Environmental fluctuations in the *Olenus* Zone (Upper Cambrian), southern Scandinavia: A geochemical approach

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The Scandinavian Alum Shale Formation (Middle Cambrian to Lower Ordovician) was deposited under generally low bottom water oxygen levels. In the formation there is a covariance between faunal composition and the level of trace element enrichment caused by their mutual dependence upon changes in the bottom water oxygen levels. A detailed profile of the V/(V+Ni) ratio through the Upper Cambrian *Olenus* Zone in the Gislövshammar-2 core, Scania, Sweden, is described. Environmental information from this zone is particularly relevant since the *Olenus* species in the zone apparently undergo iterative changes in morphology that may be linked to environmental changes. Moreover, the occurrences of *Olenus* species and *Homagnostus obesus* are almost mutually exclusive. The results indicate that the trilobitic intervals coincide with increases in oxygen levels as monitored by the V/(V+Ni) ratio. Peak oxygen levels do not appear at the base of each interval, suggesting that colonisation of the sea-floor took place when the oxygenation level reached a certain threshold but before maximum oxygen levels were reached. The distribution patterns of *Olenus* and *Homagnostus* are interpreted as reflecting differences in substrate preference since samples containing *Homagnostus* have statistically significantly higher TOC levels. The V/(V+Ni) variations in the *Olenus* bearing intervals suggest that oxygen levels fluctuated more than would be expected from morphological changes apparent in the *Olenus* species.

Key words: Alum Shale, Gislövshammar-2, olenids, agnostids, evolution, dysoxic, substrate, V/(V+Ni).

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Kaufmann (1933a, b, 1935) undertook a series of detailed studies of microevolution in the Upper Cambrian *Olenus* Zone of southern Scandinavia. The work showed that species of *Olenus* repeatedly became narrower up-section (Fig. 1). The six species investigated formed four lineages, which have been regarded as classical examples of iterative evolution (e.g. Clarkson 1988, Hoffman & Reif 1994). The middle part of the original section in Scania has recently been re-examined by Clarkson et al. (1998), who largely confirmed Kaufmann's observations. However, Clarkson et al. (1998) also studied the non-olenid fossil elements and stressed that the faunal succession is much more dynamic than previously recognised.

Since Kaufmann's pioneering work, a better understanding of the palaeoecology and depositional environment of the Alum Shale and its fauna has been established (Buchardt et al. 1997, Clarkson & Taylor 1995a, b, Clarkson et al. 1998, Schovsbo submitted, Nielsen et al. unpublished). The aim of the present paper is to use geochemical parameters to characterise the environment in which the trilobites lived and to investigate whether the faunal dynamics can be understood in terms of differences in the depositional environment. The iterative pattern seen in Figure 1 could thus reflect responses to environmental fluctuations by either adaptation (compare Sheldon 1990, 1996) or by ecophenotypic differences in the sense of Johnson (1981) and Nielsen (1995). A reassessment of Kaufmann's original section in Scania is currently being conducted, based on collections of new trilobite material (Bodil Lauridsen unpublished.). The original exposures are, however, too weathered to allow a geochemical investigation and the present paper is therefore based on fresh drill-core material from the Gislövshammar-2 core drilled 30 km south of Andrarum (Fig. 2). Although Kaufmann did not show that the morphological changes recorded at

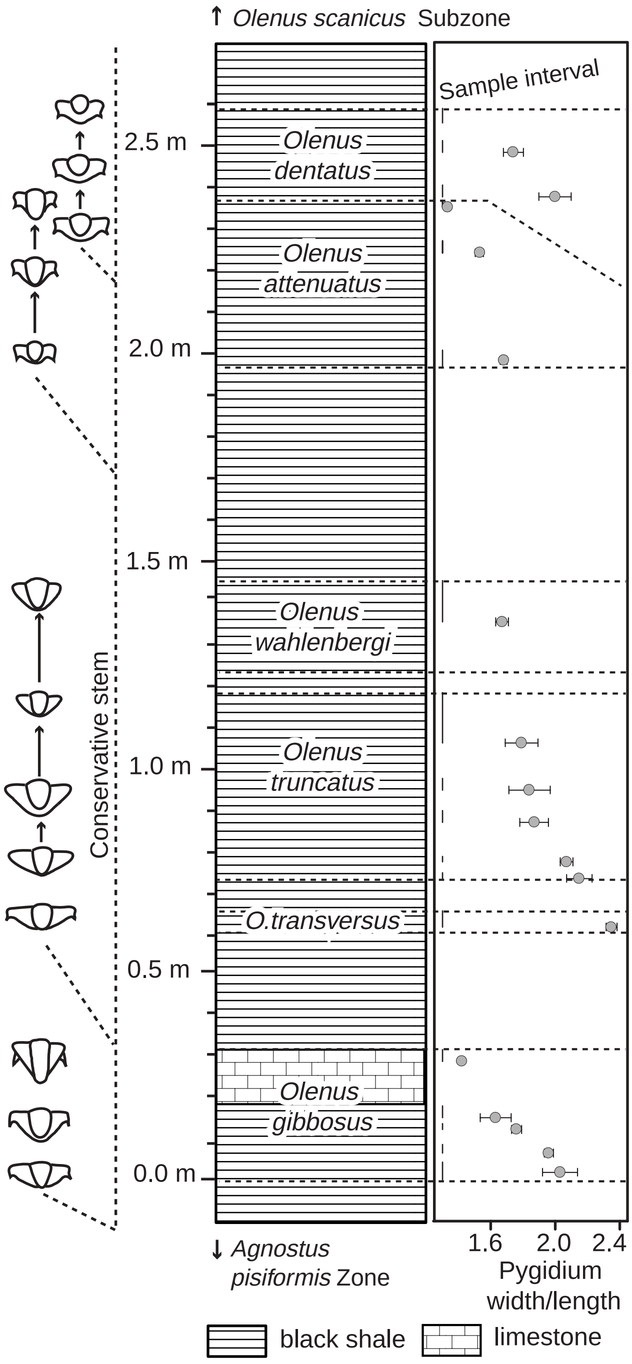

Fig. 1. Profile through the *Olenus* Zone in Andrarum. Mean and standard error of the mean pygidia width/length ratio are from Kaufmann (1933a, Table 13). The data represent the variation seen in Kaufmann's ontogenetic group 3 (pygidium that ranges from 2.6 to 3.5 mm in size) but are representative for the total data material. Based on Kaufmann (1933a) apart from outline drawings of pygidia that are redrawn from Henningsmoen (1957).

Andrarum also took place in south-eastern of Scania (Kaufmann 1933a) he nevertheless proved its regional significance by documenting it on Bornholm (Kaufmann 1933b) and on Öland (Kaufmann 1935) i.e. over distances much larger than from the Gislövshammar-2 drill-hole to Andrarum.

Depositional scenario of the Alum Shale

The Alum Shale (Middle Cambrian to Lower Ordovician), in which the *Olenus* Zone is the second trilobite zone out of six in the Upper Cambrian, was deposited in an epicontinental sea bound to the present west by the Iapetus Ocean and to the present south by the Tornquist Sea. The formation is a typical black shale unit with elevated organic carbon content and trace element levels (Andersson et al. 1985, Buchardt et al. 1997). It represents deposition in relatively deeper water, probably below storm wave base, i.e. plausibly in the range of 50–150 water depth or slightly less (Buchardt et al. 1997, Eklöf et al. 1999). The black shale facies gradually encroached on the platform in the course of a Cambrian first order sea level rise that reached a maximum in the Early Tremadoc (Buchardt et al. 1997). The bottom water environment has been viewed as being anoxic to euxinic, which prevented invasion of a benthic fauna (Thickpenny 1984, 1987). Faunal evidences suggest, however, that the environment was at least from time

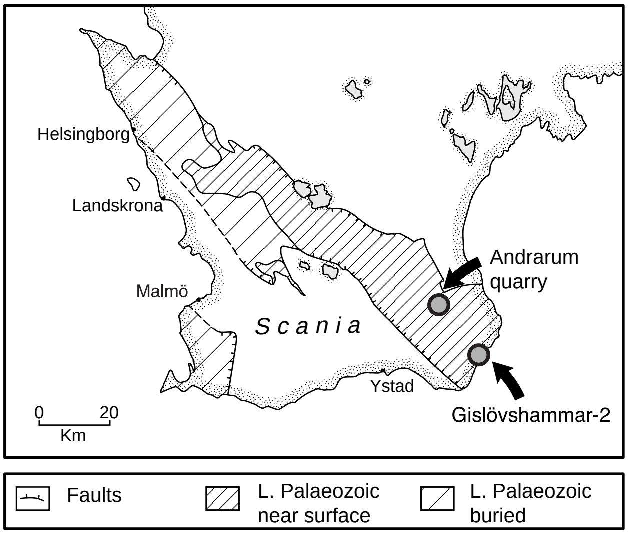

Fig. 2. Distribution of Lower Palaeozoic deposits in Scania, southern Sweden with location of the Gislövshammar-2 drill-core and Andrarum quarry. Modified from Buchardt et al. (1997).

to time sufficiently oxygenated to allow invasion and colonisation of a benthic fauna (Bergström 1980a, b, Buchardt et al. 1997, Schovsbo submitted).

The Alum Shale contains a remarkably rich fauna although rarely more than three species occur together in the Upper Cambrian (Westergård 1922, 1947). The trilobites are generally preserved as flattened moulds in the shale whereas uncompacted trilobites with the skeletons preserved can be found in diagenetically early carbonate concretions (“orsten” or anthraconite). The Mid Cambrian trilobite fauna is dominated by agnostid trilobites whereas the Late Cambrian fauna is dominated by olenid trilobites (Martinsson 1974). Non-olenid polymerid trilobites occurred occasionally in the environment during periods of relatively high oxygen levels (Bergström 1980b, Schovsbo submitted). Agnostids are also present in the Upper Cambrian, but are practically restricted to the lower two zones where they are very common; they are remarkably rare in the higher zones (Ahlberg & Ahlgren 1996). Non-trilobite faunal components include articulated and nonarticulated brachiopods, bradoriid ‘ostracods’, small crustaceans and locally sponges (Müller & Walossek 1985, 1987, Westergård 1922).

Life mode of *Olenus* and *Homagnostus*

Olenid trilobites have been regarded as a highly specialised group adapted to low-oxygen levels (Clarkson & Taylor 1995a, b, Clarkson et al. 1998, Henningsmoen 1957, Fortey 1975, Nielsen et al. unpublished). Within the Scandinavian olenids three basal morphotypes (*Olenus*, *Peltura* and *Ctenopyge*), can be recognised possibly reflecting different life-modes (Clarkson & Taylor 1995a, Henningsmoen 1957, Nielsen et al. unpublished). The *Olenus*-type olenid is a rather thin-‘shelled’ trilobite with a relatively narrow axis indicating that it did not have room for strong muscle attachments. Genal caeca are also a general feature that could be the trace of a blood system aiding respiration (Jell 1978, Clarkson & Taylor 1995b). Eyes were laterally directed with no vision below the horizontal (Clarkson & Taylor 1995b). Altogether this indicates that *Olenus*-type trilobites were not adapted to a pelagic life and they are here viewed as benthic trilobites adapted to cope with low oxygen concentrations (see also Clarkson & Taylor 1995a, b, Schovsbo submitted).

Less obvious morphological features can be used to elucidate the life mode of agnostid trilobites as illustrated by the work of Müller & Walossek (1987) on exceptionally well preserved material of *Agnostus pisiformis*. Here, some morphological details indicate a swimming or floating mode of life although these features, according to the same authors, are not in conflict with a benthic life mode (Müller & Walossek 1987: 42). Other authors have focused more on the distribution of the group. In the Cambrian, agnostids were practically restricted to black shale environments. Together with the almost pandemic distribution of some species this has led to the widely held interpretation that agnostids were pelagic organisms (e.g. Robison 1972). Their widespread distribution can, however, be explained by an extended larval stage and their strong facies dependency indicates that the adult life mode was related to the bottom environment (Conway Morris & Rushton 1988, Nielsen 1997). Hence the conclusions made by Müller & Walossek (1987) that *A. pisiformis* was not able to live an active pelagic life but was tied to the benthic environment is adopted here as a general approximation for Cambrian agnostids.

Material and data

The data represent a profile trough the *Olenus* Zone from the Gislövshammar-2 drill-core. The drill-hole situated on the east coast of Scania (Fig. 2) was placed close to the drill-site of the Gislövshammar-1 core described in detail by Westergård (1942, 1944). Samples in the present study were picked for each 5 cm. No further splitting of the core in search for fossils was conducted. Each sample was of half core width (1 inch) and approximately 1 cm thick. The fossil content was noted and macroscopic pyrite crystals were removed prior to crushing. The remaining sample procedure and analytical measurements are presented by Schovsbo (submitted) who also discussed the stratigraphical variation of the geochemical parameters.

Results and discussion

The *Olenus* Zone spans the interval from 79.49 m to approximately 71.5 m in the Gislövshammar-2 drill-core. The base of the zone is defined by the first appearance of *O. gibbosus* and the top is placed at the first appearance of *Parabolina*. Trilobites occur, however, only in the lower 2.6 m of the *Olenus* Zone and the following presentation and discussion will thus be focused on that part of the sequence (Fig. 3). This distribution of fossils is identical to that found in other parts of Scania, where trilobites are known to occur

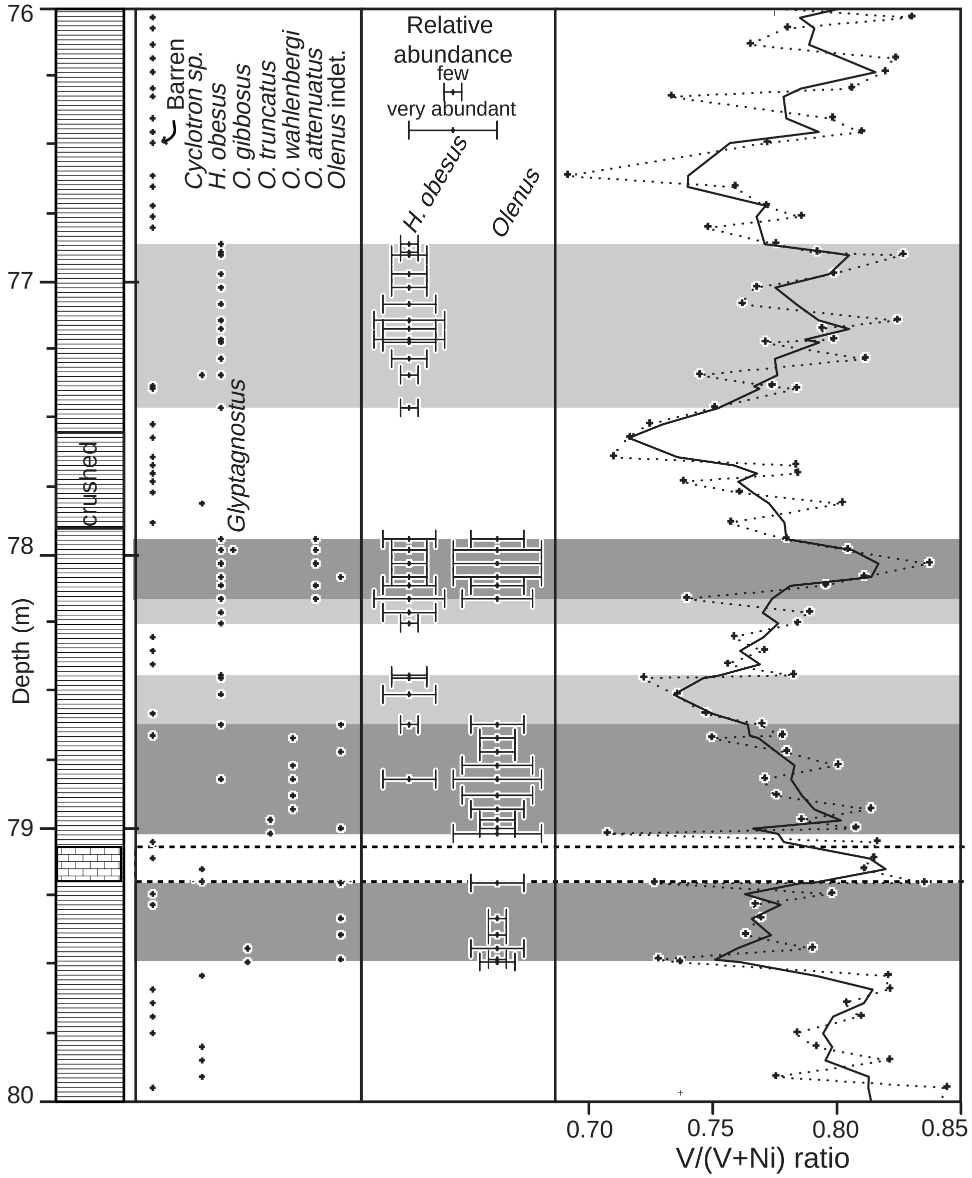

Fig. 3. Faunal range, relative abundance of *Olenus* and *Homagnostus* and profile of V/(V+Ni) ratio through the trilobitic part of the *Olenus* Zone and the uppermost part of the *Agnostus pisiformis* Zone in Gislövshammar-2 drill-core. Base of *Olenus* Zone is defined at first occurrence of *O. gibbosus* (79.5 m). The solid line represents a running average of 3 data points. Relative abundance is not based upon measurements of the genera but on visual inspection of each sample. Light shaded intervals indicate where *Homagnostus* occurs solely and dark shading where species of *Olenus* are present. See Figure 1 for legend.

frequently in the lower 5 subzones, whereas the youngest and by far the thickest *O. scanicus* Subzone is practically non-trilobitic and characterised by the bradoriid ‘ostracod’ *Cyclotron* and locally by nonarticulated brachiopods (Westergård 1922, 1944, 1947). Such non-trilobitic intervals of regional significance are probably caused by the early dissolution of calcite shells and skeletons related to increased oxygen levels at the sea floor (Schovsbo submitted).

The recorded species include *O. gibbosus, O. truncatus, O. wahlenbergi, O. attenuatus, Homagnostus obesus* and *Cyclotron* sp. (Fig. 3). Only one sample at 78.82 m included a non-olenid polymerid trilobite and one sample contained a possible *Glyptagnostus reticulatus*. The fauna is dominated by *Olenus* and *Homagnostus* that tend to occur as mutually exclusive (Fig. 3). The occurrence of species recorded from the Gislövshammar-2 core deviate slightly from that described by Westergård (1944) from the Gislövshammar-1 core. In that core Westergård recorded *O. transversus* from the shale immediately below a limestone interval. This species has not been identified with certainty in Gislövshammar-2 but a poorly preserved *Olenus* representative occurring at the same level could represent this form (Fig. 3). Westergård did not report *O. attenuatus* from the Gislövshammar-1 core. This species is, however, generally found in other parts of Scania (Westergård 1922, 1944, 1947) and its absence in the Gislövshammar-1 core probably reflects local differences in preservation. The precise ranges of the other *Olenus* species above the limestone interval differ slightly between the two cores. In the Gislövshammar-1 core *O. truncatus* and *O. wahlenbergi* have a somewhat shorter range (approx. 20 cm; Westergård 1944) as compared to 40 cm in Gislövshammar-2. This might arise from a different development of the limestone interval present in both cores. In the Gislövshammar-2 core the limestone interval is 0.15 m thick (79.05 to 79.20 m) which is notably thinner than the limestone interval in Gislövshammar-1 (0.7 m; Westergård 1944). Petrographically the limestone in the Gislövshammar-2 core resembles those fine-grained carbonate concretions that occur both in a distinct layer and in discontinuous bands in the lower portion of the *Olenus* Zone in the Andrarum quarry and elsewhere in Scania (Westergård 1922, 1944).

The precise subzone level of the *Homagnostus* bearing interval above *O. attenuatus* (Fig. 3) is not known since *O. dentatus* has not been found in either of the Gislövshammar cores. In Andrarum *O. dentatus* sparsely co-occurs with *O. attenuatus* and ranges approximately 20 cm above it (Westergård 1922, Kaufmann 1933a). In the Gislövshammar-2 core, the interval above *O. attenuatus* (77.56 to 77.92 m) was highly fractured (Fig. 3). This is probably related to the drilling procedure but small-scale faulting cannot entirely be excluded. The fractured interval in Figure 3 could thus potentially include the *O. dentatus* interval and the *Homagnostus* interval above probably represents an interval above the range of *O. dentatus*.

Faunal changes and geochemistry

According to Schovsbo (submitted) a covariance between faunal composition and geochemistry exists in the Alum Shale caused by their mutual dependence on changes in the bottom water oxygen levels. In periods of relatively high oxygen levels (upper dysoxic), nonarticulated brachiopods and non-olenid polymerid trilobites inhabited the seafloor whereas periods of low oxygen levels were characterised by communities of agnostids and olenid trilobites (lower dysoxic). By combining the whole rock V / (V+Ni) ratio with the total sulphur content of fossiliferous samples a geochemical subdivision of the oxygenation changes within the pore and bottom water was established (Schovsbo submitted). The upper dysoxic environment (sulphur <2.5 wt.%) was subdivided into an upper (D1, V / (V+Ni) <0.84) and a lower (D2, V / (V+Ni)>0.84) regime and these were interpreted to represent a build-up of pore water anoxia closer to the sediment / water interface. The lower dysoxic environment (sulphur >2.5 wt.%) was subdivided into an upper (D3, V / (V+Ni) >0.84) and a lower (D4, V / (V+Ni)<0.84) regime. This environment was interpreted to represent intense sulphate reduction at the sediment / water interface but most likely also include anoxic to euxinic bottom water conditions.

Schovsbo (submitted) argued that non-trilobitic interval could have originated from early dissolution of trilobite skeletons prior to compaction. The most likely cause for the dissolution was re-oxidation of reduced sulphide compounds related to low but unstable oxygen levels. A characteristic feature of this would be an increase in the V / (V+Ni) ratio at the base of the non-trilobitic interval and high or unstable V / (V+Ni) values in the interval. This can be seen in the upper part of the *Olenus* Zone but dissolution does not appear to control the earlier non-trilobitic intervals in the zone (Fig. 3). The trilobitic samples from the *Olenus* Zone all plot within the lower dysoxic D4 regime of Schovsbo (submitted) indicating that the oxygen levels were low during deposition and with only minor fluctuations (Fig. 4A). According to

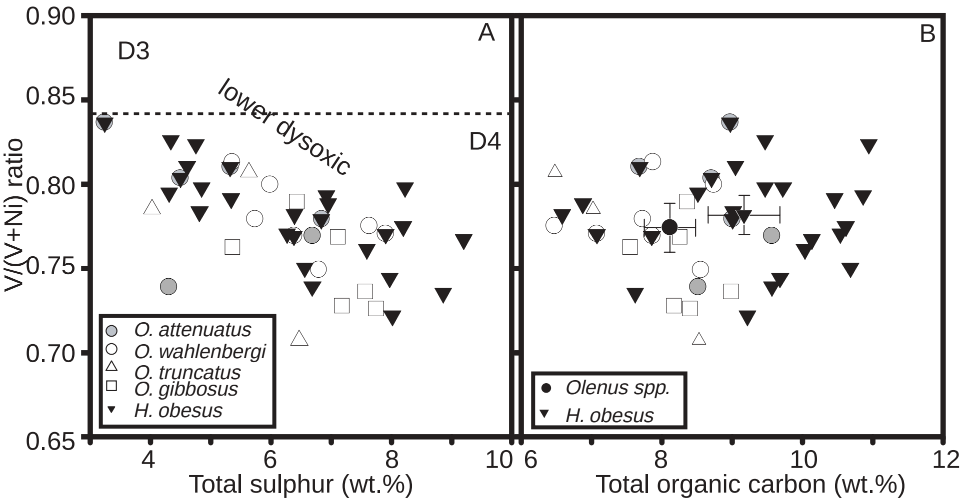

Fig. 4. V / (V+Ni) ration versus sulphur content (A) and total organic carbon (B) of trilobitic samples. Samples containing undeterminable *Olenus* spp. have been grouped together with the assumed species group. The horizontal line in A represent the boundary of the lower dysoxic D3 and D4 regimes of Schovsbo (submitted). Error bars in B indicate the confidence level (95%) on the mean value. Note that the organic carbon is thermally mature in the Gislövshammar-2 core.

Table 1. Summary of geochemical composition of trilobitic samples in the *Olenus* Zone, Gislövshammar-2 drill-core. In the calculations undeterminable *Olenus* spp. have been grouped together with the assumed species group.

	O. attenuatus			*O. wahlenbergi*			*O. truncatus*		
	TOC wt.%	S wt.%	V/(V+Ni) ppm/ppm	TOC wt.%	S wt.%	V/(V+Ni) ppm/ppm	TOC wt.%	S wt.%	V/(V+Ni) ppm/ppm
mean	8.6	5.5	0.79	7.7	6.6	0.78	7.3	5.4	0.77
std.dev	0.7	1.4	0.03	0.8	1.0	0.02	1.1	1.2	0.05
95% conf.	0.8	1.5	0.04	0.7	0.9	0.02	2.6	3.1	0.13
Number	6	6	6	7	7	7	3	3	3
min. value	9.6	6.9	0.84	8.7	8.0	0.81	6.5	4.1	0.71
max. value	7.7	3.3	0.74	6.5	5.4	0.75	8.5	6.5	0.81

	O. gibbosus			Olenids			*H. obesus*		
	TOC wt.%	S wt.%	V/(V+Ni) ppm/ppm	TOC wt.%	S wt.%	V/(V+Ni) ppm/ppm	TOC wt.%	S wt.%	V/(V+Ni) ppm/ppm
mean	8.3	6.9	0.75	8.1	6.1	0.77	9.2	6.4	0.78
std.dev	0.5	0.9	0.03	0.8	1.3	0.03	1.3	1.6	0.03
95% conf.	0.5	0.9	0.03	0.4	0.6	0.01	0.5	0.7	0.01
Number	6	6	6	22	22	22	26	26	26
min. value	7.5	5.4	0.73	6.5	3.3	0.71	6.6	3.3	0.72
max. value	9.0	7.8	0.79	9.6	8.0	0.84	10.9	9.3	0.84

Schovsbo (submitted) the D4 regime includes both lower dysoxic and anoxic oxygen levels and the non-trilobitic intervals thus most likely represent environments in which a benthic colonisation of the seafloor was prevented because of low oxygen levels.

It was anticipated, as based on Kaufmann (1933a) that each pulse of trilobites coincided with high V/(V+Ni) ratio i.e. with periods of relatively high oxygen content and that the oxygenation level would gradually decrease within each trilobitic interval (see also Pedersen 1989). The results indicated, however, a more complex interplay between faunal elements and geochemistry. In the core, each trilobitic interval does coincide with relative increases in V/(V+Ni) values although highest V/(V+Ni) values appear not at the base but 5 to 10 cm higher up (Fig. 3). It appears that the 'colonisation' commenced when the oxygen concentration reached a certain threshold but before peak oxygen levels were attained. This behaviour might also be reflected in the abundance data that tend to follow the variation in the V/(V+Ni) ratio (Fig. 3). No statistically significant differences in the selected geochemical properties (Table 1) have been observed among the different *Olenus* species indicating that they all had similar ecological requirements.

Samples containing *Olenus* and *Homagnostus* have significantly different (>95%) mean total organic carbon (TOC) values (Table 1). No statistically significant difference between the mean V/(V+Ni) values can be observed indicating similar oxygen requirements or a difference below what can be resolved by the V/(V+Ni) ratio (Table 1). The link between *Homagnostus* and higher TOC content indicates on the other hand a possible difference in substrate preference between the two groups (Fig. 4B), which may provide the explanation for their almost mutually exclusive distribution (see also distribution data and discussion in Clarkson et al. 1998). The organic carbon in the Gislövshammar-2 core is post mature with regard to oil generation (Buchardt et al. 1986, 1997) and because of hydrocarbon liberation, the organic carbon level might be 30-50% less than similar beds in immature areas (Buchardt et al. 1986). A theoretical possibility thus exists that the observed variation in TOC levels is a secondary feature related to the thermal maturation and decomposition of the organic carbon. This process is not, however, viewed as important since it would probably have generated a more random pattern than that actually observed (Fig. 4B).

Two basic mechanisms are known to affect the TOC content, namely changes in productivity and changes in the rate of deposition (Canfield 1993, Wignall 1994). Estimates of the primary productivity in the Alum Shale Sea indicate that it was low (Thickpenny 1987) probably excluding the possibility that TOC variation arose from changes in the pelagic fallout rate. Alternatively, since the organic matter in the most enriched levels occur as 0.1 to 0.5 mm thick laminae, the high TOC levels might reflect development of mat communities on the sea floor as also proposed by Buchardt et al. (1997). Guy-Ohlson & Lindqvist (1990) have provided indirect support for this. According to them the Alum Shale kerogen consist primarily of amorphous organic matter (>80 vol.%) probably having an algal origin. Moreover, Guy-Ohlson & Lindqvist (1990) found that fragments of cup-bearing mucilaginous algae remains resembling *Gloeocapsamorpha* (a marine blue-green algae) and *Botryococcus* (a fresh water green algae) occurred abundantly in Alum Shale samples of various ages. The higher TOC levels could thus reflect a higher proportion of organic matter from benthic mat communities on which *Homagnostus* might have been able to live unlike *Olenus*.

Differences in sedimentation rate are known to exercise a very important control on the organic carbon preservation in modern sediment (Canfield 1993) and on substrate conditions (Wignall 1993). Although the average depositional rate for the shale indicates that it was deposited very slowly (Lindström 1971, Thickpenny 1984), sedimentation could nonetheless have alternated with periods of non-deposition. If so, the high TOC levels could reflect periods of relative high depositional rates and opposite for the low TOC interval.

None of the explanations offered can, however, be tested although their predictions regarding the high TOC substrate are in direct opposition to each other. According to Wignall (1994) the development of benthic mats marks a fundamental change from soft to firm substrate, whereas the opposite transition is expected to take place when sedimentation rate is raised (Wignall 1993). Currently the mechanism behind incorporation of organic carbon into the Alum Shale is too poorly understood to allow the actual biological cause for the apparent different substrate preference between the agnostid and olenid trilobites to be interpreted; the strong facies dependency, however, of agnostids strongly indicates that they indeed were bottom dwellers.

Implication for the "Kaufmann Cycles"

The best-developed linear trend in the V/(V+Ni) values (judged from the running average curve in Figure 3) is seen in the *O. truncatus* to *O. wahlenbergi* Subzones. Here the gradual decrease in V/(V+Ni) values matches the narrowing of the pygidium seen in Kaufmann's data (Fig. 1). The sample to sample variation in the same interval indicates, however, that it is composed of several small-scale fluctuations (Fig. 3). A less simple stratigraphical variation in the V/(V+Ni) ratio can be seen in the *O. gibbosus* and *O. attenuatus* intervals. Here the highest V/(V+Ni) values and therefore supposedly highest oxygen levels occur in the middle part of each succession, whereas Kaufmann's data indicate a gradual upward change (Fig. 1, see also Kaufmann 1933a). In Andrarum, 30 cm of non-fossiliferous shale separates *O. gibbosus* from younger *Olenus* species (Kaufmann 19933a, Clarkson et al. 1998). This interval is not represented in the core apart from a non-continuous distribution of trilobites towards the base and above the limestone interval (Fig. 3). Likewise, since *O. dentatus* is not found in the core it could indicate that only the lower portion of the *O. attenuatus* lineage is present in Gislövshammar-2.

It thus appears that the morphological changes (Fig. 1) do not follow the variation of the V/(V+Ni) ratio (Fig. 3). This study is, however, conducted with a higher stratigraphical resolution than that of Kaufmann (1933a). Currently, a reassessment of Kaufmann's original section is in program (Bodil Lauridsen unpublished) that might shed light on the short-term variations in morphological forms. Nevertheless it seems less likely that the morphological changes were ecophenotypic. Instead, the model presented by Sheldon (1990, 1996) offers a more feasible explanation to the gradual changes seen in Figure 1. According to his model, the morphological changes should be regarded as truly evolutionary, resulting from selective pressure with morphological reversals occurring from time to time. Sheldon's model predicts that such phyletic evolution is more likely to characterise narrowly fluctuating and slowly changing environments over geological time scales. Albeit one cannot truly judge the term 'narrowly fluctuating' since it by a strict definition must be made from the animals' point of view. The geochemical composition of the *Olenus* Zone is nevertheless remarkably uniform compared with the whole Alum Shale Formation (Schovsbo submitted) suggesting that the environmental fluctuations in the *Olenus* Zone were indeed narrow.

Conclusions

- *Olenus* and *Homagnostus* occur almost mutually exclusively. Samples containing *Olenus* and *Homagnostus* differ significantly in their mean TOC values with *Homagnostus* showing preferences towards the highest values. This variation probably reflects a difference in substrate preference. No significant differences in V/(V+Ni) values between the two groups were found.
- The trilobitic intervals coincide with increases in the V/(V+Ni) ratio interpreted as reflecting increas-

ing oxygen levels. Peak oxygen levels do not occur at the base but rather 5-10 cm higher up. The reason for this could be that the start of ‘colonisation’ took place when the oxygen concentration reached a certain threshold but before peak oxygen levels were reached.
- The sample to sample variation in the *Olenus* bearing intervals suggests that the oxygen level fluctuated more than might be expected from the gradual morphological changes of the *Olenus* species if they were ascribed as ecophenotypic.

Acknowledgements

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Dansk Sammendrag

I den skandinaviske Alun Skifer Formation (Mellem Kambrium – Nedre Ordovicium) var iltsvingningerne i bundvandet styrende for faunasammensætningen og spormetalberigelsen. Denne kobling har resulteret i en kalibrering af V / (V+Ni)-forholdet med formodede ilt-inducerede faunaændringer. Et detaljeret profil af V / (V+Ni)-forholdet gennem den øvre kambriske *Olenus* Zone fra Gislövshammar-2 borekernen (østlige Skåne) beskrives og sammenholdes med ændringer i faunasammensætningen. Formålet er at undersøge om de kendte formændringer i successive *Olenus* arter beskrevet af Kaufmann (1933a, b, 1935) er sammenfaldende med ændringer i V / (V+Ni) forholdet samt at undersøge om den stratigrafiske fordeling af trilobiterne kan tilskrives ændringer i aflejringsmiljøet.

Resultaterne viser, at de trilobitførende intervaller i *Olenus* Zonen er sammenfaldende med stigende V / (V+Ni)-værdier indikative for stigende iltniveauer i bundvandet. Højeste V / (V+Ni)-forhold optræder dog først 5–10 cm over basis af intervallerne, hvilket antyder, at koloniseringen af havbunden blev muliggjort ved et lavere iltniveau end det maksimalt forekommende. Ingen statistisk signifikante forskelle i V / (V+Ni)-forholdet mellem de enkelte *Olenus* arter og *Homagnostus obesus* er konstateret, hvilket antyder samme tolerance over for iltniveauet eller en variation under detektionsgrænsen for V / (V+Ni)-forholdet. En statistisk signifikant forskel i mængden af organisk materiale mellem prøver indeholdende *Homagnostus* og *Olenus* blev fundet, hvilket tolkes som en forskel i substratvalg mellem de to trilobittyper. Denne forskel er benyttet til at forklare den stratigrafiske fordeling af *Olenus* og *Homagnostus*, idet disse to grupper tenderer til ikke at optræde sammen i *Olenus* Zonen. Ophavet til det organiske materiale er dog for uklart til at en specifik biologisk årsag kan udledes.

Prøve-til-prøve-variationen af V / (V+Ni)-forholdet antyder, at iltniveauet i de *Olenus*-førende intervaller var mere ustabilt end formændringerne af arterne indikerer. Formændringerne afspejler således ikke kortidsvariationerne i iltniveauet, som man ville forvente, hvis de var økofænotypiske, og de tolkes som repræsenterende langtids-evolutionære tendenser genereret af selektiv udvælgelse.

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