All the better to see you with: eyes and claws reveal the evolution of divergent ecological roles in giant pterygotid eurypterids

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Pterygotid eurypterids have traditionally been interpreted as active, high-level, visual predators; however, recent studies of the visual system and cheliceral morphology of the pterygotid Acutiramus contradict this interpretation. Here, we report similar analyses of the pterygotids Erettopterus, Jaekelopterus and Pterygotus, and the pterygotid sister taxon Slimonia. Representative species of all these genera have more acute vision than A. cummingsi. The visual systems of Jaekelopterus rhenaniae and Pterygotus anglicus are comparable to that of modern predatory arthropods. All species of Jaekelopterus and Pterygotus have robust crushing chelicerae, morphologically distinct from the weaker slicing chelicerae of Acutiramus. Vision in Erettopterus osiliensis and Slimonia acuminata is more acute than in Acutiramus cummingsi, but not to the same degree as in modern active predators, and the morphology of the chelicerae in these genera suggests a grappling function. The pterygotids evolved with a shift in ecology from generalized feeder to specialized predator. Pterygotid eurypterids share a characteristic morphology but, although some were top predators, their ecology differs radically between genera.

1. Background

Pterygotid eurypterids are large, cosmopolitan aquatic chelicerates known from the Silurian to the Devonian. Characterized by their large body size, huge forwardly directed chelicerae and large eyes, pterygotids have traditionally been interpreted as active, high-level, visual predators [1–3]. Recent studies of the pterygotid Acutiramus, however, revealed eyes with low visual acuity inconsistent with the lifestyle of an active predator [4] and weak chelicerae incapable of puncturing thick cuticle or grappling with struggling prey [5], contradicting this interpretation. Here, we expand this analysis to other pterygotid genera to determine whether the conclusions drawn from Acutiramus apply to this clade as a whole.

2. Material and methods

Visual acuity is primarily determined by two parameters: the number of lenses and the interommatidial angle (IOA, the angle between the optical axes of adjacent lenses) [6,7]. The IOA, in particular, distinguishes active arthropod predators today from those with other ecological roles [7], and has been used to assess the visual system of fossil arthropods [4,8]. These two parameters were measured on four species of eurypterids (table 1): the pterygotids E. osiliensis, Jaekelopterus...
Table 1. Data on the visual system of pterygotids and pterygotid relatives. Italicized values indicate average values. The value for *Pterygotus anglicus* is based on a single specimen; the values for all other species were taken from multiple specimens. Values for *Eurypterus* sp. and *Acutiramus cummingsi* were taken from previously published data [4].

<table>
<thead>
<tr>
<th>species number</th>
<th>age</th>
<th>formation</th>
<th>eye area (mm²)</th>
<th>no. lenses</th>
<th>IOA</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Erettopterus osiliensis</em></td>
<td>YPM³ 325005</td>
<td>Upper Silurian</td>
<td>Rootsikula</td>
<td>309.33</td>
<td>4392</td>
</tr>
<tr>
<td><em>Pterygotus anglicus</em></td>
<td>PWL³ 2015/5308-LS</td>
<td>Lower Devonian</td>
<td>Klerf</td>
<td>701.40</td>
<td>3160</td>
</tr>
<tr>
<td><em>Slimonia acuminata</em></td>
<td>YPM 33437</td>
<td>Upper Silurian</td>
<td>Lesmahagow</td>
<td>61.19</td>
<td>4744</td>
</tr>
<tr>
<td><em>Pterygotus osiliensis</em></td>
<td>PWL 2004/5055-LS</td>
<td>Lower Devonian</td>
<td>Klief</td>
<td>9.60</td>
<td>362</td>
</tr>
<tr>
<td><em>Eurypterus remipes</em></td>
<td>PWL 2004/5055-LS</td>
<td>Lower Devonian</td>
<td>Klief</td>
<td>9.60</td>
<td>362</td>
</tr>
<tr>
<td><em>Slimonia acuminata</em></td>
<td>NHM In 61508</td>
<td>Upper Silurian</td>
<td>Lesmahagow</td>
<td>55.73</td>
<td>3405</td>
</tr>
<tr>
<td><em>Pterygotus anglicus</em></td>
<td>NBMG³ 10000</td>
<td>Lower Devonian</td>
<td>Campbellton</td>
<td>590.53</td>
<td>4303</td>
</tr>
</tbody>
</table>

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The morphology of *Jaekelopterus rhenaniae* and *Pterygotus anglicus*, and the pterygotid sister taxon *Slimonia acuminata* (figure 1A and the electronic supplementary material). These data were compared with previously published data for the pterygotid *Acutiramus cummingsi* and for *Eurypterus* sp., a more basal eurypterid typifying the plesiomorphic generalist morphology [4].

The morphology of pterygotid chelicerae has been used as evidence of feeding habit [9,10]. Chelicer morphology is known in 14 eurypterid species, including the six for which visual acuity can be analysed. The morphology of the chelicerae was subjected to a principal coordinates analysis (PCA) of discrete characters (electronic supplementary material) and plotted in multidimensional space (figure 1B); no a priori assumptions were made about the function of specific morphologies. Phylogenetic analysis of the pterygotoida was performed using a modified version of the Lansdell & Selden matrix [11] (see the electronic supplementary material).

### 3. Results and discussion

Cheliceral morphology separates the species into three distinct groups (figure 1B), which are also differentiated on the basis of visual acuity (IOA plotted against number of lenses), with the exception of the position of *Eurypterus* (figure 2A).

The first group includes the large (up to 2.5 m long [1,2]) *Jaekelopterus* and *Pterygotus* species, and a specimen representing a new genus and species, IVPP-14593. Both *J. rhenaniae* and *P. anglicus* have high visual acuity as indicated by low IOA and a large number of lenses (figure 2 and table 1). The chelicerae of all studied species of *Jaekelopterus*, *Pterygotus* and IVPP-14593 are enlarged and robust with prominent, differentiated denticles and a curved free ramus, features associated with strong grasping and puncturing abilities in modern crustaceans [12] and scorpions [13]. Puncture wounds on the dorsal shield of a poraspid agnathan from the Devonian of Utah have been attributed to the chelicera of *Jaekelopterus howelli* [14]. The IOA values for this group fall within the range (<1) indicative of active, high level predators among modern arthropods (figure 2 and table 1) [7]. The evidence indicates that these eurypterids were active, visual predators.

The second group includes the mid-sized (<1 m long [2,15]) *S. acuminata* and *Erettopterus* species, as well as *Eurypterus remipes*. The chelicerae of *S. acuminata* are small with no denticles, similar to the typical eurypterid grasping appendages in *E. remipes* [16]. The chelicerae of *Erettopterus* are enlarged, sometimes with differentiated denticles and paired distal teeth that occlude completely, suggesting that these chelicerae were also used for grasping rather than more specialized feeding [9]. *Slimonia acuminata* and *E. osiliensis* both have high visual acuity with an IOA between 2 and 3, and a large number of lenses. Although the number of lenses is comparable to that in *Jaekelopterus* and *Pterygotus*, the IOA values are higher (table 1) [7]. Thus, the evidence indicates that, although this second group was predatory, *Slimonia* and *Erettopterus* were not as highly specialized or active as *Jaekelopterus* and *Pterygotus*. In terms of its visual system, *Eurypterus* does not cluster with *Slimonia* and *Erettopterus*, but falls between this group and the active predatory group of *Jaekelopterus* and *Pterygotus*, suggesting an intermediate visual capability.

The large (up to 2 m long [2]) *Acutiramus* species form a third group which falls farther from the other two in both plots (figures 1B and 2A). The chelicerae of all *Acutiramus* species are large with differentiated denticles, including one which is long, strongly inclined and serrated on the fixed ramus, suggesting a shearing or slicing function [5,9]. *Acutiramus cummingsi* has relatively low visual acuity, with few lenses and high IOA [4]. The separation of the *Acutiramus* species from other pterygotids, on the basis of their visual system and cheliceral morphology, indicates a distinct ecology that involved less active predation.

The variation in IOA values within *A. cummingsi* is due to changes during growth: vision is less acute in the larger specimens [4]. This is in contrast to *J. rhenaniae*, in which
vision is less acute in the smaller specimen (table 1 and figure 2). Therefore, the pterygotids may be more similar in visual capacity early in their ontogeny, with specialized morphology developing later.

The changes in pterygotid ecology associated with their evolution can be reconstructed by considering the results of this study in a phylogenetic context (figure 1a). *Erettopterus*, in contrast to *Slimonia*, has the enlarged chelicerae characteristic of pterygotids, but it lacks the giant body size or advanced visual system of *Pterygotus* and *Jaekelopterus*. The ancestor of *Pterygotus*, *Jaekelopterus* and *Acutiramus* developed giant body size, specialized chelicerae and an advanced visual system along with a predatory lifestyle, as indicated by the acute vision and strong puncturing or crushing chelicerae in *Pterygotus* and *Jaekelopterus*, and the similar chelicerae in IVPP-14593. These adaptations to active predation, except for large body size, were subsequently lost or secondarily modified in *Acutiramus*, which has very different chelicerae [10] and a weaker visual system [4], and was likely an ambush predator or scavenger upon soft-bodied organisms, possibly feeding in low-light conditions or at night [4].

Older assessments of the ecological role of the giant pterygotid eurypterids lumped them together as high-level predators on the basis of their general morphology [17]. Our new data on their visual system [4] and chelicerae yield a more detailed understanding of their lifestyles. Despite the morphological similarities between pterygotid species, their ecological roles range from a more generalized predatory arthropod (figure 2a), to high-level active predation (*Jaekelopterus*, *Pterygotus* and IVPP-14593) and specialized ambush predation or scavenging, perhaps in low light (*Acutiramus*).

Previous studies [5,9] on the ecological role of pterygotids have been driven, in part, by debates on clade selection [18,19] and clade interaction, primarily via competitive replacement [20,21]. Competitive replacement has been suggested to have played a role in the evolution of eurypterids and jawless fish [17] but this hypothesis has been largely dismissed [22]. Despite the fact that biotic competition is now generally considered to play a relatively minor role in taxon survivorship [23], the possibility of competition between eurypterids and early vertebrates has seen a resurgence in recent literature [1–3,24–26], alongside a debate about whether higher taxa (i.e. clades) exhibit distinct ecological properties [27–29]. Our results show that, even within clades with a distinct general morphology, the ecology of constituent species can vary: detailed analysis is needed before ascribing a general ecology to a group in toto. This, in turn, supports previous conclusions [30] that pterygotids were not uniformly giant active predators, comprising a clade that was outcompeted by early vertebrates.

![Figure 2. The visual systems of *Jaekelopterus rhenaniae*, *Pterygotus anglicus*, *Slimonia acuminata*, *Erettopterus osiliensis*, *Eurypterus sp.* and *Acutiramus cunningsi*. Interommatidial angle (IOA) versus number of lenses, which indicates visual acuity; the pink shading indicates IOA values in modern active predatory arthropods. (Online version in colour.)](image-url)
Author contributions. V.E.M., J.C.L., R.P.A. and D.E.G.B. designed the study; V.E.M. coordinated the research, analysed the visual systems and drafted the paper; J.C.L. analysed chelicer morphometrics and eurypterid phylogeny; M.P. and R.P.A. identified and photographed specimens. All authors interpreted data, edited the paper and approved the final version.

Competing interests. We have no competing interests.

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References