



Discovery of some 400 million year-old sensory structures in the compound eyes of trilobites

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Fossilised arthropod compound eyes have frequently been described. Among the oldest known are those from the lower Cambrian of the Chengjiang Lagerstätte (China, c 525 Ma). All these compound eyes, though often excellently preserved, however, represent just the outer shells, because soft tissues, or even individual cells, usually do not fossilise. Using modern techniques, including μ ct-scanning and synchrotron radiation analysis we present the discovery of the sensory cell system of compound eyes, belonging to trilobites around 400 million years old, which allows their description and analysis. They are interpreted as forming part of an apposition-like ommatidium, which is a basic functional type of compound eye present in arthropods of today. Considered in greater detail, it is similar to the compound eye of the horseshoe crab *Limulus*, generally regarded as a 'living fossil', which probably retained this ancient basal system successfully until today.

Excellently preserved fossilised compound eyes have been reported recently, such as those of the Emu Bay, Australia^{1,2} or the Chengjiang Lagerstätte, China^{3,4}. All these systems, however, are fossilised only as their outer shells. They are retained most often even just as fine networks, the frames of the facets, because soft tissues or even cells usually do not fossilise. Only in Eocene amber (~50 Ma) has the cellular analysis of the visual system of a fly been possible and successful⁵. It proved to be a modern-type of superposition eye as in flies living today, and remarkable as it was, the results did not offer insights to the earlier history of the evolution of vision. This must be sought in ancient arthropods, especially in trilobites, which possess well developed compound eyes. These are among the oldest invertebrates in the fossil record and which dominated the marine arthropod fauna of the Palaeozoic⁶.

Amongst modern arthropods, the most basic and most common kind of compound eye is the so-called apposition eye⁷. With up to 20,000 facets, each capping a so-called ommatidium, they form a visual system of identically repeated units. A dioptric apparatus focuses the light onto a central light-guiding structure, the rhabdom, which commonly possesses 6 to 9 sensory cells. Each of the sensory cells has a slender nerve, which combines to an optical nerve connecting the sensory cells with the central nervous system. This sensory unit is isolated by numerous pigment cells from the neighbouring ommatidia. Because the rhabdom combines all incident light which enters an individual facet, an apposition eye thus forms a mosaic-like image, and its resolution depends inter alia on the number of facets.

The eyes of the extinct trilobites, which lived between c 522 and 251 million years ago (Ma) were compound, like those of crustaceans and insects living today, but, in contrast to recent arthropods, their lenses were formed of primary calcite^{6,8,9}. Only these calcite lenses and adjacent parts of the exoskeleton are normally preserved and the sublensar structures have remained largely unknown until now. Most trilobite eyes are holochroal, that is they possess many small contiguous lenses set on a curving surface; this is the original kind of trilobite eye. One group of trilobites, however, the Suborder Phacopina (c 488–359 Ma: Lower Ordovician to Late Devonian) has schizochroal eyes, in which the lenses are much larger, fewer and separated one from another. The lenses are also internally differentiated, allowing light to focus sharply¹⁰. Each visual unit has its own thin cornea, prolonged below into a capsule with a flattish or rounded lower termination, though such thin membranous capsules are seldom preserved^{11–14}. These eyes originated by pedomorphosis from a holochroal precursor¹⁵.

Up till now, the only parts of the original sublensar elements documented were the membranous capsules. The use of μ -ct-scanning (high resolution computer tomography), and synchrotron radiation, for the first time, has given much more information about the cellular sensory structures that lay within these ancient compound eyes,



not far from being half a billion years old. Devonian phacopids investigated here include *Geesops*, *Barrandeops*, *Phacops* and *Chotecops*; the latter was investigated using light microscopy alone.

The basic concept of the investigation undertaken here is that there exist three possibilities of sensory systems which could be found in fossilised Palaeozoic compound eyes: 1. There exist numerous types of functionally differentiated compound eyes in recent arthropods, such as many forms superpose light from adjacent facets to exploit light more effectively. They derive from the most basal and widest represented visual concept in the arthropod realm. This is the apposition eye, and all more specialised forms are younger than Devonian¹⁶. The apposition eye consists of optically isolated units, the ommatidia, containing the sensory cells with a central rhabdom in common as explained above. 2. There exists a functional alternative, a small capsule floored by a tiny retina, forming a so-called ocellus. Several of these may form an aggregate eye similar to compound eyes. They are represented for example in myriapods. The ocelli are also the typical main visual system of chelicerata, except Xiphosura as *Limulus* (lateral compound eyes), onychophora^{17,18} and the related Palaeozoic lobopodians¹⁹. 3. The third alternative would be to find a new concept not known so far.

No cellular sensory structures have been found so far in the fossil record older than the relative young Eocene amber, and a discovery of such a kind would open insights to the early evolution of vision, especially of arthropod vision.

Results

Geesops. A single *Geesops schlotheimi* (Bronn, 1835) specimen, one of very many investigated, reveals remarkable details of internal structure. These phacopids originate from the Middle Devonian (Ahrdorf Formation, Eifelian, c 390 Ma) of the Gees-Gerolstein district, Eifel, Germany. The trilobites are excellently preserved in a very fine matrix, and the sensory structures have been preserved by diagenetic ‘seeding’ of a mineral film by bacteria. When the original structures decayed, the mineral shell remained. Because sensory cells decay easily, this must have taken place very soon after the death of the animal. There are two tangential ct-scans, taken at Phoenix x-ray, Munich. They show different levels within the eye, and are here clarified by black and white drawings, made from photographic enlargements, using a light table. Both scans reveal circular structures, each lying below a lens. They are of constant form and arranged in a regular pattern; it is thus unlikely that they result from an overall diagenesis. The higher scan (Fig. 1a) shows at least twelve complete or partial rosettes, with distinct cellular structures arranged in two circlets around an irregularly star-shaped unit with a central ring. In the lower scan (Fig. 1b) the rosettes are generally rather disordered and crushed together, they were probably more decayed, and somewhat displaced from the lenses before mineralisation. Figure 2 shows the capsule (Fig. 2a) and the internal structures of these rosettes in more detail. There is an inner circlet, which consists of six or seven wedge-shaped cells (Fig. 2b1, 2b2), with

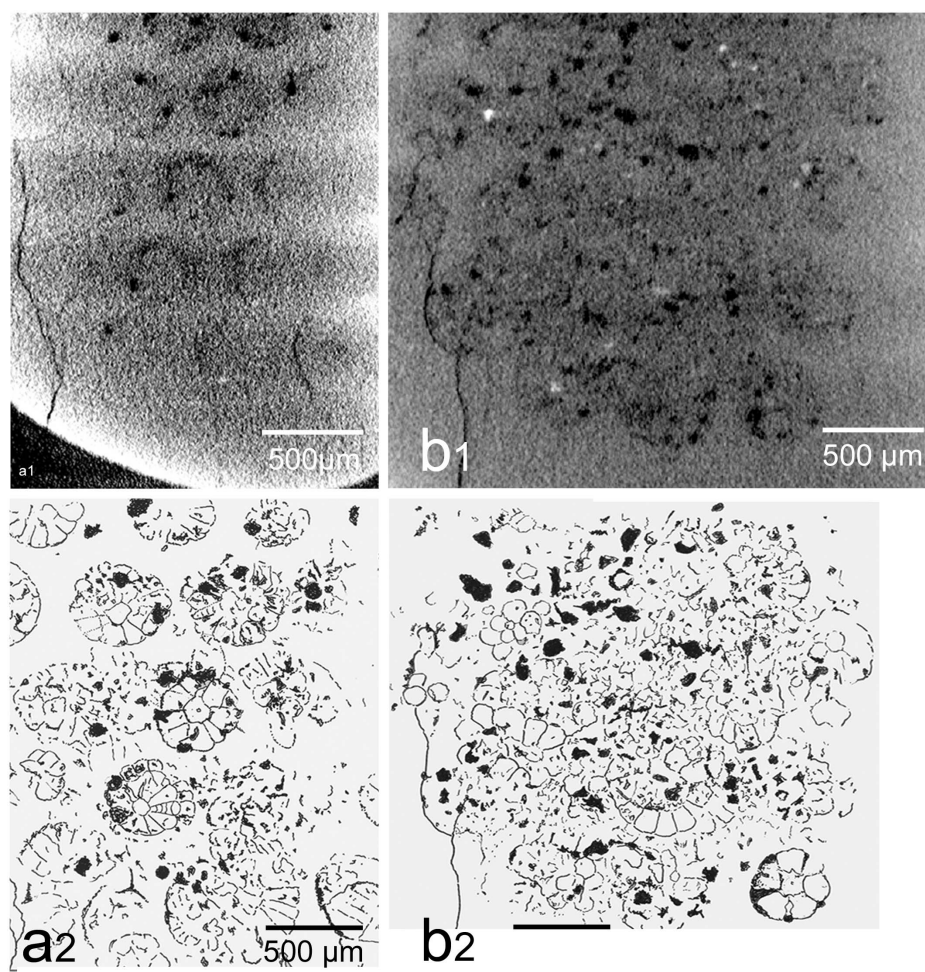


Figure 1 | Two cross sections of the (schizochroal) compound eye of *Geesops schlotheimi* (Bronn, 1835), μ ct-scanning. Age and location: Flesten Mb, Ahrdorf Fm, Middle Devonian, Gees/Gerolstein, Eifel, Germany, (a1) Cross section (slightly oblique) through the upper third of the compound eye, (a2) schematic drawing of a1. (b1) Cross section (slightly oblique) through the lower third of the compound eye. (b2) schematic drawing of b1. Both show the regular patterns of the sublensar sensory elements.

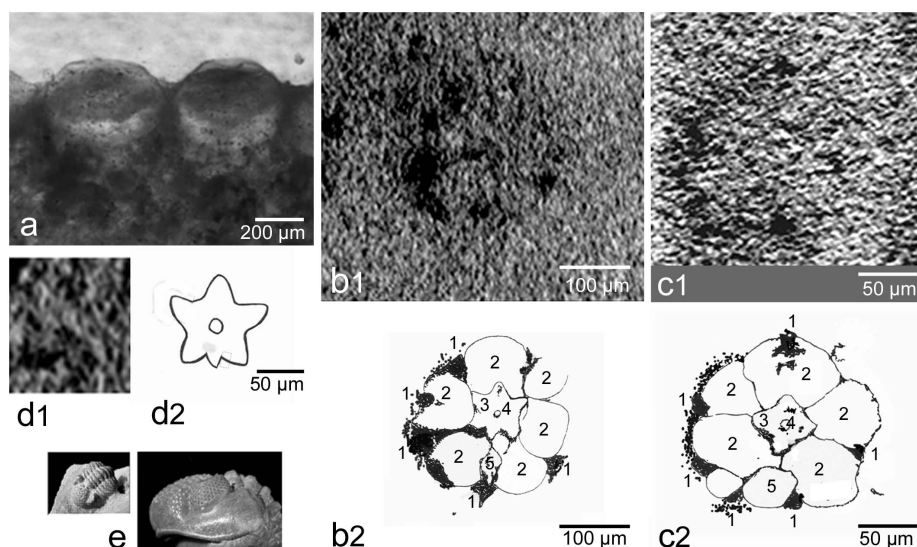


Figure 2 | ~390 Mio year old visual unit of *Geesops schlothheimi* (Bronn, 1835). Age and location: Flesten Mb, Ahrdorf Fm, Middle Devonian, Gees/Gerolstein, Eifel, Germany. (a) Light microscopic lateral aspect of the visual unit showing lens and capsule. (b1) Cross section through the upper third of the visual unit. (b2) Schematic drawing of b1. (c1) Cross section through a visual unit, slightly deeper than b. (c2) Schematic drawing of c1. (b, c, μ ct-scannings). (d1) Presumed rhabdomeric structure. (d2) Schematic drawing of d1, note the central circular structure (presumed process of the eccentric cell). (e) *Geesops schlothheimi* (Bronn, 1835), size of the specimen c1 cm if stretched. Speciman and photographs B. S. 1 presumed pigment cell, 2 presumed sensory cell, 3 star-shaped central element, presumed rhabdomeric structure, 4 central element inside of the presumed rhabdomeric structures, interpreted as the process of the excentric cell, 5 presumed excentric cell, not reaching the central axis, b–d x-ray tomography, ct-scanning.

an extra thin kite-shaped cell (Fig. 2b1, 2b2, 2c2, 5), usually not touching the centre. The outer cirlet comprises separate small black spots (Fig. 2b1, 2b2, 1; 2c1, 2c2, 1), each set at the outer margin, and at the junction between two cells of the inner cirlet. Even so several rosettes are distinct and one of these shows the original structure particularly well, though obviously affected by extra mineralisation. The inner cirlet is interpreted as the remains of original sensory cells, surrounding a rhabdom with a central rod (Fig. 2b1, 2b2 3, 4; 2c1, 2c2 3, 4) whereas the outer cirlet is likely to represent the original pigment cells (Fig. 2b1, 2b2, 1; 2c1, 2c2, 1), now preserved as hollow spaces. The narrow kite-shaped cell (Fig. 2b1, 2b2, 5; 2b1, 2c2, 5) may be equivalent to the eccentric cell in the lateral eyes of *Limulus*^{20,21}.

Barrandeops cf. granulops. (Chatterton et al. 2006), Emsian, lower Devonian (391.9 ± 3.4 Ma), Hamar Laghdad, Morocco.

In the silicified specimens the capsules themselves are preserved by a silicified film. μ -ct analysis, undertaken at the Steinmann Institute, University of Bonn and at Phoenix x-ray, Munich, revealed clearly the lower part of the sensory system, as seen from within the eye. Here (Fig. 3a) are visible some thirteen ‘cells’, like segments of an orange, arranged radially. By comparison with the ‘*Geesops*’ specimen, these must represent the original outer ring of pigment cells, like those of ‘*Geesops*’ but appreciably larger than those of *Geesops*.

Barrandeops (II). Here again, there is a star-shaped central unit with a ‘core’ (Fig. 3b1, 3b2 4,5) and an outer ring of radially arranged, wedge-shaped cells, originally about 10–12 in number, presumably pigment cells, and 5 or 6 more irregularly arranged cells between the centre and the outer ring. The center is typically star-shaped as in living arthropods, and may consequently be interpreted as the central rhabdomeric structure.

Barrandeops (III). This specimen was investigated using synchrotron radiation, undertaken at ESRF, Grenoble. The sublensar structures here are seen in lateral view, parallel with the main axis of the capsule (Fig. 3c). Although the lens has been diagenetically converted to featureless calcite the contents of the capsule are clear.

Directly below the lens are several more or less square cells with rounded lower terminations (Fig. 3c1, 3c2, 6), and a central vertical rod (Fig. 3c1, 3c2, 4) connecting the lens to an array of vertically elongated bodies (Fig. 3c1, 3c2, 2), with a number of large rounded ‘balloons’ (Fig. 3c1, 3c2, 7) below. A reasonable interpretation would be that the structures (Fig. 3c1, 3c2, 6) are the equivalent of lens-building cells, whereas the rod (Fig. 3c1, 3c2, 4) represents the rhabdom. This rod seems to preserve well and has been seen in several other instances. The elongated bodies (Fig. 3c1, 3c2, 2) are likely to be either pigment cells (Fig. 3b1, 3b2, 1; 3c, 3c2, 1), originally surrounding sensory cells (Fig. 3b, c 4), or sensory cells themselves. As yet the nature of the ‘balloons’ (Fig. 3c1, 3c2 7) remains uncertain.

Chotecops. An exceptionally well-preserved specimen of *Chotecops ferdinandi* (Kayser, 1880) from the Bundenbach Schiefer (Lower Emsian, Lower Devonian), Germany, largely confirms ct-scanning observations on *Geesops* and *Barrandeops*. Here the fossils are lightly pyritised. In this specimen the outermost surface of the eye has split off revealing in tangential light a slightly squeezed capsule below the lens. This partially pyritised lens (Fig. 4a, b 1) is attached to several darker petal-shaped structures below (Fig. 4b 2, 3). In turn, and set underneath are light-coloured elements alternating with the ‘petals’ (Fig. 4b 4). These are connected by an oblique filament (Fig. 4b 5). We interpret the ‘petals’ as sheeting pigment cells (Fig. 4b 3), and the lighter elements as sensory cells (Fig. 4b 4), each connected to a minor nerve (Fig. 4b 5). The almost squared elements (Fig. 4b 2) correspond to those of *Geesops* (Fig. 2a, right capsule) and *Barrandeops* (Fig. 3c1, 3c2, 6). Relicts of a second and similar cellular system lie adjacent to the first. These are of similar dimensions to those in *Geesops* (Fig. 2).

Discussion

Previous models for the phacopid sensory system presupposed an ocellar system, with a retina of many cells flooring the capsule^{12,13,22–25}, as it could be a basic visual system in arthropods generally. Our present investigation, on the other hand, indicates an evident

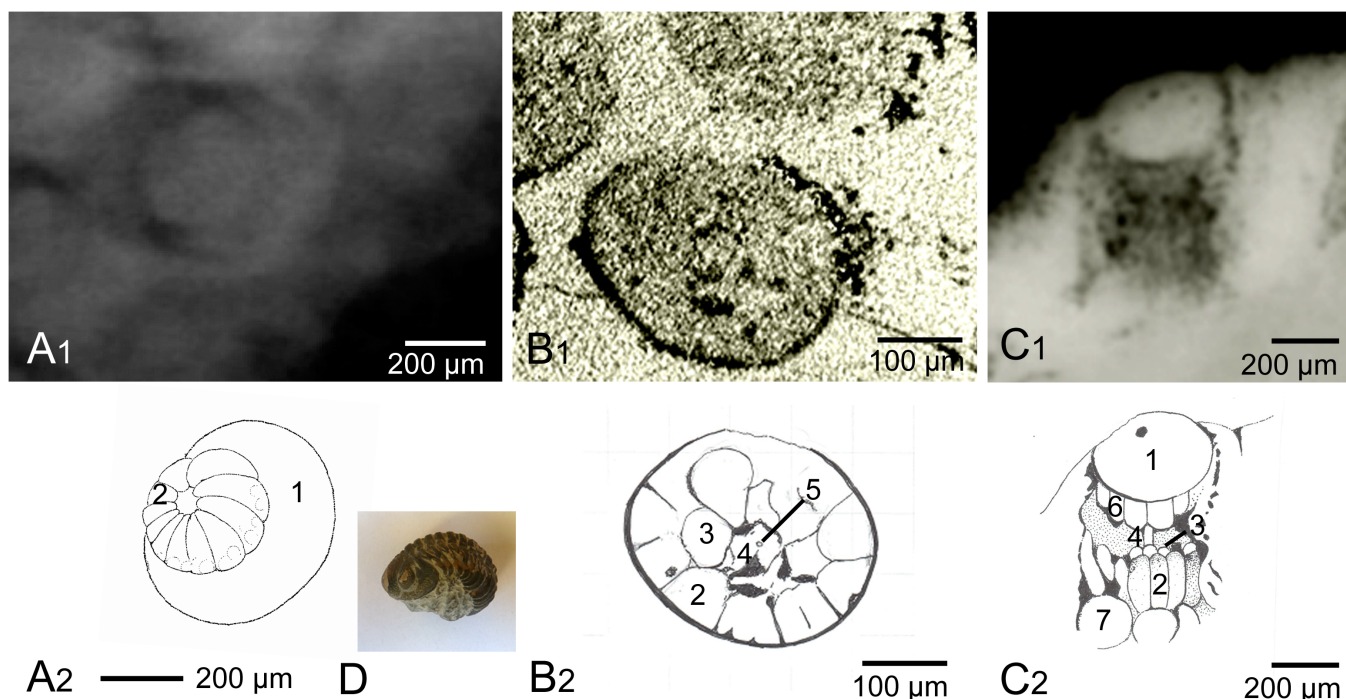


Figure 3 | The visual unit of *Barrandeops cf. granulops* Chatterton et al. 2006, Age and location: Emsian, lower Devonian (391.9 ± 3.4 Ma), Hamar Laghdad, Morocco. (a1) Three dimensional reconstruction of an individual visual unit from the rear, showing a shielding cup of ~ 11 cells, headed by the wider margin of the lower rim of the lens, which covers the visual unit (x-ray-ct). (a2) Schematic drawing of a1. (b1) Cross section of the visual unit. (b2) Schematic drawing of b1. (c) Synchrotron image of the lateral section of the visual unit of *B. cf. granulops*. (d) *Barrandeops cf. granulops* Chatterton et al 2006, size of the specimen c 3.5 cm if stretched. (Specimen and photograph B. S.) 1 lens. 2 presumed pigment cells covering the more central sensory cells. 3 presumed sensory cells, 4 rhabdomeric structure, 5 central element inside of the rhabdomeric structure (presumed process of the excentric cell). 6. ?lens-building cells.

resemblance between the phacopid sensory system and that of ommatidia in the apposition eyes of euarthropods, which was unexpected. The phacopid sensory system, however, especially the sensory cells, is very much larger than that of any insects or crustaceans (sensory cells of phacopid compound eyes: ~ 80 μm in diameter, as opposed to 2–10 μm common in modern euarthropods). In dimensions and structure, however, there is a strong resemblance between the phacopid system and that of the lateral eyes of the living *Limulus*. In the latter each ommatidium consists of 4–20 sensory cells, while the rhabdomers form a star-shaped pattern round a vertical process of an eccentric cell, itself a modified photoreceptor. Pigment cells form a sheet around the photoreceptors. In phacopids, *Geesops* in particular, but in *Barrandeops* also, there are 6 or 7 sensory cells,

arranged around a star-shaped element possibly comparable to rhabdomers within a *Limulus* ommatidium, while the central circular structure could be the process of an eccentric cell. The narrow kite-shaped cell (Fig. 2b1, 2b2 5; 2c1, 2c2 5) could be a section of the body of an eccentric cell. If these indications prove realistic then the lateral eyes of *Limulus* could have retained a fundamental archaic system which has continued to function successfully today, amongst so many other kinds of compound eye in living arthropods. This may also hold significant interest for phylogeny.

Compound eyes are a typical character for all recent Mandibulata (insects and crustaceans), and Xiphosura among the Chelicerata. In Myriapoda it is only in the Scutigermorpha that a kind of apposition eye, different from the aggregate eyes of other myriapoda, exists. Only the Xiphosura possess an excentric cell, rather similar to the phacopid trilobites investigated here.

The sophisticated internal structure of the lenses of some phacopid trilobites¹⁰ had suggested that there may be a small retina flooring the capsules below the lenses^{12,13,22–25}, and that the double lens system improved image formation. The same qualities, however, support in the same way an apposition eye, providing well focused light onto the rhabdomeres. It had been shown that the schizochroal eyes of phacopid trilobites derived by paedomorphosis from the holochroal eyes of earlier trilobites¹⁵. The holochroal eyes are the most common type of trilobite eyes and consist very often of several hundreds or even thousands of sometimes tiny facets. If the schizochroal eye derived from the holochroal eye this suggests that the holochroal eye also was an apposition eye. The sensory cells, however, must have been smaller, resulting in sizes comparable to most of the receptor cells of many modern apposition eyes. Because the lateral eyes of *Limulus*, as a “living fossil” show an excentric cell as the phacopid trilobite eyes do, it is rather probable, that *Limulus* is equipped with an archaic

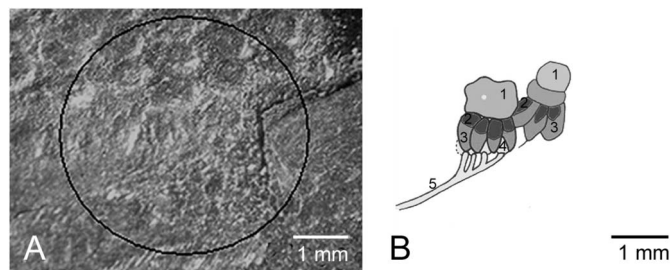


Figure 4 | Visual unit, slightly, obliquely squeezed, of *Chotecops ferdinandi* Struve,1985, Age and location: Siegenian/Emsian Stage (~ 407 million years) lower Devonian, Bundenbach, Hunsrück, Germany. (a) Obliquely ‘opened’ compound eye of *B. cf. granulops*. (b) schematic drawing of a. 1 lens, 2 ?lens-building cells 3 shielding pigment cells, 4 sensory cells, 5 efferent nerves of the sensory cells. Insert: *Chotecops ferdinandi* Struve,1985.



system, which might have been realised in the holochroal eyes also. An alternative was, that especially dense holochroal eyes with tiny lenses had even simpler systems, comparable to such as had been suggested recently for a kind of prototype of a crustacean compound eye from the upper Cambrian with just one receptor below each lens, which was forced by physical reasons in a miniscule three dimensionally preserved compound eye system²⁶. This result is in agreement with ideas about the evolution of eyes formulated by Darwin²⁷ and Gehring²⁸, where the development of visual units derive from one-cellular systems.

A third possibility was that bearers of small faceted holochroal eyes possessed ommatidia specialised to be small as in Collembola and tiny insects²⁹, or, lastly, that they had another still unknown principle.

The enormous size of the sensory cells in the phacopid trilobites found here, comparable to those of *Limulus*, indicates a convergent evolution. Because phacopid trilobite eyes show a system similar to the *Limulus*-type of apposition eye with its excentric cell, rather probably this is an archaic and basic type of compound still represented today. In the competition between prey and predator about the most effective visual system as formulated in the Light Switch Theory^{30,31} it has continued to function successfully today.

- Lee, M. S. Y. *et al.* Modern Optics in exceptionally preserved eyes of the Early Cambrian arthropods from Australia. *Nature* **474**, 631–634 (2011).
- Paterson, J. R. *et al.* Acute vision in the giant Cambrian predator *Anomalocaris* and the origin of compound eyes. *Nature* **480**, 237–240 (2011).
- Schoenemann, B. & Clarkson, E. N. K. Eyes and vision in the Chengjiang arthropod *Isoxys* indicating adaptation to habitat. *Lethaia* **44**, 223–230 (2010).
- Schoenemann, B. & Clarkson, E. N. K. The eyes of *Leancoilia*. *Lethaia* **45**, 524–531 (2012).
- Tanaka, G., Parker, A. R., Siveter, D. J., Maeda, H. & Furutani, M. An exceptionally well-preserved Eocene dolichopodid fly eye: function and evolutionary significance. *Proc. Roy. Soc. B* **276**, 1015–1019 (2009).
- Clarkson, E. N. K., Horváth, G. & Levi-Setti, R. The eyes of trilobites; the oldest preserved visual system. *Arthropod Struct. Dev.* **35**, 247–259 (2006).
- Land, M. F. & Nilsson, D.-E. *Animal Eyes*. (Oxford University Press, 2002), pp. 221.
- Towe, K. M. Trilobite eyes; calcified lenses in vivo. *Science* **197**, 1007–1009 (1973).
- Clarkson, E. N. K. The eye: morphology, function and evolution. In *Treatise on Invertebrate Paleontology, part O. Arthropoda 1. Trilobite, revised* (eds. Kaesler, R. L. *et al.*) 114–132 (The University of Kansas Press and Geological Society of America, 1997).
- Clarkson, E. N. K. & Levi-Setti, R. Trilobite eyes and the optics of Des Cartes and Huygens. *Nature* **254**, 663–667 (1975).
- Clarkson, E. N. K. Fine structure of the eye in two species of *Phacops* (Trilobita). *Palaeontology* **10**, 603–616 (1967).
- Clarkson, E. N. K. The evolution of the eye in trilobites. *Fossils & Strata* **4**, 7–31 (1975).
- Campbell, K. S. W. The functional anatomy of trilobites: musculature and eyes. *J. Proc. Roy. Soc. New South Wales* **108**, 168–188 (1975).
- Bruton, D. J. & Haas, W. The puzzling eye of *Phacops*. *Spec. Pap. Palaeontol.* **70**, 349–361 (2003).
- Clarkson, E. N. K. & Zhang, X.-g. Ontogeny of the Carboniferous trilobite *Paladin eichwaldi shunnerensis* (King 1914). *Trans. Roy. Soc. Edinburgh, Earth. Sci.* **82**, 277–296 (1991).

- Gaten, E. Eye structure and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contrib. Zool.* **67**, 223–235 (1998).
- Eakin, R. M. & Westfall, J. A. Fine structure of the eye of *Peripatus* (Onychophora). *Z. Zellforsch.* **68**, 278–300 (1965).
- Mayer, G. Structure and development of onychophoran eye: what is the ancestral visual organ in arthropods? *Arthropod Struct. Dev.* **35**, 231–245 (2006).
- Schoenemann, B., Liu, J.-n., Shu, D.-g., Han, J.-a. & Zhang, Z.-f. A Miniscule Optimised Visual System in the Lower Cambrian. *Lethaia* **42**, 265–273 (2009).
- Fahrenbach, W. H. The morphology of the eyes of *Limulus* II. Ommatidia of the compound eye. *Z. Zellforsch.* **93**, 451–483 (1969).
- Barlow, R. B. & Powers, M. Seeing at night and finding mates: the role of vision 83–102 in *The American Horseshoe Crab* (eds. Shuster, C. N., Barlow, R. B. & Brockman, H. J.) 1–427 (Harvard University Press 2003).
- Clarkson, E. N. K. The visual system of trilobites. *Palaeontology* **22**, 1–22 (1979).
- Buschbeck, E., Ehmer, B. & Hoy, R. Chunk Versus Point Sampling: Visual Imaging in a Small Insect. *Science*, **86** (5442), 1178–1180 (1999).
- Fordyce, D. & Cronin, T. W. Comparison of fossilized schizochroal compound eyes of phacopid trilobites with eyes of modern marine crustaceans and other arthropods. *Journal of Crustacean Biology*, **9**(4), 554–569 (1989).
- Fordyce, D. & Cronin, T. W. (1993). Trilobite vision: a comparison of schizochroal and holochroal eyes with the compound eyes of modern arthropods. *Paleobiology*, **19**, 288–303.
- Schoenemann, B. The eyes of a tiny ‘Orsten’ crustacean – A compound eye at receptor level? *Vision Research* **76**, 89–93 (2013).
- Darwin, C. On the origin of Species by means of natural selection. John Murray, London (1859).
- Gehring, W. J. The evolution of vision. *Wires Developmental Biology*. DOI: 10.1002/wdev.96 (2012).
- Paulus, H. F. Eye Structure and the Monophyly of the Arthropoda in *Arthropod Phylogeny* (ed. Gupta, A. P.), 299–383 (Van Nostrand Reinhold Co., New York (1979), pp. 762.
- Parker, A. R. Colour in Burgess Shale animals and the effect of light on evolution in the Cambrian. *Proc. Roy. Soc. B* **217**, 177–189 (1998).
- Parker, A. R. *In the Blink of an Eye*. Perseus, New York (2003).

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Author contributions

B.S. and E.C. conducted the analyses, wrote the main manuscript text, and prepared the figures. All authors reviewed the manuscript.

Additional information

Competing financial interests: The authors declare no competing financial interests.

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