



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.

compound eye | visual system | arthropod | evolution | Cambrian

Vision is one of the key factors in triggering evolutionary changes. In many groups of animals, it is an essential support for finding social partners for mating and it provides information about the nature and settings of the environment. The “race” between predator and prey and the need “to see” and “to be seen” or “not to be seen” were drivers for the origin and subsequent evolution of efficient visual systems, as well as for protective shells, systems of camouflage, and many adaptations and strategies for survival, as the “light switch theory” (1, 2) formulates. Effective vision was an important tool that aided survival in the world of competition and selection.

The origin of vision still “lies the dark.” At the boundary between the Precambrian–Cambrian (~541 Ma), there is a sudden appearance in the fossil record of entirely new organisms that can be considered as the ancestors of most modern animal groups. This event, known as the “Cambrian Explosion” or the “Cambrian Radiation,” is a relatively short interval of time [*ca.* 20 (3, 4)–25 (5, 6) My]. The early origins of complex animal life, however, actually started in the Precambrian to continue during the Cambrian Explosion and the “Great Ordovician Biodiversification Event” (7).

Marine invertebrates of the Cambrian Explosion are, for example, excellently represented in the Chengjiang Biota of China (8, 9), Burgess Shale Fauna (10, 11), and Sirius Passet (12, 13), as “Orsten” fossils (14, 15) and at other Lagerstätten. Many of these organisms were equipped with eyes. Primordial single-lens eyes existed in the lobopodians (16), worm-like creatures with legs, which are now placed systematically among the Ecdysozoa, and perhaps even camera eyes were present in the early chordates and vertebrates of Chengjiang. The faunas of this period were dominated by arthropods, showing basic compound eyes, but there were also sophisticated lens systems, densely and hexagonally packed, sometimes with several thousand facets (16–20). Some of these arthropods even possessed a second eye system, which is typical for modern euarthropods, the ocellar median eyes (18, 21, 22). Most spectacular were the highly acute compound eyes of organisms that lived in the slightly younger Emu Bay Formation of Australia (23, 24). Some of these

compound eyes have been assigned to the most impressive arthropods of their time, anomalocaridids (radiodontids) (24).

The dominant preserved group among the early Cambrian arthropods, however, was the trilobites, which were well equipped with compound eyes from their very beginning. To have insight into the internal structures of a lower Atdabanian trilobite’s eye, an arthropod from one of the earliest of all trilobite records of the Cambrian, would surely provide us with critical information about the oldest documentable compound eyes so far, as well as the state of visual organs at the beginning of the metazoan fossil record.

Characterization of *Schmidtellus reetae* Bergström, 1973 and its Stratigraphic Assignments

The eye structures studied here are preserved in the holotype specimen of *Schmidtellus reetae* Bergström, 1973 (25) (Fig. 1A), which is deposited at the Institute of Geology at Tallinn University of Technology, Estonia, under repository number GIT 294-1.

S. reetae Bergström, 1973 (25) belongs to the group of Olenelloidea (superfamily), occurring on all paleocontinents, that presumably gave rise to all other groups of trilobites, because they were simply the only trilobites at the beginning and the first of all (26–29). The origin of trilobites is still unclear in general (26–29), so no further phylogenetic discussion is possible at this point.

In Estonia, the lower Cambrian is represented by shallow marine terrigenous sediments (clay, silts, and sandstones) of which the alternations mark several water level low stands and uplifts (30–32). The lower Cambrian sediments accumulated in a relatively shallow epicontinental basin on the Baltica Paleoterrane. Subsequently, different regions of Baltoscandia were affected by postdepositional heating in different ways. The most altered sediments are those in Norway, where temperatures

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.

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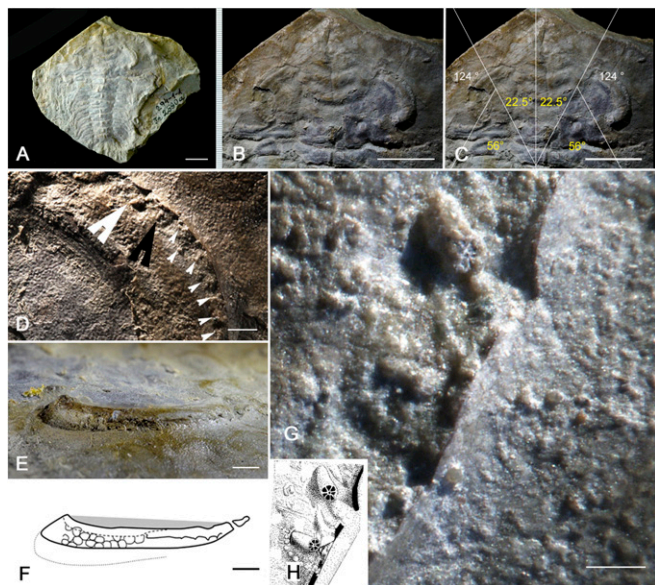


Fig. 1. Trilobite *S. reetae* Bergström, 1973 (25) (GIT 294-1) and its compound eye. (A) Holotype. (B) Head region of A. (C) Fields of view. (D) Abraded part of the right eye. Arrowheads indicate the ommatidial columns. (E) Lateral view of the right eye. (F) Schematic drawing of E. (G) Two visual units (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 μ m.)

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 *Schmidtellus 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 *Schmidtellus*. The alternating successions of clay and silt in the Lükati Formation of the Dominopolian 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 accepted, however, that the oldest trilobite fossils were preceded by arthropod (possibly trilobite) traces (40) as reported here. It has been demonstrated, unequivocally in a very few cases, when in trace fossils like *Rusophycus* and *Cruziana*, trilobite specimens have actually been found in the trace they were making, but not, so far as we are aware, for any Cambrian examples as old as the cases we are referring to [those were upper Cambrian (48)]. *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 Atabanian) (40)] are slightly younger (5, 39) (Fig. S1).

Baltoscandian trilobites are among the earliest in the world (40). They occur coevally with the assemblages of the lower Atdabanian of Siberia [*Profallotaspis*, *Bigotinella*, *Bigotina* (Olenelloidea, at the base of the Atdabanian)], Laurentia (olenellids of the *Fritzaspis* zone, uppermost part of the Begadean 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 (*Lemdadella* lower Ovetian stage, correlated to the lower Atdabanian), while the oldest trilobites from Morocco (*Bigotina*, *Eofallotaspis*, *Fallotaspis*, and *Lemdadella* Issendalenian) and the redlichiid 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 Guzhangian, ~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 *Rehbachella kinnekullensis* from upper Cambrian limestone concretions collected in southern Sweden, where fine setae and setulae (<1 μ m) were shown to be present on its appendages (14).

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 and other Cambrian fossils; 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 eodiscids 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 calcareous 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

solid phosphate. This is what seems to have happened to our specimen of *Schmidtellus*.

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 dioptric 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. reetae* lived as benthos. Gliding over the sea floor it had, in common with all (more or less) contemporary genera of olenellid trilobites, such as *Holmia*, *Lemdadella*, *Fallotaspis*, and others, reniform eyes with a narrow slit-like visual surface oriented toward the front and especially toward the lateral horizon (Fig. 1 *B, C, E*, and *F*). Conspicuously, the top of the eye is covered by a lenseless top surface, the “palpebral lobe,” and the visual field does not extend upward more than $25\text{--}30^\circ$ 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. reetae* covers $\sim 2 \times 124^\circ$ (Fig. 1 *B* 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 ($< \sim 100$), relatively large lenses (~ 50 μm) (Fig. 1 *E* 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. reetae* 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 relicts 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. 1*D*).

In the best preserved of these (Figs. 1 *D, G*, and *H* and 2 *B–D* and *J*), the lenses (~ 1 mm in diameter), broken across, are extremely flat and thin, showing no convexity (Figs. 1 *G* and *H* and 2 *C, D*, and *J*). Beneath the lens lies a basket-like structure, consisting of spherical elements, perhaps former cells (Figs. 1 *G* and *H* and 2 *B–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 seven elements of similar but different sizes (~ 50 μm) grouped around a central core (Figs. 1 *G* and *H* and 2 *B–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

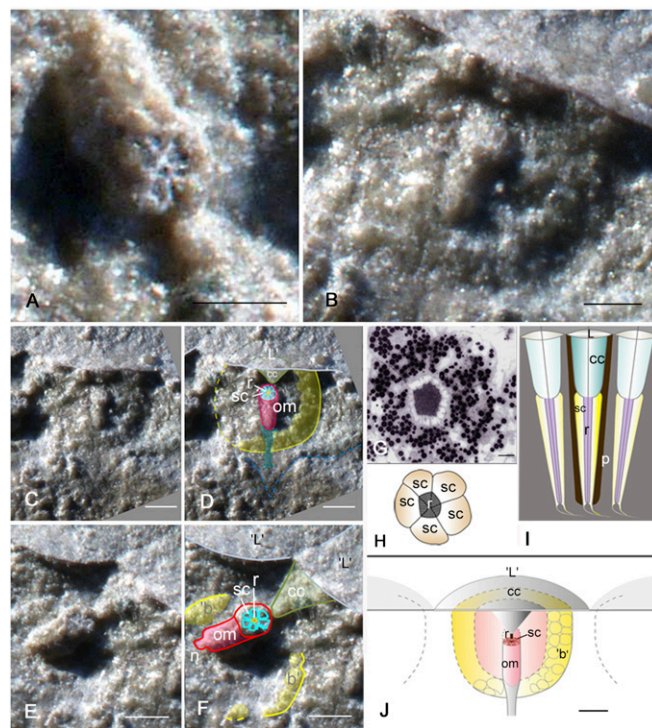


Fig. 2. Internal structures of the functional visual unit. (A) Ommatidium. Note the cellular elements (relicts of receptor cells) arranged radially around the central core (relict of the rhabdom). (B) Ommatidium positioned in a basket. Note the cellular elements (relicts of receptor cells) arranged radially 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. reetae*. 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 ($\sim 500 \mu\text{m}$ long, $\sim 70 \mu\text{m}$ \varnothing 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 ($\sim 56 \mu\text{m}$ high, $\sim 350 \mu\text{m}$ wide) can be seen, positioned directly below the lens (Figs. 1*G* and 2*B–D* and *J*). Distally from the tube, a regular, triangular element ($\sim 56 \mu\text{m}$ high, $\sim 350 \mu\text{m}$ 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. 1*D*, *G*, and *H* and 2*A*, *E*, *F*, and *J*). It has a total length of $\sim 364 \mu\text{m}$, and is $\sim 208 \mu\text{m}$ wide. It ends proximally in a small tube $\sim 70 \mu\text{m}$ in diameter, which sinks into the depth of the matrix. There are seven triangular elements (largest: $\sim 70 \mu\text{m}$, smallest: $56 \mu\text{m}$) that surround a central circular structure (diameter $\sim 20 \mu\text{m}$). The difference in the diameter of both tubular systems of about $\sim 48 \mu\text{m}$ ($\sim 160 \mu\text{m}$ vs. $\sim 208 \mu\text{m}$) 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. 1*G* and *H* and 2*E*, *F*, and *J*).

In comparison to many modern, compact systems, such as those of bees or dragonflies, the large distance (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 m^2 of an extended standardized source, and this would enable a comparison between the ancient visual system investigated here and the sensitivities of recent arthropods:

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

[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 photopigment [0.69% per micrometer; lobster (72), after Land 1981 (70)], x (μm) length of the perceiving structure (rhabdom), here $338 \mu\text{m}$ (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 $\sim 2.91 [\text{m}^2 \cdot \text{sr}]$. Thus, the approximate estimated sensitivity of *S. reetae* Bergström, 1973 (25) is very similar to that of the branchiopod crustacean *Artemia salina* (Linnaeus, 1758) (73) [$S = 2.3 [\text{m}^2 \cdot \text{sr}]$ (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, $f \approx 156 \mu\text{m}$. Furthermore if we take, as discussed, the upper width of the crystalline cone as aperture $A \approx 350 \mu\text{m}$, 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 (Φ_{crit}), which is given by $\arcsin(n_1/n_2)$. The refractive index of sea water is about $n_1 = 1.34$ (35% salinity, 20°C), and $n_2 = 1.36\text{--}1.40$ for the rhabdom (ref. 66, p. 59). The results are an acceptance angle for the rhabdom of $20\text{--}30^\circ$ and overlapping visual fields of each system, as is quite common in modern compound eyes. The interommatidial angle ($\Delta\phi$) lies at about 10° . In terrestrial systems not suffering from light absorbance, such as insects, they often range from $1\text{--}5^\circ$ (74). In aquatic crustaceans and xiphosurans 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 $\sim 9^\circ$, 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

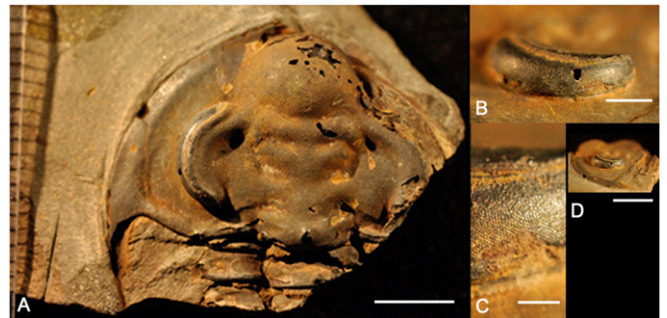


Fig. 3. *H. kjerulfi* (Linnarsson, 1871) (85) (Natural History Museum at the University of Oslo, PMO 73168). (A) Head region of *H. kjerulfi*. (B) Left eye of A. (C) Dense facets in B, hexagonally packed. (D) Lateral aspect of the head. (Scale bars: A and D, 1 cm; B, 2 mm; and C, 500 μm .)

estimate the anatomical resolution, which can be defined as the highest spatial frequency (of a sinusoidal grating) (ν_s) that is resolved by such an array of sampling stations (ommatidia): $\nu_s = 1/2\Delta\phi$ [cycl/rad] (70, 75–79), which allows a good comparison with other investigated systems. The ν_s results here to 2.87 [cycl/rad], revealing an anatomical resolution lower than that of *Limulus* (4.8 [cycl/rad]) but higher than that of *Cirolana* (1.9 [cycl/rad]) (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 chelicerata; 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 relicts 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 kjerulffi* (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. kjerulffi (Linnarsson, 1871) (85), described by Kiaer (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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