THE EYES OF BOHEMIAN TRILOBITES

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Abstract

There are trilobites of the Bohemian area, which belong to the best preserved in the world. Their compound eyes were first studied in detail by Hawle and Corda in 1847, but especially by Barrande (1852, 1872), whose original observations are still of great value. More recently both holochroal and schizochroal eyes have been documented from Bohemian material, their visual fields plotted, growth geometry established, and thin-sections and polished surfaces used for determining the internal structure of the lenses. Modern physiological methods have great potential for determining the nature of the light environment to which even extinct animals were adapted, and thus have an important bearing on their ecology. The use of the eye parameter, which can be determined from the diameter and angle between adjacent lenses is discussed here. This approach, along with further detailed structural investigations should allow many new insights to accrue over the next few years.

Introduction

When Barrande (1846, 1852, 1872) published his comprehensive work on Central Bohemian trilobites, he took great care also to describe and illustrate details of eye morphology in his extraordinarily beautiful and precise drawings. While these drawings were made by his artist, Mr. Josef Fetters, Barrande supervised him at every stage, and the eyes are shown in the greatest detail observable in that time. Although trilobite eyes had been subsequently illustrated on Swedish material by Lindström (1901) it was not until the 1960s that the structure of the lenses, and other aspects of eye morphology were investigated, and this was based to a great extent on superbly preserved Silurian and Devonian material from Bohemia. Sometimes this is re-crystallised, but this is not always so, and thus Clarkson (1968) using polished surfaces and thin-sections of the eyes of *Reedops* showed that the intralensar bowls discussed and illustrated by Lindström were original components of the lenses and not diagenetic artefacts. Likewise in *Ananaspis fecunda* a sublensar capsule was recognised for the first time (Clarkson 1969) and such structures have been abundantly confirmed since. Ordovician *Ormathops* from Bohemia was used in studies of the generation and packing of lenses and distribution (Clarkson 1971) and many other Bohemian eyes have been illustrated, and their visual fields set out graphically (Clarkson 1973, 1975, 1997). Of the trilobite eyes illustrated in six plates by Clarkson (1975), three-

quarters were from Bohemia, using material stored in British collections. Moreover, *Dalmanitina* eyes were used by Clarkson & Levi-Setti (1975) in investigations of lens-function. Budil and colleagues published articles about Middle Devonian Bohemian trilobite eyes (e. g. Budil 1996, 1999, Budil – Hörbinger 2007), but there remains scope for further studies on how they may have functioned, what their internal structure may have been, and what these eyes could tell us about the light environments to which these eyes were adapted – and thus their owners – the trilobites of the Prague Basin.

In many of the trilobites of the Barrandian area, the eyes are exceptionally well preserved, as good as, or better than, any in the world. They are all compound eyes, like those of arthropods such as insects or crustaceans living today. Functionally, the visual organs of trilobites are almost certainly of, or at least base on the so-called apposition type, still present in most diurnal arthropods of the present day, such as bees, dragonflies and many crustaceans active during the day. More evolved types, such

Fig. 1: Principles of compound eyes in trilobites: A – Holochroal eye of *Gerastos (Longiproetus) glandiferus glandiferus*; B – Schizochroal eye of *Dalmanites* sp.; C – Functional principle of an apposition eye: contrast distribution of the environment (1) inside the visual field of the ommatidium (2) is focused by the dioptric apparatus (3) onto the central rhabdom, which is part of the sensory cells (4); D – Explanation of the parameters: $\Delta\varphi$ opening angle of the visual unit (ommatidium), D lens diameter, aperture.

Fig. 2: Holochroal eyes: A – Moulting of *Pricyclopyge binodosa* (Salter 1859); B – Facetted eyes of *P. binodosa*; C – Pattern of the facets of the compound eye of *P. binodosa*.

as the different kinds of superposition eyes (neural superposition eyes and all kinds of optical superposition eyes), compound eyes adapted to poorer light conditions, are not known before Jurassic times (Gaten 1998).

There are two main functional types in trilobite eyes. The holochroal eye (fig. 1 A, fig. 2), is composed of up to several thousands of units which can make up a compound eye, with densely packed round or hexagonal facets (fig. 2 B, C). A second type arose in the suborder Phacopina in the Early-Middle Ordovician, where the lenses remain separated from each other. The lenses are remarkably larger than in holochroal eyes (sometimes larger than 1 mm), and normally are less numerous. This type is called schizochroal eye (fig. 1 B, fig. 3). It has been shown recently by x-ray tomography that the schizochroal eyes of the Devonian trilobites
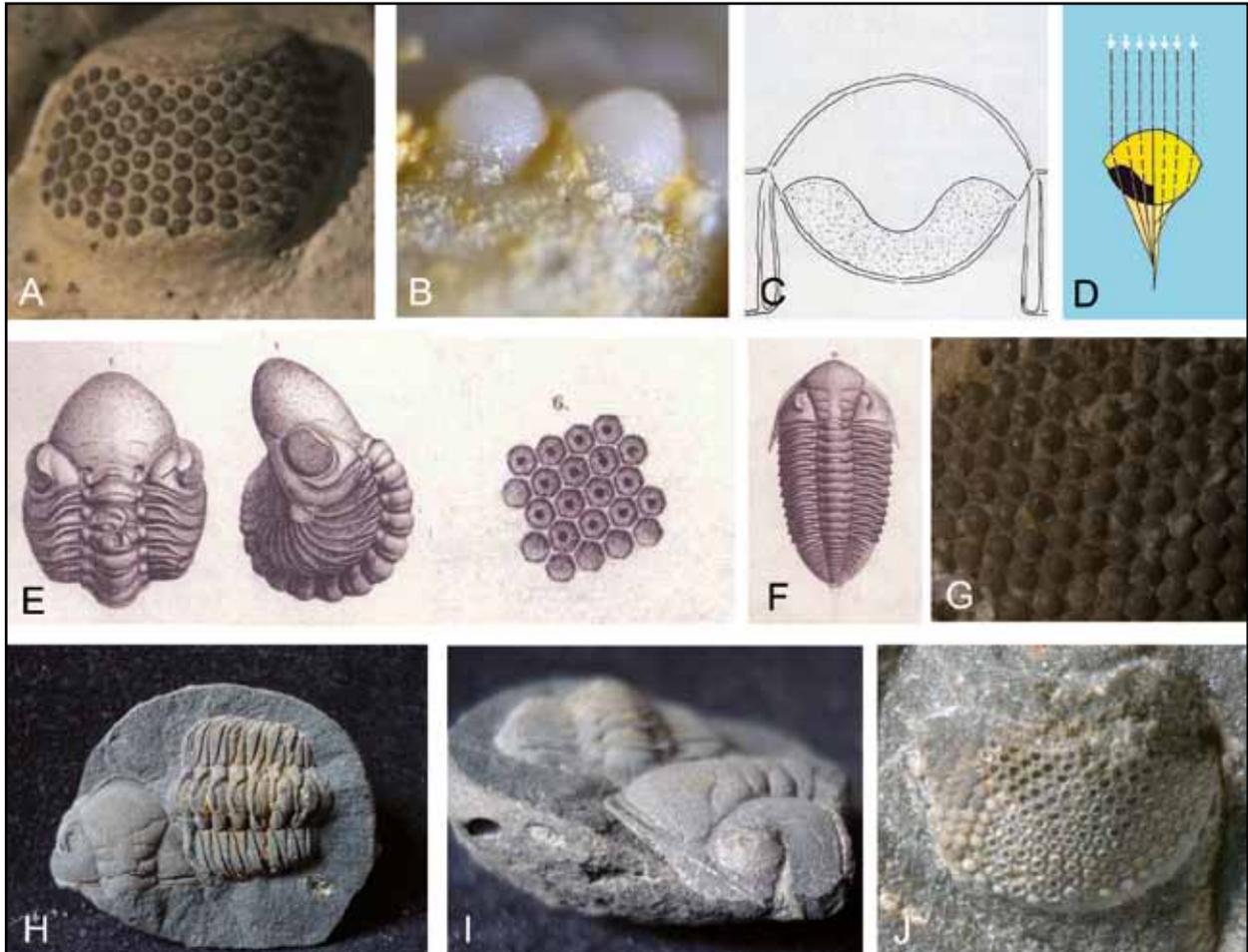
Fig. 3: Schizochroal eyes: A – Schizochroal eye of *Chotecops auspex*; B – Lens doublet of a small Bohemian phacopid trilobite; C – Schematic drawing of the lens doublet, the functional structure of a phacopid lens (after Levi-Setti 1975); D – Functioning of the lens doublet: right side: the rays at the periphery of the lens are focused at a different point from those which enter more centrally, thus the image will be blurred. Left side: the aplanic interfaces focuses all rays into one point, thus it results a sharp image; E – *Reedops cephalotes* (Hawle & Corda 1847) enrolled. In the center of the lenses the third internal structure, the core, is illustrated (Barrande, 1852, pl. 20, figures 1., 2., 6., as *Phacops cephalotes* Cor.); F – *Dalmanitina socialis* (Barrande, 1852), (Barrande 1852, pl. 26, fig. 16., as *Dalmanites socialis*); G – Visual surface of *Dalmanites* sp. (unknown locality, Silurian); H, I – *Ormathops atava*; J – Eye of specimen in H and I..

Geesops schlotheimi (Bronn 1835) from the German Trilobitenfelder/Gees show an internal structure identical to that of the apposition eyes of modern diurnal arthropods, although most previous models proposes a retinal eye. Because the schizochroal eye very probably originated by paedomorphosis (Clarkson – Zhang 1991) from an holochroal ancestror the holochroal eye ought to have the same functional structure, being an apposition eye too.

Methods of analysis of fossilised eyes and their chances of prospects for further insights

The apposition compound eye is composed of independent repetitive units, separated physically and functionally. Each unit, the so-called ommatidium (fig. 1 C), consists of a dioptric apparatus, which focuses the incident light onto a light-guiding structure, the so-called rhabdom, which is part of the sensory cells and contains the visual pigments. The energy of the entering rays changes the stereometric form of the visual pigment molecules and causes, in consequence, a low electrical signal, which can be processed by the nervous system of the arthropod. Because all the light captured inside the opening angle of the ommatidium is combined inside of the rhabdom, all contrasts inside the visual field of one facet is averaged to a single mean light intensity. Thus, an individual ommatidium does not transmit a complete image of the environment, but just a single point. The images from all the ommatidia form a mosaic-like image, in the same way that a pixel contributes to a computer graphic. The more pixels are available, the higher is the acuity of vision (at least in the first approxiamtion, other parameters may be taken into consideration too, but those are rather secondary). In modern arthropods like in certain dragonflies, but also in trilobites (for example among the Cyclopygidae), several thousands of "pixels" per eye are established. This performance of a compound eye is comparably low with regard to human camera lens eyes with several millions of sensory cells, but the circumspectant view at all times and into three dimensions is one of the great advantages of the compound eye system.

Modern physiology has developed advanced tools to describe the performances of apposition compound eyes, such as acuity (Snyder 1977, 1979, Snyder et al 1977, Horrdige 1977) and sensitivity (Land 1981). They have been applied to many recent forms, to characterise and to compare them (for an overview see Land 1981, Land & Nilsson 2002). Recently these methods have been used for diverse arthropods belonging to the Chengjiang Fauna and also for trilobites (Schoenemann – Clarkson 2010, 2011 a, b, c, McCormick – Fortey 1998).

A higher sensitivity gives an ability to live under poorer light conditions, in other words a crepuscular life style or at greater depth. This depends normally on a sufficient size of the facets, because larger lenses can capture more light than smaller ones. A high acuity however demands for as many visual units as possible, and thus in the limited space of a compound eye, they should be as small as possible. Thus, adapted to the light conditions of their environment, there results in compound eyes

a "conflict" between the demands of acuity and sensitivity. As a result there is a compromise between highest acuity at threshold perception of light and the need to gather as much light as possible. This theoretical concept has led to the development of the so-called eye parameter p, characterising this compromise. When the facets are hexagonal: $p_{hex} = \frac{1}{2}.D.\Delta\varphi.\sqrt{3}$ [μm rad].D Lens diameter, the greater D the higher the sensitivity, because the more light can be yielded per unit, $\Delta\varphi$ opening angle of the visual unit (fig. 1 D), the smaller the angle, the finer the pattern of scanning of the surrounding and the higher is the acuity, Snyder (1977, 1979), Snyder et al 1977, Horridge (1977). Horridge (1977) investigated the eye parameter of many arthropods and showed how the eye parameter can be a useful tool for assigning the arthropods, in terms of the design of their compound eyes, to light environments to which they are adapted. This technique has been successfully used many since (for overview see Land 1981).

Using these methods of modern physiology it has been shown that of the more than half a billion year old fossilised *Isoxys* from the Chengjiang Fauna there exist two forms – one living close to the shore, and another one in deeper areas of the sea (Schoenemann – Clarkson 2010). Estimation of the eye parameter made it possible for McCormick and Fortey (1998) in a detailed analysis to assign the Ordovician telephinid trilobite *Carolinites killaryensis utahensis* to be pelagic, while *Pricyclopyge bindosa* was interpreted as mesopelagic. These theoretical tools have not yet been used further to characterise the environments to which Bohemian trilobites were adapted, but such an approach would undoubtedly be worth while, as will be shown here subsequently.

The eyes of Bohemian trilobites

Bearing in mind these principles, it seems appropriate to give a general preliminary characterisation of Bohemian trilobite vision, for even the outer shape, as the way to "wear" an eye, indicates much about a trilobite´s life-style. Holochroal eyes in particular reflect the mode of life of their owners. Most similar to the eyes of the predatory dragonflies are the impressive eyes of the Ordovician Cyclopygidae, which likewise possess several thousands of facets, small enough to indicate a diurnal, light adapted life-style. The compact and strong shape of their bodies indicate a powerful, free-swimming trilobite (fig. 2 A), and the high acuity of the eye allows the assumption that these trilobites were pelagic predatory arthropods, orientating themselves visually and so capturing their prey. This assumption is strengthened by the convergence and fusion of the lateral eyes anteriorly among in pricyclogidids. Finally *Ellipsotaphrus* possesses functionally just a single eye, panoramic and highly acute. Other impressive examples are among the remopleurid *Amphitryon*, body shaped like a modern jet fighter, and equipped with a highly resolving view in a wide ranging visual field (but offering only narrow, sub-horizontally oriented strip of closely packed sub-hexagonal ommatidia with very limited possibility to see dorsally and, especially, ventrally).
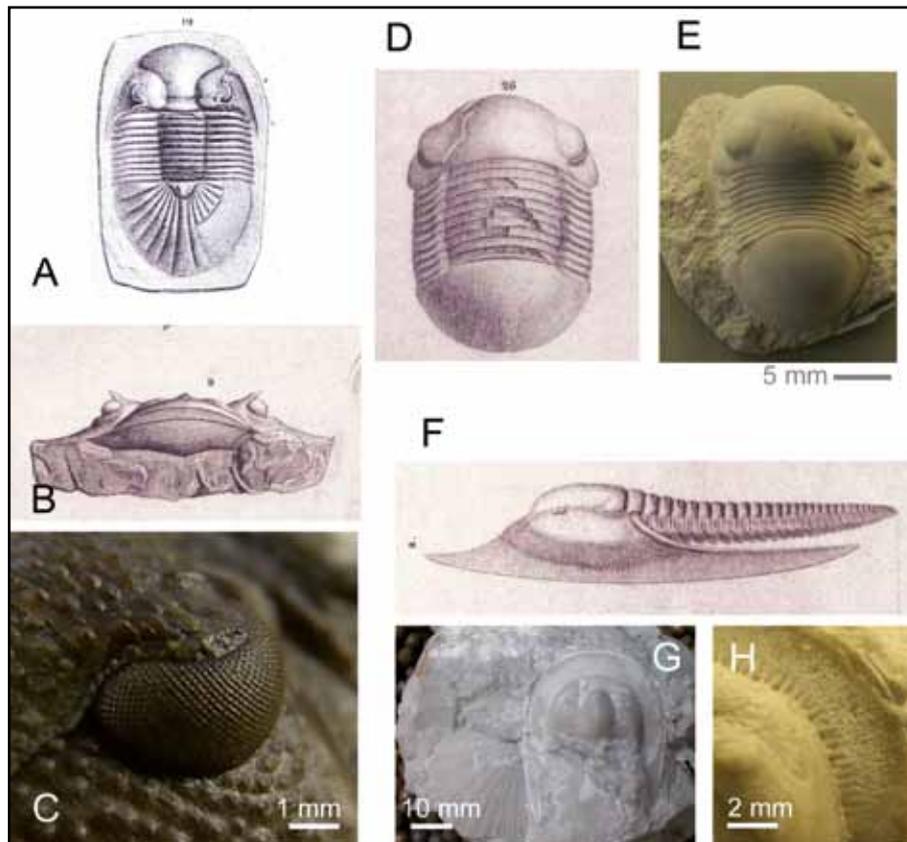
Fig. 4: Special adaptations and eye reduction: *Scabriscutellum (S.) caelebs caelebs* (Barrande, 1852, pl. 46, fig. 19, *Bronteus caelebs* (Barr.); B – Frontal view of *Radioscutellum intermixtum* (Hawle & Corda 1847) (Barrande 1852, plate 45, fig. 9., as *Bronteus palifer* Beyr.); C – Holochroal eye of *Scutellum geesense* Rud. & E. Richter 1956 (Middle Devonian, Germany); D – *Liolalax bouchardi* (Barrande, 1846), (Barrande, 1852, pl. 34, fig. 26., as *Illaenus bouchardi* Barr.) ; E – *Bumastus* sp.; F – *Bohemoharpes (Unguloharpes) ungula ungula* (Sternberg 1833) (Barrande 1852, pl. 9, fig. 2., as *Harpes ungula* Stern.) ; G, H – *Lioharpes venulosus* (Hawle & Corda, 1847). Note the delicate pores of cephalic rim.

Other holochroal eyes, with hundreds of fine delicate lenses can be found amongst the proetid and illaenid trilobites (fig. 4 A–E). These indicate a high acuity but they also require a high light intensity to function, thus a diurnal life-style not too far from the well lit water surface. Many of these eyes are covered by a kind of lid, the so-called palpebral lobe, which protects the eye from flickering light downwelling from the water surface, and thus concentrating the view mainly to the wide lateral horizon enabling the detection of possible predators. However, many of Bohemian illaenids are blind. The scutelloids show an impressive compound eye, each rather with a remarkable field of view, in a similar way. In the scutelloids the lenses may be slightly larger, however, indicating also that they were adapted to poorer light conditions. So, for example *Paralejurus campanifer* comes from the peri-reef environment, on the other hand, *Paralejurus brongniarti* from deeper part of the basin; a closer investigation of their visual systems would be of worth.

Besides the few pelagic probably predatory trilobites mentioned before, the detection of predators is a primary task for the facetted eyes of trilobites, and an effective facility for the detection of motion is one of the great advantages of this system. A temporal change in the pattern of light distribution across the facets indicates a moving object in the environment, and this detection is the finer the smaller are the facets. For small organisms especially it may be advantageous to have set the visual field onto long stalks, because the angle over the ground for scanning the horizon may be enlarged (Zeil et al. 1986, Zeil – Hemmi 2006). This principle is appropriate for example for the delicate forms of acidaspids, especially *Miraspis mira* (Barrande 1852, fig. 5 A). Notably, when coupled with an ability for enrollment, stalked eyes may enable such trilobites to see over the margins of their own bodies, as in *Cyphaspis* and allied genera (Barrande, 1852, plate 18) (fig. 5 D, E).

The need for detecting predators, social partners or simply to orientate optically may be of less importance in certain habitats and may lead to reduced compound eyes like the holochroal eyes of *Agraulos ceticephalus* (fig. 5 H, I); especially when other sensory organs may overtake the orientation function or help to find adequate food. This may be true especially for the harpetids, gliding over the ground with their wide cephalic margins, equipped with thousands of fine pores (fig. 4 F–H), which in our view may be traces of tiny chemosensory organs. The eye is reduced to 2 (*Bohemoharpes vittatus*) or 3 facets. Because they contribute, as explained before, just 3 "pixels", and thus are unable to form any image, they may have functioned just as light detectors, informing the trilobite about the state of the day or may have given rough and limited information about moving patterns in the environment. The relatively large size of the lenses indicates again an adaptation to darker environments.

Blindness is regarded to be secondary in trilobites, and blind trilobites like *Conocoryphe sulzeri* (fig. 5 G) or the elegant forms of *Ampyx* (fig. 5 B, C) are restricted to a benthic habitat, probably with poor light conditions.

The schizochroal eye, which is represented only in the suborder Phacopina, originated from the holochroal eye probably paedomorphically (Clarkson – Zhang 1991). The lenses of the Silurian dalmanitids as in many geologically younger phacopids, show a highly differentiated internal structure, which is not as yet completely understood. The impressive schizochroal eyes like those of *Dalmanites*

(fig. 3 F, G) or Ormathops (fig. 3 H–J), have a wide field of view, and their almost spherical lenses remain close to each other, even if not as close as in holochroal eyes. It was shown by Clarkson and Levi-Setti in 1975, that the lenses of Bohemian *Dalmanitina socialis* Barrande 1852 are actually lens-systems (fig. 3 C), consisting of two parts, which under certain conditions allow a sharp focusing, even without spherical aberration (fig. 3 D). This sophisticated system suggested an underlying retina, able to form real images. In other phacopid trilobites, like the Middle Devonian *Geesops schlotheimi* (Bronn 1835), from the German Trilobitenfelder in Gees, it has been shown however, by x-ray tomography, made in Bonn, the sublensar elements were of apposition type, which represents the oldest traces of sensory cells known so far (Schoenemann – Clarkson 2011c).

In some phacopid trilobites even a third internal structure exists, a central more or less drop-like shaped core, which may act as an additional internal lens or may have some other optical function. This core can already be seen in the precise drawings of Barrande´s *Reedops cephalotes* (Barrande 1852, plate 20) (fig. 3 E). These structures occasionally have been discussed as diagenetical, but it could be shown that they are primary structures (Lee et al. 2007).

However sophisticated the visual system of phacopid trilobites may have been, eye reduction can be observed also in Bohemian phacopid trilobites, as in the comparably small but robust *Denckmannites volborthi*, which possesses small eyes, with less than 20 facets within each (fig. 5 F). Because the lenses are orentated anteriorly and the reduction starts in the posterior part of the eye, this eye could still well protect the trilobite by vision or to help to unearth prey. To see movements outside still would be possible, but the acuity of vision became rather low.
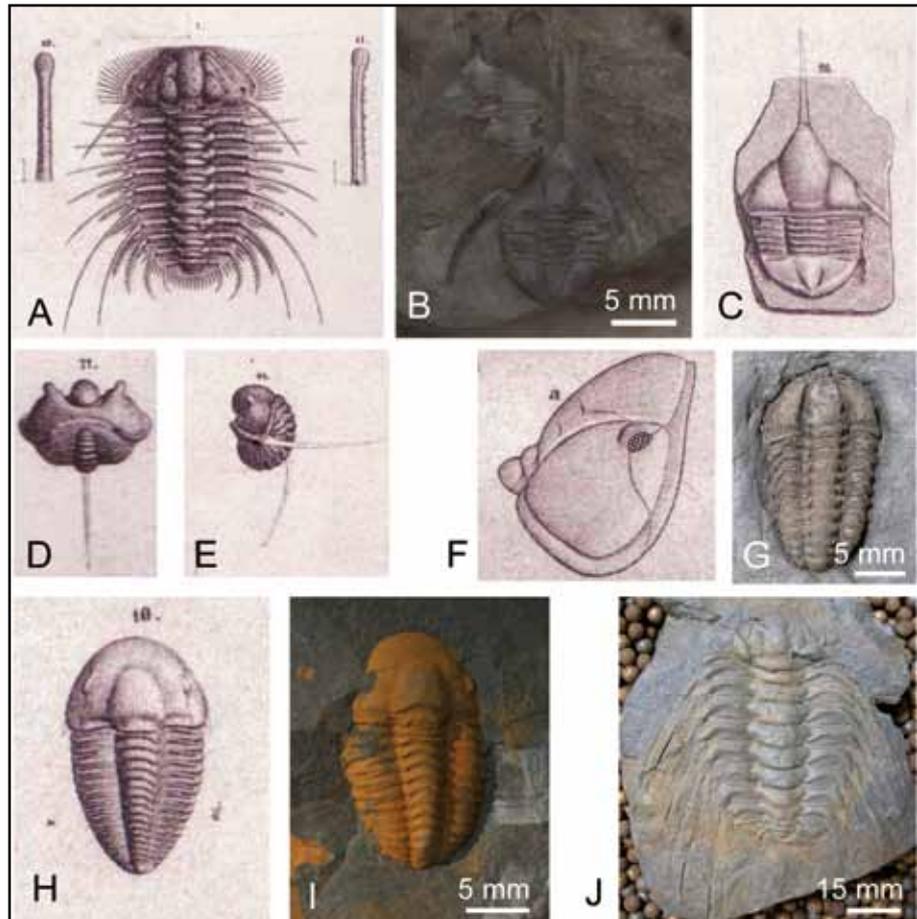
Fig. 5: Special adaptations and eye reduction: Stalked eyes of *Miraspis mira* (Barrande 1852, pl. 39, figures 1., 10., 11., as *Acidaspis mira* Barr.); B – *Ampyx nasutus* Dalman 1827, a blind trilobite (Ordovician, Morocco); C – *Lonchodomas porthlocki* (Barrande 1846) (Barrande 1852, pl. 30, fig. 26., as *Ampyx porthlocki* Barr.); D, E – *Cyphaspis barrandei* (Hawle & Corda 1847), (Barrande 1852, pl. 18, figures 43., 44., as *Cyphaspis barrandei* Cord.) enrolled, looking over the margins of the body; F – Eye reduction in schizochroal eyes *Deckmannites volborthi* (Barrande 1852) (Barrande 1982, pl. 3, fig. 26., as *Phacops volborthi* Barr.); G – *Conocoryphe sulzeri sulzeri* (Schlotheim 1823), a blind trilobite; H, I – *Agraulos (A.) ceticephalus* (Barrande, 1846), (Barrande 1852, as *Arionellus ceticephalus* Barr.); J – *Selenopeltis* sp., a huge ground-living trilobite.

In this short article only a few of the different kinds of eyes in the Bohemian trilobite fauna have been discussed here, along with a general overview of physiological principles, which should help in understanding them further. There is scope for so much more work to be undertaken on the superbly preserved eyes of Bohemian trilobites, and it is highly likely that their exceptional quality will allow many new insights to accrue over the next years.

References

Barrande, J. (1846): Notice priliminaire sur le Systime Silurien et les trilobites de Boheme. – pp. 8–22, Leipzig.

Barrande, J. (1852): Systeme Silurien du Centre de la Boheme. (Not paginated), 51 plates, Prague.

Barrande, J. (1872): Systeme Silurien du Centre de la Boheme, Supplément au Volume I. Trilobites, crustacés divers et poissons. 647 pp., 35 plates, Prague.

Budil, P. (1996): Representatives of genera *Mucronaspis* and *Songxites* (Trilobita) from the Bohemian Upper Ordovician. – Bull. Czech Geol. Soc. 63–78. Praha.

Budil, P. (1999): Some comments on the genus Ormathops Delo from the Bohemian Ordovician. – Acta Univ. Carol. Geol. 43 (1/2), 373–376. Praha.

Budil, P. – Hörbinger, F. (2007): Exoskeletal structures and ultrastructures in Lower Devonian dalmanitid trilobites of the Prague Basin (Czech Republic). – Bulletin of Geosciences 82(1), 27–36. Prague.

Clarkson, E. N. K. (1969): On the schizochroal eyes of three species of Reedops (Trilobita: Phacopidae) from the Lower Devonian of Bohemia. – Transactions of the Royal Society of Edinburgh 68, 183-205, Edinburgh.

Clarkson, E. N. K. (1971): On the early schizochroal eyes of *Ormathops* (Trilobita, Zeliszkellinae). – Memoires du Bureau des recherches géologiques et miniéres 73, 51–63. Orleans.

Clarkson, E. N. K. (1973): Structure of the eye of *Crozonaspis struvei* (Trilobita, Dalmanitidae, Zeliszkellinae). – Senckenbergiana Lethaea , 49, 383–392.

Clarkson, E. N. K. (1975): The evolution of the eye in trilobites. – Fossils & Strata 4, 7–31. Oslo.

Clarkson, E. N. K. (1997): The Eye, Morphology, Function and Evolution. – In: Kaesler, R. L. (ed.): Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita, revised. –Volume 1: Introduction, Order Agnostida, Order Redlichiida. The Geological Society of America, Inc. & The University of Kansas, 114–132, Boulder, CO , Lawrence, KA.

Clarkson E. N. K. – Levi-Setti, R. (1975): Trilobite eyes and the optics of Des Cartes and Huygens. Nature, 254, 663–667. London.

Clarkson, E. N. K. – Zhang, X-g. (1991): Ontogeny of the Carnoniferous trilobite *Paladin eichwaldi shunnerensis* (King, 1914). – Transactions of the Royal Society of Edinburgh 82, 277–295. Edinburgh.

Gaten, E. (1998): Eye structure and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). – Contributions to Zoology, 67, 223-235. Washington DC.

Hawle, I. – Corda, A. J. C. (1847): Prodrom einer Monographie der böhmischen Trilobiten. Calve, Prague, 176 pp.

Horridge, G. A. (1977): Insects which turn and look. – Endeavour 1, 7–17. Amsterdam.

Land, M. F. (1981): Optics and vision in invertebrates. – In: Vision in invertebrates. (Handbook of sensory physiology, vol. VII/6B), (H. Autrum H. ed.), 471–592. Berlin, Heidelberg, New York: Springer Verlag.

Land, M. F. – Nilsson, D.-E. (2002): Animal eyes. University Press, pp. 244, Oxford.

Lee, M. R. – Torney, C. – Owen, A. W. (2007): Magnesium-rich intralensar structures in schizochroal trilobite eyes. – Palaeontology, 50 1031–1037. London.

Levi-Setti, R. (1975): Trilobites. Chicago University Press. – pp. 213, Chicago.

Lindström, G. (1901): Researches of the visual organs of the trilobites. – Kongliga Svenska vetenskapsakademiens handlingar 34, 6–86, 6 Pl., Oslo.

McCormick, T. – Fortey, R. A. (1998): Independent testing of a paleobiological hypothesis: the optical design of two Ordovician pelagic trilobites reveals their relative paleobthymetry. – Palaeobiology 24, 235–253. Alexandria, VA, USA.

Schoenemann B. – Clarkson, E. N. K. – Ahlberg, P. – Dies Álvarez, M. E. (2010): A tiny eye indicating a planktonic trilobite. – Palaeontology 53, 695–701. London.

Schoenemann, B. – Clarkson, E. N. K. (2011): The eyes of *Isoxys* – Eye morphology indicates the ecological habitat of an a half million year old animal. – Lethaia, 44 (2), 223–230. Copenhagen.

Schoenemann, B. – Clarkson, E. N. K. (2011 a): The eyes of *Leanchoilia*. Lethaia under review. Copenhagen.

Schoenemann, B. – Clarkson E. N. K. (2011 b): At First Sight – Functional Analysis of Lower Cambrian eye systems. – Palaeontographica A (accepted). Bonn.

Schoenemann, B. – Clarkson, E. N. K. (2011c): Sublensar Structures in Trilobite Eyes are Revealed by CT-Scanning, for the First Time. – Science under review. Washington

Snyder, A. W. (1977): The acuity of compound eyes: physical limitations and design. – Journal of comparative Physiology, 116, 161–182. Berlin.

Snyder, A. W. (1979): Physics of Vision in *Compound* Eyes. – In: Autrum H. (ed.): Vision in invertebrates. – Handbook of sensory physiology, vol. VII/6A, 225–313. Springer Verlag. Berlin.

Snyder, A. W. – Stavenga, D. G. – Laughlin, S. B. (1977): Spatial information capacity of compoud eyes. – Journal of com parative Physiology, 116, 183–207. Berlin.

Zeil J. – Nalbach, G. – Nalbach, H.-O. (1986): Eyes, eye stalks and the visual world of semi-terrestrial crabs. – Journal of comparative Physiology 159, 801–811. Berlin.

Zeil, J. – Hemmi, J. M. (2006): The visual ecology of fiddler crabs. – Journal of comparative Physiology 192, 1–25. Berlin.