



## Arthropod eyes: The early Cambrian fossil record and divergent evolution of visual systems



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### ABSTRACT

Four types of eyes serve the visual neuropils of extant arthropods: compound retinas composed of adjacent facets; a visual surface populated by spaced eyelets; a smooth transparent cuticle providing inwardly directed lens cylinders; and single-lens eyes. The first type is a characteristic of pancrustaceans, the eyes of which comprise lenses arranged as hexagonal or rectilinear arrays, each lens crowning 8–9 photoreceptor neurons. Except for Scutigermorpha, the second type typifies Myriapoda whose relatively large eyelets surmount numerous photoreceptive rhabdoms stacked together as tiers. Scutigermorph eyes are faceted, each lens crowning some dozen photoreceptor neurons of a modified apposition-type eye. Extant chelicerate eyes are single-lensed except in xiphosurans, whose lateral eyes comprise a cuticle with a smooth outer surface and an inner one providing regular arrays of lens cylinders. This account discusses whether these disparate eye types speak for or against divergence from one ancestral eye type. Previous considerations of eye evolution, focusing on the eyes of trilobites and on facet proliferation in xiphosurans and myriapods, have proposed that the mode of development of eyes in those taxa is distinct from that of pancrustaceans and is the plesiomorphic condition from which faceted eyes have evolved. But the recent discovery of enormous regularly faceted compound eyes belonging to early Cambrian radiodontans suggests that high-resolution faceted eyes with superior optics may be the ground pattern organization for arthropods, predating the evolution of arthropodization and jointed post-protocerebral appendages. Here we provide evidence that compound eye organization in stem-group euarthropods of the Cambrian can be understood in terms of eye morphologies diverging from this ancestral radiodontan-type ground pattern. We show that in certain Cambrian groups apposition eyes relate to fixed or mobile eyestalks, whereas other groups reveal concomitant evolution of sessile eyes equipped with optics typical of extant xiphosurans. Observations of fossil material, including that of trilobites and eurypterids, support the proposition that the ancestral compound eye was the apposition type. Cambrian arthropods include possible precursors of mandibulate eyes. The latter are the modified compound eyes, now sessile, and their underlying optic lobes exemplified by scutigermorph chilopods, and the mobile stalked compound eyes and more elaborate optic lobes typifying Pancrustacea. Radical divergence from an ancestral apposition type is demonstrated by the evolution of chelicerate eyes, from doublet sessile-eyed stem-group taxa to special apposition eyes of xiphosurans, the compound eyes of eurypterids, and single-lens eyes of arachnids. Different eye types are discussed with respect to possible modes of life of the extinct species that possessed them, comparing these to extant counterparts and the types of visual centers the eyes might have served.

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## 1. Introduction

Despite considered discussions that eye morphologies could contribute to an understanding of arthropod relationships, conflicting views persist regarding the ancestral origin of eyes (Paulus, 2000; Harzsch and Hafner, 2006; Harzsch et al., 2007). To complicate matters there is ambiguity even about what structure should be classified as an “eye” and what terms to use to designate such a structure as an integral component of a visual system.

In this account, we use the word “eye” in reference to any dioptric apparatus (compound lenses/lens cylinders or a single lens) that focuses light on an underlying array of photoreceptor neurons that provide relay neurons with encoded information to successive retinotopically organized neural centers, the circuits of which reconstruct relevant features of a taxon's visual environment. This “eye + visual system” as a distinct attribute of the arthropod protocerebrum is implicit in Holmgren's (1916) neuro-anatomical observations across two extant panarthropod phyla, Onychophora and Arthropoda (Chelicerata + Mandibulata). Visual systems so defined explicitly exclude optical structures whose underlying photoreceptor neurons do not provide afferents to discrete visual neuropils but supply relays that distribute to modulatory centers of the brain's protocerebrum as exemplified by crustacean nauplius eyes and covert internal photoreceptive cells of some malacostracans (Elofsson, 2006; Sandeman et al., 1990). This specific distinction of functionally perceptive visual systems from light sensitive modulatory pathways should impact all future interpretations of structures commonly referred to as “ocelli”, which are claimed to be widespread across Arthropoda (Bitsch and Bitsch, 2005; Mayer, 2006). Many publications and modern glossaries (Richter et al., 2010) confuse eyes of visual systems, as defined above, with light sensitive channels subtending lenses, but which do not supply retinotopic neuropils. The lenses of Onychophora (Strausfeld et al., 2006), the paired median lenses of xiphosurans (Harzsch et al., 2006), single lenslets of Chilopoda (Müller et al., 2007), and the lenses of Chelicerata, including Pycnogonida, all supply light to photoreceptor neurons that connect to retinotopic neurons comprising discrete visual neuropils belonging to the protocerebral neuromere of the brain (Strausfeld et al., 2006; Harzsch et al., 2006; Strausfeld, 2012; Lehmann et al., 2012; Lehmann and Melzer, 2013). In contrast, the nauplius eyes of crustaceans and the ocelli of insects, their likely homologues, supply sparse outputs to distributed areas in the central protocerebrum but not to specialized visual neuropils (Nässel and Hagberg, 1985; Lacalli, 2009; Fritsch and Richter, 2010).

That an “ocellus” (Latin: little eye) differs from a single-lens eye was already admitted during the golden age of comparative morphology, exemplified by Korschelt and Heider's (1899) synthesis that drew attention to distinctions between the corneal structure of single-lens eyes of spiders and that of median ocelli of insects. Korschelt and Heider referred to the classical study by Lankester and Bourne (1883) that compared single-lens structures and their underlying organization of photoreceptor clusters (their “retinulae”) in scorpions (*Androctonus funestus*, *Euscorpis italicus*) with the compound eyes of *Limulus polyphemus*, which Lankester had identified in 1881 as a chelicerate. Not only did these authors therefore posit that the scorpion eye was a derivation of a compound *Limulus*-type organization, but their 1883 work stressed commonality with respect to the composition of their retinulae (groups of photoreceptor neurons and supporting cells), noting that the composition of arachnid retinulae is distinct from retinulae of a crustacean ommatidium (their “ommateum”). A clear distinction between arachnid and crustacean eyes was thus established long before the identification eighty years later of eccentric cells, post-receptor neurons unique to chelicerates originating within the

retina's retinulae (Hartline et al., 1952; Schwartz, 1971; Schliwa and Fleissner, 1979).

Lankester and Bourne's comparisons between chelicerate and crustacean retinas opened the debate as to whether compound eyes evolved once or twice and whether single-lens eyes such as found in scorpions and spiders had evolved from compound retinas. The recognition that within mandibulates the structure and development of the compound eyes of crustaceans and insects share so many characters yet, with the exception of Scutigermorpha, differ so profoundly from the clustered lenses of myriapods has further enlivened debates about visual system origins (Harzsch and Hafner, 2006).

Many studies have demonstrated that the organization of insect and crustacean compound eyes is highly conserved despite divergent modifications that allow superposition optics and numerous other eye types, including box mirror optics in the paraphyletic Crustacea (Nilsson, 1990). Indeed, the greatest variety of divergently evolved compound eye optics is found within Anomura (hermit crabs, king crabs, etc; Nilsson, 1988). Nevertheless, even taxa that as adults have superposition or other optical arrangements, as pelagic larvae they all possess apposition eyes (Nilsson, 1983). Such distinctive eye characters allow phylogenetic approaches in the reconstruction of crustacean relationships (Richter, 1999; Paulus, 2000). In addition, across Pancrustacea (Hexapoda + “Crustacea”), each visual unit of the eye – the ommatidium – contains a highly conserved arrangement of eight (in some species nine) photoreceptor neurons and four cone cells that secrete the crystalline cone lying beneath the cuticular lens (Melzer et al., 1997; Paulus, 2000; Richter, 2002), the two comprising the ommatidium's dioptric apparatus. Exceptions to this arrangement include some species of very small beetles, in which the cone cells have undergone secondary reduction or loss resulting in “Limulus-like” optics (see Caveny, 1986).

This highly conserved suite of compound eye characters in Pancrustacea differs profoundly from visual systems of Myriapoda where, in the great majority of taxa, the visual apparatus consists of a field of relatively large lenslets each surmounting numerous photoreceptor neurons arranged to provide two tiers of microvilli (Müller and Meyer-Rochow, 2006). In pleurostigmophoran Chilopoda the lenslets may provide a superficially hexagonal arrangement, whereas in Diplopoda the lenslets – sometimes referred to as lateral ocelli (Müller and Meyer-Rochow, 2006) – are spaced well apart. Only one group of Chilopoda, the Scutigermorpha, has hexagonally faceted eyes and only this group and diplopods, belonging to the penicillate Synxenidae, possess cone cells (Müller et al., 2003, 2007).

Myriapoda are mandibulate arthropods that differ markedly from Pancrustacea in that their body morphology is homonomous except for their five most anterior segments and one caudal segment. The only pancrustacean taxa approaching such simplicity are the anchialine Remipedia and the Cephalocarida (Fanenbruck and Harzsch, 2005; Stegner and Richter, 2011). The brain organization of the former suggests affinities to Malacostraca, whereas brain organization in cephalocarids suggests a more ancient crustacean ancestry. Until the late 1990s the notion was still entertained that because Myriapoda demonstrate a number of anatomical attributes in common with Hexapoda, their status was that of the sister group or ancestral grade to Hexapoda, with Hexapoda and Myriapoda together comprising “Tracheata” (Kraus, 1998). Shared attributes include, amongst others, trachea, the single pair of (deutocerebral) antennae, and uniramous appendages. Although some still adhere to the Tracheata concept (Wägele and Kück, 2014), it is strongly contradicted by a large body of molecular evidence (Giribet and Edgecombe, 2013), including the recently published genome sequence of *Strigamia maritima*, which reveals many

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