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The remarkable eyes
of the Cambrian
ocean's top
predator **PAGE 237**



NEUROSCIENCE

OUT OF BODY EXPERIENCES

What body illusions tell
us about ourselves

PAGE 168



POLITICS

UNHEALTHY COMPETITION

Asia's space race is sowing
seeds of conflict

PAGE 171

COSMOLOGY

TEN BILLION SUNS

New contenders for title of
'biggest black hole'

PAGES 187 & 215

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Acute vision in the giant Cambrian predator *Anomalocaris* and the origin of compound eyes

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Until recently¹, intricate details of the optical design of non-biomineralized arthropod eyes remained elusive in Cambrian Burgess-Shale-type deposits, despite exceptional preservation of soft-part anatomy in such Konservat-Lagerstätten^{2,3}. The structure and development of ommatidia in arthropod compound eyes support a single origin some time before the latest common ancestor of crown-group arthropods⁴, but the appearance of compound eyes in the arthropod stem group has been poorly constrained in the absence of adequate fossils. Here we report 2–3-cm paired eyes from the early Cambrian (approximately 515 million years old) Emu Bay Shale of South Australia, assigned to the Cambrian apex predator *Anomalocaris*. Their preserved visual surfaces are composed of at least 16,000 hexagonally packed ommatidial lenses (in a single eye), rivalling the most acute compound eyes in modern arthropods. The specimens show two distinct taphonomic modes, preserved as iron oxide (after pyrite) and calcium phosphate, demonstrating that disparate styles of early diagenetic mineralization can replicate the same type of extracellular tissue (that is, cuticle) within a single Burgess-Shale-type deposit. These fossils also provide compelling evidence for the arthropod affinities of anomalocaridids, push the origin of compound eyes deeper down the arthropod stem lineage, and indicate that the compound eye evolved before such features as a hardened exoskeleton. The inferred acuity of the anomalocaridid eye is consistent with other evidence that these animals were highly mobile visual predators in the water column^{5,6}. The existence of large, macrophagous nektonic predators possessing sharp vision—such as *Anomalocaris*—within the early Cambrian ecosystem probably helped to accelerate the escalatory ‘arms race’ that began over half a billion years ago^{7,8}.

Anomalocaridids are broadly acknowledged to be the top predators in Cambrian and Ordovician ecosystems^{6,9}. Predatory habits are inferred on the basis of their large size (body length more than 91.5 cm, ref. 9), robust spinose frontal appendages, mouth with a dentate inner margin¹⁰, size and form of the midgut glands¹¹, predation damage to associated biota^{10,12} and interpretation of coprolites as having an anomalocaridid origin^{6,13}. The streamlined profile of the body, inferred function of the lateral body flaps (‘swim flaps’¹⁴) in locomotion, and the large tripartite tail fan preserved in a few taxa indicate strong swimming capabilities^{5,15,16}. The large, stalked eyes of anomalocaridids, emerging from the dorsolateral side of the head, provide additional evidence for prey detection and tracking consistent with predatory habits. Although the eyes are preserved in several anomalocaridid genera^{13,15,17,18}, they have until now been known solely from their outlines. The inference that they were probably compound eyes¹⁸ has been based on size, shape and the phylogenetic placement of anomalocaridids in the arthropod stem group^{18–20} rather than on direct evidence of surface detail (such as preserved lenses).

Exceptionally preserved eyes from the early Cambrian (Series 2, Stage 4) Emu Bay Shale²¹ at Buck Quarry, Kangaroo Island, South

Australia, are much larger, and have very different morphology, than those of another arthropod documented from this locality¹. The visual surface is pyriform (pear-shaped) rather than hemispherical, and the ommatidia are more than five times as numerous, yet much smaller in maximum size, with no evidence of a distinct ‘bright zone’. The specimens are registered in the collections of the South Australian Museum. SAM P45920a,b (part and counterpart) is a pair of eyes (Fig. 1) that are in contact with each other at their proximal ends, their long axes diverging from each other at 45 degrees. Both eyes are of the same size and morphology, and a chance association can be ruled out; they are identified as the left and right eyes of a single individual; although the eyes in most other anomalocaridids are widely spaced^{10,13,17,18}, the preserved orientation of the eyes in SAM P45920 is similar to that of *Amplectobelua symbrachiata* from China (figure 15A in ref. 15) and probably results from lateral or oblique compression of the head. They are each composed of a pyriform visual surface with a very large number of small, hexagonal ommatidial lenses. In the more complete of the pair (Fig. 1d), the long axis of the visual surface is 21.8 mm long, its maximum width 12.2 mm (including a fracture, Fig. 1b). Part of this eye is overprinted across its width by a different structure of undetermined nature (‘us’ in Fig. 1b, d). It is preserved in positive relief on the part, with its lenses concave. The other eye has a maximum width of 12.7 mm; it is preserved in negative relief on the part, and its lenses are convex. In the counterpart, the concavity/convexity of the visual surface and lenses is reversed. We interpret the sediment in the proximal portion of this eye as having in-filled the collapsed cavity, and the cuticle is now replicated by iron oxide. Lenses range from ~70–110 µm in diameter, with variability throughout the visual field attributed to surface irregularities. The lenses are consistently arranged with regular hexagonal packing relative to their neighbours (Fig. 1c, e). Extrapolating from the regions with the best preserved lenses across the area of the entire visual surface of the eye in Fig. 1d indicates that an estimated 16,700 lenses are present on one side of the eye. The proximo-distal axis of the visual field is established on the basis of the preservation of the eye stalk on the left eye, with a sharp delineation from the visual surface (Fig. 1b, d). The eye stalk lacks obvious surface sculpture and is more strongly developed along one side of the visual surface than the other. A second specimen of a single eye, P46330a,b (Fig. 2b and Supplementary Fig. 1a–e), is even larger, 16.9 mm wide, and has patches of well-preserved lenses, but is too incomplete to measure its length.

Scanning electron microscopic energy dispersive spectrometry (SEM-EDS) analysis of SAM P45920a shows that the visual surface is composed of iron oxide with detectable traces of sulphur (Fig. 2a), probably indicating limonite after pyrite. Limonite pseudomorphs of microcrystalline pyrite are often found concentrated beneath and between non-trilobite arthropod cuticle in the Emu Bay Shale (figure 7 in ref. 22), as are peripheral haloes of iron oxide around a variety of fossils, suggesting that pyritization was a common preservation mode

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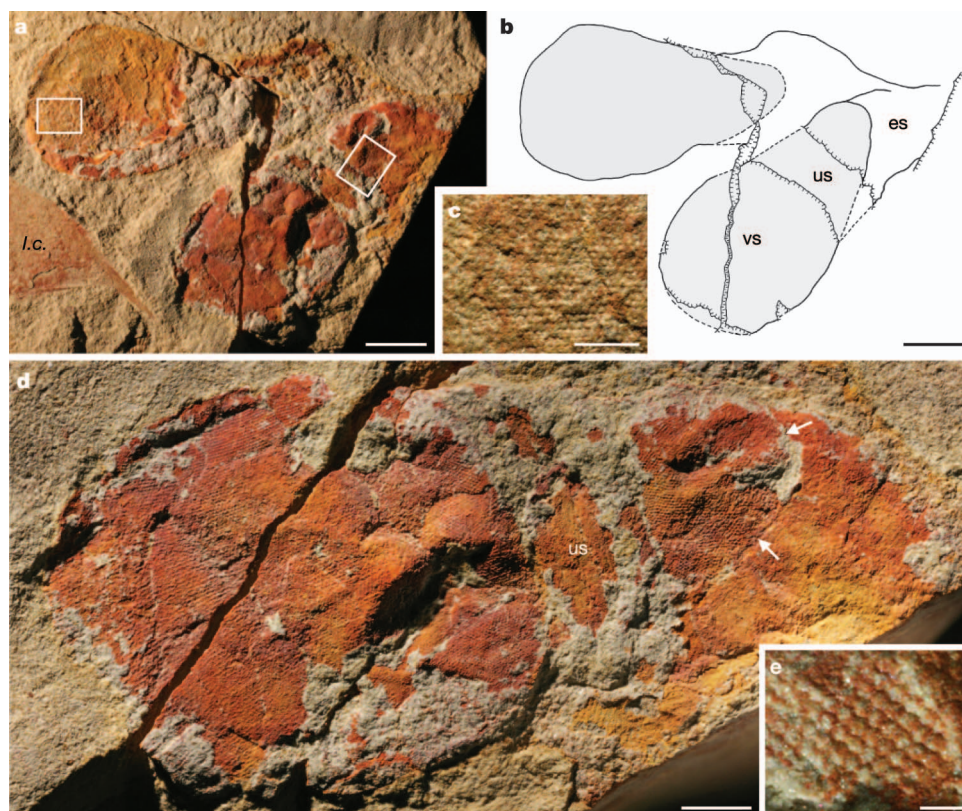


Figure 1 | *Anomalocaris* eyes from the Emu Bay Shale. **a–d**, Eye pair, SAM P45920a, level 10.4 m.

a, b, Overview and camera lucida drawing. Scale bars, 5 mm. Grey fill in **b** represents visual surface, the proximal part in the upper eye extrapolated from the lower eye. **c**, Detail of ommatidial lenses located by horizontal white box in **a**. Scale bar, 1 mm. **d**, More complete eye, showing transition between visual surface and eye stalk (white arrows). Scale bar, 2 mm. **e**, Detail of ommatidial lenses in counterpart SAM P45920b. Scale bar, 0.3 mm. **es**, eye stalk; **I.c.**, *Isoxys communis*; **us**, undetermined structure; **vs**, visual surface. Tilted white box in **a** represents area analysed using SEM-EDS, with elemental maps shown in Fig. 2a.

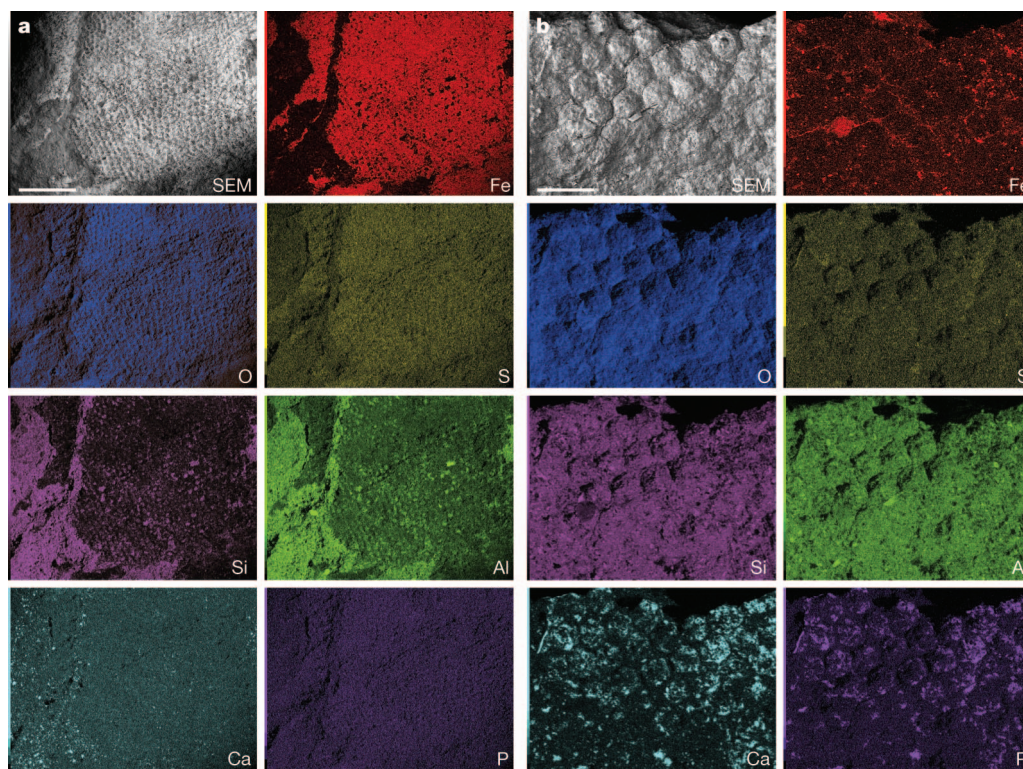


Figure 2 | SEM-EDS analyses of *Anomalocaris* eyes. **a**, SAM P45920a. Scale bar, 1 mm; see Fig. 1a for area analysed. **b**, SAM P46330b. Scale bar, 0.3 mm; see Supplementary Fig. 1e for area analysed. Accelerating voltage of 20 kV. Each map depicts the relative abundance of each element, with brighter colours indicating greater abundance. SEM, backscattered electron image of area analysed. **Al**, aluminium (green); **Ca**, calcium (cyan); **Fe**, iron (red); **O**, oxygen

(dark blue); **P**, phosphorus (purple); **S**, sulphur (yellow); **Si**, silicon (pink). The visual surface of SAM P45920a in **a** contains elevated amounts of iron, oxygen and sulphur, indicative of limonite after pyrite; the matrix (at left of each image) shows high levels of silicon and aluminium, reflecting muscovite and aluminosilicate clay minerals. The lenses of SAM P46330b in **b** contain elevated amounts of calcium and phosphorus, indicative of calcium phosphate.

within this deposit. Moreover, *Anomalocaris* frontal appendages and lateral body flaps (Supplementary Fig. 1f) from the Emu Bay Shale are often preserved as iron oxide, suggesting that pyritization of the entire body was possible, as in the anomalocaridids from the Ordovician Fezouata Biota in Morocco⁹ and *Schinderhannes bartelsi* from the Devonian Hunsrück Slate in Germany¹⁹. Early diagenetic pyritization of soft tissues is also common in the Chengjiang Biota and requires high concentrations of iron in pore waters and low organic content within the sediment to promote reactions between iron minerals and H₂S generated by anaerobic bacterial sulphate reduction²³. These specific conditions seem to have been present during the deposition of the fossiliferous interval of the lower Emu Bay Shale, the mudstones being iron rich but extremely low in total organic carbon²². Interestingly, an SEM-EDS analysis of SAM P46330b (Fig. 2b) reveals that the lenses contain elevated amounts of calcium and phosphorus (and only minor traces of iron), suggesting that phosphatization (rather than pyritization) was the taphonomic pathway in this instance. The role of phosphatization was also important in preserving the eyes of a different arthropod in the Emu Bay Shale¹, demonstrating that disparate styles of early diagenetic mineralization can replicate the same type of extracellular structure (in this case, the cuticle of the visual surface) within a single Burgess-Shale-type deposit. This contrasts with many other Cambrian Konservat-Lagerstätten, wherein recalcitrant tissues (such as cuticle) typically preserve as carbonaceous films²⁴ and may therefore explain why intricate details of the visual surface (especially in non-biomineralizing arthropods) are rarely preserved¹.

These Emu Bay Shale eyes (Fig. 1 and Supplementary Fig. 1a–e) are identified as belonging to anomalocaridids. Two species of *Anomalocaris* occur in the Emu Bay Shale, *A. briggsi* Nedin, 1995, and *Anomalocaris* sp. nov.²⁵. Both taxa are present in Buck Quarry as well as at the locality on the coastline at Big Gully. Frontal appendages and lateral body flaps of *Anomalocaris* are present at the levels (10.4 and 11.3 m) from which the eyes were collected, and are common within a 2-m interval that includes these levels (Supplementary Figs 1f and 2). The large size of the eyes rules out an assignment to all other arthropods known from the Emu Bay Shale, but is consistent in size with the eyes of anomalocaridids known from articulated specimens from other Cambrian Konservat-Lagerstätten (Supplementary Table 1). The shape of the Emu Bay Shale eyes compares closely to that of *Anomalocaris*^{13,17}, *Amplectobelua*¹⁵, *Laggania*¹⁰ and *Hurdia*¹⁸, all being variably pyriform or ovoid; the length:width ratio (1.8:1) of the present elements falls well within the variation in anomalocaridids as a whole (1.3:1–2.0:1) (Supplementary Table 1). The width of the eye stalk relative to the width of the distal pyriform section of the eye (that bears the visual surface in SAM P45920a) likewise resembles the stalked eyes of articulated anomalocaridids. Considering eye length in articulated specimens of *Anomalocaris* from Canada¹⁷ and China¹³ relative to the length of the frontal appendages, the Emu Bay Shale eyes are of an appropriate size relative to the frontal appendages of *A. briggsi*. We thus identify the specimens as *Anomalocaris*, the only anomalocaridid genus known from the Emu Bay Shale.

The number of ommatidia in the *Anomalocaris* eyes would almost certainly have greatly exceeded the count based on the exposed surface of the eye alone. If the flattened surface in the fossils is even partly mirrored on the other side, as suggested by the fact that the three available specimens each have lenses over the entire exposed area of the fossils, but factoring in possible asymmetry to provide cuticular support of the visual surface, the total count could be substantially greater than the observed 16,000+ lenses. If this is indeed the case, few living arthropods have as many ommatidia, and these eyes would certainly have functioned with a high degree of acuity²⁶. Assuming that SAM P46330 has the same proportions as the more complete SAM P45920, a length of the visual surface in excess of 3 cm is inferred, with the likelihood of an even greater ommatidial count than in SAM P45920. Throughout the geological history of Arthropoda, compound eyes have rarely exceeded this size; very large Siluro-Devonian pterygotid

eurypterids and some Jurassic thylacocephalans represent some of the rare examples with eyes larger than those of *Anomalocaris*.

The discovery of compound eyes in *Anomalocaris* provides compelling support for arthropod affinities^{13,18}. Dense, hexagonal packing of ommatidia in compound eyes has been demonstrated to have been unequivocally present in *Schinderhannes bartelsi*, a Devonian species resolved as the immediate sister group to the arthropod crown group¹⁹ (Fig. 3). The eyes of *Schinderhannes* resemble those of *Anomalocaris* in being large, stalked, having an ovoid outline of the visual surface, and a highly elevated number of lenses. The finding that *Anomalocaris*, resolved more basally than *Schinderhannes* in the arthropod stem group¹⁹, possesses the same kind of ommatidial packing as in *Schinderhannes* and crown-group arthropods pushes the origin of compound eyes further down the arthropod stem group. As such, compound eyes evolved earlier than the origin of a hardened tergal exoskeleton and biramous trunk limbs (the latter characters being present in *Schinderhannes* but not anomalocaridids). We infer that the stalked eyes of all Radiodonta¹⁷ (that is, anomalocaridids) are arthropod-type compound eyes. Previous inferences of this character distribution¹⁸ based on gross morphology (size and stalks) now have direct support. The mode of growth of the anomalocaridid eye is presumed to be the same as in other arthropods, in which new elements are added at the margins of the visual field⁴. The next most stem-ward (basal) taxon in the arthropod stem group^{18,19}, *Opabinia*, also has stalked eyes, but direct observation of ommatidia is needed to ascertain whether they are compound.

The resolving power of compound eyes depends to a large extent on the angle between ommatidia; smaller angles mean denser image sampling and higher acuity. Although exact angles in the *Anomalocaris* eyes cannot be determined owing to extensive compression, upper limits on average angles can be estimated (see Supplementary Methods). Assuming the preserved visual surface does not curve more than 180°, average interommatidial angles would be <1.4°; even this conservative estimate suggests greater acuity than most living arthropods²⁷. The interommatidial angle and average lens diameter of ~95 µm yields a low 'eye parameter' value of <2, characteristic of diurnal taxa living in

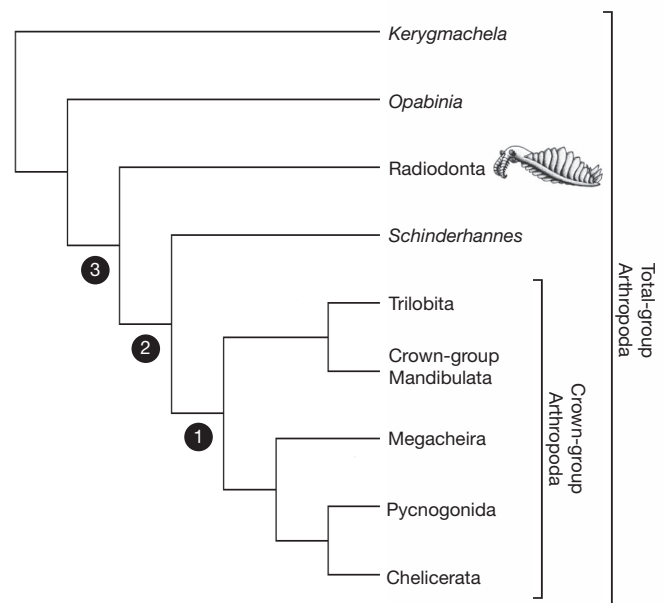


Figure 3 | The early evolution of compound eyes, and the position of anomalocaridids (Radiodonta), in the arthropod stem group. Numbers refer to the inclusiveness of the monophyletic group that can be confidently inferred to possess compound eyes: (1) based on extant taxa alone; (2) based on discovery of *Schinderhannes*¹⁹; and (3) based on new data herein. Phylogeny after ref. 19.

well-lit marine environments²⁷, and is consistent with suggestions that anomalocaridids were midwater predators in the photic zone⁶.

The very large size of anomalocaridid compound eyes and the visual acuity inferred from the elevated lens number and low interommatidial angles suggest that processing of visual information would have required the optic neuropils and brain to be of comparable complexity to crown-group (that is, modern) arthropods. In the crown group, two optic neuropils are reconstructed in the most recent common ancestor, transmitting to a protocerebrum with a median unpaired neuropil, the central body²⁸. The eyes of *Anomalocaris* expand the known diversity of visual adaptations in the early Cambrian: low-resolution organs with <100 ommatidia (eodiscoid trilobites), higher-resolution eyes with a distinct bright zone that might have functioned in low light¹, and very large eyes with a uniformly dense visual field adapted to bright environments.

Functional morphological arguments from the structure of raptorial frontal appendages and large, spherical eyes in various Cambrian arthropods indicate that visual predation in the water column was already established as an important component in early Cambrian food webs^{29,30}. The large absolute size and huge number of ommatidial lenses in the eyes of *Anomalocaris* confirm its status as a highly visual apex predator⁶. The presence of sophisticated nektonic predators with acute vision, such as anomalocaridids, within Cambrian communities would have placed considerable selective pressures on prey that would have influenced the 'arms race' that began during this important phase in early animal evolution^{7,8}.

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