The lower and middle Cambrian of Sweden: trilobites, biostratigraphy and intercontinental correlation

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Department of Geology
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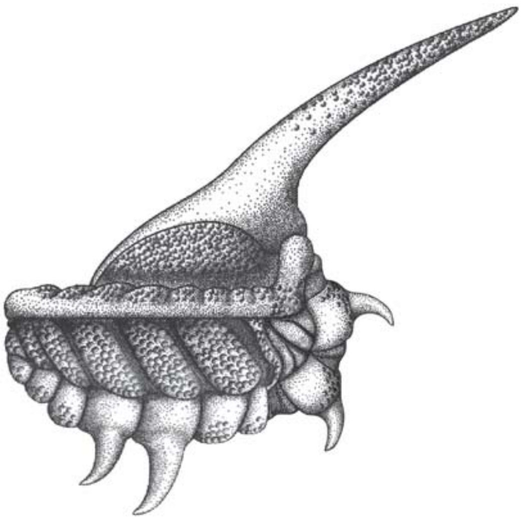

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LUND UNIVERSITY
DEPARTMENT OF GEOLOGY

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The lower and middle Cambrian of Sweden: trilobites, biostratigraphy and intercontinental correlation

Abstract

This thesis is based on studies of Cambrian successions in Sweden, with particular focus on the middle Cambrian biostratigraphy and its correlative relationship to the proposed global agnostoid zonation. The investigated material, mainly trilobites, was collected from both outcrops and drill cores from five provinces in Sweden: Skåne (Scania), Öland, Västergötland, Jämtland and Lapland.

The Almbacken drill core penetrated *c*. 30 m of Cambrian strata, constituting one of the stratigraphically most complete successions of this age in Scania. Thirty-two trilobites were identified to species level and used to subdivide the core into seven biozones; from the *Ptychagnostus gibbus* Zone of the lower middle Cambrian to the *Lejopyge laevigata* Zone of the upper middle Cambrian. Another drill core (Andrarum-3) was taken at Andrarum, south-eastern Scania. It covers *c*. 29 m of middle Cambrian to Furongian (upper Cambrian) strata. Based on the fossil content, the core was subdivided into eight biozones; from the middle Cambrian *P. atavus* Zone to the Furongian *Parabolina spinulosa* Zone. A series of alum shale samples yielded a positive $\delta^{13}C$ excursion corresponding to the globally recognisable Steptoean Positive Carbon Isotope Excursion (SPICE). This is the first time SPICE is documented in Baltica, and based on organic matter from an alum shale setting.

New material collected from Västergötland showed that the *P. punctuosus* and *Goniagnostus nathorsti* zones are considerably more extensively developed in this area than previously thought. Trilobites collected from eight localities show that the two zones are represented in a 15 cm thick and impersistent conglomeratic limestone at both Mount Kinnekulle and in the larger area of Falbygden-Billingen. Moreover, the classical locality of Gudhem yielded a trilobite fauna including several widespread key agnostoid species. In particular, *L. laevigata* (Dalman, 1828) was studied as its first appearance datum (FAD) currently is proposed to define the base of the uppermost stage in the Cambrian Series 3. We suggested that the base of the *L. laevigata* Zone of Scandinavia should be defined by the FAD of the eponymous species. Of similar global stratigraphical importance is *P. atavus* (Tullberg, 1880). Its FAD is proposed to define the base of the middle stage of the Cambrian Series 3. A syntype series collected from the Forsemölla-Andrarum area of Scania of both this species and the closely similar *P. intermedius* (Tullberg, 1880) were studied. It was concluded that they are conspecific, and that *P. intermedius* is the junior synonym of *P. atavus*.

A revision of the conspicuous eodiscoid *Dawsonia oelandica* (Westergård, 1936) was made, based on well preserved material from Mon, Jämtland. Reconstructions of this species were presented, and its functional morphology and relationship to closely related taxa were discussed. Associated trilobites placed the material stratigraphically within the lower middle Cambrian *P. praecurrens* Zone. Another eodiscoid fauna, including the first reported occurrence from Scandinavia of *Neocobboldia* aff. *dentata* (Lermontova, 1940) and *Chelediscus acifer* Rushton, 1966, was also studied. These eodiscoids, recovered from the Luobákti section, Lapland, offered a tentative correlation between the uppermost lower Cambrian strata of Baltica and eastern and western Avalonia.

From the studies included in this thesis it has been shown that the proposed global zonation can be applied to Swedish middle Cambrian successions, substituting the traditional zonation in our overall strive for a common global zonation. Accordingly, eight biozones can be recognised (in ascending order): the *Eccaparadoxides insularis*, *P. praecurrens*, *P. gibbus*, *P. atavus*, *P. punctuosus*, *G. nathorsti*, *L. laevigata* and *Agnostus pisiformis* zones.

Key words:
Palaeontology, Cambrian, biostratigraphy, trilobites, correlation, Sweden

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To my wife Petra,
and my mother and father Margareta and Leif

Contents

Abstract

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Populärvetenskaplig sammanfattning

Popular summary in Swedish

Kambrium är ett tidsavsnitt av jordens historia som spänner från ca 542 till 488 miljoner år sedan. Under denna tid utvecklades livet, främst djur, i en rasande takt genom något som brukar kallas den kambriska explosionen, en ekologisk förändring utan dess like. Bland de nya livsformer som fick de kambriska haven att koka av liv märks skalbärande djur som små armfotingar (brachiopoder), primitiva blötdjur (mollusker) och trilobiter som tillhör leddjuren. Under tidens gång har sediment avsatta på de kambriska havsbottnarna och dess inkapslade djurrester omvandlats till bergarter samt fossil. I Sverige finns en mängd olika lokaler, allt från diken och vägskärningar till nerlagda eller aktiva stenbrott, där sådana kambriska bergarter är tillgängliga. Framförallt i Skåne, Västergötland, Närke och på Öland finns viktiga lokaler som innehåller rikligt med välbevarade fossil. Även i andra områden som Jämtland, Norrland och Östergötland kan kambriska bergarter och fossil påträffas.

Lagerföljderna utgörs främst av sandstenar, vilka överlagras av skiffer med horisonter av kalksten. Sandstenarna avsattes i tidig kambrium då havet steg över land, skiffern avsattes på större vattendjup medan kalkstenslagren i regel motsvarar tider av havsytesänkningar. I Västergötland och Skåne, två viktiga lokaler på den geologiska världskartan, är den sk. alunskiffern vanligt förekommande. Den har studerats intensivt under drygt 300 år och har fått sitt namn efter alun, ett salt som förr utvanns genom bränning och lakning av skiffern och därefter användes bland annat för garvning av läder, färgning av garn eller som blodstillande medel. Under 1700-talet och första halvan av 1800-talet var brytningen av alunskiffer en storskalig industri som resulterade i en mängd stenbrott runtom i Sverige. Mest omfattande var kanske verksamheten vid Andrarum i Skåne och på Kinnekulle i Västergötland. Skiffern är svart på grund av sin höga halt av organiskt material, och bildades under syrefattiga förhållanden i kambrium och början av ordovicium. Karakteristiska kalkstenslinser, även kallade orstenar, som ligger insprängda i skiffern innehåller ibland mycket välbevarade fossil. Orstenarna skapades efter att det skifferbildande materialet avsatts på havsbottnen, kanske genom upplösning och utfällning av karbonater i det ursprungliga sedimentet.

Kambrium kan delas in i tre enheter (eller serier): underkambrium, mellankambrium och furong (överkambrium). Denna doktorsavhandling fokuserar huvudsakligen på den mellersta delen av kambrium. I Sverige är den artrika och varierade trilobitfauna som finns representerad i mellankambriska avlagringar anmärkningsvärd. Denna ersätts i furong av en betydligt magrare fauna bestående av endast ett fåtal släkten och familjer. I underkambrium är fossil relativt ovanliga och representerade framför allt av spår efter grävande organismer samt en del trilobiter, armfotingar och blötdjur.

Trilobiterna var en mycket framgångsrik djurgrupp som kom att spela en viktig roll i haven under kambrium och ordovicium, för omkring 542 till 444 miljoner år sedan. Under tidig ordovicium började trilobiterna att avta i antal och artrikedom, till fördel för andra organismer. Knappt 200 miljoner år senare, i slutet av perm, försvann de för alltid från jordens yta. Trots detta kan vi studera dom än idag, till synes omärkbart förändrade efter att bevarats inneslutna i sedimentära bergarter under hundratals miljoner år.

Trilobiterna är en klass leddjur som uteslutande levde i havet och var mycket mångformiga och framgångsrika. I dagsläget har det beskrivits mer än 5000 släkten och, uppskattningsvis, 20 000 arter i flertalet olika former och storlekar, och fortfarande beskrivs många nya arter årligen. Trilobiter är inte bara fascinerande på grund av sin vackra form, de är också användbara inom en rad olika geologiska och paleontologiska forskningsområden, främst kanske biostratigrafi.

Biostratigrafi är ett verktyg för att göra relativa åldersbestämningar och skiljer sig således från absoluta dateringar, där man med hjälp av radioaktiva isotoper kan få fram en mer eller mindre exakt ålder i antal år hos, låt säga, en bit ben eller en bergart. Biostratigrafi bygger på att dokumentera förekomst av fossil i en serie bergarter. Med hjälp av fossilen (både vad avser olika arter samt antalet individer) kan man dela in bergarterna (lagerföljden) i olika enheter, så kallade biozoner. Generellt kan sägas att en biozon uppvisar ett fossilinnehåll som skiljer sig från under- och överliggande zoner. Biozonerna i den studerade lagerföljden kan därefter jämföras med andra fossilförekomster jorden över. Hittar man samma arter på olika platser kan man anta att lagerföljderna vid de olika lokalerna bildades ungefär samtidigt. På så sätt kan man påvisa relativ ålder med hjälp av fossil, trots att lagren man hittar dom i kan variera stort både vad gäller tjocklek och bergartstyp. Ofta har varje biozon ett unikt namn, uppkallat efter ett inom zonen vanligt förekommande eller karakteristiskt fossil. Detta fossil kallas ledfossil och för att kunna klassas som ett sådant ställs det vissa krav. Fossilet ska helst finnas i rikliga mängder och ha en global geografisk spridning. Det ska inte vara faciesbundet (man ska kunna hitta det i olika typer av sedimentära bergarter), ha en snabb evolutionär utveckling (hittas inom ett så kort tidsintervall som möjligt) och vara lätt att identifiera (även om man endast hittar delar av det). Många trilobiter uppfyller dessa kriterier och klassas därför som goda ledfossil.

Den internationella subkommissionen för kambrisk stratigrafi (ISCS) är en internationell organisation vars mål är att indela kambrium i underavdelningar, vilkas gränser i största möjliga mån ska kunna identifieras i så många områden som möjligt på olika kontinenter, något som är ett svårt och tidskrävande arbete. Den biostratigrafiska indelningen av mellankambrium i Sverige grundades framför allt av paleontologen Anton H. Westergård i ett arbete från 1946. Westergård indelade mellankambrium i nio biozoner och samlade dessa inom tre s.k. etager och hans arbete har varit av mycket stor betydelse för den moderna kambriska forskningen, inte bara i Sverige. Även om Westergårds arbete står sig väl än idag har forskningsresultat de senaste 60 åren medfört ett behov av att förnya hans indelning för att på bästa möjliga sätt kunna knyta de svenska lagerföljderna till den globala indelning ISCS arbetar med.

Lejonparten av denna doktorsavhandling omfattar arbeten som behandlar den biostratigrafiska indelningen av mellankambrium där noggranna undersökningar av faunan har gjorts för att studera om den globala indelningen kan appliceras även under de förutsättningar som råder i Sverige. Materialet som har undersökts kommer från Jämtland, Lappland, Västergötland och Öland samt två borrkärnor från Skåne. Resultaten visar att den globala indelningen mycket väl kan appliceras på våra svenska mellankambriska lagerföljder. Vidare har specifika trilobitarter, användbara för att länka samman Sveriges under- och mellankambrium till likåldriga lagerserier utomlands, studerats mer ingående. Det har även gjorts en studie där kolisotoper har använts. Kolisotoper som ^{12}C, ^{13}C och ^{14}C är naturligt förekommande varianter av grundämnet kol och det som skiljer dom åt är uppbyggnaden av deras atomkärna. Isotoperna kan bevaras i de sediment som avsätts på havsbottnen och som sedan förvandlas till bergart. Detta innebär att vi kan mäta halten av en viss isotop i t.ex. en 500 miljoner år gammal bergart och få reda på vilken isotopsammansättning havet hade vid denna tid. Eftersom denna sammansättning påverkas av omfattande biologiska och fysiska händelser som istider, massutdöenden och skiftningar i havskemin kan isotoperna användas för att spåra förändringar i miljön. En sådan isotopförändring hittades i en av borrkärnorna från Skåne och kunde användas som ett viktigt komplement till den biostratigrafiska indelningen.

1. Introduction

This thesis is the result of seven papers (I–VII below) dealing with trilobites from Sweden and their use in primarily middle Cambrian biostratigraphy and intercontinental correlation. Papers related to this subject but not included in the thesis are those of Axheimer (2003, 2004), Axheimer & Ahlberg (2001*a*, *b*, 2004), Axheimer *et al*. (2005*a, b*) and Ahlberg *et al*. (2004*a*, *b*, 2006*a*), Terfelt *et al*. (2003) and Calner *et al*. (2006). Specimens illustrated in this synthesis are housed at the Department of Geology, Lund University (LO). The thesis is compiled to meet the formal requirements set for academic dissertations at universities in Sweden.

2. Summary of papers

Paper I

Axheimer, N. & Ahlberg, P. 2003: A core drilling through Cambrian strata at Almbacken, Scania, S. Sweden: trilobites and stratigraphical assessment. *GFF 125*, 139–156.

Summary: This paper deals with a drill core taken in 1949 at Almbacken, near the small community of Södra Sandby, Scania (Fig. 1). The core is *c*. 30 m long and consists of middle and lower Cambrian strata. The middle Cambrian part of the core is *c*. 28.3 m thick, and it is one of the stratigraphically most complete successions of this age in Scania. It is represented by dark grey to black alum shales and occasional layers and lenses of dark grey to black limestone (stinkstone or *orsten*). The lowermost *c*. 1.50 m consist of siltstone and a minor limestone bed at the very bottom of the core. These presumably lower Cambrian deposits are scarce in fossils and yielded only indeterminate brachiopod valves and fragments of polymerid trilobites. Accordingly, the lower–middle Cambrian boundary could not be precisely located and was tentatively placed at the top of a series of siltstones.

The drill core was logged and its faunal content was recorded centimetre by centimetre, resulting in 32 trilobites identified to species level. These species were used in a high-resolution biostratigraphical subdivision of the core. Fossils were found in both the shale and limestone. Three major and richly fossiliferous limestone beds were documented; the Andrarum Limestone, the Exsulans Limestone and the ”Fragment” Limestone. The preservation of the fossils is generally good, and often with full convexity in the limestone intercalations, allowing also documentation of the growth stages in the pygidia of *Ptychagnostus punctuosus* (Angelin, 1851). In total, seven biozones could be recognised using Westergård's (1946) scheme (in descending order): the *Lejopyge laevigata* Zone, the *Solenopleura*? *brachymetopa* Zone, the *P. lundgreni–Goniagnostus nathorsti* Zone, the *P. punctuosus* Zone, the *Hypagnostus parvifrons* Zone, the *Tomagnostus fissus–P. atavus* Zone and the *P. gibbus* Zone. The biostratigraphical subdivision of the middle Cambrian established by Westergård (1946) was also compared to the global scheme adopted by Peng & Robison (2000), and it was shown that both are applicable to the Almbacken drill core.

Paper II

Weidner, T. R., Ahlberg, P., Axheimer, N. & Clarkson, E. N. K. 2004: The middle Cambrian *Ptychagnostus punctuosus* and *Goniagnostus nathorsti* zones in Västergötland, Sweden. *Bulletin of the Geological Society of Denmark 51*, 39–45.

Summary: The aim of this paper was to present new trilobite findings, collected at eight localities in Västergötland, south-central Sweden (Fig. 1). Västergötland holds several classical localities with middle Cambrian (as well as Furongian) deposits, and the table mountain of Kinnekulle has been studied for more than two hundred years. The more extensive area of Falbygden-Billingen is, however, less well known. The middle Cambrian of Västergötland differs from that of Scania in several aspects. The richly fossiliferous Andrarum Limestone is poorly developed in Västergötland and is, in part, represented merely by the conspicuous Exporrecta Conglomerate. The similarly highly fossiliferous Exsulans Limestone of the *Ptychagnostus gibbus* Zone, as well as the *Acadoparadoxides* [or *Paradoxides* (*Plutonides*); Fletcher *et al*. 2005] *oelandicus* Superzone, are not represented in Västergötland. Thus, the faunal diversity of the middle Cambrian of Västergötland seems to be restricted and reaches its peak values in the 'Exsculptus-layer', within the stinkstone lenses of the *Lejopyge laevigata* Zone.

The biostratigraphical zonation and correlation table of Västergötland was erected by Westergård (1946), and has since remained unchanged. His scheme shows an absence of both the *P. lundgreni–Goniagnostus nathorsti* and the *P. punctuosus* zones. Although a few specimens of *P. punctuosus* have previously been recorded, their stratigraphical position has not been confirmed. The material collected from the eight localities by the senior author, however, yielded numerous well preserved specimens of *P. punctuosus*, *P. lundgreni* (Tullberg, 1880) and *G. nathorsti* (Brøgger, 1878). These agnostoids were found in both loose boulders and outcrops at Kinnekulle,

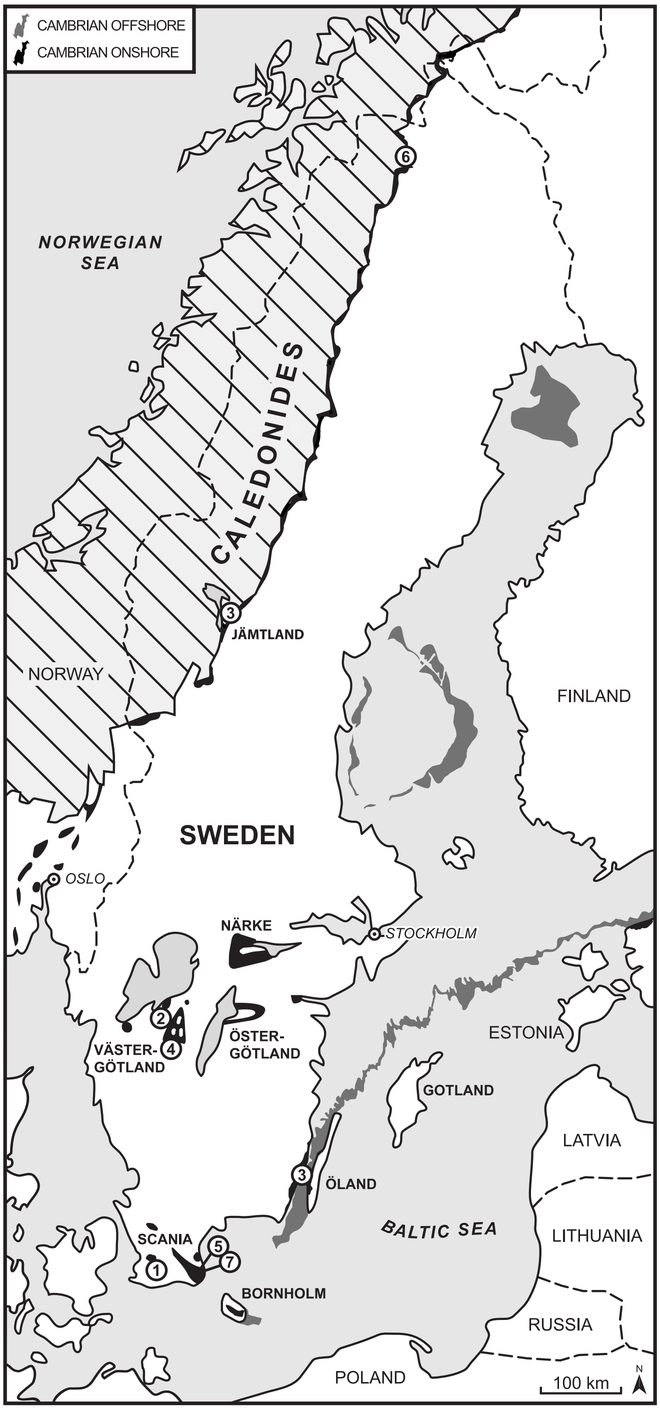

Fig. 1. Map showing the distribution of Cambrian strata in Sweden and adjacent areas. Locally, Cambrian strata are also present in the Caledonides, which is marked by slanting lines. The numbers 1–7 show the origin of the material studied. 1. Almbacken drill core, Scania (Paper I). 2. Västergötland (Paper II). 3. Mon, Jämtland, and Öland (Paper III). 4. Gudhem, Västergötland (Paper IV). 5. Forsemölla-Andrarum, Scania (Paper V). 6. Luobákti, Lapland (Paper VI). 7. Andrarum-3 drill core, Scania (Paper VII). The map is in part based on Martinsson (1974), Bergström & Gee (1985) and Axheimer *et al*. (2006*a*: paper VI).

Mösseberg and Ålleberg. At seven of the localities, a previously unrecognised conglomeratic limestone with a thickness of up to 15 cm was discovered, situated between the ”Hypagnostus limestone bank” and the Exporrecta Conglomerate. The upper part of this limestone is richly fossiliferous and yielded a mixed fauna of the three species together with eight other trilobites identified to species level, in addition to hyoliths and brachiopods. The conglomeratic limestone has been found previously also at Djupadalen (locality 8), and together with the new discoveries from localities 1–7 its faunal content warrant the presence of both the *P. punctuosus* and the *G. nathorsti* zones in Västergötland. The restricted thickness of the conglomeratic limestone, however, suggests that the two zones most likely are incomplete.

Paper III

Axheimer, N. 2006: The middle Cambrian eodiscoid trilobite *Dawsonia oelandica* (Westergård, 1936). *Journal of Paleontology 80*, 193–200.

Summary: The eodiscoid trilobite *Dawsonia oelandica* (Westergård, 1936) is reviewed in this paper. The species was originally described from Sweden by Westergård (1936), based on material collected at the island of Öland, south-eastern Sweden; two cephala were recovered from a drill core and one pygidium was collected from a locality near the small community of Mössberga. New, well preserved, material was collected by T. R. Weidner (Juelsminde, Denmark) from a block of dark grey limestone at a road section near the community of Mon, south of Östersund in Jämtland, central Sweden (Fig. 1). This material consists of five cephala and two pygidia, allowing for a thorough redescription and discussion of the species. Associated trilobites allow the material to be placed stratigraphically within the lower middle Cambrian *Ptychagnostus praecurrens* Zone. The species has also been reported from Siberia and Germany, and its affinity to closely related species from, e.g., New Brunswick, Newfoundland and Wales is discussed.

Dawsonia oelandica is a conspicuous eodiscoid with an elaborate granulation on major parts of both the cephalon and pygidium. The preglabellar field is strongly depressed and the cephalic border is subdivided into numerous distinct ”segments”. The occipital ring is extended into a long glabellar spine of approximately the same length as the cephalon. The pygidium is strongly convex and displays five pleural bands, separated by distinct pleural furrows directed backwards. The pygidia from Jämtland shows semi-circular damages on the third and fourth axial rings, which led to the interpretation that these rings were extended into small spines or spine-like tubercles. A new latex cast of the holotype (a pygidium) from Öland yielded a previously unknown axial spine on the attached thoracic tergite. Clearly, *D. oelandica* sported an impressive display of spines.

Paper IV

Axheimer, N., Eriksson, M. E., Ahlberg, P., & Bengtsson, A. 2006*b*: The middle Cambrian cosmopolitan key species *Lejopyge laevigata* and its biozone: new data from Sweden. *Geological Magazine 143*, 447–455.

Summary: The fourth paper deals with the upper middle Cambrian agnostoid *Lejopyge laevigata* (Dalman, 1828), its

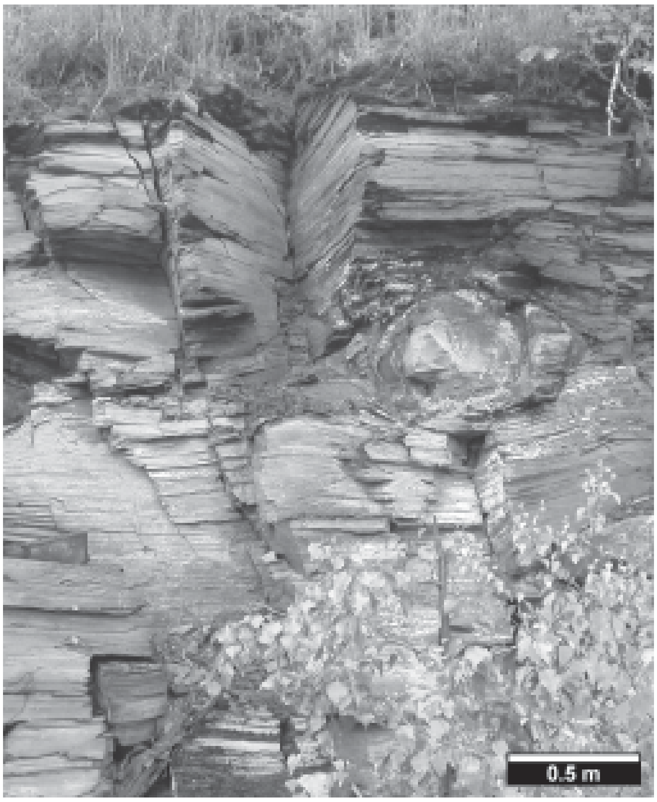

Fig. 2. A typical alum shale succession with an intercalated stinkstone lens; the *Lejopyge laevigata* Zone at the Gudhem quarry, Västergötland, south-central Sweden (see Axheimer *et al*. 2006*b*: paper IV).

biozone and applicability in intercontinental correlation. Work currently in progress by the International Subcommission on Cambrian Stratigraphy (ISCS) have shown that at least ten biohorizons have potential for global correlation in the upper half of the Cambrian, one of these being the first appearance datum (FAD) of *L. laevigata*. This species is globally distributed and used in many areas of the world, including Sweden, as a zonal index fossil. Currently, the FAD of *L. laevigata* is considered as a potential stage boundary level for the base of the upper stage of the third Cambrian series (Babcock *et al*. 2005). As such, it was of great importance to document the faunal succession in the *L. laevigata* Zone at the classical locality of Gudhem, Västergötland, south-central Sweden (Fig. 1). This locality is probably also the type locality of the closely related and associated *L. armata* (Linnarsson, 1869). The quarry is situated *c*. 0.7 km west of the city of Falköping, and three sections were investigated and sampled. The sections are well exposed and consist of a series of unfossiliferous alum shale with three to four levels of richly fossiliferous limestone lenses (Fig. 2). The combined thickness of the *L. laevigata* Zone in the three sections was measured to *c*. 4.3 m, which is the thickest reported from Västergötland.

The *L. laevigata* Zone succeeds the *Solenopleura*? *brachymetopa* Zone, which, by common practice, has been used to be defined by the lower and upper limits of the Andrarum Limestone. Although the Andrarum Limestone is important for regional correlations, a biozone defined by a spatially restricted lithological unit is unfortunate; this limestone is, for instance, poorly developed or even missing in Västergötland. Furthermore, the original definition of the *L. laevigata* Zone is vague, seemingly based upon local taxon abundance and not stratigraphical range. Furthermore, the nominal species has been recorded well below the base of the traditional *L. laevigata* Zone. Although such observations were not made at the studied locality, *L. laevigata* has been found below the Andrarum Limestone in a drill core from Scania, as noted in this paper (see also Ahlberg *et al*. 2006*b*). Therefore, it was suggested that the *L. laevigata* Zone in Scandinavia should be extended to include the traditional *S.*? *brachymetopa* Zone, and, following Peng & Robison (2000), its lower boundary should be defined by the FAD of *L. laevigata*. The base of the succeeding *Agnostus pisiformis* Zone has traditionally been defined by the lowest level where *A. pisiformis* (Wahlenberg, 1818) occur in abundance. As this is a vague definition of a zonal boundary, we suggested that the base of the *A. pisiformis* Zone should be placed at the last appearance datum (LAD) of *L. laevigata*. In addition to *L. laevigata*, the Gudhem succession yielded several other geographically widespread agnostoid species, such as *Clavagnostus spinosus* (Resser, 1938), *Glaberagnostus altaicus* Romanenko, 1985 and *Tomagnostella sulcifera* (Wallerius, 1895), which together with the zonal index provide a high correlative potential with sections outside Scandinavia.

Paper V

Ahlberg, P., Axheimer, N. & Robison, R. A. 2006*c*: Taxonomy of *Ptychagnostus atavus*: a key trilobite in defining a global Cambrian stage boundary. *Submitted to GeoBios*.

Summary: This paper deals with the common, globally distributed agnostoid *Ptychagnostus atavus* (Tullberg, 1880). Originally described from Andrarum, Sweden, the taxonomy of this species and its relationship to *P. intermedius* (Tullberg, 1880) have been confused, in part because of inadequate or erroneous illustrations of specimens from the syntype series. A proposal to define the middle stage of the third Cambrian series by the FAD of *P. atavus* was recently approved by ISCS, justifying a clarification of its taxonomy and a review of the type material.

Ptychagnostus atavus was originally described by Tullberg (1880) and rudimentarily illustrated by four sketches. The syntype material, one cephalon and one pygidium, were collected from a loose stinkstone (*orsten*) at Forsemölla in the Andrarum area, Scania (Fig. 1). An associated cephalon, illustrated by Westergård (1946), could not be located in the collections at Lund University. Tullberg (1880) also described *P. intermedius* from the same area, based on *c*. 50 cephala and pygidia collected from alum shale within the *P. atavus* Zone, and noted its similarity to *P. atavus* and *P. affinis* (Brøgger, 1878). Later, Westergård (1946) concluded that the differences between *P. atavus* and *P. intermedius* were insignificant and synonymised the two names. However, *P. intermedius* was independently reinstated by several authors in the 1980's as a valid species.

Close examination of the type material of *P. intermedius* provided new information regarding the taxonomy and affinity of the species. For example, the median tubercle is prominent

and medially indents the F2 resulting in a distinctly hexagonal M2, similar to that in the syntype pygidium of *P. atavus*. Hence, it was concluded that *P. intermedius* is a subjective junior synonym of *P. atavus*, as noted by Westergård (1946).

Paper VI

Axheimer, N., Ahlberg, P. & Cederström, P. 2006*a*: A new lower Cambrian eodiscoid trilobite fauna from Swedish Lapland and its implications for intercontinental correlation. *Submitted to Geological Magazine*.

Summary: This paper deals with a new eodiscoid fauna recovered from the top of the Torneträsk Formation (upper lower Cambrian) at the Luobákti section, south of Lake Torneträsk, northern Sweden (Fig. 1). The section studied consists of sandstones alternating with siltstone- and shale-dominated units, and subordinate limestone and conglomerate beds (Moberg 1908; Kulling 1964; Thelander 1982). The succeeding Alum Shale Formation is unfossiliferous, but possibly of middle Cambrian age. The material described was collected by PC from a bioclastic limestone in a ravine at the northern flank of Mount Luobákti (Fig. 3). The dense limestone is dark grey to black in colour. The fauna is dominated by trilobites, followed by phosphatic-shelled brachiopods, rare helcionellid molluscs and a bradoriid. Trilobites found were: *Holmia* sp., *Orodes*? *lapponica* (Ahlberg, 1980), *Strenuaeva inflata* Ahlberg & Bergström, 1978 and the eodiscoids *Chelediscus acifer* Rushton, 1966 and *Neocobboldia* aff. *dentata* (Lermontova, 1940).

The generic composition of the Luobákti trilobite fauna indicates a late early Cambrian age, and in terms of Scandinavian biostratigraphy it was recovered either from the *Holmia kjerulfi* or the *Ornamentaspis*? *linnarssoni* Assemblage Zone. The presence of a species of *Holmia* may suggest that the fauna comes from the *H. kjerulfi* Assemblage Zone, but that genus ranges upwards into the *O.*? *linnarssoni* Assemblage Zone (Nikolaisen 1986). The stratigraphical position of the fauna, at the top of the lower Cambrian and just below the Alum Shale Formation, suggests that it belongs to the *O.*? *linnarssoni* Assemblage Zone.

Intercontinental correlation within the lower Cambrian is often difficult, hampered by the strongly provincial character of the trilobite faunas (e.g., Palmer 1968). Several genera and species of eodiscoids seem, however, to have a wider geographical distribution than polymerid trilobites, and hence are important for long-distance correlations in the upper lower Cambrian (e.g., Robison *et al.* 1977; Fletcher 2003; Geyer 2005). Since the *Neocobboldia* species recovered from the Luobákti section could not be adequately identified it was of little use for high-resolution correlation. *Chelediscus acifer*, however, provides a novel tie-line between lower Cambrian successions in Baltica and Avalonia.

Fig. 3. Aerial photograph of the northern flank of Mount Luobákti, south of Lake Torneträsk, northern Sweden. The lower Cambrian Torneträsk Formation crop out in the foreground. The section described in Axheimer *et al.* (2006*a*: paper VI) is located in the ravine. Photograph by John Ahlgren (Mariestad).

Paper VII

Ahlberg, P., Axheimer, N., Eriksson, M. E., Schmitz, B. & Terfelt, T. 2006*b*: Cambrian high-resolution biostratigraphy and carbon isotope chemostratigraphy in Scania, Sweden. *In manuscript*.

Summary: This paper deals with the biostratigraphy and the discovery of a positive $\delta^{13}C$ excursion in the middle Cambrian–Furongian interval from a drill core (Andrarum-3) that was taken near the Great Quarry at Andrarum, south-eastern Scania, Sweden (Fig. 1). The core has a diameter of 71 mm and comprises 28.90 m of dark grey or black, finely laminated mudstones and shales with early concretionary carbonate lenses (stinkstones or *orsten*) and a few primary carbonate beds, including the middle Cambrian Andrarum Limestone. The Furongian part of the core comprises 11.55 m, whereas the middle Cambrian covers the remaining 17.35 m. The lithology and faunal content of the core were examined in cm-scale. Four trilobite and three phosphatocopid genera were recovered from the Furongian interval, whereas the middle Cambrian part of the core yielded 19 trilobite genera and two phosphatocopid genera. These fossils were used to subdivide the core into eight biozones, spanning from the Furongian *Parabolina spinulosa* Zone to the middle Cambrian *Ptychagnostus atavus* Zone.

Fiftyeight samples were taken from the core, each containing approximately three grams of ground and washed alum shale, and processed for $\delta^{13}C_{org}$ analysis. An additional 19 samples were taken from the limestones for $\delta^{13}C_{carb}$ analysis, for

comparisons to the organic carbon signal. The data from the carbonates showed values consistent with diagenetic alteration in the limestones and, hence, could not be used in the study. The $\delta^{13}C_{org}$ values, however, revealed a curve spanning the interval from the *P. atavus* Zone into the lower *P. brevispina* Subzone. The curve becomes increasingly positive through the middle Cambrian *Lejopyge laevigata* and *Agnostus pisiformis* zones and display peak values of *c*. –28.00 ‰ $\delta^{13}C_{org}$ in the upper part of the lower Furongian *Olenus wahlenbergi* Subzone through the middle part of the *O. attenuatus* Subzone. Thereafter there is a gradual decrease, reaching significantly lower values in the upper *O. scanicus* and lower *P. brevispina* subzones. This excursion corresponds to the Steptoean Positive Carbon Isotope Excursion (SPICE), which is one of the largest positive $\delta^{13}C$ excursions of the Palaeozoic. It was initially recorded from the eastern Great Basin, USA (Brasier 1993; Saltzman *et al*. 1998), and is recognized here, for the first time, in Scandinavia.

The onset of the SPICE is quoted to be coeval with the FAD of *Glyptagnostus reticulatus* (Angelin, 1851) (see, e.g., Peng *et al*. 2004), whereas in the Andrarum-3 drill core the onset can be noted at a lower stratigraphical level. This diachrony may be explained by uncertainties in the biostratigraphical resolution of the vastly thicker successions in, e.g., the Great Basin, USA, Kazakhstan and South China. The SPICE in the Andrarum-3 core appears to be a net shift of +1.50–2.00 ‰ $\delta^{13}C$, which is approximately half the magnitude of the SPICE recorded in other regions (see Saltzman *et al*. 2000; Peng *et al*. 2004). This may be explained by the fact that the present analyses were made on organic matter as opposed to the whole-rock carbonate analyses from other regions. It may also be related to temporal variations in the type, origin and/or burial history of the organic fraction analysed. The stratigraphic fit of the recorded excursion, however, corresponds well with the SPICE as documented elsewhere.

3. Material and methods

All studied material derives from the Cambrian of Sweden. The Almbacken drill core (Paper I) was taken in 1944 and is stored at the Department of Geology, Lund University. Thomas R. Weidner collected the material from Kinnekulle and the Falbygden-Billingen area in Västergötland (Paper II), as well as the material of *Dawsonia oelandica* from Jämtland (Paper III). Anders Bengtsson collected the bulk of the material from Gudhem, Västergötland, described in Paper IV. Additional material was collected by the senior author and Per Ahlberg. The type specimens of *Ptychagnotus atavus* and *P. intermedius* described in Paper V were collected by Sven A. Tullberg at Andrarum, Scania. The lower Cambrian material from Luobákti, Swedish Lapland, was collected by Peter Cederström (Paper VI). The Andrarum-3 drill core (Paper VII) was made by Upplands Miljö- och Kärnborrning AB, Knutby.

Of the multi-authored papers (I, II, IV, V, VI and VII) included in this paper I have been deeply involved in composing and revising the text. In paper VII, I have contributed with text and revisions for all chapters except for the discussion on biomeres and the Furongian interval. In all papers (excluding the SEM-photographs in paper VI and figs. 3Q–T in paper VII), I have taken all photographs. Furthermore, I have made all line drawings and other illustrations except for those in paper VII, which were created by me, Mats E. Eriksson and Fredrik Terfelt.

All work was carried out at the Department of Geology, Lund University, except for the SEM photography (Department of Zoology, Lund University). Studies of the type material of *Dawsonia sculpta* (Hicks, 1871) were conducted at the Sedgwick Museum in Cambridge, England. The majority of the fossils (except Paper I) were photographed with a digital camera (Nikon Coolpix 990), using the following technique: several photos (3–5) of each specimen were taken with different depth of focus. The series of images were then processed in the freeware program *CombineZ*, written by Alan Hadley, by stacking and combining them to provide a merged image with an optimal focus. For further information of the material and methods used, reference is given to the separate papers included in this thesis.

4. The Cambrian of Sweden

The Palaeozoic of Sweden (and Scandinavia in general) has been studied for well over 200 years, initiated by the works of Carl Linnaeus in the middle of the 18th century. Ever since, the Cambrian of Sweden has continued to receive attention of palaeontologists and some of the more important and long-lasting works that can be recognized are those of, e.g., Wahlenberg (1818), Dalman (1827), Torell (1870), Tullberg (1880), Angelin (1854) and Linnarsson (1869). More recent papers, largely focused on trilobites, which have been of great importance for studies on the middle Cambrian, are the detailed works of Westergård (1936, 1942, 1944, 1946, 1948, 1950, 1953).

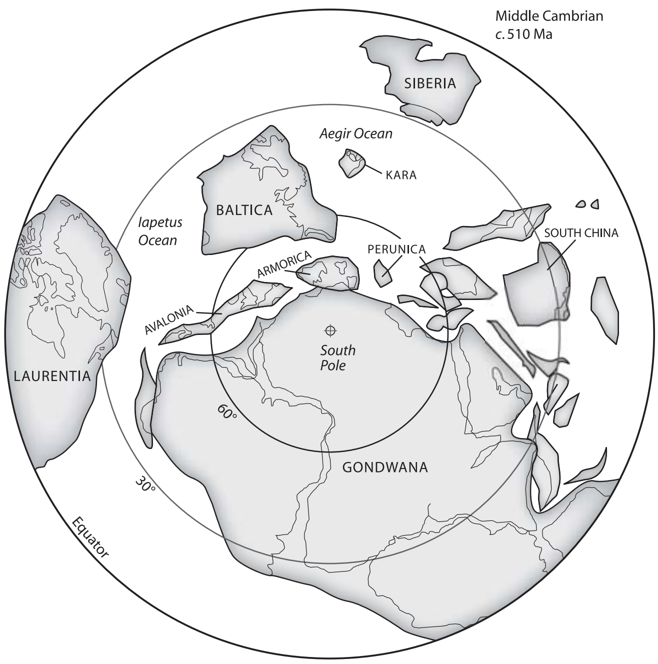

Fig. 4. Global palaeogeographical map of the middle Cambrian. Modified from Cocks & Torsvik (2002, 2005) and Landing (2005).

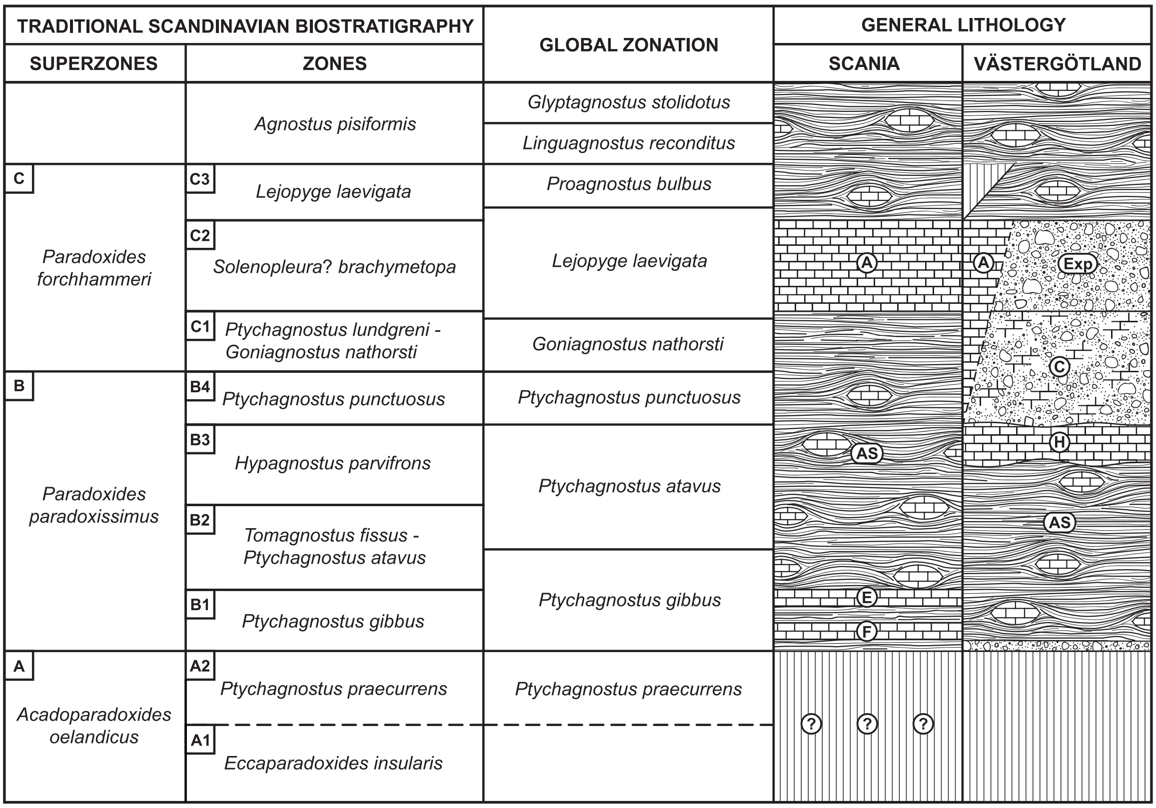

Fig. 5. Generalised middle Cambrian stratigraphy of Scania and Västergötland, Sweden, and correlation between the traditional biostratigraphy of Scandinavia (Westergård 1946; Ahlberg 1989) and the global zonation (Robison 1982, 1984; Peng & Robison 2000). The lettering system (A1–C3) of Westergård (1946) is also shown. A = Andrarum Limestone; AS = alum shale with lenses and beds of limestone (*orsten*); C = Conglomeratic limestone; E = Exsulans Limestone; Exp = Exporrecta Conglomerate; F = ”Fragment” Limestone; H = ”Hypagnostus limestone bank”. Note that the thicknesses of the different lithological units and the corresponding extension of the biozones are approximate and illustrated for a general review only. Based mainly on Axheimer & Ahlberg (2003: paper I), Weidner *et al*. (2004: paper II) and Axheimer *et al*. (2006*b*: paper IV).

Major outcrop areas of Cambrian strata in Sweden can be found in the southern and south-central parts, on the island of Öland in the south-east and along the eastern margin of the Caledonian Front (Fig. 1). The accessibility of these outcrops is in the south and south-east generally restricted to old quarries and shoreline exposures. In the central and south-central parts of Sweden, i.e., in Västergötland, Östergötland and Närke, outcrops can be principally found in old quarries, for example in the table mountains of Västergötland. The Cambrian of Öland is mainly known from borings and scattered outcrops along the western shoreline. In a sinuous belt, *c*. 2000 km long, along the eastern Caledonian Front, Cambrian outcrops are discontinuously found in both the Autochthon and in the allochthonous units. Except for the Caledonides and neighbouring areas, the Cambrian deposits in Sweden have escaped tectonism and are generally completely unmetamorphosed, witnessing stable tectonic conditions in Baltica during the Cambrian Period.

The final break-up of Baltica from Laurentia occurred near the end of the Precambrian, opening up the Iapetus Ocean between these two terranes (Cocks & Torsvik 2002, 2005). Baltica, which includes Scandinavia and north-central Europe together with European Russia, was located between 60°S and 30°S during the Cambrian (Fig. 4). To the south of Baltica, the massive continent of Gondwana occupied large parts of the area surrounding the South Pole. Laurentia, positioned to the west of Baltica, moved northwards towards the equator where it remained to early Silurian times (Cocks & Torsvik 2002). Siberia was also an isolated continent, located north-east of Baltica. The generally thin succession of middle Cambrian and Furongian strata in Baltica and its vast lateral extent suggests that this palaeocontinent was low in topography and sediment supply, hence submerged under the sea for the major part of the Cambrian (Cocks & Torsvik 2005). There are no evident tectonic events that may have caused the flooding of Baltica, but the composition of the Cambrian successions is a tell tale-sign of a general transgression (Cocks & Torsvik 2005).

In most areas the Cambrian successions rest with a profound unconformity on a peneplained Proterozoic crystalline basement. Locally along the Caledonian front, however, lower Cambrian strata rest on late Proterozoic sedimentary rocks (e.g., Greiling *et al*. 1999). A series of sandstones on top of this peneplain reflects flooding of Baltica in early Cambrian times. These lower Cambrian sandstones are in the central Baltic and south-central Sweden commonly referred to as the File Haidar Formation (Bergström & Gee 1985). The lower Cambrian deposits are a few tens of metres thick in south-central Sweden and thicken southwards towards Scania (Hardeberga Formation), south-eastwards towards Gotland, and northwards in the Caledonides where they attain a thickness of up to 200 m. In general, the lower Cambrian of Sweden is poorly fossiliferous, but has yielded trilobites, arcritarchs and ichnofossils along with, for example, a few brachiopods and molluscs.

The base of the middle Cambrian varies from being transitional to sharp with development of conglomerates. The lower part of the series is missing in Västergötland and possibly also in Scania. The middle Cambrian and Furongian (upper Cambrian) in Sweden are largely represented by the Alum Shale Formation (which extends into the Ordovician), which predominantly consists of dark grey or black, kerogen-rich mudstones and shales with lenses or beds of dark grey limestone (Figs. 2, 5). The stratigraphy, palaeontology and geochemistry of the Scandinavian alum shales have been extensively studied (see, e.g., Westergård 1922; Bergström & Gee 1985; Andersson *et al*. 1985; Buchardt *et al*. 1997; Ahlberg 1998 and Schovsbo 2000, for general reviews). The lenses of limestone are commonly referred to as stinkstones (or *orsten*). The formation of these lenticular limestones is not fully known, but they are thought to have been formed by post-depositional, early diagenetic, precipitation of calcium carbonate in the sediment, triggered by an increased alkalinity in the pore water possibly due to bacterial growth (Buchardt *et al*. 1997). The mudstones and shales are finely laminated and contain up to 28% organic matter, which gives their dark colour. These values vary, however, throughout Sweden as the maturity of the alum shales differs from area to area, in part related to heating by local intrusions of Permo–Carboniferous dykes or, as in the Caledonides, by low-grade metamorphism (Andersson *et al*. 1985). In addition to organic matter, the alum shale is rich in various trace elements, such as uranium and vanadium. The name alum shale is derived from the salt alum (a potassium aluminium silicate), which, for various practical purposes, was extensively extracted from the shales in the eighteenth to early nineteenth century. The alum shales are thought to have been accumulated at a very slow rate in oxygen depleted waters, minimizing the bacterial-induced decay of organic matter (Thickpenny 1984, 1987; Andersson *et al*. 1985; Buchardt *et al*. 1997). The Alum Shale Formation is primarily exposed in Scania, Västergötland, Östergötland, Närke and Öland, and along the Caledonides, e.g., in Jämtland. The shales thin out towards the east and are poorly represented in, for example, the subsurface of Gotland (e.g., Ahlberg 1989). On northernmost Öland, the Alum Shale Formation is merely one metre thick, whereas a thickness of 130 metres has been reported from the Terne drill core taken off-shore, north-west of Scania (Michelsen & Nielsen 1991).

In addition to alum shale and stinkstones, the middle Cambrian of Sweden contains some prominent, but spatially restricted, limestone layers. In Scania, a *c*. 0.4 m thick bioclastic limestone bed occurs in the lower middle Cambrian. It is commonly referred to as the ”Fragment” Limestone, because of its richness in indeterminate fossil fragments. The Exsulans Limestone (*c*. 0.4 m thick) slightly above and the Andrarum Limestone (*c*. 1 m thick) in the upper middle Cambrian are both well known for their rich and well preserved fossil content. These three limestones represent shallow-water facies and are well-developed in Scania. In Västergötland, the ”Fragment” Limestone and the Exsulans Limestone are missing, whereas the Andrarum Limestone is represented only by a less prominent counterpart on Hunneberg and Kinnekulle (see Weidner *et al*. 2004: paper II), or by the conspicuous Exporrecta Conglomerate (Fig. 5). The Andrarum Limestone facies extends westwards as far as the Ritland area, south-western Norway (Bruton & Harper 2000), and southwards to the island of Bornholm, Denmark (e.g., Berg-Madsen 1985*a*). As mentioned above, the Furongian of Sweden is also represented by the Alum Shale Formation and exhibit few lithological differences from the middle Cambrian.

5. Middle Cambrian faunas – a review

The Cambrian Period was a time of evolution and major biological diversification of an unchallenged magnitude. The rise of brachiopods, molluscs, trilobites and other shell-bearing body fossils left behind an invaluable fossil record. Although the fossil content in the lower Cambrian of Sweden is scarce (generally restricted to a few representatives of trilobites, brachiopods, microfossils such as arcritarchs and trace fossils) exemplary localities in other parts of the world, such as the Chengjiang lagerstätten in China (e.g., Hou & Bergström 1997), have shown that already in the earliest Cambrian, life on earth was thriving. In the upper lower Cambrian, however, diversity increases and amongst the fossil fauna a variety of olenellid and ellipsocephalid trilobites, a few eodiscoids, lingulate and other inarticulated brachiopods, molluscs, hyoliths and a few bradoriids have been recorded (e.g., Bergström & Ahlberg 1981).

During the middle Cambrian, fossil diversity reached its peak values in Sweden, especially regarding the trilobite faunas. Approximately 155 species of trilobites are known from the middle Cambrian of Scandinavia and they form the basis for the biostratigraphical subdivision of the series (see chapter 6). Trilobites are found throughout the major part of the middle Cambrian Alum Shale Formation, both in the shale and in the concretionary limestones, although the shale facies is notably fossiliferous only in Scania and the Oslo Region (Andersson *et al*. 1985). The fossils found in the shale are mostly flattened, whereas preservation in the limestones is often considerably better. For instance, exceptionally well preserved arthropods with appendages have been chemically extracted from upper middle Cambrian and Furongian stinkstones from Västergötland (e.g., Müller & Walossek 1985, 1987, 2003). The fossil faunas from both the Exsulans and Andrarum limestones are on the whole rich. The latter holds the greatest trilobite diversity recorded from a single lithological unit in the Cambrian of Scandinavia and has yielded more than 30 trilobite species (e.g., Berg-Madsen 1985*a*, p. 136).

The middle Cambrian trilobite faunas of Sweden (and Scandinavia in general) are dominated by agnostoids (Fig. 6). Polymerid trilobites occasionally occur in abundance but chiefly in the few major limestones mentioned above. Most prevalent among the polymerids are paradoxidids, solenopleurids and conocoryphids. Other, generally rare, trilobites include burlingiids, anomocarids (Fig. 7) and

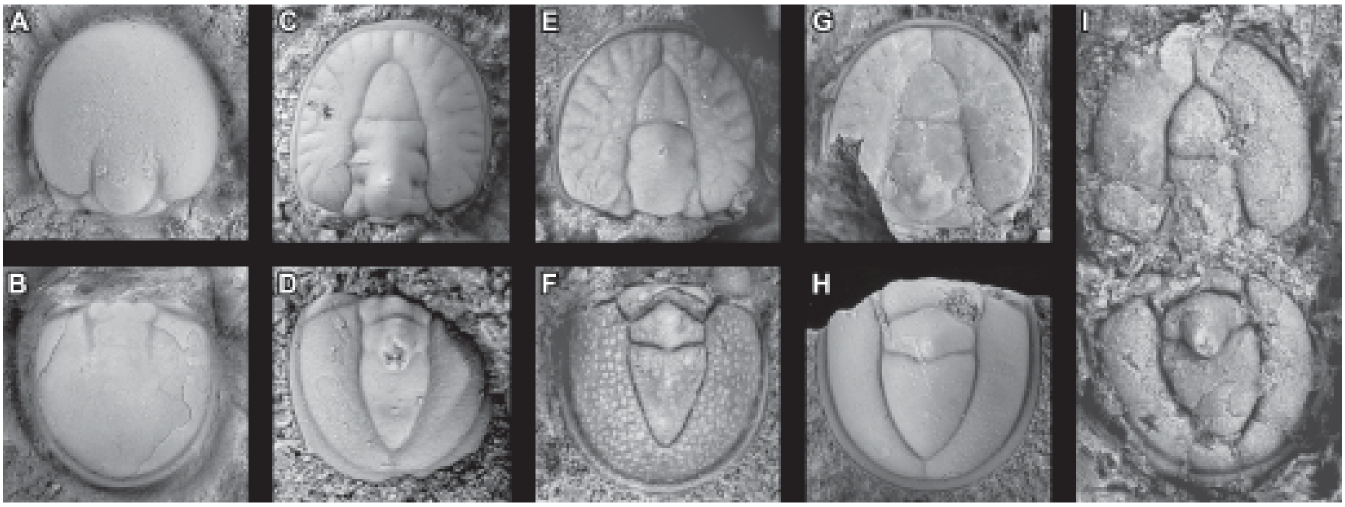

Fig. 6. Selected agnostoid index species from the middle Cambrian of Sweden. A, B. *Lejopyge laevigata* from Gudhem, Västergötland. A. Cephalon, original of Axheimer *et al*. (2006*b*, fig. $6a_1$), LO9600t, ×7. B. Pygidium, original of Axheimer *et al*. (2006*b*, fig. $6a_2$), LO9601t, ×8. C, D. *Goniagnostus nathorsti* from Vilske stream, Falbygden. C. Cephalon, original of Weidner *et al*. (2004, fig. 3N), LO9563t, ×9. D. Pygidium, original of Weidner *et al*. (2004, fig. 3R), LO9567t, ×13. E, F. *Ptychagnostus punctuosus*. E. Cephalon from Vilske stream, Falbygden, original of Weidner *et al*. (2004, fig. 3A), LO9547t, ×11. F. Pygidium from the Almbacken drill core, Scania, original of Axheimer & Ahlberg (2003, fig. 5L), LO9205t, ×7. G, H. *Ptychagnostus atavus* from Forsemölla, Scania. G. Cephalon, lectotype, original of Ahlberg *et al*. (2006*c*, fig. 2.1), LO354T, ×6. H. Pygidium, syntype, Ahlberg *et al*. (2006*c*, fig. 2.3), LO355t, ×9. I. *Ptychagnostus gibbus* from the Almbacken drill core, Scania, original of Axheimer & Ahlberg (2003, fig. 5E), LO9198t, ×6.

corynexochids. A plethora of the ”Swedish” agnostoids have been reported also from other continents, such as Siberia, South China, south-eastern Newfoundland and Great Britain, whereas a majority of the polymerids seem to have been strongly provincial. These distributional differences were likely related to different modes of life (e.g., Robison 1976). The often cosmopolitan agnostoids, commonly found in open-marine deposits, are generally thought to have been pelagic, allowing them to spread across vast areas (e.g., Robison 1975; Bruton & Nakrem 2005 but see, e.g., Müller & Walossek 1987; Nielsen 1997). By contrast, many polymerids were probably adapted to a benthic mode of life on the shelf, hence restricting their occurrence to individual palaeocontinents or specific areas (e.g., Rowell *et al*. 1982; Samson *et al*. 1990). Furthermore, physical barriers must have affected their ability to migrate over long distances. The Iapetus Ocean (Fig. 4), for example, seems to have been an efficient oceanic barrier preventing long-distance migration of most benthic polymerids. It is likely, however, that the larvae of specific polymerids were able to passively migrate considerable distances with the aid of currents.

Despite their endemic nature and often being strongly facies controlled, polymerid trilobites have commonly been used for interregional correlation. Although their endemism reduces the potential for intercontinental correlation, polymerids are important for palaeogeographical reconstructions. The polymerid trilobite faunas from the middle Cambrian of Scandinavia most closely resemble those of south-eastern Newfoundland, New Brunswick, Massachusetts and England, i.e., eastern and western Avalonia. The location of Baltica and, for instance, Armorica, Perunica and Avalonia, in close proximity of south-polar latitudes during the Cambrian (Cocks & Torsvik 2002), suggests that these palaeocontinents experienced cool-water environments. Several palaeobiogeographic studies have indicated that faunal dispersal between isolated or neighboring terranes was strongly related to temperature gradients in the oceans (e.g., Conway Morris & Rushton 1988; Shergold 1988; Babcock 1994*a*, *b*; Cocks & Torsvik 2002). This would explain the differences in polymerid faunas between Baltica and for example Laurentia, of which the latter was located closer to the equator in Cambrian times, hence experiencing considerable warmer environments (Samson *et al*. 1990).

Polymerids of both Laurentian and Baltic aspect, however, have been reported from the Innuitian margin of the Laurentian palaeocontinent, showing that not all polymerids were endemic (Babcock 1994*a*, *b*). Genera reported from deep-water, outer shelf deposits of the Henson Gletscher and Kap Stanton formations of North Greenland include, for example, *Anomocarina* (Fig. 7), *Centropleura*, *Parasolenopleura* and *Solenopleura*, all of which are common taxa in cold-water, shallow deposits of Baltoscandia (see, e.g., Angelin 1851; Westergård 1950, 1953). Similar distributional patterns have been recognized to occur between other palaeocontinents. For instance, the genera *Anomocarina* and *Solenopleura* have also been documented from Kara and Siberia (Bogolepova *et al*. 2001). The distribution of these genera suggests that, at least some, polymerids were affected by oceanic temperature gradients and had access to open ocean waters (Babcock 1994*b*).

6. Stratigraphy and correlation

The work on a chronostratigraphically standardized Cambrian System is supervised by the International Subcommission on Cambrian Stratigraphy (ISCS), an organization aiming also at developing and publishing regional and global stage-level chronostratigraphical classification charts of the Cambrian System. With one exception, the Cambrian System is lacking

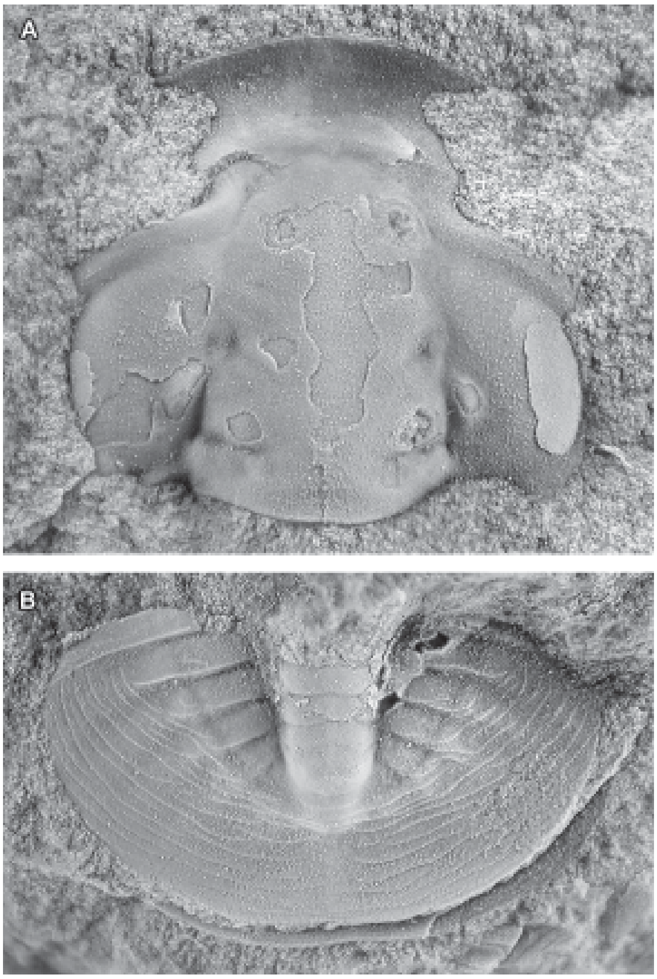

Fig. 7. *Anomocarina excavata* (Angelin, 1851) from the Andrarum Limestone, Andrarum, Scania (coll. S. A. Tullberg). The genus has been recorded from several palaeocontinents and the species from, e.g., Baltica, Laurentia (North Greenland) and Siberia (Westergård 1950; Babcock 1994*a*, *b*). A. Cranidium, LO9801t, ×6. B. Pygidium, LO9802t, ×6.

formally defined international stages, partly reflecting the scarcity of suitable biostratigraphical markers for intercontinental correlation. So far, only the system boundaries and the lower boundary of the uppermost series, the Furongian, and its lowermost stage, the Paibian, have been ratified. The latter two units are defined by the first appearance datum (FAD) of the globally occurring agnostoid *Glyptagnostus reticulatus* (Peng *et al*. 2004). The traditional lower and middle Cambrian series are subject to change. Currently, three series below the Furongian have been proposed for the chronostratigraphical subdivision for the Cambrian System, hence abandoning the traditional tripartite division (e.g., Babcock *et al*. 2005; Peng *et al*. 2006). These, yet undefined, series have been accepted by the International Commission on Stratigraphy (ICS), and shall be based on Global Standard Stratotype Sections and Points (GSSPs), i.e., not substituting the traditional Cambrian subunits but instead representing new stratigraphic intervals. They are provisionally named (in ascending order): Cambrian Series 1, Series 2 and Series 3. The base of Series 2 has been proven difficult to define because of the lack of reliable fossils, and is suggested to be defined by the lowest occurrence of trilobites (Babcock *et al*. 2005). Although not yet ratified, the base of Series 3 is likely to be defined by the FAD of the polymerid *Oryctocephalus indicus* (Reed, 1910) or at a slightly lower level (e.g., Peng *et al*. 2004; Geyer 2005). As these three series are pending ratification, the subdivision of the Cambrian System into the traditional lower and middle Cambrian and the Furongian is used in this thesis. Accordingly, the former two are spelled with a lowercase ”l” and ”m”, respectively.

The biostratigraphy of the middle Cambrian in Sweden is based predominantly on trilobites. Much of the pioneer work made on the biozonation was carried out by Westergård (1936, 1944 and 1946), who subdivided the series into three superzones (or ”stages”) and nine zones (A1–C3; Fig. 5), largely based on the occurrence of agnostoids (Fig. 6) and paradoxidids. His studies and interpretations were preceded by pioneer biostratigraphical works of, e.g., Tullberg (1880), Linnarsson (1869, 1883) and Nathorst (1869, 1877). The lowermost of the three superzones, the *Acadoparadoxides* [or *Paradoxides* (*Plutonides*); Fletcher *et al*. (2005)] *oelandicus* Superzone, is locally missing, e.g., in Västergötland and possibly Scania (Fig. 5). The succeeding *Paradoxides paradoxissimus* and *P. forchhammeri* superzones are generally more complete, particularly in Scania, but may be partially or completely missing (e.g., Westergård 1946; Martinsson 1974). Although his work is known as a reference standard, Westergård (1946) neither explicitly described the nine zones, nor did he give thorough definitions of their boundaries. Such descriptions are important as work in progress is aiming for a viable globally subdivision of the middle Cambrian Series. In the proposed global agnostoid zonation of Robison (1982, 1984) and Peng & Robison (2000), the base of each zone is defined by the FAD of a single species selected for its abundance, wide geographical distribution and relatively short stratigraphic range. Nine zones, more or less globally recognizable, have been identified for the middle Cambrian (Fig. 5). The majority of the papers in this thesis address Westergård’s (1946) zonation and its applicability to this global standard.

Two of Westergård’s zones, the *Ptychagnostus lundgreni–Goniagnostus nathorsti* and the *Tomagnostus fissus–P. atavus* zones, were given more than one index species. According to Westergård (1946), this was because of one of the species may be predominant and the other one rare, or even absent, at a given locality. The *P. atavus* Zone (*sensu* Peng & Robison 2000) broadly correlates with Westergård’s (1946) *T. fissus–P. atavus* and *H. parvifrons* zones. The latter zone has been incorporated into the global *P. atavus* Zone, based on the fact that *H. parvifrons* (Linnarsson, 1869) appears already within the lower parts of the *P. atavus* Zone (Westergård 1946, p. 45). Thus, the original designation of the *H. parvifrons* Zone as a standalone zone was based on local taxon abundance rather than stratigraphical range (Berg-Madsen 1985*b*; Peng & Robison 2000). Although *Tomagnostus fissus* (Linnarsson, 1879) is known as a common and widely distributed species, it has been reported not only co-occurring with *P. atavus*, but also with *P. gibbus* (Linnarsson, 1869) below (Peng & Robison 2000). Its use as an index fossil is therefore restricted. For further discussion on the *P. atavus* Zone, see Ahlberg *et al*. (2006*c*: paper V). *Ptychagnostus lundgreni* has a long stratigraphical range and does not always co-occur with *G. nathorsti*. Hence, it is also not suitable as an index fossil. The validity of the *P.*

lundgreni–G. nathorsti Zone was thoroughly discussed by Berg-Madsen (1985*b*; see also Peng & Robison 2000). Another major discrepancy between the traditional Swedish zonation and the global scheme is the *Solenopleura*? *brachymetopa* Zone. This zone is of considerable importance for regional correlations, and reflects a facies change recorded by the Andrarum Limestone and the Exporrecta Conglomerate, and in Scania also by strata just below, including the Hyolithes Limestone. As noted by Westergård (1944, 1946; cf. Daily & Jago 1975), and further discussed in Axheimer *et al*. (2006*b*: paper IV), *Lejopyge laevigata* already appears near the base of the *S*.? *brachymetopa* Zone. Recently, *L. laevigata* was recorded even below this zone in the Andrarum-3 drill core from Scania, Sweden (Ahlberg *et al*. 2006*b*: paper VII). As noted by Peng & Robison (2000, p. 7), the *L. laevigata* Zone of Sweden was seemingly based on local taxon abundance and not stratigraphical range, and it was proposed in Axheimer *et al*. (2006*b*: paper IV) that the *S*.? *brachymetopa* Zone should be abandoned, and that the base of the *L. laevigata* Zone should be lowered to the FAD of the nominal species.

The uppermost zone of the middle Cambrian of Sweden, the *Agnostus pisiformis* Zone (formerly lowermost upper Cambrian; prior to the selection of a GSSP for the base of the Furongian), is difficult to define. Its base has traditionally been defined by local abundance of the taxon. As its FAD lies within the *L. laevigata* Zone, it was decided also in Axheimer *et al*. (2006*b*: paper IV) that the base of *A. pisiformis* Zone should be defined by the LAD of *L. laevigata*. The upper boundary of the *A. pisiformis* Zone is defined by the base of the succeeding *Olenus* & *A.* (*Homagnostus*) *obesus* Zone (or the base of the *Glyptagnostus reticulatus* Zone). In conclusion, the middle Cambrian of Sweden can for the most parts be tied well to the global agnostoid zonation of Robison (1982, 1984) and Peng & Robison (2000).

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