Structure and function of a compound eye, more than half a billion years old

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Until now, the fossil record has not been capable of revealing any details of the mechanisms of complex vision at the beginning of metazoan evolution. Here, we describe functional units, at a cellular level, of a compound eye from the base of the Cambrian, more than half a billion years old. Remains of early Cambrian arthropods showed the external lattices of enormous compound eyes, but not the internal structures or anything about how those compound eyes may have functioned. In a phosphatized trilobite eye from the lower Cambrian of the Baltic, we found lithified remnants of cellular systems, typical of a modern focal apposition eye, similar to those of a bee or dragonfly. This shows that sophisticated eyes already existed at the beginning of the fossil record of higher organisms, while the differences between the ancient system and the internal structures of a modern apposition compound eye open important insights into the evolution of vision.

Significance

An exceptionally well-preserved arthropod fossil from near the base of the lower Cambrian shows the internal sensory structures of a compound eye, more than half a billion years old. The trilobite to which it belongs is found in a zone where the first complete organisms appear in the fossil record; thus, it is probably the oldest record of a visual system that ever will be available. This compound eye proved to possess the same kind of structure as the eyes of bees and dragonflies living today, but it lacks the lenses that are typical of modern eyes of this type. There is an elegant physical solution, however, of how to develop a quality image of modern type.
ranged between 150 °C and 200 °C during the Caledonian Orogeny (33), while superb preservation of acritarch organic material in Estonia indicates temperatures well below 100 °C (34). Here, the cuticular exoskeletons of the trilobites are exceptionally well preserved in contrast to those in some other regions of the world, which have been demineralized and may have vanished altogether.

The nearly complete specimen of S. reetae Bergström, 1973 (25) described here was collected from the Saviranna section below the beds with Schmidtiellus mickwitzi (Schmidt, 1888) (35) but above the beds with Rusophycus trace fossils, which supposedly mark arthropod (likely trilobite) traces, and contains fragmentary unidentified trilobites, possibly also Schmidtiellus. The alternating successions of clay and silt in the Lükati Formation of the Domnonial regional stage correlate with the lowermost part of the Atdabanian (22, 36–40) or may extend down into the underlying Tommotian as suggested by the global acritarch succession (41, 42). Consequently the trilobite described here may be older than the fauna represented in the “Chengjiang Fauna,” which is correlated to the Qiongzhusian (43, 44), a stage correlated with the late Atdabanian stage in Siberian sequences of the middle of the lower Cambrian (44–47).

The stratigraphy of the lower lower Cambrian is an object of intense research and discussion; it is broadly demonstrated and intense research and discussion; it is broadly demonstrated and intensely debated (23, 24). Therefore, the oldest trilobites have cuticles of calcite set in an organic base (57). This is most unlikely to be primary, considering that all other trilobites have cuticles of calcite set in an organic base (57). Secondary phosphatization, however, is quite common in trilobites from Russia and other Cambrian fossil-bearing areas and other Cambrian fossil-bearing areas and other Cambrian fossil-bearing areas and other Cambrian fossil-bearing areas. Cases that come immediately to mind are the magnificently preserved Orsten crustaceans and other fossils, with perfectly preserved appendages, from the Furongian of central Sweden (58, 59). Other examples are the lower Cambrian bradoriids and codicids in perfect preservation from South China (60). Finally, there is evidence of the preservation of ommatidia in lower Cambrian radiodontans (61), and the preservation of ommatidia by phosphatization has also been reported recently in a Jurassic crustacean (62).

The availability of vast quantities of phosphate in the Cambrian (63) was apparently set in motion by a massive marine transgression at the beginning of the Cambrian that generated substantial upwelling. The phosphorus and other vital elements that had accumulated on the late Precambrian ocean floors for millions of years were thus released into the upper waters of the sea, to be made available both for the formation of organophosphatic shells, as in inarticulated brachiopods, and for the proliferation of phosphate bacteria, which covered the surfaces of calcarious and other shells in micrometric deep layers, producing a thin but durable shell, replicating outer and inner surfaces. Solution-containing carbonate rocks, containing such fossilized shells in weak acids, release the replicas, which are then available for study (63). South China was a major center of such phosphatic replication in lower Cambrian times; however, by the middle Cambrian, this center had shifted to Australia. It is likely that phosphatization spread to the inner parts of the shells in some instances, so that what had been entirely calcite became

Baltoscandian trilobites are among the earliest in the world (40). They occur coevaly with the assemblages of the lower Atdabanian of Siberia [Profallotaspis, Bigotinella, Bigotina (Olenelloidea, at the base of the Atdabanian)], Laurentia (olenellids of the Frittsaspis zone, uppermost part of the Begadane stage, which is correlated to the lower Atdabanian of Siberia), the bigotinid trilobites from southern Europe, Spain, and France (lower Ovetian, correlated to the lower Atdabanian), and the assemblages of Antarctica (Lemdaddella lower Ovetian stage, correlated to the lower Atdabanian), and the oldest trilobites from Morocco (Bigotina, Eofallotaspis, Fallotaspis, and Lemdaddella Issendalenian) and the redlichid trilobites of China (Abadiella, Abadiella zone correlates with the upper Atdabanian and Australia (Abadiella) are slightly younger (39, 40).

The Cambrian Explosion or Cambrian Radiation started about 542 Ma (3–6, 46, 50), and the Cambrian Radiation of rich arthropod faunas is known mainly from rare “time windows” preserving fossil Lagerstätten. The best known and studied are the Chengjiang Biota (~520 Ma) in China (e.g., refs. 8, 9); Sirius Passet Biota in Greenland (~518 Ma) (e.g., refs. 51, 52); Emu Bay Formation on Kangaroo Island, Australia (~514 Ma) (e.g., refs. 53, 54); and the biotas of the Kaili Formation in China (~510 Ma) (e.g., refs. 44, 45), or the slightly younger fauna of the middle Cambrian Burgess Shale Formation in British Columbia, Canada (~508 Ma) (e.g., refs. 10, 11); the middle Cambrian Weeks Formation (late Guzhangan, ~497–500.5 Ma) in Utah (e.g., refs. 55, 56); and the Orsten fossils (e.g., refs. 14, 15). Meanwhile more than 50 of these Burgess Shale-type biotas have been described so far (e.g., ref. 56). The critical point here is that the Baltoscandian trilobites are older than any of these famous Lagerstätten (Fig. S1).

The cuticle of S. reetae is preserved as calcium phosphate, which often allows the record of finest details, such as, for example, in the filter-feeding branchiopod Rehbachiella kinnekullensis from upper Cambrian limestone concretions collected in southern Sweden, where fine setae and setulae (~1 μm) were shown to be present on its appendages (14).

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Fig. 1. Trilobite S. reetae Bergström, 1973 (25) (GIT 294-1) and its compound eye. (A) Holotype. (B) Head region of A. (C) Fields of view. (D) Abraded part of the right eye. Arrowheads indicate the ommatidal columns. (E) Lateral view of the right eye. (F) Schematic drawing of E. (G) Two visual units (big arrows in D). (H) Schematic drawing of G. (Scale bars: A–C, 1 cm; D, 1 mm; E and F, 2 mm; and G, 200 μm.)

S. mickwitzi (Schmidt, 1888) (35) and S. reetae Bergström, 1973 (25) belong to an early trilobite assemblage comparable to those of the oldest assemblages of the lower Atdabanian of Siberia and lower Ovetian of France, Spain, and Antarctica, or the earliest trilobites of Morocco [Issendalenian (approximately lower Ovetian) (49)] and Laurentia (Montezuman). All these trilobites are more or less coeval. The early trilobites of China [Nangao (approximately middle Ovetian, upper Atdabanian) (40)] are slightly younger (5, 39) (Fig. S1).
solid phosphate. This is what seems to have happened to our specimen of *Schmidtiiellus*.

Another possibility is that increasingly deep bioturbation in the early Cambrian disturbed the surface layers of the sediment and released minerals from the lower layers (64).

**Results**

Compound eyes of apposition type are typical of modern diurnal arthropods, whereas more advanced and sensitive systems (superposition eyes) may not have existed before the Devonian [419.2 ± 3.2 Ma–358.9 ± 0.4 Ma (65)].

Apposition compound eyes are composed of numerous identically repeated visual units, the ommatidia. Recognizable externally as facets, they consist, among the Mandibulata, of a cuticular “corneal lens” and a so-called “crystalline cone” focusing the incident light onto the tip of a central light-guiding structure, the rhabdom, lying underneath “[focal apposition eye,” sensu Land and Nilsson (66)]. In its longitudinal section, the crystalline cone often forms an approximately triangular shape. In aquatic systems, the difference in optical density between water and the organic material that forms the lens is not high enough to supply the capacity for effective refraction; thus, normally, it is the crystalline cone instead of the lens that forms an effective dioptic apparatus. The central rhabdom is part of the receptor cell system; these cells lie arranged around it like a rosette. The number of receptor cells is variable and depends on the species; very commonly, there are eight of them. In a focal apposition eye, all stimuli within the visual field of each facet are focused, and thus concentrated on the distal tip of the rhabdom, averaged to one mean light impression. Screening pigment cells, differing in number among species, optically isolate the visual units from each other. Thus, the focal apposition eye as a whole provides a perceived mosaic-like image (67, 68). The acuity of such eyes depends, among other factors, on the number of facets: The more there are, the higher is the quality of the image (in the same way that pixels define the quality of a computer graphic).

The acuity of the image relates also to the acceptance angle of the rhabdoms [between 0.8° and 10° for most compound eyes (69)], and the sensitivity of the eye also depends, among other factors, upon the latter.

As with all coeval trilobites, *S. rectae* lived as benthos. Gliding over the sea floor it had, in common with all (more or less) contemporary genera of onellid trilobites, such as *Holmia, Lemidella, Fallotaspis*, and others, reorient, form eyes with a narrow slit-like visual surface oriented toward the front and especially toward the lateral horizon (Fig. 1B, C, E, and F). Conspicuously, the top of the eye is covered by a lensless top surface, the “palpebral lobe,” and the visual field does not extend upward more than 25–30° above it. This is a common pattern in early trilobites generally, but why that is so remains an open question. It is likely that the vertically narrow visual field limited the distracting effect of bright light signals from the lower surface of the water. The horizontal visual field of *S. rectae* covers ~2 x 124° (Fig. 1B and C); thus, the eye was able to scan the seafloor anterolaterally around the trilobite. There were certainly free-swimming predators capable of tackling trilobites, which, in a more or less homogeneous environment on the sea floor, could be detected already from a distance by this wide, horizontally directed visual field.

The eye of the specimen investigated here is about 10 mm long and 4.5 mm wide. The lateral aspect of the compound eye shows that the elongated, crescentic visual surface has just a few (<~100), relatively large lenses (~50 μm) (Fig. 1E and F). Functionally, even a small number of such lenses could pick up the movement of potential predators passing within the field of view, as a result of change in light intensity detected by one ommatidium after another. Thus, the system probably worked as a movement detector rather than as an image-forming eye, but also as an obstacle detector when scanning the environment.

In the specimen *S. rectae* Bergström, 1973 (25) GIT 294-1-1, the palpebral lobes are present, although their papillated upper surfaces are slightly abraded. While all structures are destroyed superficially in the left eye, this is not so with the right eye, which allows extraordinarily rare insight into its internal structures. Several internal reliefs ranged against the ocular suture may be seen here, which presumably, on account of their position, belonged to the lowest part of the eye. There may be as many as seven of these, some in situ and others slightly displaced (Fig. 1D).

In the best preserved of these (Figs. 1D, G, and H and 2B–D and J), the lenses (~1 mm in diameter), broken across, are extremely flat and thin, showing no convexity (Figs. 1G and H and 2C, D, and J). Beneath the lens lies a basket-like structure, consisting of spherical elements, perhaps former cells (Figs. 1G and H and 2B–D and J). It is about 460 μm high and probably about 1.3 mm wide. In its center is a conical tube, broken at its upper side. The distal surface shows the conical tube to consist of several elements of similar but different sizes (~50 μm) grouped around a central core (Figs. 1G and H and 2B–D and J), what must be a sensory complex in the form of seven radially arranged, more or less triangularly shaped elements (receptor cells) grouped around a central structure (rhabdom). This conical tube has a diameter of ~160 μm and a length of ~338 μm, and

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**Fig. 2.** Internal structures of the functional visual unit. (A) Ommatidium. Note the cellular elements (relicts of receptor cells) arranged radially around the central core (relict of the rhabdom). (B) Ommatidium positioned in a basket. Note the cellular elements (relicts of receptor cells) arranged radially around the central core (relict of the rhabdom). (C) General aspect of B for interpretation in D. (E) General aspect of A for interpretation in F. (G) Cross-section of the ommatidium of the extant crustacean *Dulichia porrecta* (Bate, 1857) (87) (Crustacea, Amphipoda) (88). (H) Schematic drawing of the elements of a typical sensory system in the aquatic compound eye in G. (I) Schematic drawing of a longitudinal section of an ommatidium. (J) Schematic drawing of the visual unit of *S. rectae*. b, basket; cc, crystalline cone; l, lens; om, ommatidium; p, pigment screen; r, rhabdom; sc, sensory (receptor) cells. (Scale bars: A, B, E, F, and J, 200 μm; C and D, 100 μm; and G, 1 μm.)
it connects centrally with a long thin tube that is directed inward (~500 μm long, ~70 μm Ø in diameter). The total length cannot be described because the proximal end of the system plunges downward outside the bottom of the “basket.” Distally from the tube, a regular, triangular element (~56 μm high, ~350 μm wide) can be seen, positioned directly below the lens (Figs. 1G and 2B–D and J). Distally from the tube, a regular, triangular element (~56 μm high, ~350 μm wide) can be seen, positioned below the “lens,” which slightly covers this triangular element. It can be interpreted as a kind of crystalline cone because of its triangular shape (from a side view) and its relative position between lens and sensory complex. These elements and their arrangement are typical for compound eyes of the appositional type, as explained before. The typical position within of the unit of a compound eye excludes other possibilities for explaining this pattern, formed so characteristically for an ommatidium. Additionally, at least we do not know of any plant-based pattern, protozoan structure, or mineral structure that would be similar.

Close to it, on the left-hand side, and at a distance of about 1 mm from the first, a second conical tube-like structure similar to the first, although displaced and rotated, can be clearly seen (Figs. 1D, G, and H and 2A, E, F, and J). It has a total length of ~364 μm, and is ~208 μm wide. It ends proximally in a small tube ~70 μm in diameter, which sinks into the depth of the matrix. There are seven triangular elements (largest: ~70 μm, smallest: 56 μm) that surround a central circular structure (diameter ~20 μm). The difference in the diameter of both tubular systems of about ~48 μm (~160 μm vs. ~208 μm) can be explained by a difference in structure: the second system is embraced by a wide membrane-like sheet, while the sheet of the first system described is thinner. Another difference between the two systems is that inside the seven elements of the first system, just a dark irregular spot can be seen, while in the second system, dark areas surrounded by a membrane can be more clearly made out. In their principal structure, however, both elements are congruent. This system seems to have a triangular element between the lens and tubular element also; this, however, appears distorted (Figs. 1G and H and 2E, F, and J).

In comparison to many modern, compact systems, such as those of bees or dragonflies, the large size (one system’s diameter is ~1 mm) between the ommatidial cones is remarkable, and may have provided or supported an effective optical isolation of the individual visual units.

We are aware that due to the limited amount of data, only a generalized description of the performance of this early eye is possible. There exist measurable parameters, however, that allow an approximate estimation, and thus a rough characterization, of this early visual system. In comparison to terrestrial visual systems, aquatic vision suffers by the absorbance of light in water; thus, in principle, the compound eyes of aquatic arthropods, at the same time of the day, require a higher sensitivity than those of terrestrial organisms. This is all the more so the deeper the arthropod lives in the water column. Under low-light conditions, vision appears very “noisy” because the low photon numbers show relatively large random fluctuations. This improves with receptors capable of a high photon capture rate. This photon capture rate can be increased by a wide aperture (lens diameter) A, a large diameter of the receptor (rhabdom) d, and a sufficient length of the absorbing structure (rhabdom) x (70, 71). Land (70, 71) defined a fine measure to describe the capacity of a receptor in a compound eye to capture light: the sensitivity S. It describes the rate of photons absorbed by each receptor to the number of photons emitted per steradian by 1 m² of an extended standardized source, and this would enable a comparison between the ancient visual system investigated here and the sensitivities of recent arthropods:

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S = \left(\frac{\pi}{4}\right) \cdot \left(\frac{A}{f}\right)^2 \cdot \left(1 - e^{-fD}\right) = 0.64 \cdot \left(350/156\right)^2 \cdot \left(1 - e^{-0.0069\cdot 338}\right) = 2.91 \text{ m}^2 \cdot \text{sr}^{-1}
\]

[S sensitivity (0.64) is derived from the circular shape of the system (70). A aperture (μm)), f focal length, k absorption coefficient of the phototipoid (0.69% per micrometer; lobster (72), after Land 1981 (70)), x (μm) length of the perceiving structure (rhabdom), here 338 μm (length of the rhabdom approximates length of the tubular structure, which is interpreted as an ommatidium).]

For the first discussed system the sensitivity results to ~2.91 [m² · sr]. Thus, the approximate estimated sensitivity of S. retacea Bergstrom, 1973 (25) is very similar to that of the branchiopod crustacean Artemia salina (Linnaeus, 1758) (73) [S = 2.3 [m² · sr] (71)] when it is dark-light–adapted. A. salina is a shallow water inhabitant, and the results presented here are in accordance with sedimentological evidence, which indicates that this benthic trilobite inhabited shallow waters also.

An effective parameter describing an eye’s light-gathering capacity is the F-number: F = f/D, where f is the focal length and D is the diameter of the lens. It is familiar to all photographers that cameras with low F-numbers produce bright images (ref. 69, p. 75). If we accept that this eye is a focal apposition eye because of the conical shape of the crystalline cone, the system suggests that the focused light fell on the tip of the rhabdom; thus, f ≈ 156 μm. Furthermore if we take, as discussed, the upper width of the crystalline cone as aperture A = 350 μm, the F-number can be calculated as 2.2. This value matches F-numbers typical for lenses of recent apposition eyes, which normally show F-numbers of about 2 (69, 70, 71).

As mentioned, the resolution of this early compound eye is rather low. Because the rhabdom acts as a light-guiding structure, the light is trapped into the system only up to a critical angle (θcrit), which is given by arcsine (n1/n2). The refractive index of sea water is about n1 = 1.34 (35% salinity, 20 °C), and n2 = 1.36–1.40 for the rhabdom (ref. 66, p. 59). The results are an acceptance angle for the rhabdom of 20°–30° and overlapping visual fields of each system, as is quite common in modern compound eyes. The interommatidial angle (Δϕ) lies at about 10°. In terrestrial systems not suffering from light absorbance, such as insects, they often range from 1°–5° (74). In aquatic crustaceans and xiphosurae with apposition eyes, however, this value is quite common, so we find in the xiphosuran Limulus, active at night, an interommatidial angle of 8°; for Artemia, a shallow water branchiopod, an interommatidial angle of ~9°; and in Cirolana, a deep sea isopod, an interommatidial angle of 15° (71). Thus, an interommatidial angle of 10° is not uncommon in aquatic arthropods. Due to the interommatidial angle, it is possible to...
estimate the anatomical resolution, which can be defined as the highest spatial frequency (of a sinusoidal grating) ($\nu_I$) that is resolved by such an array of sampling stations (ommatidia): $\nu_I = \frac{\nu}{2\Delta \phi \text{[cy]}}$ (70, 75–79), which allows a good comparison with other investigated systems. The $\nu$ results here to 2.87 [cy] and $\nu_I$, revealing an anatomical resolution lower than that of *Limulus* (4.8 [cy]) but higher than that of *Cirolana* (1.9 [cy]) (67). So, in total, the system of the trilobite *S. reetae* is in a state similar to modern aquatic arthropods, even without a lens.

**Discussion**

In discussion of these findings, it is remarkable that very little lens structure can be clearly distinguished. There are indications of round lens-like discs when the eye is studied from the outside, but from the internal aspect, no convexities that could effectuate any refraction of light can be made out. Also lens cylinders, such as in xiphosurans of the genus *Limulus* (68), cannot be recognized here. Even calcite as typical material for trilobite lenses, with a high refractive index, may not have been effective enough to refract light in water if there were not surfaces curved sufficiently enough, forming a “real convex lens.” Differing from *S. reetae* in aquatic crustaceans of today, the refractive element is commonly built by a massive cellular crystalline cone, often with an index gradient (70, 71). It is possible that at the time *S. reetae* was living in this marine environment, the dioptric apparatus of these early trilobites was, in some respects, relatively simple. If the small triangular structure underneath the lens was indeed an early type of crystalline cone, this might suggest, among other things, a relationship of the trilobites with the Mandibulata, because no crystalline cones can be observed in cheliceratae; alternatively, it may have been an indication of convergent development in this special case. The crystalline cone has been considered to be a synapomorphy of either Mandibulata or Pancrustacea (80–84). To have any refractive power and focusing, even in this ancient system, an index gradient then might be assumed to have existed.

Different from typical modern apposition eyes, the sensory apparatus lies in a kind of probably cellular basket. Inside of the basket-like unit in *S. reetae*, the seven elements arranged like a rosette around the central axis (Figs. 1 G and H and 2 A–F and J) clearly can be interpreted as relics of former sensory cells, grouped around a central fused rhabdom, underneath a small crystalline cone; it is a typical ommatidium of a focal apposition eye (70, 71) (Fig. 2 G–J). The arrangement of both systems described is almost identical: The small differences in diameter and the covering sheet may arise by diagenetic processes, or the systems may be of different function but identical principle. Unlike those of most modern compound eyes, the ommatidial systems lie very isolated from each other, and pigment cells, shielding the units against each other optically would not have been necessary.

One hypothesis may suggest that the circular discs (lenses) had only been more or less transparent parts of the cuticle, and that, as explained, the rhabdom itself overtook all light-gathering functions. This also may explain, why in most early Cambrian trilobites, where the visual surfaces are preserved, no distinct facets can be made out in their compound eyes. The very few visual units of this compound eye (Fig. 1 E and F), resulting in a pixilated mode of vision, surely did not provide an image formation but probably functioned as a movement detector discovering objects passing by, but without any detailed impression of the surroundings in its shallow water environments.

It may be mentioned that another trilobite, *Holmia kjerulfi* (Linnarsson, 1871) (85) from Norway, Botoman Formation, thus just less than 2 My younger, already had established densely packed compound eyes (Fig. 3), comparable to those of modern dragonflies.

In summary, the oldest compound eye so far known from the fossil record, which is that of the trilobite *S. reetae* Bergström, 1973 (25), was a focal apposition eye. In its principal structure, it was simpler than, but otherwise almost identical to, that of the modern compound eyes of bees and dragonflies living today; thus, the focal apposition eye is more than half a billion years old.

**Materials and Methods**

The holotype specimen of *S. reetae* Bergström, 1973 (25) is deposited at the Institute of Geology at Tallinn University of Technology, Estonia, under repository number GIT 294-1.

H. *kjerulfi* (Linnarsson, 1871) (85), described by Klaer (86), from Tomten, Ringsaker, Norway, is deposited in the Natural History Museum at the University of Oslo under repository number PMO-73168. The photographs were taken with a Nikon D7000 camera and a Nikon AZ100 microscope.

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