



Research

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Palaeontology

What big eyes you have: the ecological role of giant pterygotid eurypterids

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Eurypterids are a group of extinct chelicerates that ranged for over 200 Myr from the Ordovician to the Permian. Gigantism is common in the group; about 50% of families include taxa over 0.8 m in length. Among these were the pterygotids (Pterygotidae), which reached lengths of over 2 m and were the largest arthropods that ever lived. They have been interpreted as highly mobile visual predators on the basis of their large size, enlarged, robust chelicerae and forward-facing compound eyes. Here, we test this interpretation by reconstructing the visual capability of *Acutiramus cummingsi* (Pterygotidae) and comparing it with that of the smaller *Eurypterus* sp. (Eurypteridae), which lacked enlarged chelicerae, and other arthropods of similar geologic age. In *A. cummingsi*, there is no area of lenses differentiated to provide increased visual acuity, and the interommatidial angles (IOA) do not fall within the range of high-level modern arthropod predators. Our results show that the visual acuity of *A. cummingsi* is poor compared with that of co-occurring *Eurypterus* sp. The ecological role of pterygotids may have been as predators on thin-shelled and soft-bodied prey, perhaps in low-light conditions or at night.

1. Introduction

Pterygotid eurypterids ranged through nearly 40 Myr, with a global distribution from Silurian to Lower Devonian [1,2]. They have been interpreted as apex predators in shallow water near shore basins [3–5]. A study of the chelicera of the pterygotid *Acutiramus cummingsi* (Pterygotidae), however, concluded that it could at best ‘trap, grasp and slice soft-bodied and relatively weak prey’ [6]. Predatory arthropods are normally equipped with acute vision to allow them to locate and capture prey [7]. The large lenses of *A. cummingsi* are often evident to the naked eye, whereas the small ones of *Eurypterus* sp. are usually invisible. We discovered that imaging with backscattered electrons on a scanning electron microscope (SEM) reveals these much smaller lenses without the need to extract the cuticle from the rock [8]. This allowed us to analyse and compare vision based on exceptionally preserved co-occurring specimens of these two eurypterids as an additional source of evidence of their relative ecological roles.

2. Material and methods

The visual system of *A. cummingsi* was investigated based on five specimens and compared with that of *Eurypterus* species based on 25 specimens (i.e. *E. remipes* and *E. lacustris*, which are closely similar, and some that could not be distinguished) from the ca 423–419 Myr old Williamsville Member of the Bertie Formation at Ridgemount Quarry-South, Ontario, Canada [9] (figure 1*a,d*; electronic supplementary material, tables S1, S2, and figure S1). The specimens are preserved within planar-laminated grey dolostone, interpreted to represent a brackish estuarine setting [10]. The modern horseshoe crab *Limulus* [11] was examined for comparison. Photomicrographs of the eye of *A. cummingsi* were taken using a Leica MZ16 optical microscope combined

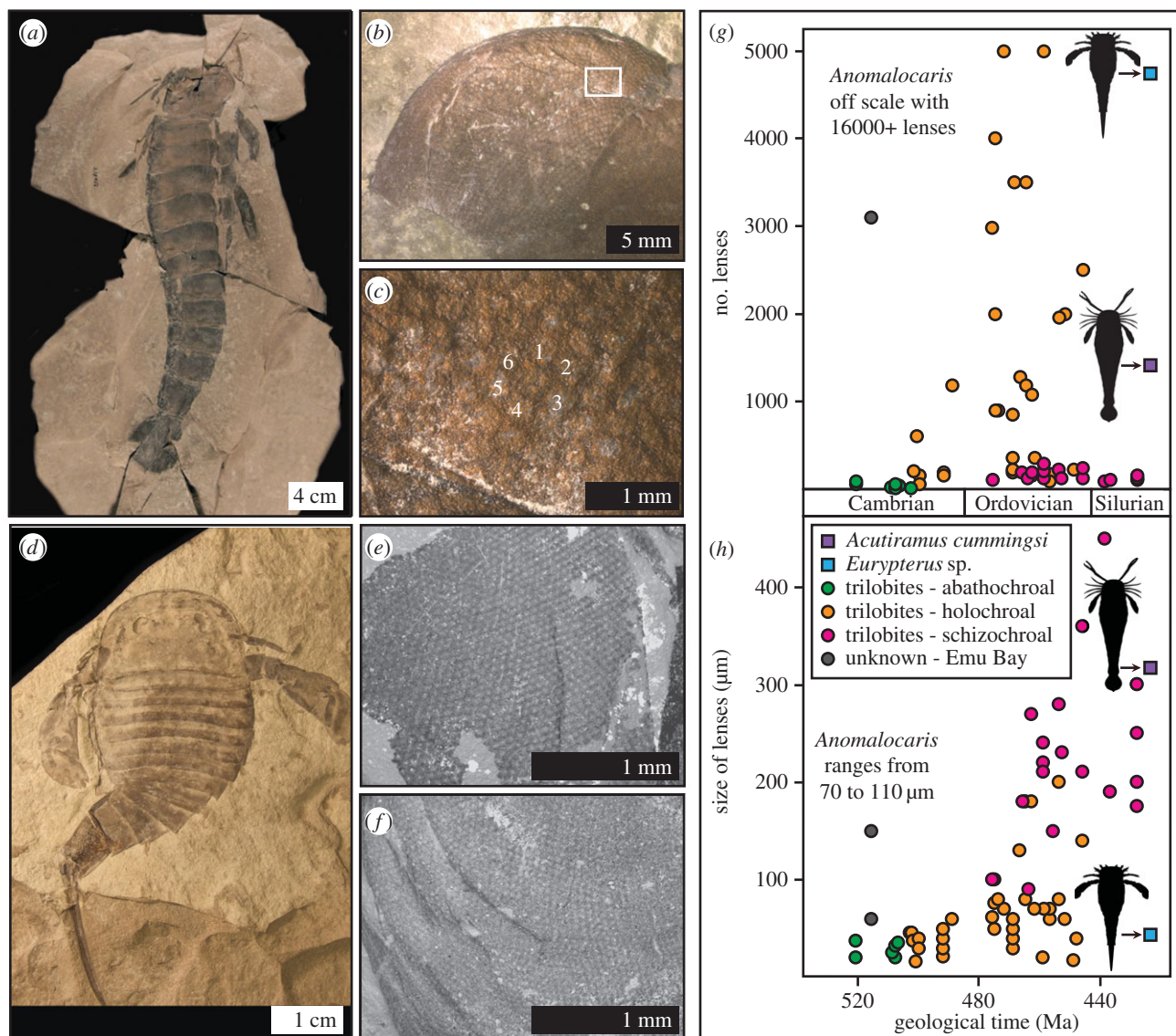


Figure 1. (a) *Acutiramus cummingsi*, YPM 218956. (b–c) *Acutiramus cummingsi*, YPM 210042. (b) Area of visual surface showing lenses and wrinkling of organic cuticle. (c) Area of visual surface showing hexagonal arrangement of lenses with central lens surrounded by six immediate neighbours (1–6). (d) *Eurypterus dekayi*, YPM 403886. (e–f) *Eurypterus* sp., backscatter electron micrograph of visual surface showing lenses. (e) YPM 208527. (f) YPM 216603. (g,h) Complexity of eurypterid visual system compared to that of other Palaeozoic arthropods. (g) Number and (h) maximum preserved dimension of lenses (size) from the Cambrian to the Silurian. Circles, data from the literature; squares, data measured in this study (electronic supplementary material, table S2). Eurypterids are unremarkable in terms of number and size of lenses compared with other arthropods.

with a Leica DFC420 camera and polarizing filters (figure 1*b,c*). The eyes of *Eurypterus* sp. were imaged with backscattered electrons on a variable pressure SEM (electronic supplementary material) with the electron beam set at 25 kV so as to penetrate the cuticle (figure 1*e,f*). The longitudinal and transverse axes of the eyes, the total area of the eye and the length of the perimeter were measured using quantitative imaging software. Lenses were counted per unit area and the maximum dimensions recorded. These counts were extrapolated over the area of the eye to calculate the total number of lenses per eye (electronic supplementary material). The interommatidial angle (IOA) was calculated by reconstructing the angle subtended by a number of transects across the eye (electronic supplementary material, figure S2).

3. Results

The kidney-shaped eyes of *A. cummingsi* (table 1) are positioned at the antero-lateral margin of the carapace; part of the eye may be preserved beyond the carapace margin [12]. The smaller eyes of *Eurypterus* sp. (table 1) are also kidney-shaped but they are

positioned further from the margin of the carapace. In both eurypterids, eye area correlates with carapace maximum width ($R^2 = 0.75$ *A. cummingsi*, 0.76 *Eurypterus* sp.).

Visual acuity in arthropods depends on several variables including the number and size of lenses (figure 1*g,h*) and the angle between their optical axes, i.e. the IOA [13]. Generally, the more lenses in the eye, the denser the sampling of the visual field. The mean number of lenses per eye (table 1) in the sample of *A. cummingsi* is 1407 in contrast to *Limulus* with 680. The number in *Eurypterus* sp. is 4746. These values are exceeded in the eyes of some trilobites [14] and the Cambrian predator *Anomalocaris* (at least 16 000 lenses per eye) [15] (figure 1*g*).

In general, the size of the lenses is an indicator of the brightness of the image falling on the photoreceptors [7]. The mean maximum preserved dimension of lenses (table 1) in *A. cummingsi* (0.32 mm) is larger than in *Limulus* (0.14 mm) (figure 1*h*). The lenses of schizochroal eyes in some trilobites are comparable in size to those of *A. cummingsi* but those of most trilobites and *Anomalocaris* are significantly smaller [14,15]. As in other arthropods, the size of the lenses in *A. cummingsi* increases

Table 1. Data on eyes.

	<i>Acutiramus cummingsi</i>	<i>Eurypterus</i> sp.	<i>Limulus</i>
eye size (mm ²)			
range	190–224	3–34	
mean \pm s.d.	198 \pm 37.1	16.141 \pm 6.37	
<i>n</i> (eyes, individuals)	7, 5	38, 25	
number of lenses			
range (estimates based on extrapolation)	1150–1608	3156–6733	426–944
mean \pm s.d.	1407 \pm 225	4746 \pm 1100	680 \pm 174
<i>n</i> (eyes, individuals)	7, 5	15, 13	8, 8
size of lenses (mm)			
range	0.30–0.38	0.029–0.065	0.09–0.26
mean \pm s.d.	0.32 \pm 0.042	0.045 \pm 0.011	0.14 \pm 0.057
<i>n</i> (eyes, individuals, lenses per eye)	7, 5, 20	15, 13, 20	7, 7, 20
IOA (°)			
range	1.8–2.9	0.9–1.8	1.7–3.7
mean \pm s.d.	2.01 \pm 0.582	1.13 \pm 0.274	2.87 \pm 0.743
<i>n</i> (eyes, individuals)	5, 5	13, 11	7, 7
eye parameter (<i>P</i>)			
range	6–17	0.4–1.5	
mean \pm s.d.	11.96 \pm 4.18	0.79 \pm 0.331	
<i>n</i> (eyes, individuals)	5, 5	13, 11	

with increasing area of the eye [7,14]. The lenses of *Eurypterus* sp. are strikingly smaller than in *A. cummingsi* (0.045 mm), but are not unusually small relative to the size of the eye (electronic supplementary material, figure S3).

Mean lens size does not always determine the intensity of light entering the eye. The eyes of most modern predatory arthropods include an area where lenses are 1.61–2.71 times larger than those on the eye margins, often giving the benefit of enhanced sensitivity or greater sampling of the visual field [7]. To determine whether there is such an area in the eyes of the eurypterids, lenses were measured in two or three separate areas of the eye and maximum preserved lens dimension was averaged in each area (electronic supplementary material, figures S4 and S5). In most specimens analysed, lenses in the central area of the eye are significantly larger than those on the margin ($p < 0.01$; electronic supplementary material, tables S3 and S4). However, the size gradient in the lenses of *A. cummingsi* is substantially less than that in modern arthropods with a zone of larger lenses [7] and in an unidentified Cambrian arthropod from the Emu Bay Shale (2.5 : 1) [14]. Thus, there is little evidence for a discrete area of larger lenses in the eyes of *A. cummingsi* and the same applies to *Eurypterus* sp.

The best measure of visual acuity in fossils is the angle between the optical axes of adjacent lenses (the IOA). Generally, the smaller the IOA, the greater the density at which the visual field is sampled [7]. The values we obtained for the IOA in *A. cummingsi* increased with the size of the carapace, ranging from 1.8° to 2.9° (table 1 and figure 2). This suggests that acuity declined as the animal grew and contrasts with the decrease in IOA with size we observed in *Limulus* (electronic supplementary material, figure S5). The IOAs in *A. cummingsi* are comparable to those in many modern arthropods (1° to 5°

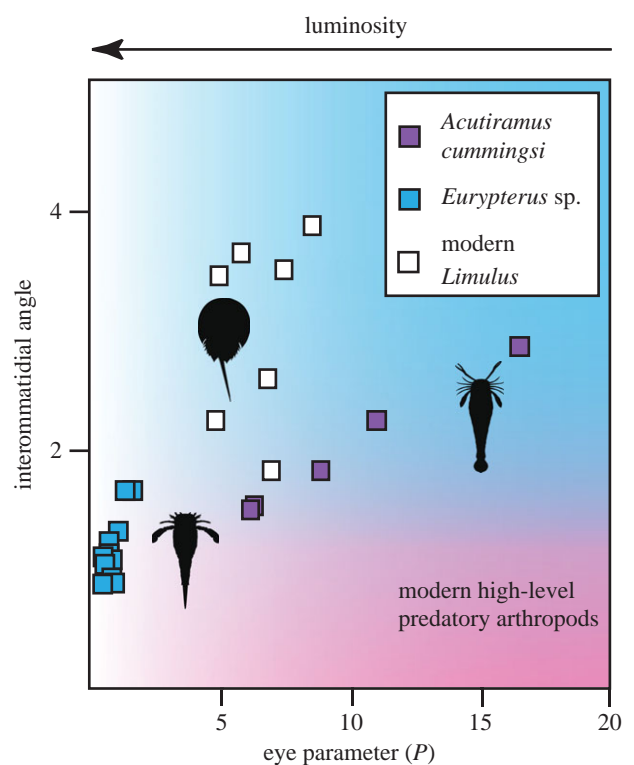


Figure 2. Eurypterid IOA plotted against *P*, eye parameter. *Acutiramus cummingsi* has a higher eye parameter than *Eurypterus* sp. Modern *Limulus* is plotted for comparison. IOAs in modern high-level predatory arthropods are less than 1° [7].

[7]), including *Limulus* (1.7° to 3.7°: table 1), and in holochroal trilobites (1.43° to 2.9° [16]). Yet, they are inconsistent with IOAs of high-level arthropod predators such as mantis shrimps

and dragonflies, which employ their visual system to track prey as either mobile or 'sit-and-wait' predators—the IOAs can be as low as 0.2° in the acute zone and 1° elsewhere in these predators [7]. We cannot distinguish between mobile and sit-and-wait predators on the basis of the visual system of the fossil forms. IOAs in *Eurypterus* sp. range from 0.9° to 1.8° (table 1) and are similar to those of *Anomalocaris* (less than 1.4°) [15], approaching values in modern arthropods that exhibit high-level predatory behaviour [7]. These values suggest a higher visual acuity in *Eurypterus* sp. than in *A. cummingsi* and are consistent with its interpretation as a more agile swimmer [17].

Combination of the IOA with the maximum dimension of each lens yields the eye parameter P (electronic supplementary material) [18], which provides an indication of the ambient light of the habitat in which the arthropod lived. The fossil data allow calculation of an average IOA and maximum lens dimension, yielding an average eye parameter (figure 2). Values of P for *A. cummingsi* range from 6 to 17 (table 1). These values are high compared with many modern arthropods, particularly diurnal marine crustaceans, which typically show P -values between 2 and 4 [19] and suggest that *A. cummingsi* lived in a low-luminosity environment (less than 0.03 cd m^{-2}) [18,19]. Eye parameter values for *Eurypterus* sp. range from 0.4 to 1.5 (table 1), and most are less than 1 (figure 2). These low values are indicative of higher-luminosity habitats (more than 1 cd m^{-2}) [18,19] and are characteristic of diurnal insects [19],

suggesting that *Eurypterus* sp. lived in shallow clear water or at least close to the surface.

4. Discussion

Eurypterus sp. is interpreted as highly manoeuvrable, using its paddle-shaped sixth prosomal appendage for lift-based swimming to pursue prey or escape predators [20–22]. The eye of *A. cummingsi*, in contrast to that of *Eurypterus* sp., comprises fewer lenses and most significantly displays larger IOAs than other Palaeozoic arthropods and modern high-level predators [7,14,15]. *Acutiramus cummingsi* is found in association with *Eurypterus* sp. in an environment interpreted as a shallow marginal marine carbonate platform [10], but the larger lenses may indicate that it inhabited low-light habitats or fed at night. Our results suggest that not all pterygotid eurypterids pursued actively swimming armoured prey, a conclusion consistent with the biomechanical analysis of the chelicerae [6]. The diet of *A. cummingsi*, at least, may have been comparable to that of *Limulus*, with predation on thin-shelled and soft-bodied animals [23].

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