THE LIFE AND TIMES OF THE OLENID TRILOBITES

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Abstract

The Middle Cambrian of Bohemia contains a widespread fauna which can be traced from eastern Newfoundland, through central Britain, Scandinavia and the Montagne Noire in France and further east. Whereas the upper Cambrian (Furongian) in Bohemia consists of volcanics and alluvial sediments, in the Scandinavian (Baltica) and Avalonian successions, dysoxic facies prevail, dominated by the olenid trilobites. The Furongian of southern Sweden forms a superb natural laboratory for studying processes and patterns of evolution in the olenids. The rapid turnover of species and superb preservation of the fossils allows evolutionary changes to be assessed stratophenetically, and at the microevolutionary scale. Also, the dynamics of the evolving faunas can be assessed and their relations with environmental fluctuations established by bed-by-bed collecting and analysis. Moreover since all trilobite growth stages often occur along with the adults, it is possible to establish the complete or partial ontogeny of many species, and to explore the relationhips between ontogeny and phylogeny. Information gained from various lines of evidence from the faunas can be used, along with geochemical approaches to build up a coherent picture of an extinct environment and its inhabitants; this paper summarises old and new explorations in this field.

Introduction

The Barrandian syncline is surely one of the world's richest and most famous localities for well-preserved trilobites. Yet in the Cambrian, marine sediments containing them are confined to the Jince Formation of the Middle Cambrian. The Lower Cambrian consists mainly of continental conglomerates, and the later Middle Cambrian and Upper Cambrian are mainly alluvial, the latter deposited in an active and long-continued volcanic setting (Havlíček 1971, Geyer et al. 2008). The characteristic general of the Jince Formation include *Paradoxides*, *Ellipsocephalus*, *Conocoryphe* and others, immortalised in one of Zdeněk Burian's paintings, and these are elements of a very diverse and widespread fauna which can be traced from eastern Newfoundland, through southern France and northern Spain, Wales and central England, and Scandinavia.

The Scandinavian Cambrian successions are likewise rich in trilobites, and it is interesting to compare and contrast these with the Bohemian faunas. The Lower Cambrian in Scandinavia consists mainly of sandstones, with trilobites in shales at a few horizons. Then, with the deposition of the middle to upper Cambrian shale sequence we are in a unique facies known as the Alum Shales. The Middle Cambrian consists mainly of genera such as those of the Jince Formation; it is remarkably rich and diverse. In southern Sweden alone there are two horizons of limestone, in which there are 12 and 15 agnostoid and 7 and 13 polymeroid genera respectively. Above these there is a remarkable transition, testifying to a major environmental perturbation, for the highest horizon of the Middle Cambrian consists almost entirely of the agnostoid trilobite *Agnostus pisiformis* which literally occur in uncountable millions. (Terfelt et al. 2008). The base of the overlying Furongian is defined as the FAD of *Glyptagnostus reticulatus*, following which is a sequence of beds dominated by trilobites of the Family Olenidae, the main subject of this presentation. These do not, of course, occur in Bohemia since the Furongian sediments are continental. Would there have been a similar sequence in the Barrandian if there had been marine sediments? It is tempting to think so. In Newfoundland, and in Wales and England, the Furongian faunas are dominated by olenids, but by contrast, the coeval trilobites in the Montagne Noire in southern France is quite different, with a strongly Chinese aspect (Shergold et al. 2000).

The Alum Shales of Scandinavia

Before going further, we should consider the paleogeography of the time (fig. 1). During the Cambrian, the

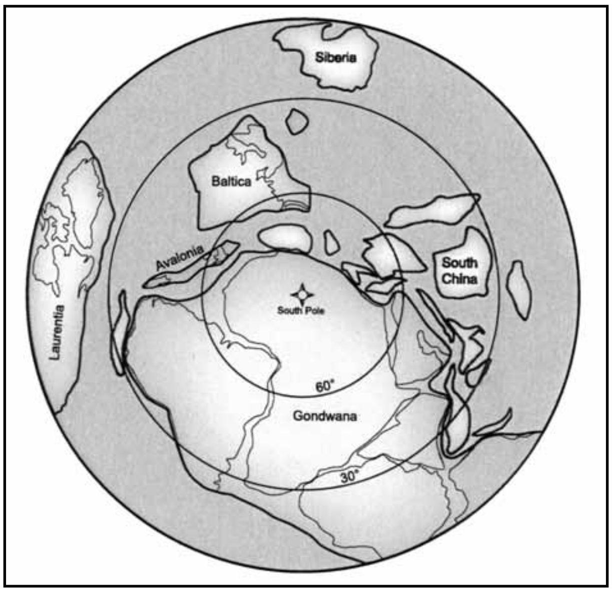

Fig. 1: The Late Cambrian world with the position of Baltica in southern latitudes (from Terfelt).

Laurentian continent sat astride the equator, as it did for the later Palaeozoic. On the other side of the globe lay Gondwana, not yet split into separate landmasses, and in between were the free continents of Kazachstania and Siberia, while in higher southerly latitudes there resided the continent of Baltica, now Scandinavia and Russia west of the Urals. This was the 'heartland' of the olenid trilobites, and it was here, in cool dysoxic waters where they evolved and proliferated, and from where they migrated to other areas. They were able also to colonise the cool deep water surrounding other continents where the temperature was similar to that to which they were accustomed. We shall consider first the Scandinavian olenid faunas of Furongian time, later we shall examine the final stages of their evolution.

We have noted the vast numbers of *Agnostus pisiformis* at the top of the Middle Cambrian. Occasional specimens of the earliest olenid, *Olenus alpha* are found therein. Above this the fauna is dominated by other olenid trilobites, the type genus *Olenus* belonging to the earliest zones of the Furongian where it occurs at certain levels with *Homagnostus obesus*. Interestingly, agnostoids become very rare above this level; there are only a few occurrences, but these are of great value in providing tie points with other continental masses, since the agnostoids have a very wide distribution. Likewise there are rare instances of large polymeroids ("tourists" to use the apt words of Anna Żylińska) from other continental masses which can be used in the same way (Rushton 1967, 1983, Żylińska 2000). The spectacular change from the high-diversity Middle Cambrian trilobite fauna to the low-diversity Furongian fauna is far from well understood at the present time.

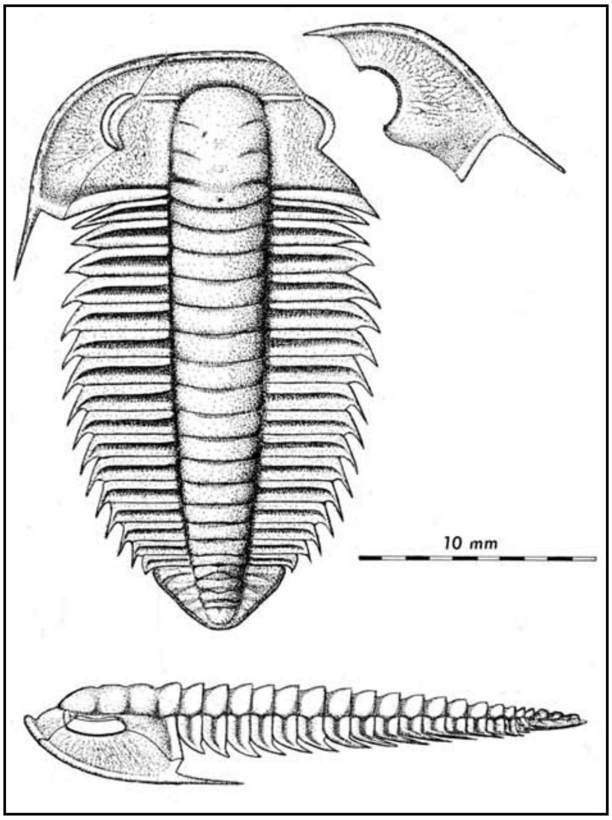

Fig. 2: Reconstruction of *Olenus wahlenbergi* Westergård in dorsal and lateral views. Andrarum, Skåne, Sweden.

Andrarum, Skåne, Sweden

The best place to study the Furongian succession is at the old quarries at Andrarum, in eastern Skåne, the southernmost part of Sweden. Here some 80 metres of Furongian sediment are exposed, overlying 30 metres of Middle Cambrian; they are mainly dark shales with some limestone beds, and very many calcareous concretions. They were exploited for the extraction of alum between 1636 and 1912, and the remains of the old workings are still visible, as well as the red heaps of shale from which the alum has been boiled out. The olenids occur in countless numbers in some parts of the shale sequence, but are almost universal, and often superbly preserved in the concretions.

The Andrarum succession forms a superb natural laboratory for studying very many aspects of trilobite evolution, the relationship of the trilobites to changing environments and the other organisms within it, changing diversity, biotic turnovers, and the overall environment. Our intention over many years of research, and for the foreseeable future, has been to elucidate as much as possible about the Alum Shale environment and its faunas, using as many kinds of diverse evidence as possible, and to try to link them in to a common synthesis.

Biostratigraphy and olenid evolution

Although there are four 'barren intervals' within the Furongian sequence, the succession is otherwise remarkably complete. The rate of faunal turnover is very high, and in consequence the olenid trilobites are of great use in stratigraphy. The overall succession has been known for at least 150 years. A basic scheme of evolutionary relationships was given by Westergård (1922) and elaborated further by Henningsmoen (1957). A recent biostratigraphical revision (Terfelt et al. 2008) links four agnostoid zones with 28 zones based on olenids. In ascending order these are the zones of *Olenus* (6), *Parabolina* (2), *Leptoplastus* (6), *Ctenopyge* (8), *Parabolina lobata* (1). *Peltura* (3) *Westergaardia* (1) and *Acerocare* (1) Since there is only one olenid species in each zone in the lower part of the sequence, evolutio-

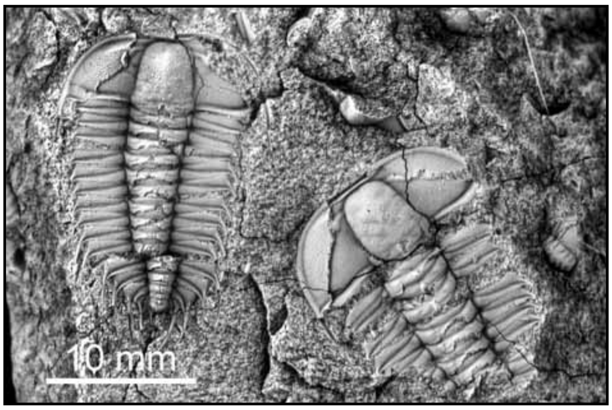

Fig. 3: Type specimens of *Parabolina spinulosa* Wahlenberg. Andrarum, Skåne, Sweden.

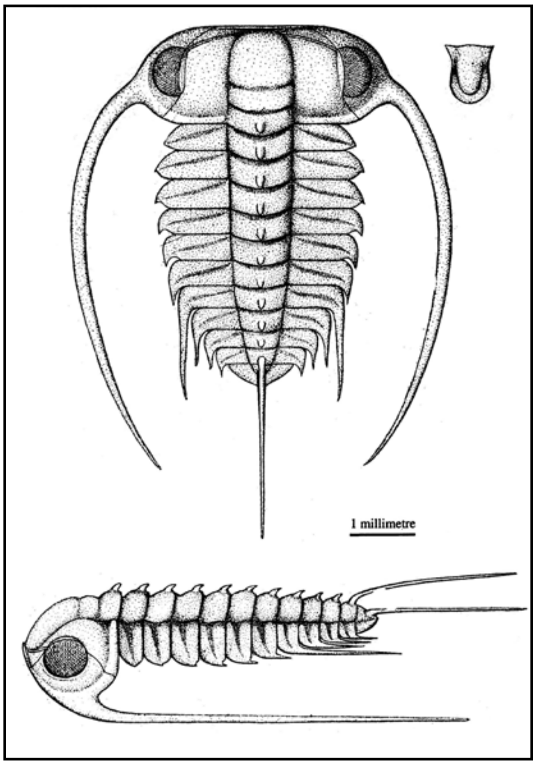

Fig. 4: *Ctenopyge angusta* Westergård. Adult specimen, reconstructed. The long genal spines would support the body above the sea floor, the gills above the dysoxic sea floor. Västergötland, Sweden.

nary relationships at the generic and specific level are easy to determine stratophenetically. The *Olenus* and overlying *Parabolina* zones (fig. 2, 3) have only one species at each level and are dominated by rather 'ordinary-looking' trilobites. Above this, in the *Leptoplastus* zone, some very interesting things begin to happen. (Ahlberg et al. 2006). Firstly the rate of evolutionary change and faunal turnover speeds up dramatically. Secondly, new morphotypes originate, especially forms with very long genal spines. Such morphology provided a springboard for later innovations in the *Ctenopyge* zones (figs 4–6). Thirdly there may be up to four olenid species co-existing. Towards the top of the Furongian, such bizarre forms disappear, and more standard olenid types prevail. Evolutionary convergence is common and some morphotypes are virtually 'repeats' of earlier ones, presumably suggesting similar adaptations.

Microevolution and faunal dynamics

Species-to-species transitions in olenids, and at the same time, faunal dynamics within populations can readily be undertaken by band-by-band collection and counting within a quadrat. The first such analysis was undertaken by Kaufmann (1933) on limestone beds within barren shale intervals in the *Olenus* zones, and indicated four successive trends involving the lengthening and narrowing of the pygidium. Further studies were undertaken in fossiliferous shales of the same age, elsewhere in the quarry (Clarkson et al. 1998), confirming at least one of these microevolutionary trends, and showing that agnostoids and olenids could either occur separately or together. Further studies, with broadly similar conclusions (though more critical of Kaufmann's work), were presented by Lauridsen – Nielsen (2005). Another, very detailed bed-by-bed study, in the *Leptoplastus* zones (Ahlberg et al. 2006) showed that particular faunal associations are often confined to discrete sedimentary packages, or arise after an unfossiliferous interval. Some species may range through several sedimentary changes. Here there are three or even four olenid species at some levels.

Olenid ontogenies

The preservation of many olenids in the concretions is exquisite, and they are often still well-preserved, though flattened, in the shales. Moreover, the juveniles are frequently preserved with the adults which enables detailed studies of ontogeny, i. e. development from early larva to adult, to be undertaken. The use of the scanning electron microscope has greatly facilitated this end. So far, the ontogenies of ten or more olenid species have been worked out and these studies are continuing (figs 4–6) (Clarkson – Taylor 1995a, 1997, Clarkson – Ahlberg 2002, Clarkson et al. 2003, 2004, Tortello – Clarkson 2003, 2008). These studies also shed light on the relationship between ontogeny and phylogeny: *Parabolina*, for example, is a direct descendant of *Olenus*, the

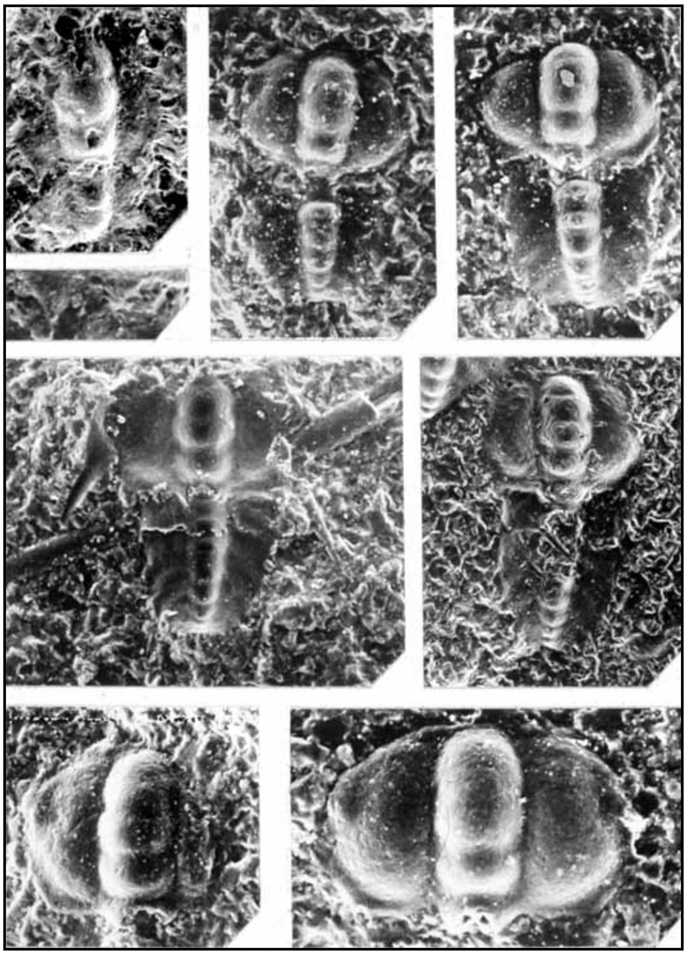

Fig. 5: *Ctenopyge angusta*. Westergård. Juvenile stages of ontogeny (SEM photographs, for size compare the scale bar at the fig. 6) Västergötland, Sweden.

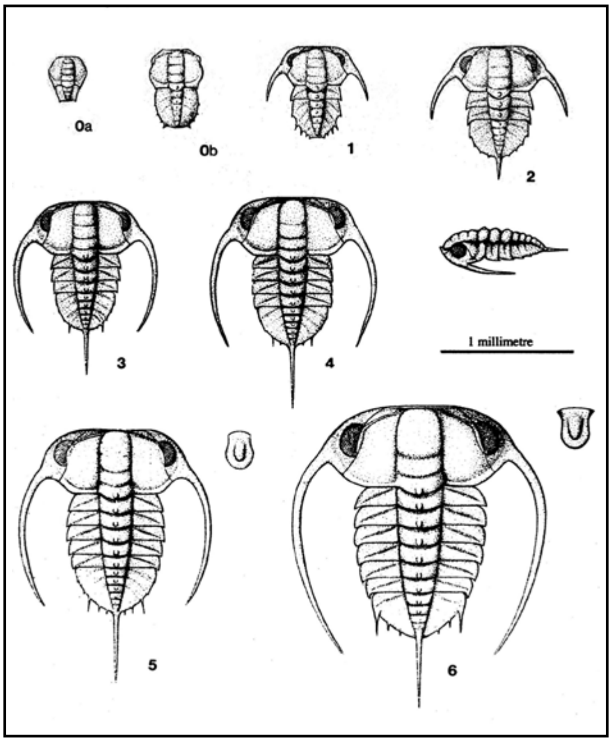

Fig. 6: *Ctenopyge angusta*. Westergård. Juvenile stages, reconstructed. Västergötland, Sweden.

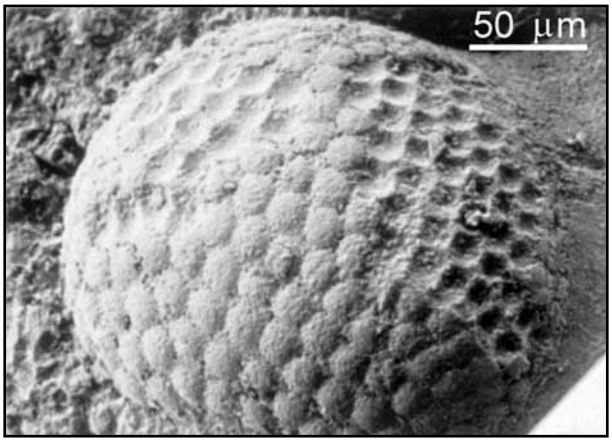

Fig. 7: *Ctenopyge angusta*. Westergård. Holochroal compound eye. SEM photograph.

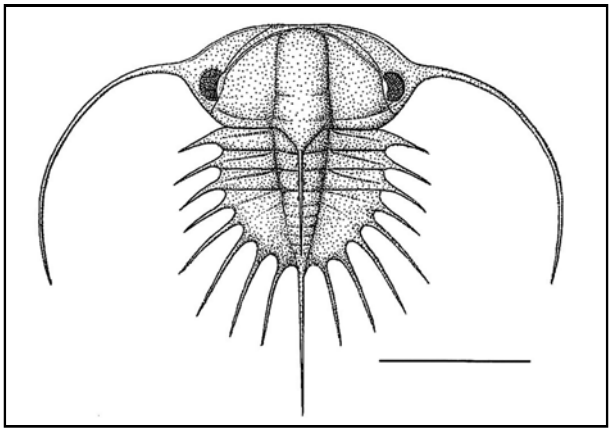

Fig. 8: *Ctenopyge ceciliae* Clarkson & Ahlberg, a planktonic olenid, reconstructed. Scale bar 500 microns. Skåne, Sweden.

'new' characters having arisen by mosaic heterochrony (Clarkson – Taylor 1995a). Moreover, ontogenetic development in some olenids is tightly constrained, with sizes of instars plotting out in discrete groups. In others, however, especially *Parabolina* and *Protopeltura* there seems to be much less restraint on developmental variability, a subject being actively investigated now.

Olenid life habits and functional morphology

The excellent preservation gives plenty of scope for investigations of functional morphology and life habits. Olenids seem to have lived as vagrant benthos, adapted to low oxygen conditions. Some may have fed on the kind of chemosynthetic bacteria typical of such environments (Fortey 2000). The compound holochroal eyes of some olenids (Clarkson 1973) are often well-preserved and offer much scope for detailed optical analysis (fig. 7). One miniaturised and spiny species, *Ctenopyge ceciliae*, (Clarkson – Ahlberg 2002, Schoenemann – Clarkson 2010) (fig. 8) became planktonic, as indicated not only by its tiny size and spinosity, but also from the optics of its eyes, adapted to strong light. The most extreme modification of the basic olenid ground plan began in the *Leptoplatus* zone. In this and the following *Ctenopyge* zones some olenids developed very long genal spines (probably used for resting on the sea floor keeping the gills well above the dysoxic or anoxic sea-floor mud) Clarkson – Taylor 1995b, Clarkson et al. 2003, 2004) (fig. 4). But the body spinosity of these remarkable trilobites, so evident in many olenids at this stratigraphical level, is not fully explained, even though they can be reconstructed from various angles. It is not easy to interpret, for example, the strange morphology of *Ctenopyge ahlbergi* (fig. 9). Many of these species are superficially similar in form to odontopleurids. Interestingly, towards the top of the Furongian, the olenids reverted to much more normal and less bizarre morphology. A specialised fauna of late Cambrian – Tremadocian olenids found in northern Norway (Nikolaisen – Henningsmoen 1985) include forms with unusual morphologies which would well repay studies of their life habits.

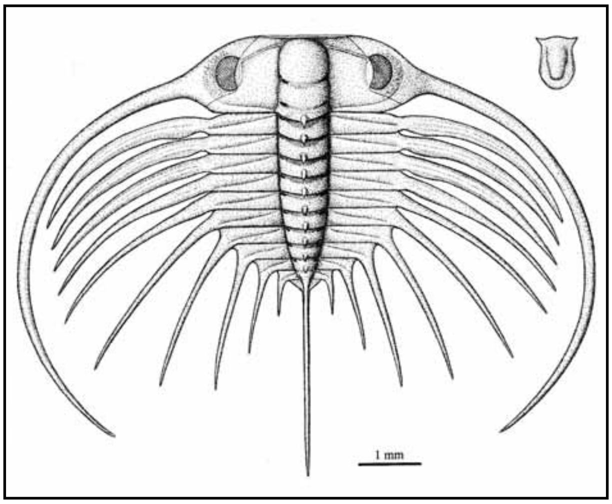

Fig. 9: *Ctenopyge ahlbergi* Clarkson, Ahlgren & Taylor, reconstructed, one of the most highly modified of all olenids. Västergötland, Sweden.

Brachiopods

Brachiopods are uncommon in the Furongian, apart from the articulated benthic finkelbergine *Orusia*. This occurs in great abundance in the *Parabolina* zone, sometimes alone, and forming substantial monospecific assemblages, and sometimes together with *Parabolina*. It is found in Scandinavia, in north Wales, and has recently been discovered in the Montagne Noire, southern France (D. A. T. Harper, pers. comm.). Its presence must represent times when the sea floor was firm and probably more oxygenated than usual, and its geographical and detailed stratigraphical distribution are being investigated at present, as an important component in the overall history of changes in the Alum Shale environment.

Other associated faunas

The associated faunas, which give further insights into the environments of the time are of two main kinds. Firstly there are the astonishingly well-preserved *Agnostus*, stem-group crustaceans, pentastomids etc. described by the active research groups in Bonn and latterly Ulm. (Müller – Walossek 1985 and many subsequent references). The crustaceans and other groups may well have inhabited the flocculent layer on the sea floor, and formed an active part of the benthos. These were first discovered in 1975 when a search was being made for conodonts, the latter subsequently described by Müller – Hinz (1991). They are preserved as a thin bacterial film which spread over the whole surface after the death of the arthropods. Secondly a fauna of phosphatised olenid fragments, beautifully preserved, was found at the top of the *Peltura scarabaeoides* zone (Ahlberg et al. 2005). Amongst the fragmentary olenids, perhaps the best preserved so far known, were chaetognaths and conodonts, pelmatozoa columnals, a possible camaroid, a possible conulariid, and fossils of unknown affinity. These must have lived in dysoxic rather than almost anoxic conditions, and the sea floor must at that time have been firm enough to allow colonisation by sessile organisms.

Geochemistry

The Alum Shales have long been known for their heavy elements, V, Mo, Ni, U etc., Schovsbo (2001, 2003) has documented shoreward enrichment in uranium, and environmental fluctuations within the *Olenus* zone based on geochemistry. Further work in progress at Lund University seeks to provide a carbon isotope curve, calibrated against a high reolution biostratigraphy for the Middle Cambrian though Furongian. So far two major excursions have been recorded, the negative DICE (DrumIan Carbon Isotope excursion) in the *Pt. atavus* zone of the Middle Cambrian, and the SPICE (Steptoean Positive Carbon Isotope Excursion) in the lower Furongian *Olenus* and *Homagnostus* obesus zone (Ahlberg et al. 2009, 2–16). These link with global changes in other continents.

Barren intervals

The lack of fossils in the barren intervals may be the result of a complete lack of oxygen during sedimentation. But there is good geochemical evidence that some, at least, resulted from an excess of oxygen at the time remobilising the unconsolidated mud and dissolving the fossils (Schovsbo 2000, 2002). The barren intervals are not necessarily barren of all fossils, but only of trilobites, brachiopods and other organisms with calcareous shells. They may contain phosphatocopines, which are small bivalved arthropods; one such instance where the phosphatocopines in aggregates; the faeces of some predator, has recently been described from the *Agnostus pisiformis* zone (Eriksson – Terfelt 2010).

Changing sea levels

There is no question that many of the enviroinmental fluctuations within the Furongian are closely linked to changing sea-levels. A major flooding event has been recognised at the base of the Middle Cambrian, likewise several fluctuations within the Furongian. The *Parabolina* zone, for example seems to have been a time of relatively low sea-level. There is much scope for further detailed investigations, linking sea-level fluctuations seen in Scandinavia with global events.

An extinct environment

Not only do living organisms become extinct, but the environments they inhabited may become extinct too. Although there may be some resemblances to sediments on the anoxic or dysoxic shelves of the Atacama and Namibian deserts, the Alum Shales environment is best regarded as both unique and extinct (fig. 10).

The later history of the olenids

Olenid trilobites are well known from Middle Ordovician rocks in Jämtland, Sweden (Månsson 1998), in Argentina (Harrington – Leanza 1957, Balsiero et al. 2010) and North America, where the long-ranging genus *Triarthrus* persists until towards the end of the Ordovician (Ludvigsen – Tuffnell 1995). In most cases, however, the olenids form part of a more diverse and 'normal' fauna

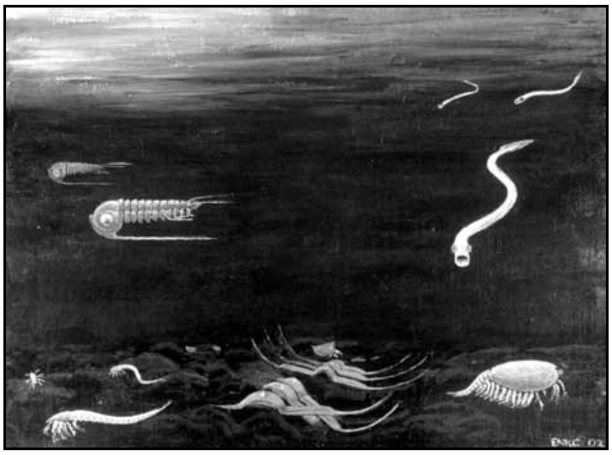

Fig. 10: Reconstruction of the Swedish Alum Shales environment in the late Middle Furongian, with *Ctenopyge angusta* and conodont animals (swimming), moulted C. (*Mesoctenopyge*) fragments, and small crustaceans in the flocculent layer on the sea floor.

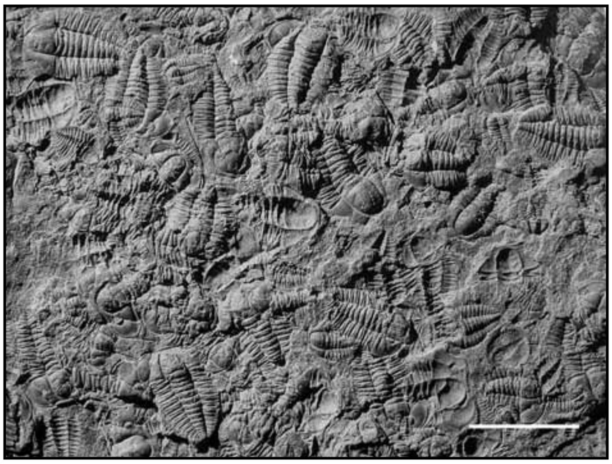

Fig. 11: *Leptoplastides salteri* Raw. A monospecific assemblage of an olenid from the Tremadocian Shineton Shales, Shropshire, England. Scale bar 20 mm.

during the Ordovician. Though they may form spectacular monospecific assemblages (fig. 11) they appear to have lost their specialised adaptation to dysoxic facies, and during the Ordovician lived in waters of more standard oxygen levels (Balseiro et al. 2010). An interesting case of survival in changing circumstances.

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References

Ahlberg, P. – Månsson, K. – Clarkson, E. N. K. – Taylor, C. M. (2006): Faunal turnovers and trilobite morphologies in the upper Cambrian *Leptoplastus* Zone at Andrarum, southern Sweden. – Lethaia, 39, 97–110.

Ahlberg, P. – Szaniawski, H. – Clarkson, E. N. K. – Bengtson, S. (2005): Phosphatised olenid trilobites and associated fauna from the Upper Cambrian of Västergötland, Sweden. – Acta Palaeontologica Polonica, 50, 429–440.

Ahlberg, P. – Axheimer, N. – Eriksson, M. – Schmitz, B. – Terfelt, F. (2008): Cambrian high-resolution biostratigraphy and carbon isotope chemostratigraphy in Scania, Sweden; first record of the SPICE and DICE excursions in Scandinavia. – Lethaia, 42, 2–16.

Balseiro, D. – Waisfeld, B. – Buatois, L. (2010): Unusual trilobite biofacies from the Lower Ordovician of the Argentine Cordillera Oriental: new insights into olenid palaeoecology. – Lethaia, 44, 1–18.

Clarkson, E. N. K. (1973): Morphology and evolution of the eye in upper Cambrian Olenidae (Trilobita). – Palaeontology, 16, 735–763.

Clarkson, E. N. K. – Ahlberg, P. (2002): Ontogeny and structure of a new, miniaturised and spiny olenid trilobite from southern Sweden. – Palaeontology, 45, 1–22.

Clarkson, E. N. K. – Ahlberg, P. – Taylor, C. M. (1998): Faunal dynamics and microevolutionary investigations in the upper Cambrian Olenus Zone at Andrarum, Skåne, Sweden. – GFF, 120, 257–267.

Clarkson, E. N. K. – Ahlgren, J. – Taylor, C. M. (2003): Structure, ontogeny, and moulting of the olenid trilobite Ctenopyge (Eoctenopyge) angusta. Westergård, from the upper Cambrian of Västergötland, Sweden. – Palaeontology, 46, 1–27.

Clarkson, E. N. K. – Ahlgren, J. – Taylor, C. M. (2004): Ontogeny, structure, and functional morphology of some spiny Ctenopyge species (Trilobita) from the upper Cambrian of Västergötland, Sweden. – Transactions of the Royal Society of Edinburgh; Earth Sciences 94, 115–143.

Clarkson, E. N. K. – Taylor, C. M. (1995a): Ontogeny of the tribobite Olenus wahlenbergi Westergård 1922 from the upper Cambrian Alum Shales of Andrarum, Skåne, Sweden. – Transactions of the Royal Society of Edinburgh: Earth Sciences, 86, 13–34.

Clarkson, E. N. K. – Taylor, C. M. (1995b): The lost world of the olenid trilobites. – Geology Today, 11, 147–154.

Eriksson, M. E – Terfelt, F. (2007): Anomalous facies and ancient faeces in the latest middle Cambrian of Sweden. – Lethaia, 40, 69–84.

Fortey, R. A. (2000): Olenid trilobites: the oldest known chemoautotrophic symbionts? – PNAS, 97, 6574–6578.

Geyer, G. – Elicki, O. – Fatka, O. – Żylińska, A. (2008): Cambrian. – In: McCann, T. (ed.): Geology of Central Europe, 155–202, Geological Society of London.

Havlíček, V. (1971): Stratigraphy of the Cambrian of Central Bohemia. – Sborník geologických Věd, Geologie, 20, 7–52.

Henningsmoen, G. (1957): The trilobite family Olenidae, with description of Norwegian material and remarks on the Olenid and Tremadocian series. – Norske Vetenskaps-Akademi i Oslo Skrifter. 1. Matematisk- Naturvedenskap Klasse 1. 1–303.

Ludvigsen, R – Tuffnell, P. (1995): The last olenacean trilobite: *Triarthrus* in the Whitby Formation (Upper Ordovician) of southern Ontario. – Bulletin of the Geological Society of Canada, 48, 183–212.

Kaufmann, R. (1933): Variationsstatistiches Untersuchungen über die 'Artabwandlung' und 'Artumbildung' an der Oberkambrische Gattung *Olenus* Dalm. – Abhandlungen des Geologisches-Paläontologisches Institut der Universität Greifswald, 10, 1–54.

Lauridsen, B. W. – Nielsen, A. T. (2005): The upper Cambrian trilobite *Olenus* at Andrarum, Sweden, a case study of iterative evolution? – Palaeontology, 48, 1041–1056.

Månsson, K. (1998): Middle Ordovician olenid trilobites (*Triarthrus* Green and *Porterfieldia* Cooper) from Jämtland, central Sweden. – Transactions of the Royal Society of Edinburgh: Earth Sciences, 89, 47–62.

Müller, K. J. – Hinz, I. (1991): Upper Cambrian conodonts from Sweden. – Fossils & Strata 28, 1–153.

Müller, K. J. – Walossek, D. (1985): A remarkable arthropod fauna from the Upper Cambrian "Orsten" of Sweden. – Transactions of the Royal Society of Edinburgh: Earth Sciences, 76, 161–172.

Nikolaisen, F. – Henningsmoen, G. (1985): Upper Cambrian and lower Tremadoc olenid trilobites from the Digermul peninula, Finnmark, northern Norway. – Norsk geologiske undersokning. Bulletin 400, 1–49.

Rushton, A. W. A. (1967): The upper Cambrian trilobite Irvingella nuneatonensis (Sharman). – Palaeontology, 10, 339–348.

Rushton, A. W. A. (1983): Trilobites from the upper Cambrian *Olenus* Zone in central England. – Special Papers in Palaontology, 30, 117–139.

Schovsbo, N. H. (2000): Environmental fluctuations in the *Olenus* Zone (Upper Cambrian), southern Scandinavia: a geochemical approach. – Bulletin of the geological society of Denmark, 47, 53–61.

Schovsbo, N. H. (2001): Why barren intervals? A taphonomic study of the Scandinavian alum shale and its faunas. – Lethaia, 34, 271–285.

Shergold, J. – Feist, R. – Vizcaino, D. (2000): Early Late Cambrian trilobites of Australo-Sinian aspect from the Montagne Noire, Southern France. – Palaeontology, 43, 599–632.

Terfelt, F. – Eriksson, M. E. – Ahlberg, P. – Babcock, L. E. (2008): Furongian Series (Cambrian) biostratigraphy of Scandinavai – a revision. – Norwegian Journal of Geology, 88, 73–87.

Schoenemann, B. – Clarkson, E. N. K. –, Ahlberg, P. – Alvarez, M. A. E. (2010): A tiny eye indicating a planktonic trilobite. – Palaeontology, 53, 695–702.

Tortello, M. F. – Clarkson, E. N. K. (2003): Ontogeny of the Early Ordovician trilobite *Jujuyaspis keideli* Kobayashi from north-western Argentina. – Ameghiniana 40, 257–275.

Tortello, M. F. – Clarkson, E. N. K. (2008): Ontogeny, structure, and moulting of *Parabolina frequens argentina* (Kayser) (Trilobita, Olenidae) from the Furongian of northwestern Argentina. – Ameghiniana 45, 13–31.

Westergård, A. H. (1922): Sveriges Olenidskiffer. – Sveriges Geologiska Undersökning. Ca 18, 1–205.

Żylińska, A. (2001): Late Cambrian trilobites from the Holy Cross Mountains, Central Poland. – Acta Geological Polonica, 52, 217–238.