THE UPPER CAMBRIAN TRILOBITE *OLENUS* AT ANDRARUM, SWEDEN: A CASE OF ITERATIVE EVOLUTION?

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Abstract: The morphological changes in four species-level lineages of the Late Cambrian trilobite *Olenus* from the Alum Shale at Andrarum, south-east Scania, Sweden, have been analysed with the aim of re-examining the classical study of iterative evolution by Kaufmann (1933*a*). New material comprising 647 pygidia was collected for a restudy of *Olenus*, and for comparison the skeletal development of 918 cephala and 568 pygidia from the associated *Homagnostus obesus* were included. The re-examination shows that (1) only pygidia of the *O. transversus* – *O. truncatus* – *O. wahlenbergi* lineage display a statistically significant directional change towards a narrower shape; (2) all other lineages, including the agnostids, show net morphological stasis; (3) hence iterative directional evolution cannot be confirmed. Based on morphological investigations it is tempting to conclude that the lineage *O. transversus* – *O. truncatus* – *O. wahlenbergi* represents just one species displaying gradual morphological changes. Whether this is an evolutionary or an ecophenotypic phenomenon remains uncertain. The vertical distributions of olenids and agnostids are compared by using vanadium/(vanadium + nickel) ratios from the *Olenus* Zone of the nearby Gislövshammar-2 drill-core. It appears that incursions of olenids were linked to increases in bottom-water oxygen levels and that *Homagnostus obesus* was tolerant of lower dysoxia than olenids.

Key words: trilobites, olenids, agnostids, Upper Cambrian, evolution, palaeoecology.

The Middle Cambrian – Lower Ordovician Alum Shale Formation of Scandinavia comprises black mudstones with bituminous limestone layers and concretionary nodules (see Westergård 1922; Martinsson 1974; Thickpenny 1984; Bergström and Gee 1985; Buchardt *et al.* 1997 for reviews). A few thin, dark grey limestone layers are intercalated in the Middle Cambrian succession. The formation has a high content of pyrite and organic carbon, and is known for its significant trace-element enrichment (Buchardt *et al.* 1986; Lewan and Buchardt 1989; Pedersen 1989). The Alum Shale was deposited in an epicontinental sea that covered most parts of Baltica, and the remaining rather small and deeply peneplaned land areas produced very little clastic material. As a result the muds were deposited very slowly with a maximum average accumulation rate of 16 mm/1000 years in Scania, southern Sweden (post-compaction values from Schovsbo 2001). The formation represents deposition in relatively deep water on the shelf below storm wave-base. Depositional depths have been estimated in the range of 50–150 m (Buchardt *et al.* 1997). The bottom environment was probably dysoxic most of the time whereas the pore-water generally must have been anoxic, as suggested by the high content of microscopic pyrite and organic carbon in the Alum Shale (Schovsbo 2001). The distribution of macroscopic pyrite could in theory reflect periods with higher levels of oxygen in the bottom water, i.e. the opposite of what was assumed by Fortey (2000). Iron is transported in the oxygenated state and relatively high levels of oxygen in the bottom water thus facilitated growth of pyrite in the sediments just below the sea floor (Schovsbo 2001). If the bottom water was anoxic, pyrite formed in the water column and quickly settled as small particles, preventing formation of (early) macroscopic pyrite. Intervals with real anoxia in the bottom water seem to have been few and short-lived, judging from the common presence of benthic trilobites (Schovsbo 2001). The distribution of macroscopic pyrite does not match the geochemical or the morphological variations, and this parameter is therefore not used further.

Trilobites occur in great abundance in many limestone concretions, and locally also in the shale. Early dissolution

seems to have been responsible for the absence of calcite-shelled fossils at many levels (Schovsbo 2001). Olenid and agnostid trilobites strongly dominate the fossil fauna, whereas other trilobites are rare in the Upper Cambrian part of the Alum Shale. Non-trilobite faunal elements include articulated and non-articulated brachiopods, bradoriid arthropods, small crustaceans and sponges (Westergård 1922; Müller and Walossek 1985; Williams et al. 1994). Agnostids, notably Agnostus pisiformis and Homagnostus obesus, are very common in the uppermost zone of the Middle Cambrian and lowermost zone of the Upper Cambrian Alum Shale, but are rare at higher strati-graphical levels (Westergård 1922; Ahlberg and Ahlgren 1996). Usually the olenid trilobites occur in profusion as monospecific assemblages, but occasionally two species occur together. It is uncommon to find three or more species associated at any one level except in the Peltura Zone. The high density and low diversity of the trilobites are strongly suggestive of an opportunistic mode of life. The palaeoecology of the Alum Shale trilobite faunas has been discussed by Henningsmoen (1957), Fortey and Wil-mot (1991), Clarkson and Taylor (1995a, b), Buchardt et al. (1997), Clarkson et al. (1998), Fortey (1999, 2000) and Schovsbo (2000, 2001). It is beyond the scope of the present paper to address the palaeoecology of olenid trilo-bites in general; suffice it to state that there is a consensus of opinion that they were adapted to cope with low oxy-gen levels (Henningsmoen 1957; Fortey 1999, 2000; Sch-ovsbo 2001). Agnostids have been regarded as pelagic by some workers and variations in lateral and vertical distri-bution have been thought to reflect differences in the presence of oxygen and nutrients in the upper surface waters (e.g. Robison 1975; Clarkson et al. 1998). How-ever, like olenids, most agnostids are typical of 'black shale' environments and this strong facies dependency

rather suggests a benthic way of living. In Scandinavia, agnostids are very common in the Middle Cambrian Alum Shale of Scania–Bornholm, whereas the coeval silt-stones of nearby Öland contain no agnostids except for sporadic occurrences in a conglomerate at the very top (Westergård 1946). The relatively shallow-water Exsulans and Andrarum limestones that are intercalated within the Middle Cambrian Alum Shale of Scania–Bornholm con-tain, with few exceptions, only rare or very rare agnostids, and among those present other genera dominate, com-pared with the black shale (cf. Westergård 1946). The pronounced facies dependency led Nielsen (1997) to con-clude that agnostids most likely were benthic and with regard to Cambrian taxa generally were adapted to live under dysoxic conditions. A large spat production is to be anticipated under such conditions, which would pro-vide agnostids with considerable migration potential, in particular if the larval stage were long-lasting. This paper also shows that agnostids do not occur scattered through-out the section investigated, as would be anticipated if they lived high in the water column.

The Kaufmann study

The Upper Cambrian Alum Shale of Scandinavia is divi-ded into eight trilobite biozones of which the Olenus Zone traditionally was the second zone from the base (Henningsmoen 1957). Recently the Middle/Upper Cam-brian boundary was redefined so that the Olenus Zone is now the first zone of Upper Cambrian, the Paibian Stage and Furongian Series (Peng et al. 2002). Kaufmann (1933a) studied olenid trilobites from the lower part of this zone at Andrarum, southern Sweden (Text-fig. 1), where the six species, O. gibbosus, O. transversus,
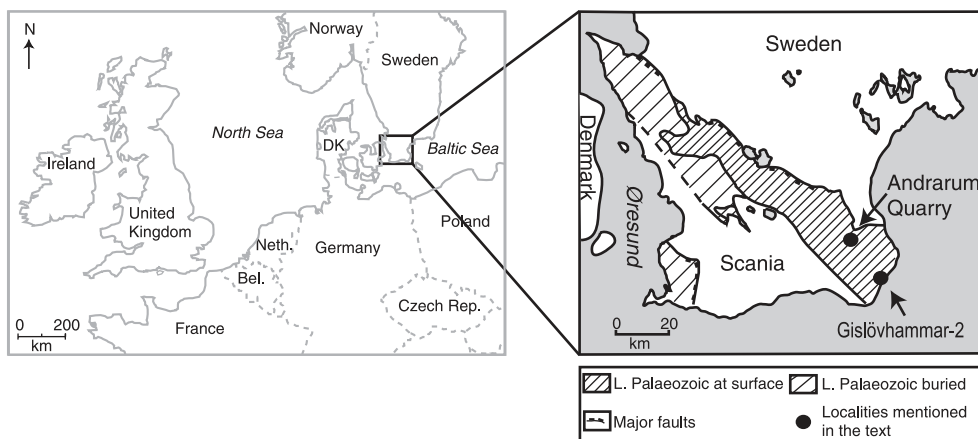
TEXT-FIG. 1. The distribution of Lower Palaeozoic strata in Scania, southern Sweden, and location of the Andrarum Quarry and the Gislövhammar-2 borehole.
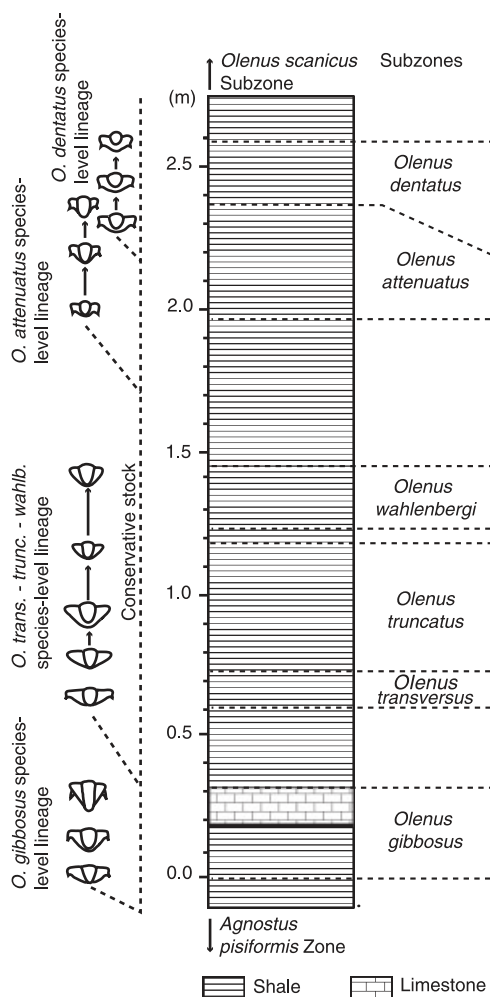
TEXT-FIG. 2. Modified version of Kaufmann (1933*a*, table 2). The four species-level lineages and the supposed gradualistic evolution of the pygidia are indicated. The hypothetical 'Conservative Stock' is marked at the base of each species-level lineage. The thicknesses of subzones are showed in the right-hand column.

O. truncatus, O. wahlenbergi, O. attenuatus and *O. dentatus*, occur in a sequence approximately 2 m thick; examples are shown in Plate 1. The associated and rather common *Homagnostus obesus* was not included in the study. The olenid species succeed one another or show partial stratigraphical overlap. Kaufmann (1933*a*) measured a number of cranidial and pygidial characters, and conducted a simple biostatistical study of 680 pygidia and 1048 cranidia. The measurements were presented only graphically as mean values at specific levels; the original raw data are not available for statistical reinvestigation. Besides, the material analysed came only from selected levels and was not sampled continuously bed-by-bed. Kaufmann (1933*a*) combined his olenid material into four lineages: (1) *O. gibbosus*, (2) *O. transversus* – *O. truncatus* – *O. wahlenbergi*, (3) *O. attenuatus* and (4)

O. dentatus. He concluded that each lineage displays distinct directional evolution of the pygidium, gradually changing from being wide to narrow through time. Associated cranidial changes were less obvious. Kaufmann (1933*a*, table 2) summarised his results in a diagram showing sketches of typical pygidia from selected levels in the section investigated (here Text-fig. 2) and suggested that the four lineages followed an iterative pattern of evolution. He hypothesised that they were derived independently and at different times from an unknown conservative stock. Offshoots from this hypothetical ancestral stock migrated into the area, possibly from Great Britain, when conditions for survival were suitable. Kaufmann (1933*b*, 1935) also analysed the succession of *Olenus* species in the Upper Cambrian of Bornholm (Denmark) and Öland (Sweden), largely confirming the pattern seen at Andrarum. He (Kaufmann 1933*a*) explained the pattern of evolution as examples of orthomutation indirectly triggered by the regression of the Alum Shale sea during *Olenus* Zone time.

The pioneering study of Kaufmann (1933*a*) has been regarded as a classical example of iterative evolution (e.g. Simpson 1953; Raup and Stanley 1978). Kaufmann (1933*a*, *b*, 1935), however, never defined iterative evolution in his studies but referred to earlier works where the concept was discussed (e.g. Dacqué 1921; Abel 1929; Schindewolf 1929; Beurlen 1930). Iterative evolution has been defined as 'a periodic continual appearance with the same (or almost the same) morphotype coming from one single species level lineage' (Hoffman and Reif 1994, p. 72). Levinton (1988, 2001) and Hoffman and Reif (1994) discussed the theories of iterative evolution based on the data presented by Kaufmann (1933*a*, *b*, 1935). Levinton (1988) suggested that widespread and relatively unspecialised taxa have a greater probability of producing new, and more specialised descendants. This idea fits well with the concept of a conservative stock as the source of repeated evolutionary iteration. When representatives of closely related taxa invade the same environment, it is possible that they evolve in a similar way, thus producing an iterative pattern. Levinton (1988) accordingly suggested that iterative evolution is a valid pattern in a modern evolutionary context. Iterative evolution can also be used as an indicator of longevity if the pattern (seen as radiations following extinctions) is comparable among fossil groups (Levinton 2001). Sheldon (1993) suggested that reversals within a single lineage possibly account for some cases of iterative evolution. In this case, lineages of short duration showing similar trends bud off repeatedly from a hypothetical conservative stock. Reversals supposedly occur when traits other than the one under consideration are selected. For further discussion on the concepts of iterative evolution, see Raup and Stanley (1978), Kennedy (1989),

Hoffman and Reif (1994), Clarkson (1998, p. 247) and Levinton (1988, 2001).

The original material investigated by Kaufmann (1933a) seems to have been lost during the Second World War. New sampling was therefore undertaken at Andrarum in south-east Scania, Sweden, in order to duplicate his study and at the same time test the results using a modern analytical approach. The aim of the study is thus primarily to reinvestigate the previously described directional morphological changes displayed by the pygidia of *Olenus*. In addition the pygidia and cephala from the contemporary *H. obesus* were also measured in order to investigate whether they show comparable morphological changes.

MATERIAL AND METHODS

This study is based on the material collected by Clarkson *et al.* (1998) in combination with supplementary specimens collected by us in the Andrarum Shale Quarry. The pooled material covers the interval from the first occurrence of *O. gibbosus* to some decimetres above the last occurrence of *O. dentatus*, i.e. the same succession as that studied by Kaufmann (1933a). The material analysed by Clarkson *et al.* (1998) was collected from a 1·3-m-thick interval ranging from the top of the limestone in the *O. gibbosus* Subzone to the base of the *O. attenuatus* Subzone (Text-fig. 8). The new material that we sampled derives from two sections covering the *O. gibbosus*, *O. attenuatus* and *O. dentatus* subzones. These supplementary sections partly overlap with the section studied by Clarkson *et al.* (1998) and the total stratigraphical thickness investigated is 2·9 m. All new material was collected in 10-mm intervals, whereas Clarkson *et al.* (1998) sampled in intervals of 10–30 mm. The limestone in the *O. gibbosus* Subzone, used as the datum level for measuring the sections, was not sampled (Text-fig. 7). This limestone is henceforth referred to as the limestone marker bed.

The material studied by Clarkson *et al.* (1998) is housed in the Department of Historical Geology and Palaeontology, University of Lund (LO catalogue numbers on Pl. 1), while the material we collected is stored at the Geological Museum, University of Copenhagen (MGUH catalogue numbers on Pl. 1).

The surfaces of the shale samples were whitened with ammonium chloride and about 5000 photographs were taken with a digital camera (Text-fig. 3). Each skeletal element used for species identification and/or morphological analysis was measured using the computer program Northern Eclipse (Copyright 2001; Empix Imaging, Inc.). The number of agnostids and olenids used for the palaeoecological analysis were also counted using the same program. Altogether, 15 articulated olenid skeletons, 1897 olenid cranidia, 748 free cheeks and 746 pygidia were registered in addition to 918 agnostid cephala and 568 agnostid pygidia. At least 50 cm^2 of shale was investigated at each level, but at some levels up to 200 cm^2 was studied. In order to facilitate comparisons, the number of skeletal elements on each surface was later averaged to equal that of 25 cm^2.

All data were collected as simple random samples. It is assumed that all the biometrical data are normally distributed. The PAST program (Hammer *et al.* 2001) was used to test whether the growth pattern displayed by the *Olenus* species and *H. obesus* were iso- or allometric. The species identifications of the six *Olenus* species are based on their stratigraphical distribution in combination with the taxonomic attributes emphasised by Westergård (1922). However, isolated skeletal parts of *O. truncatus* and *O. wahlenbergi* from the interval approximately 50–70 cm above the limestone marker bed proved impossible to assign safely to species, and the transition is strongly suspected to be gradual. Typical representatives of *O. truncatus* are broader overall than those of *O. wahlenbergi* (notably free cheeks and pygidia; cf. Westergård 1922), but with a gradual transition the distinction remains arbitrary. Only the number of thoracic segments, 13 in *O. truncatus* and 15–16 in *O. wahlenbergi*

EXPLANATION OF PLATE 1

Fig. 1. *Olenus truncatus* (Brünnich, 1781), almost entire specimen, LO 7539; levels +22–25 cm; ×2.

Figs 2, 13–14. *O. dentatus* (Westergård, 1922). 2, negative counterpart (positive damaged); the only semi-entire specimen reported in the literature so far; note hypostome in front of cephalon; MGUH 27143; level +187 cm; ×4. 13, MGUH 27149; level +185 cm; ×14. 14, MGUH 27150–27151, level +183; ×8.

Fig. 3. *O. attenuatus* (Boeck, 1838), entire specimen, MGUH 27144; level +137 cm; ×2·5.

Figs 4–5. *O. gibbosus* (Wahlenberg, 1821), pygidia. 4, MGUH 27145; level −45 cm; ×6·5. 5, MGUH 27146; level −43 cm; ×9.

Figs 6–7. *O. truncatus*, pygidia. 6, LO 7536; level +77 cm; ×10. 7, LO 7541; levels +22–25 cm; ×6.

Fig. 8–10. *O. wahlenbergi* (Wahlenberg, 1821), pygidia. 8, LO 7573; level +73 cm; ×11. 9, LO 7579; level +78 cm; ×16. 10, LO 7529; level +78 cm; ×12.

Figs 11–12. *O. attenuatus*, pygidia. 11, MGUH 27147; level +168 cm; ×18. 12, MGUH 27148; level +157 cm; ×25.

All levels noted are above the limestone marker bed apart from those in 4 and 5, which are below it.

PLATE 1
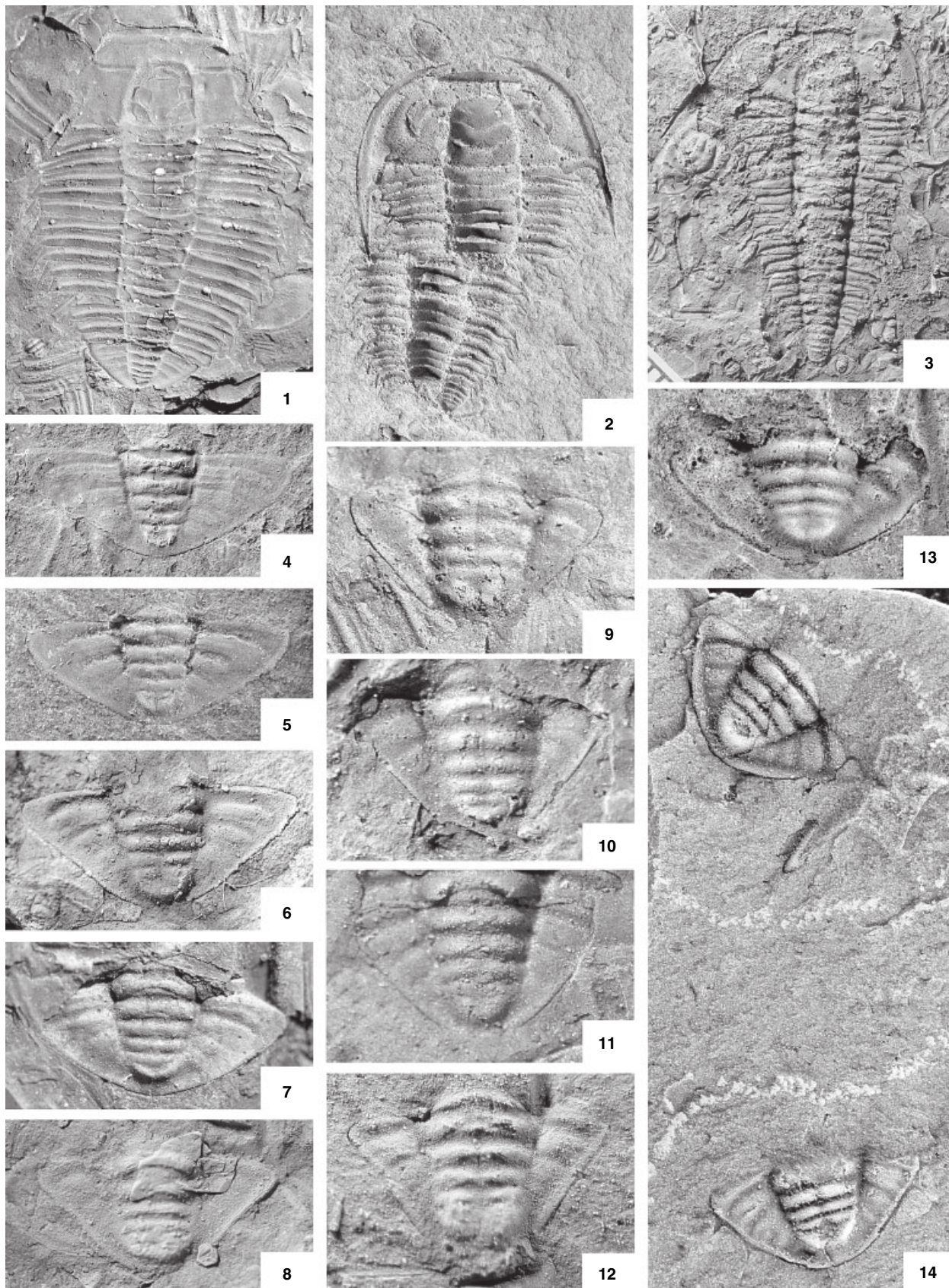
LAURIDSEN and NIELSEN, *Olenus*

TEXT-FIG. 3. Example of a shale surface from level 84 cm above the limestone marker bed (*O. transversus* – *O. truncatus* – *O. wahlenbergi* lineage); ×6. The high densities of fossils at certain levels are clearly shown on the surface. Cranidia, free cheeks, pygidia and thoracic segments from olenids are seen as well as pygidia and cephala from *H. obesus*.

according to Westergård (1922), remains as a possible diagnostic difference, but complete specimens are uncommon in the sections investigated. Eleven complete specimens from 23·5 to 43 cm above the limestone marker bed have 13 thoracic segments, whereas an almost complete specimen from 88·5 cm above the limestone marker bed has more than 14 segments. No articulated specimens are available from the interval where *O. wahlenbergi* and *O. truncatus* supposedly co-occur and it is an open question as to whether the increase in number of thoracic segments is gradual (as we would expect) or abrupt. Further studies of complete specimens are needed to settle whether the species distinction between *O. truncatus* and *O. wahlenbergi* is warranted. For these reasons the two species were treated together in the present study.

The changes in shape of the pygidia of *Olenus* and the cephala and pygidia of *H. obesus* were tested in order to reveal directional patterns in the succession that might reflect evolution. Following Kaufmann (1933a) focus has been on the shape [width (AA)/length (CH) ratio] of the *Olenus* pygidia (Text-fig. 4A). *O. transversus*, *O. truncatus* and *O. wahlenbergi* were analysed as one continuous lineage as suggested by Kaufmann (1933a). The shapes of both cephala and pygidia of *H. obesus* are defined as the maximum width of the axis compared with the length of either the cephalon or the pygidium (Text-fig. 4B). This measurement was chosen
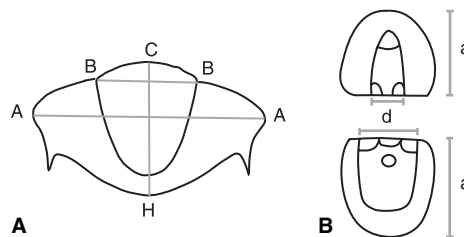
TEXT-FIG. 4. Measurements used for species identification and morphological changes. A, in the pygidia of *O. gibbosus*, *O. truncatus*, *O. wahlenbergi*, *O. attenuatus* and *O. dentatus*, width (AA) is compared with length (CH). B, in *H. obesus* the maximum width of the axis (d) is compared with the length (a) of either the cephalon or pygidium.

because it was easier to measure in a consistent way rather than measuring the maximum width of the respective shields.

The morphological changes for each species lineage were analysed by calculating the arithmetical mean value (X_m) and the standard deviation (σ) at each level. All levels containing more than one measurement were included in the analysis. To test for any directional changes the means of the first and last shape in each lineage were compared using the *t*-test. In addition, the values from each level in all species lineages were compared with those of the succeeding level, an approach that also reveals temporary reversals. When there was a

significant difference in shape between two levels, a histogram based on size (i.e. pygidia length in *Olenus* species and cephala or pygidia length in *H. obesus*) was constructed. This was done to test whether the detected shape difference could be due simply to size differences (reflecting allometric growth). A Kolmogorov-Smirnov test for goodness of fit was used to test the outcome. This test was selected because it is especially powerful when dealing with small sample sizes.

In examining the plotted results, it became obvious that the shifts at some levels resembled reversals. The significance of the difference of mean values between these levels was therefore tested and again positive outcomes were assessed by *t*-tests and the Kolmogorov-Smirnov test for goodness of fit, as described above.

For palaeoecological analysis, abundance diagrams were constructed for the sections investigated. The skeletal elements used for these diagrams show no signs of abrasion or wear and a wide spectrum of sizes is present. It is concluded that the material has not been transported, although only a few articulated specimens have been found.

The palaeoecological diagrams are constructed in the same way as was done by Clarkson *et al.* (1998) and they are calibrated to display the number of skeletal elements on a 25-cm^2 shale surface (hence the number of elements present is most often not an equal number).

RESULTS

Measurements of fossils found in shale may suffer from distortion related to compaction and other taphonomic processes (Hughes 1999; Webster and Hughes 1999). Our study is based mainly on olenid pygidia, which are rather small and not very inflated in comparison with the larger and more strongly convex cranidia. Hence they are less likely to undergo strong deformation during compaction. All specimens were collected from shale and it is therefore assumed that the same taphonomic processes have affected the entire material. The results are therefore considered comparable and internally consistent. The agnostid specimens are probably relatively more distorted by compaction, being rather highly vaulted when unflattened, but as long as the measurements are not compared with uncompacted material we consider the adopted approach tenable. An additional problem is to obtain consistent measurements based on photographs because the specimens are often preserved slightly inclined relative to the bedding surface and photographs should be taken normal to the horizontal plane of the specimen and not to the bedding surface. In this case we argue that all specimens were measured with the same technique making any errors consistent. The measuring error as well as the effect

of compaction quite possibly amplifies the biological variation range.

A first step in the analysis was to investigate whether the growth patterns in *Olenus* and agnostid species are iso- or allometric by checking the value of the alpha slope. The statistical analyses showed that the growth patterns for all species are allometric (Text-fig. 5) but that juveniles (particularly) show rather deviating morphological ratios as compared with adults. Juvenile olenids, defined as specimens in which the length of the pygidia is less than 0·5 mm, were therefore excluded from the stratigraphical study of length/width ratio variations. It should be noted that because the specimens display allometric growth it is possible that the intercepts of the rare mean axis on the *y*-axis can differ, even though the slopes are not significantly different. In this case the pattern of growth may have changed. We were not able to find an appropriate statistical test for checking this.

Morphological changes in the pygidia of Olenus *and the cephala and pygidia of* Homagnostus obesus

The morphological changes within each species level lineage are shown in Text-figure 6. This figure displays the mean value and standard deviation of the measured character at each level. The probability and direction of shape variation are marked with an arrow, and a dotted line pinches into the levels with a positive outcome. The Kolmogorov-Smirnov test was conducted to test if the changes at these levels could be due just to changes in the mean size. The Kolmogorov-Smirnov test rejected this hypothesis. H0 means that 'there is no difference in the size of the individuals from the two investigated levels' in all cases except for levels 27–29·5 cm and levels 43–45 cm of the *O. transversus – O. truncatus – O. wahlenbergi* lineage (marked with a thick arrow and bold values of probability), only here the size of the individuals was not the reason for the statistically significant shape variation. The shape changes are in both cases from a broad to narrow pygidia.

Testing for directional changes between the first and the last occurrence within each of the lineages showed that the *O. transversus – O. truncatus – O. wahlenbergi* lineage (levels 20–83 cm) exhibits a statistically significant shape difference at the 1 per cent level. The cephala from *H. obesus* (from levels −52 to +190 cm) also display a statistically significant shape difference at the 2 per cent level. Histograms based on size were then constructed. Because the lowermost value in the *O. transversus – O. truncatus – O. wahlenbergi* lineage is based on only two specimens, the histogram values were pooled from the lowermost and uppermost 5 cm, respectively (i.e. interval 20–25 cm and interval 81·5–86·5 cm). A Kolmogorov-Smirnov test for goodness of fit was conducted and

this confirmed the H0 in the *O. transversus* – *O. truncatus* – *O. wahlenbergi* lineage, but rejected it in the *H. obesus* (cephalon) lineage. The change in shape displayed by the

pygidia of the former lineage is, therefore, not due to changes in the mean size of the specimens whereas the difference in the *H. obesus* lineage is size related.
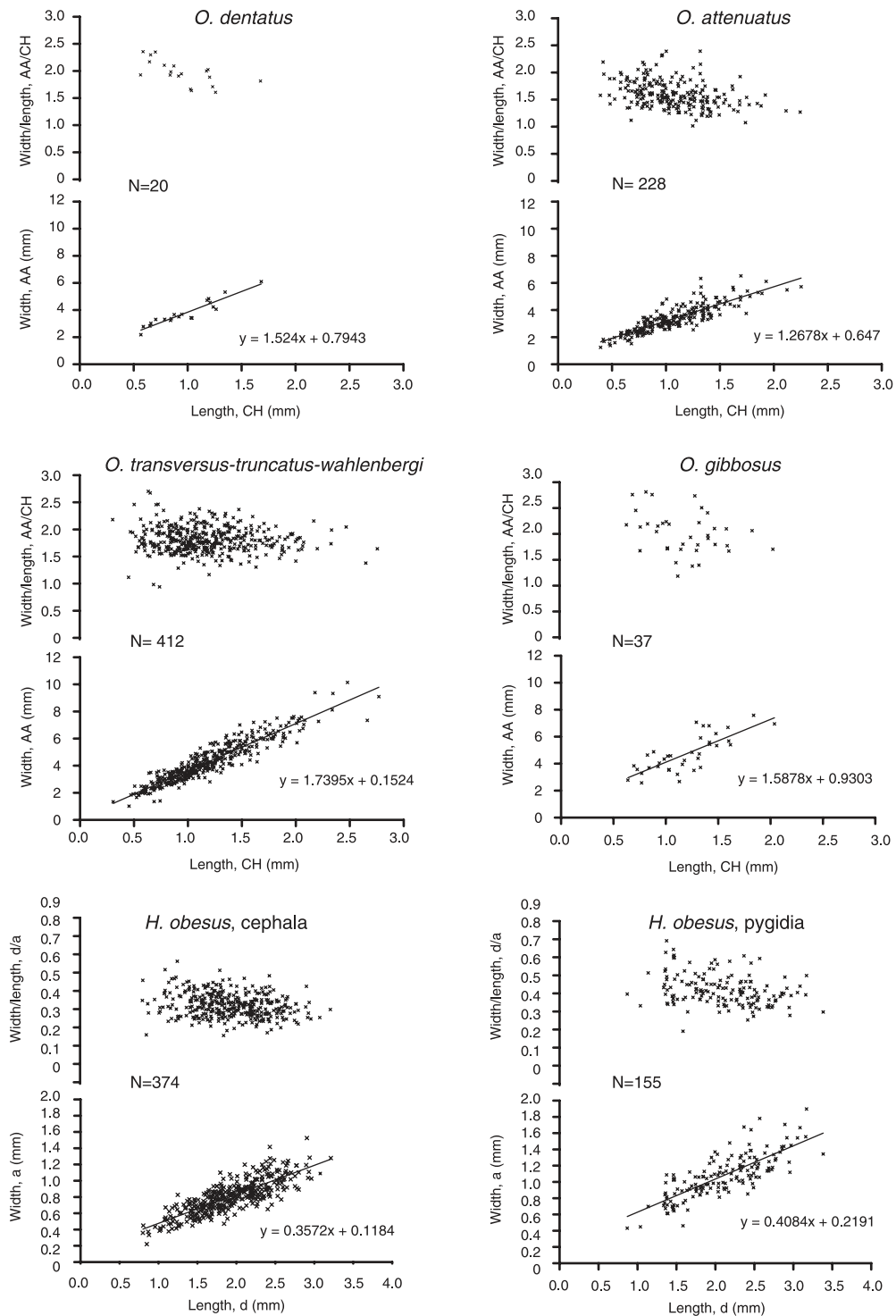
TEXT-FIG. 5. Allometric curves of *O. gibbosus*, *O. truncatus*, *O. wahlenbergi*, *O. attenuatus*, *O. dentatus* and *H. obesus*. For each species the relation between both the length/width and the length/(width/length) are shown. Specimens with a pygidial length of less than 0·5 mm were excluded from the study.
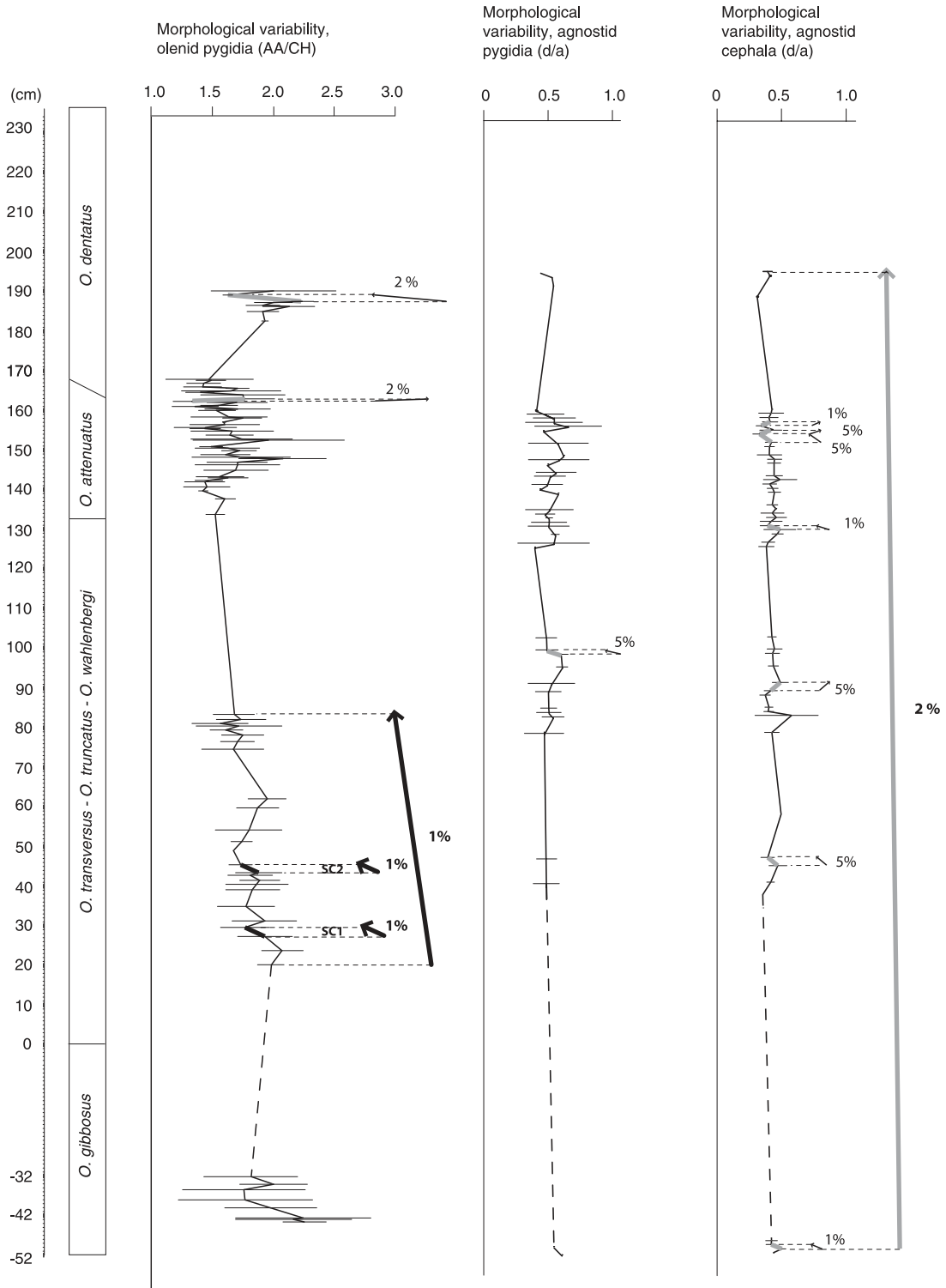
TEXT-FIG. 6. Morphological changes in pygidia of *Olenus* and cephala and pygidia of *Homagnostus obesus*. The variations in morphological variability defined as width/length ratios are compared for each species. The probability and the direction of the shape variation are marked with an arrow. A dotted line pinches into the levels with a positive outcome. The numbers indicate the values of probability. Only in levels 27–29·5 cm (SC1), 43–45 cm (SC2) and 20–83 cm are the significant changes in morphology not size related.
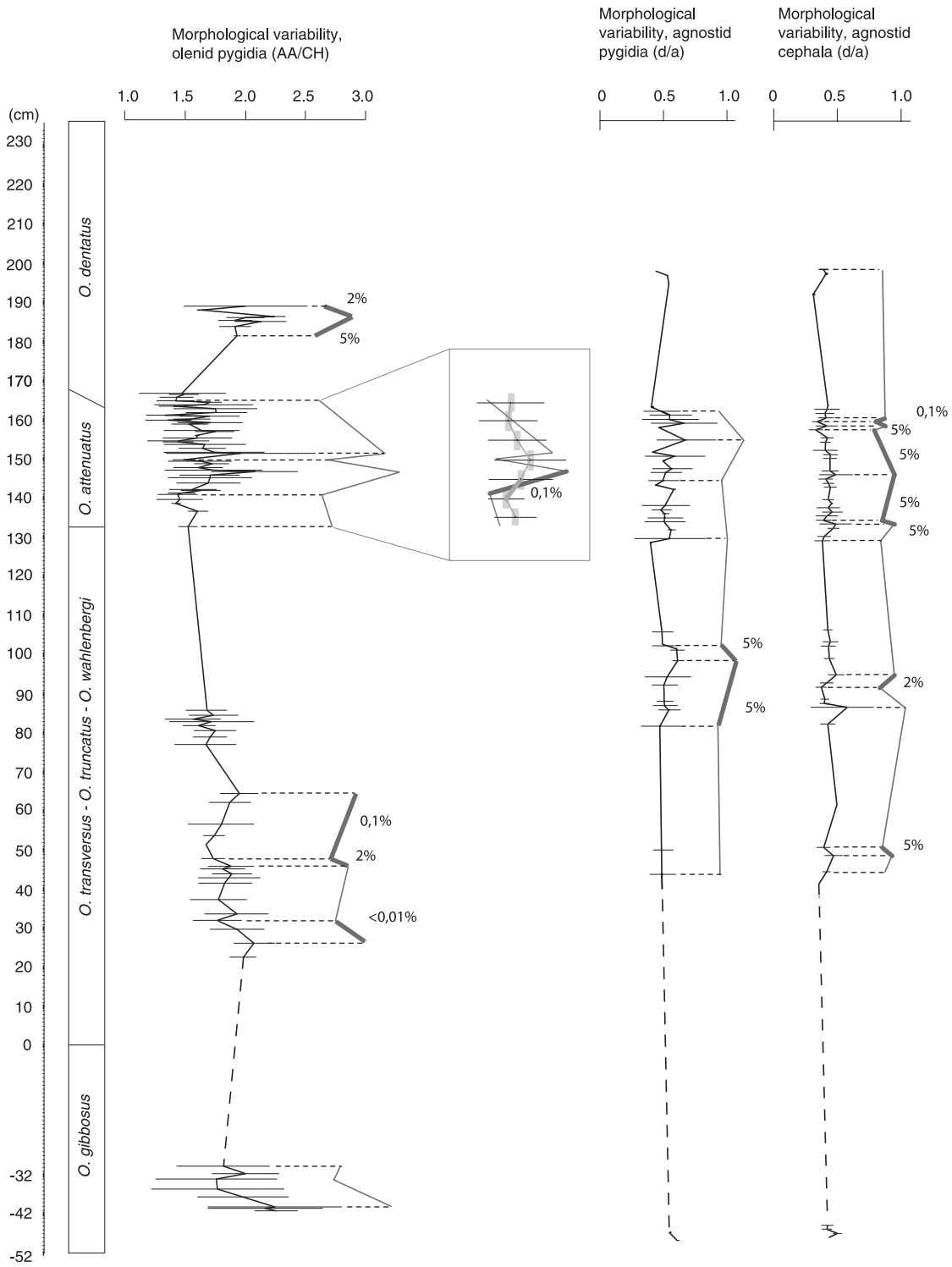
TEXT-FIG. 7. A similar diagram to Text-fig. 6, but displaying tests for reversals in shorter segments (see text). The thick lines indicate when a significant difference is recorded in a series. The numbers indicate the probabilities. However, all the changes can be ascribed to size differences. The box inserted in the *O. attenuatus* Subzone shows a statistical analysis based on specimens pooled from 5-cm intervals instead of 1-cm intervals.

Judging from Text-figure 6, it is possible that a test based on only first and last occurrences is too crude and overrules shorter-term temporary changes, including reversals, which might be significant. In order to examine

this idea the significance of the difference of mean values in shorter intervals was tested using the *t*-test: the intervals analysed are indicated on Text-figure 7; they were selected to reflect major kinks in the average curve. On this figure the thin lines on the right-hand side of each curve indicate the selected series and the thick lines indicate when a significant difference is recorded. At first it appeared that the *O. transversus* – *O. truncatus* – *O. wahlenbergi* and *O. dentatus* lineages both show significant changes at some intervals, whereas none of the changes in the *O. gibbosus* and *O. attenuatus* lineages proved statistically significant. Moreover the pygidia and cephala of *H. obesus* show significant shape changes at various levels (Text-fig. 7). However, all significant changes were subsequently tested with the Kolmogorov-Smirnov test and without exception this rejected the H0. The changes are, therefore, attributable to size differences and not to real shape changes. Theoretically the lack of changes in *O. attenuatus* could be due to small sample sizes, and an additional statistical analysis was performed based on specimens pooled from 5-cm rather than 1-cm intervals (Text-fig. 7). Only one level showed a difference with this method, but also in this case the Kolmogorov-Smirnov test revealed that size differences are involved. It is, therefore, concluded that *O. attenuatus* displays no significant shape changes throughout its range.

Palaeoecological investigations

The distribution of *Olenus* species, *Homagnostus obesus* and *Glyptagnostus reticularis* is shown in Text-figure 8. Only two specimens of *G. reticularis* were found; it is not, therefore, considered further. The diversity of species is no more than two at most levels and only a few levels in the *O. gibbosus* Subzone contain three different species. This is in sharp contrast to the abundance of specimens, which varies considerably, as is apparent from Text-figure 8. Both agnostids and olenids are common and occur together in the uppermost part of the *O. transversus* – *O. wahlenbergi* Subzone (from 46–52 and 83–90 cm above the limestone marker bed) and all the way through the *O. attenuatus* Subzone (130–165 cm above the marker bed). At other levels agnostids occur alone in high densities (84–107 cm above the marker bed). A rather constant ratio of skeletal elements within each genus (cranidia + cephala represent approximately two-thirds of all skeletal elements found) is also apparent from Text-figure 8.

The variations in faunal abundance are not associated with any obvious changes in lithology, pyrite content or presence/absence of baryte rhombs. Pyrite seems essentially omnipresent; it occurs disseminated and as larger nodules or thin layers. At some levels it replaces rhomb-shaped baryte crystals.
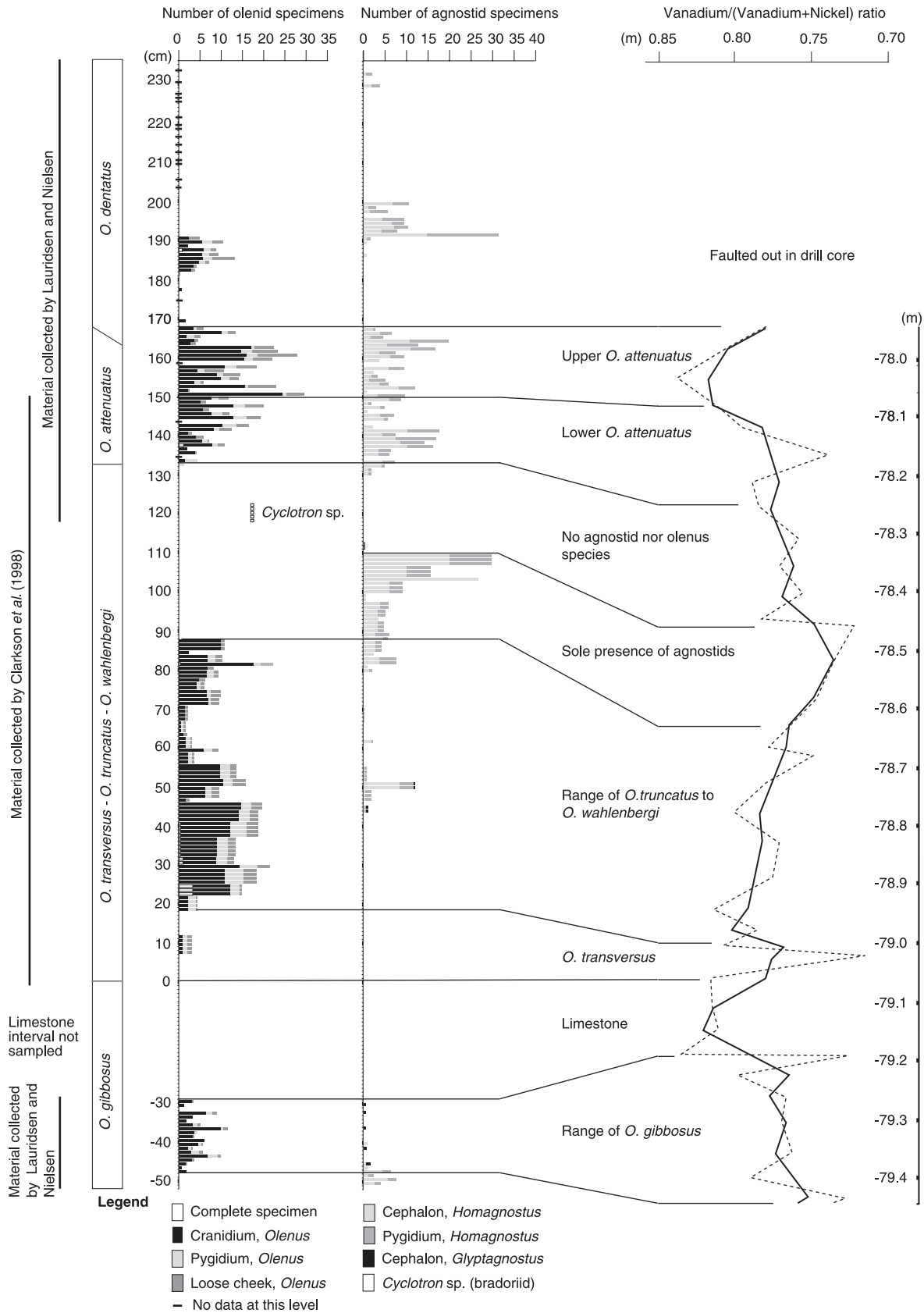
For comparison, the $V/(V + Ni)$ ratios measured through the same stratigraphical interval in the nearby Gislövshammar-2 core are also shown on Text-figure 8 (data from Schovsbo 2000, 2001). The Gislövshammar-2 drill-site is located 20 km south-east of the Andrarum Shale Quarry (Text-fig. 1). The lower *Olenus* Zone interval is thinner in the core than at Andrarum, but the nearly identical distribution pattern of *Olenus* species and *Homagnostus obesus* allows a detailed combination of the results of this study with the geochemical data published by Schovsbo (2000, 2001). It is emphasized that the $V/(V + Ni)$ curve from the Gislövhammar-2 core is calibrated by aligning the tops of the marker limestone bed and the tops of *O. attenuatus* Zone (Text-fig. 8). The scaling of the thinner core section is then adjusted accordingly. Hence, there is not a strict one-to-one match between the sections. The whole rock $V/(V + Ni)$ ratio combined with the sulphur content is interpreted as a proxy of the average oxygen content in the depositional environment (see Schovsbo 2001 for details). The sulphur content is not shown here because its distribution parallels the variation of $V/(V + Ni)$ (Schovsbo 2000, fig. 4). Overall the variation in the $V/(V + Ni)$ ratio in the *Olenus* Zone is low compared with the rest of the Alum Shale Formation (Schovsbo 2000, 2001). This suggests that the oxygen fluctuations in the *Olenus* Zone were comparatively narrow. No significant difference in preferences for $V/(V + Ni)$ ratios between the *Olenus* species and *H. obesus* is apparent (Schovsbo 2000).

The fossil densities in the interval from the top of the marker bed up to 130 cm above it (Text-fig. 8) are somewhat different from those presented by Clarkson *et al.* (1998, fig. 2), generally showing much lower abundance. This is somewhat surprising inasmuch as our data are based on the material collected by Clarkson and co-authors. Our numbers are based on a total count of all fossils on all surfaces, calibrated down to equal that of 25 cm^2, whereas Clarkson *et al.* (1998) used a spot count method by randomly placing a 5×5-cm grid on the shale surfaces. The results demonstrate that it is difficult to place such a grid impartially, and a count based on a larger surface appears preferable.

DISCUSSION AND CONCLUSIONS

Morphological changes

The main focus of our study has been to reinvestigate the iterative morphological changes displayed by the pygidia of *Olenus*, as originally described by Kaufmann (1933*a*). Somewhat unexpectedly it showed that only the *O. transversus* – *O. truncatus* – *O. wahlenbergi* lineage displays a significant shape difference from first to last occurrence

Number of olenid specimens

Number of agnostid specimens

Vanadium/(Vanadium+Nickel) ratio

Faulted out in drill core

Upper *O. attenuatus*

Lower *O. attenuatus*

Cyclotron sp.

No agnostid nor olenus species

Sole presence of agnostids

Range of *O.truncatus* to *O. wahlenbergi*

O. transversus

Limestone

Range of *O. gibbosus*

Material collected by Lauridsen and Nielsen

O. dentatus

O. attenuatus

O. transversus - O. truncatus - O. wahlenbergi

Material collected by Clarkson *et al.* (1998)

O. gibbosus

Limestone interval not sampled

Material collected by Lauridsen and Nielsen

Legend

☐ Complete specimen

■ Cranidium, *Olenus*

☐ Pygidium, *Olenus*

▨ Loose cheek, *Olenus*

— No data at this level

☐ Cephalon, *Homagnostus*

▨ Pygidium, *Homagnostus*

■ Cephalon, *Glyptagnostus*

☐ *Cyclotron* sp. (bradoriid)

(Text-fig. 6). This lineage also includes two levels (significant change intervals 1 and 2 on Text-fig. 6) where notable, rapid shape changes are evident. In both cases the lineage follows the overall pattern towards a narrower morphology. The net directional change in the *O. transversus – O. truncatus – O. wahlenbergi* species lineage may indeed be a genuine example of evolutionary change, whereas the three other *Olenus* lineages and the *H. obesus* lineage all show no statistically significant shape changes. All the detected changes are simply due to size variations. With only one lineage displaying directional changes and three lineages displaying stasis, it is evident that the *Olenus* species do not provide an example of iterative evolution, as previously proposed by Kaufmann (1933a). Whether the one case with directional shape change in fact reflects evolution or is an ecophenotypic phenomenon remains unsettled. As is apparent from Text-figure 8, the morphological change is coincident with a gradual decrease in oxygen in the depositional environment, judging from the V/(V + Ni) ratios; a causal relationship is thus likely. Several different factors could explain the different outcomes of Kaufmann's and our study. Firstly, the fact that Kaufmann (1933a) did not statistically investigate whether size differences were of importance could be a reason, but we do not consider this to be likely because he had a relatively large collection of specimens to hand from each level. He also analysed the individual ontogenetic stages separately (see Kaufmann 1933a, table 13), demonstrating that he was well aware of size-related morphological differences.

Secondly, *O. gibbosus* has not been sampled in the marker limestone bed in our study. Apparently Kaufmann had five, seemingly rather narrow pygidia from the limestone (his *O. gibbosus* posterior 2; cf. Kaufmann 1933a, tables 2, 13). However, there is no statistically significant narrowing from Kaufmann's *O. gibbosus* anterior to *O. gibbosus* posterior 1 in the material we have analysed; thus we cannot repeat his results. This remains unexplained.

Furthermore, and also apparent from Kaufmann (1933a, tables 2, 13), there is no major difference in pygidial outline in the *O. dentatus* line; according to our restudy there is no statistically significant narrowing. Our study does, however, confirm the overlap between *O. dentatus* and *O. attenuatus*.

Although the two studies are based on roughly the same number of pygidia, our material covers a larger interval, being sampled bed-by-bed. Hence the number of specimens at each level is lower than in Kaufmann's study. This obviously has importance for the statistical treatment. In order to test this factor we tried to pool material from 5-cm intervals and apply statistical analysis, now based on a larger material from each level. The outcome was almost identical to the un-pooled analysis. We therefore conclude that there are no significant morphological changes except in the *O. transversus – O. truncatus – O. wahlenbergi* lineage. Based on the difficulties in separating the three species on the characteristics defined by Westergård (1922) it is tempting to conclude that the species-level lineage represents just one species undergoing gradual evolution or ecophenotypic changes due to lowering of oxygen in the environment, eventually making survival impossible for the olenids.

As it appears, we cannot explain the differences between Kaufmann's study and ours based on newly collected material. We conclude that we have not been able to reproduce Kaufmann's data with the exception of the *transversus – truncatus – wahlenbergi* line, which obviously is rather disturbing.

Palaeoenvironment

The *Olenus* Zone marks a distinct faunal change when compared with the underlying *A. pisiformis* Zone. This change from relatively diverse agnostid-dominated faunas of Middle Cambrian aspect to Late Cambrian-type low-diversity, olenid-dominated faunas coincides with the SPICE event (Steptoean Positive Carbon Isotope Excursion) recognized by Saltzman *et al.* (2000). This event seems to signal a palaeoenvironmental shift associated with a significant expansion of the oxygen minimum zone, thus causing more widespread dysoxia in the Baltoscandian epicontinental sea. The spread of dysoxia may not be only a local phenomenon (Nielsen and Schovsbo unpublished). In addition it is obvious, judging from the lithofacies distribution throughout Baltoscandia, that the *Olenus* Zone was initiated by a pronounced lowering of

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TEXT-FIG. 8. Palaeoecological diagram showing densities of the faunal elements in the lower part of the *Olenus* Zone at Andrarum. Note that the number of specimens on the figure differs from the total count mentioned in the text. This is because the number of skeletal elements on the figure was averaged down to equal that of 25 cm^2. The V/(V + Ni) curve is from the equivalent level in the Gislövhammar-2 drill-core (from Schovsbo 2000). The solid line though the individual V/(V + Ni) data points is a running average between mean values at each level. Low V/(V + Ni) values are interpreted as low oxygen levels in the bottom water. In the core, the *O. truncatus-wahlenbergi* lineage ranges up to −78·6 m and the interval with sole presence of agnostids above ranges up to −78·4 m, i.e. matches the interval with low V/(V + Ni) ratios. *O. attenuatus* ranges from −78·2 to −77·9 m, i.e. matching the interval with high V/(V + Ni) ratios. Tie lines indicate correlatable levels (based on fossil evidence).

sea level (Kaufmann 1933a; Nielsen and Schovsbo in prep.). The SPICE event was also associated with a major regression in Laurentia (Saltzman *et al.* 2000). The exact interaction, connection and timing between the sea-level fall and the resulting environmental changes remain uncertain. It is logical, however, to infer that the change from a relatively diverse agnostid-dominated community to a low-diversity olenid-dominated community somehow reflects more widespread dysoxia in the sea. The $V/(V + Ni)$ ratios support a more dysoxic state of the bottom waters during the *Olenus* Zone by comparison with the underlying *A. pisiformis* Zone (Schovsbo 2000, 2001).

Fluctuations in the oxygen levels could have been a primary factor in triggering morphological changes as well as variable faunal abundances. However, the $V/(V + Ni)$ ratio may to some extent be considered to represent a time-averaged proxy of the oxygen levels in the bottom water, and could therefore be too crude to track important short-term variations that influenced the trilobite abundance (e.g. seasonal dysoxia). Apparently incursions of olenids do match high-oxygen intervals [high $V/(V + Ni)$ ratios; Text-fig. 8]. Schovsbo (2000) envisaged that the start of the colonisation by olenids took place when the oxygen concentration reached a certain threshold. The decline in olenid abundance through the *O. transversus* – *O. truncatus* – *O. wahlenbergi* lineage is also linked to a well-defined decline in oxygen content. There is also clear evidence that maximum abundances of agnostids and olenids do not coincide, as noted previously by Clarkson *et al.* (1998). Thus, from below, a peak of agnostids at around 50 cm below the limestone marker bed (see Text-fig. 8) is followed by sparse agnostids and a spike of olenids at −30 to −40 cm. Above the limestone marker bed, a small incursion of agnostids a little above +50 cm is associated with a decrease in olenid abundance, and upwards the agnostids become very abundant as the olenids disappear above +90 cm. Thereafter follows a barren interval before agnostids and olenids reappear. However, the maximum abundance of olenids at around +150 to +160 cm is flanked by maxima of agnostids below and above. After another almost barren interval, an incursion of olenids is followed by a burst of agnostids. In all cases the olenids are most abundant in relatively oxygen-rich intervals, judging from the $V/(V + Ni)$ curve, and the slightly offset peak abundances of agnostids are associated with slightly lower oxygen levels.

According to Schovsbo (2000) olenids and agnostids differ significantly with regard to the TOC (total organic carbon) content of the host sediment, with *H. obesus* showing a preference towards the highest TOC values. This variation may reflect different substrate preferences (Schovsbo 2000). According to our interpretation, the differences in TOC values may reflect lower oxygen concentrations and hence lower levels of breakdown of organic material in the palaeoenvironment.

The outlined distribution pattern suggests that *H. obesus* was tolerant of slightly greater dysoxia than olenids. Even though this contrasts with the general idea outlined above regarding the shift from agnostid-dominated 'Middle Cambrian' faunas to 'Upper Cambrian' olenid-dominated faunas, we do not think that it necessarily invalidates it, since some genera are likely to have been more tolerant than others. We particularly stress that the *Olenus* Zone contains only one dominant agnostid species in association with one rare species (*Glyptagnostus reticulatus*), whereas most Middle Cambrian zones are characterized by numerous agnostid species (cf. Westergård 1946) as well as a limited number of polymerid trilobites.

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