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Review

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Crustacean conundrums: a review of opsin diversity and evolution

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Knowledge of crustacean vision is lacking compared to the more well-studied vertebrates and insects. While crustacean visual systems are typically conserved morphologically, the molecular components (i.e. opsins) remain understudied. This review aims to characterize opsin diversity across crustacean lineages for an integrated view of visual system evolution. Using publicly available data from 95 species, we identified opsin sequences and classified them by clade. Our analysis produced 485 putative visual opsins and 141 non-visual opsins. The visual opsins were separated into six clades: long wavelength sensitive (LWS), middle wavelength sensitive (MWS) 1 and 2, short wavelength or ultraviolet sensitive (SWS/UVS) and a clade of thecostracan opsins, with multiple LWS and MWS opsin copies observed. The SWS/UVS opsins were relatively conserved in most species. The crustacean classes Cephalocarida, Remipedia and Hexanauplia exhibited reduced visual opsin diversity compared to others, with the malacostracan decapods having the highest opsin diversity. Non-visual opsins were identified from all investigated classes except Cephalocarida. Additionally, a novel clade of non-visual crustacean-specific, R-type opsins (Rc) was discovered. This review aims to provide a framework for future research on crustacean vision, with an emphasis on the need for more work in spectral characterization and molecular analysis.

This article is part of the theme issue 'Understanding colour vision: molecular, physiological, neuronal and behavioural studies in Arthropods'.

1. Introduction

The crustaceans are a paraphyletic group that is comprised of all members of the clade Pancrustacea excluding hexapods. Although approximately 75% of the 67 000+ described extant species inhabit marine environments [1], crustaceans are an ecologically diverse group, occupying nearly every habitat from abyssal ocean depths to snowy mountain peaks. The variation in light environments across these habitats, along with the morphological and behavioural diversity found across lineages, have produced an extreme degree of visual system diversity within the group, yet studies of the molecules involved in crustacean vision are still taxonomically limited.

As in all animal eyes, the molecular foundation of vision in crustaceans is the opsin protein. Opsins, when bound to a vitamin A-derived chromophore, form a visual pigment that can absorb photons of light and initiate a cellular signalling cascade. Depending on the amino acid sequence of the opsin and the particular vitamin A derivative used as the chromophore, a visual pigment may have peak sensitivity ranging anywhere from the ultraviolet (UV) through the visible (violet to red) spectrum of light. Most animal visual pigments use the same form of chromophore, making the variation in light sensitivity primarily due to variation in the opsin sequence.

The first opsin sequence fully characterized was bovine rhodopsin [2,3], which has served as a template for those that followed. As more arthropod visual opsins were characterized, it became clear that they were evolutionarily distinct from vertebrate ciliary (C-type) opsins, and were termed R-type opsins based on the rhabdomeric photoreceptor cells found in arthropod visual

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systems [4–6]. Although the physiological function of crustacean visual pigments has been studied for over 60 years [7–11], the first crustacean opsin sequence was not characterized until 1993 from the crayfish *Procambarus clarkii* [12]. Following this breakthrough, molecular studies of crustacean opsins remained scarce compared to those focused on insect species [13–15]. It was not until the advent of next-generation sequencing (NGS) that studies of opsin evolution from a diversity of crustacean species became more common [16–19].

Based on studies of visual anatomy and physiology (see below) crustacean eyes have typically been characterized with one or two spectrally distinct types of photoreceptors [20–22]. Until studies of crustacean visual opsins became more commonplace, it was assumed that visual opsin diversity mirrored the measured photoreceptor spectral diversity (similar to the pattern observed in many insects). Most species were predicted to express two opsins forming visual pigments, each with a distinct spectral sensitivity—one to blue or blue-green light, the second to violet or UV light. However, the second crustacean in which the visual opsin sequences were characterized belied this hypothesis. In 1996, two opsins were sequenced from the crab *Hemigrapsus sanguineus*, but the opsins were co-expressed in the same set of cells sensitive to blue light (480 nm) rather than in separate sets of cells with different sensitivities [13]. The next group of crustaceans investigated deviated even further from initial expectations. Oakley & Huber [15] found that two ostracod species expressed up to eight opsins in their eyes, launching the idea that unlike well-studied insect species, crustaceans expressed multitudes of recently duplicated opsins. As more species were studied, it became apparent that higher opsin diversity than photoreceptor physiology was the norm, rather than the exception in crustaceans [23].

With increased ability to detect expressed opsins using NGS approaches, studies of the evolutionary history of crustacean opsins became possible. By combining spectrally characterized visual pigments with opsin sequence phylogenetic analyses, crustacean visual opsins have been broadly characterized into three major evolutionary clades: long wavelength-sensitive (LWS: greater than 500 nm), middle wavelength-sensitive (MWS: approx. 400–500 nm) and short- or ultraviolet-sensitive (SWS/UVS: less than 400 nm) [16,17]. In the SWS/UVS clade, despite a shared history with blue-sensitive (SWS) insect opsins, spectral [20,24–26] and molecular [23,27,28] characterizations indicate that crustacean opsins form violet- or UV-sensitive visual pigments. In terms of predicted sensitivity, the ancestral pancrustacean lineage is suggested to have four spectral clades of visual opsins: one LWS, two MWS and one SWS [18].

NextGen Sequencing also aided in discovery of opsins that detect light in non-visual contexts [18,29–32]. Based mostly on data from insects and chelicerates, arthropod non-visual opsins form five clades: Rh7, arthropsins, pteropsins, peropsins and neuropsins. Although non-visual opsins had been characterized from arthropods for several decades [33–37], finding them in crustaceans has been exceedingly rare, and none have been spectrally or functionally characterized.

To date, no reviews have included opsin data from the full taxonomic diversity of crustaceans encompassing the known diversity of eye types in the subphylum. Given the preponderance of data for arthropods and relative paucity of data for crustaceans, we focused on crustacean opsin diversity within all classes with publicly available data, encompassing more than half (30 of 58; figure 1) of the currently described extant orders. To place this expanded view of crustacean opsin diversity in context, we start with brief reviews of crustacean visual systems and visually mediated behaviours. Although this comprehensive approach significantly expands our knowledge, it also highlights how much is still unknown about the overall function and molecular evolution of crustacean opsins.

2. Morphology of crustacean visual systems

Crustaceans have evolved a wide range of visual system morphological diversity based on a multitude of eye types, optical designs and structures for colour and polarization vision [44]. All of the morphological diversity observed stems from two basic structural arrangements: naupliar versus compound eyes. Naupliar eyes are structurally less complex, often formed from single chambers or small clusters of photoreceptor cells [32,45]. Compound eyes, in contrast, are multifaceted and complex, typically composed of numerous, small, nearly identical units called ommatidia that each contain photoreceptor cells underneath light-focusing structures [46]. There are many documented modifications to both eye types, which allow for changes in visual acuity and spatial resolution [47,48]. Associations between eye types, structural modifications and opsin diversity have yet to be extensively studied. Although 'typical' eye designs in some crustaceans express little opsin diversity (e.g. crayfish and brachyuran crabs [49,50], barnacles [51,52], some amphipods and cave isopods [30,53,54]), sparse literature suggests that in some species highly modified visual structures equate to exponentially increased opsin diversity (e.g. stomatopods [55,56]), while in others even relatively simple photoreceptor set-ups have revealed similarly high opsin diversity (e.g. diplostracans, ostracods and copepods [15,19,31,32,57]). This glimpse of the relationship between visual structures and opsin diversity suggests that other factors, such as behaviour, are integral to understanding the sometimes overwhelming diversity of visual opsins characterized from crustacean eyes.

3. Visually mediated behaviours

Visually mediated behaviours come in many forms and functions across habitats but would not be possible without the use of light. Light provides a fast, high-fidelity signal especially over relatively short distances where scattering is not a concern. Perhaps the most impressive visual behaviour, in terms of scale, is diel vertical migration (DVM) performed by a taxonomically diverse set of aquatic species. DVM represents the greatest daily migration on earth in terms of biomass, with individuals moving across depths of metres to hundreds of metres [58], and is primarily driven by light cues (see review [59]). As the primary animal light detector, the role of opsin diversity and differential expression in DVM is not yet clear. However, some evidence from vertically migrating oplophorid shrimp suggests a pattern of diel fluctuation in co-expression of opsins that may be used to tune visual systems during the migratory process [60]. A similar pattern of unexpectedly high opsin diversity can be found in other vertical migrators (e.g. krill, copepods and

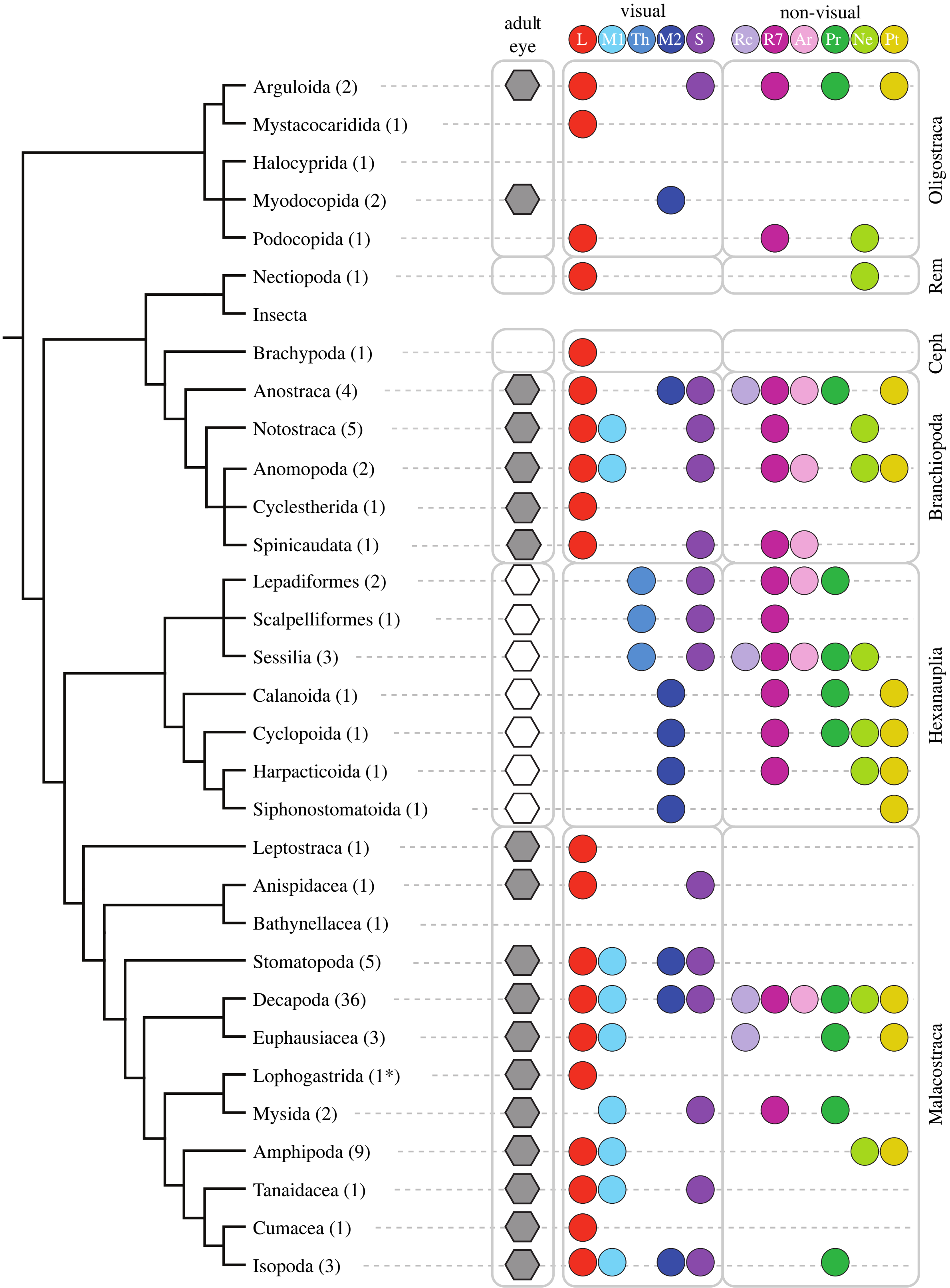

Figure 1. The presence or absence of crustacean opsin clades identified from publicly available transcriptome data mapped across a phylogenetic supertree of crustacean orders. Ordinal relationships were reconstructed from multiple recently published phylogenies [38–42]; dark grey dashed-line boxes group orders by either class or superclass (Rem, Remipedia; Ceph, Cephalocarida). The numbers in parentheses after each order indicate the number of species included in represented opsin data; * = data from a published PCR-based study only [43]. For each order, the dominant eye morphology in adults is indicated (compound eye, grey hexagon; simple eye, white hexagon; no eyes, X), as well as which visual and non-visual clades contained at least one opsin sequence within the order. Visual opsin clades: L, red circles: long wavelength-sensitive; M1, light blue circles: middle wavelength-sensitive 1; Th, medium blue circles: thecostracan-specific; M2, dark blue circles: middle wavelength-sensitive 2; S, dark purple circles: short-wavelength/ultraviolet-sensitive. Non-visual opsin clades: Rc, light purple circles: non-visual crustacean opsin; R7, dark magenta circles: Rh7 clade; Ar, pink circles: arthropsin clade; Pr, green circles: peropsin clade; Ne, lime green circles: neuropsin clade; Pt, yellow circles: pteropsin clade.

ostracods), potentially allowing for broadened spectral sensitivity to aid in visual function in different light environments at depths [18,29,57,60].

Expanded opsin diversity is also likely to play a role in communication for many crustaceans. Perhaps most notable are the stomatopods with more than 33 visual opsins [56], which use both colour and polarization cues to guide behaviours such as mate recognition and aggressive interactions [61–63]. In areas of low light, some crustacean species even have the ability to produce their own light for means of communication. Male ostracods (*Vargula annecohenae*) perform intricate bioluminescent displays to attract females and have also been found to possess a high degree of opsin duplications [15,64]. These behaviours are not limited to the aquatic realm, as terrestrial and semi-terrestrial crabs often use visual signals in the form of reflective carapace to communicate aggression or signal to potential mates [65–67].

Predation and predator avoidance are another set of visually guided behaviours. Some crustaceans use transparency as camouflage both to avoid visual predators and as a means to disguise themselves from potential prey [68,69]. However, the use of transparent tissues for defense is less effective against predators sensitive to UV light [70], suggesting a role for increased UV visual sensitivity in pelagic, predatory crustaceans. Conversely, some species light up to avoid detection by using bioluminescent photophores positioned ventrally to disrupt the visible shadow that they would otherwise produce, a phenomenon known as counter-illumination [71]. Although the mechanisms by which bioluminescent crustaceans are able to match downwelling irradiance are not known, it has been suggested that photosensitivity in the photophores of these animals may play a role [72]. More work in this area is needed to elucidate the potential use of extraocular opsin expression in bioluminescent camouflage.

These are far from the only visually mediated behaviours described from crustaceans, and it is likely that vision plays an important role in behaviours that have yet to be investigated. In order to understand how visual stimuli influence behaviour, a better understanding of crustacean vision is needed and there is still much to learn about how opsin diversity may influence behaviour in crustaceans.

4. Crustacean opsin diversity

Establishing the evolutionary relationships among these successful arthropods continues to be a work in progress, with regular modifications to taxonomic classifications [70]. Using previously published crustacean opsin studies, along with searches of publicly available transcriptomic data generated primarily from eye, nervous system and whole-body tissue (electronic supplementary material, table S1), we present the most complete view of crustacean opsin diversity to date. Transcriptomic data were gathered from 29 of the 30 extant crustacean orders included here and from all major crustacean habitat types (e.g. marine, brackish, freshwater and terrestrial). The use of transcriptomic data allows us to focus on opsins that are expressed and may be translated to functional proteins, rather than the full repertoire of opsins that a species may use in its lifetime (see electronic supplementary material, data for methods). Spectral sensitivity, labelling or targeted PCR studies were collected for opsins from 17 species in 6 orders (electronic supplementary material, table S1). For the majority of crustacean opsins, additional data on sensitivity, tissue localization or associated behaviours are lacking, highlighting the need for further research in this area.

Visual opsins from these data formed five clades—LWS, MWS 1 and 2, SWS, and the thecostracan opsins, a clade that is composed exclusively of opsins from barnacles. Non-visual opsins included Rh7, arthropsins, peropsins, neuropsins, pteropsins and a new putatively crustacean-specific, non-visual rhodopsin group abbreviated here as 'Rc'. Evidence for lineage-specific opsin duplication was noted when a species possessed multiple opsin copies within a defined spectral clade. Potential opsin duplications at the species level were also summarized (figure 2). We outline what is known about opsin diversity relative to characterized visual systems for each order with available data below.

(a) Superclass Oligostraca

(i) Arguloida

The order Arguloida consists of over 200 aquatic, primarily fish ectoparasites. This group has prominent compound eyes that are used in selecting fish hosts and foraging [73]. From two freshwater species of *Argulus* up to nine visual opsins were identified: five and seven LWS opsins for *Argulus siamensis* and *Argulus foliaceus*, respectively, and two SWS/UVS opsins were identified in each species. Non-visual opsins were also identified from the Rh7, pteropsin and peropsin clades, adding Rh7 and pteropsin to the known repertoire of this group.

(ii) Mystacocaridida

This order is represented by a handful of mesopsammic species, which are not expected to be highly visual due to their lack of eyes and light-sensitive frontal organs [74]. Though a prominent organ of Bellonci has been observed in *Derocheilocaris remanei*, light reception of this organ has been ruled out as immunohistological studies found no innervation to the central nervous system [75]. From a single transcriptome assembled for *D. remanei*, only one predicted LWS visual opsin was identified and was reduced in size (approx. 7% reduction), suggesting functional degradation.

(iii) Halocyprida

The order Halocyprida is a group of anchialine cave-adapted ostracods that lack eyes. Unsurprisingly, no opsins were found in the transcriptome of *Obtusoecia obtusa* analysed here.

(iv) Myodocopida

There are approximately 800 described members of this order that subsist in marine and brackish environments, with some species known to use bioluminescence in complex mating rituals [76,77]. Within the class Ostracoda, the Myodocopida are easily identified by their large compound eyes. Eye-specific RT-PCR expression in two species, *Skogsbergia lerneri* and *Vargula hilgendorfii*, found at least 8 orthologs of predicted R-type opsins [15]. Although the sequences from *S. lerneri* were mostly too short to include here, seven full length visual opsins identified from transcriptomic data for *V. hilgendorfii* confirmed the original PCR data. All opsins found were in the MWS2 group of visual opsins and no non-visual opsins were identified.

(v) Podocopida

The order Podocopida consists of over 1500 marine, freshwater and semi-terrestrial species of ostracods that have only a single naupliar eye [78]. One transcriptome from the freshwater pool-dwelling species *Heterocypris incongruens*

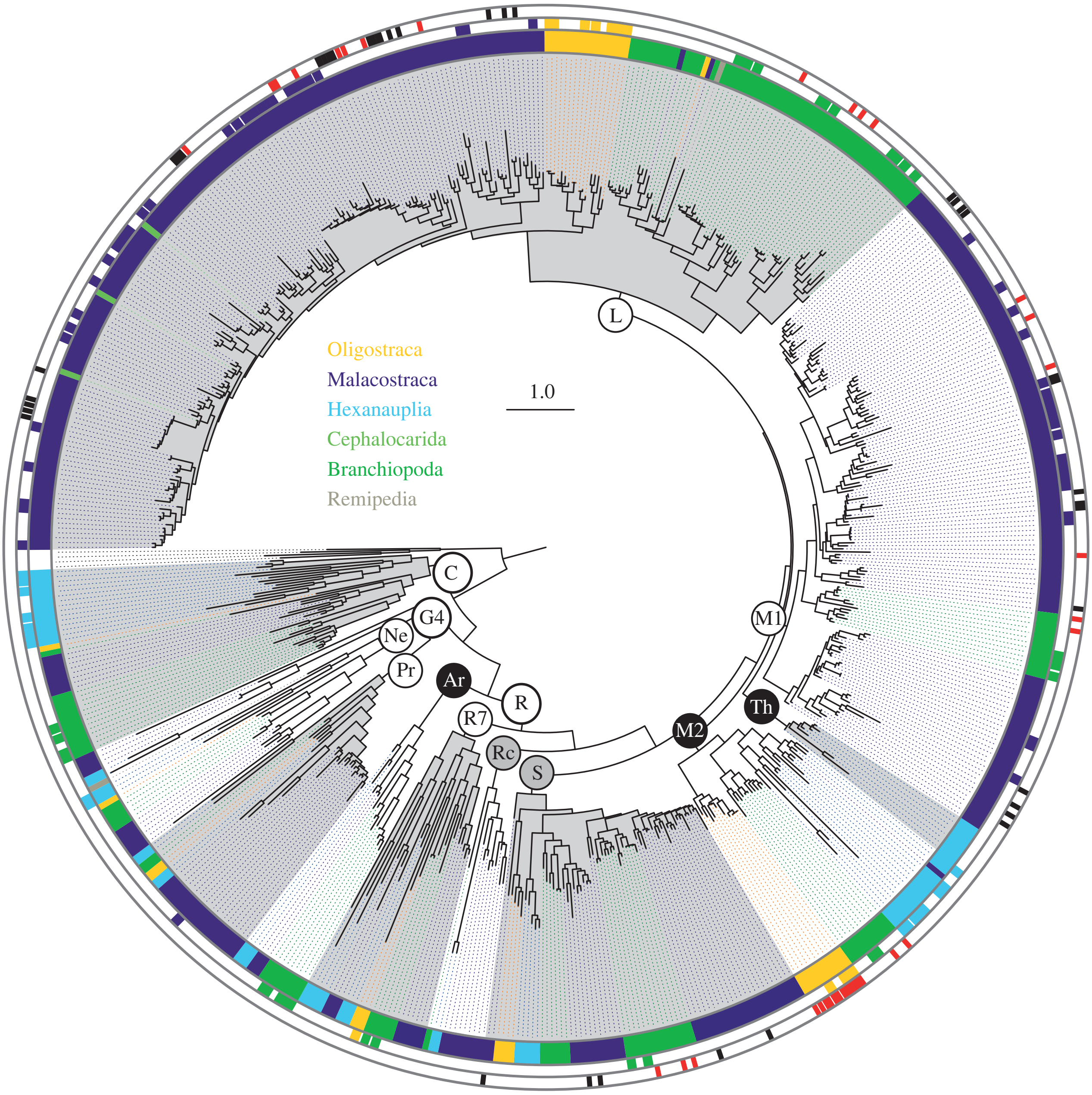

Figure 2. Maximum-likelihood phylogeny of opsin proteins from crustacean orders using placozoan opsins as an outgroup (uncoloured; see electronic supplementary material, table S2 for sequence information). Major groups are labelled at the nodes and coloured by bootstrap support value: 90–95% (grey) and 96–100% (black). Groups include: C, C-type pteropsins; G4, tetraopsins; Ne, neuropsins; Pr, peropsins; R, rhabdomeric opsins; Ar, arthropsins; R7, rhodopsin 7; Rc, crustacean rhabdomeric opsin; S, short/ultraviolet wavelength-sensitive; M1, M2, middle wavelength-sensitive; Th, thecostracan visual opsins; L, long wavelength-sensitive. Innermost ring is coloured by superclass or class, the second ring indicates species-specific and monophyletic duplications, and the outermost ring indicates confirmation of opsin sequences either with associated spectral or labelling (black bars) or PCR (red bars) studies.

contained exclusively LWS visual opsins (five transcripts) as well as two Rh7 opsins and one neuropsin. Greater sampling across species from different habitat types is necessary to further understand the visual capabilities of this order.

(b) Class Remipedia

(i) Nectiopoda

The eyeless order Nectiopoda contains only 28 species of anchialine cave-adapted crustaceans. One of these species, *Xibalbanus tulumensis*, had been investigated for opsin diversity by Henze & Oakley [18], and none were identified. Here, we have added the analysis of a transcriptome from *Lasionectes entrichoma*, and identified a single LWS opsin, as well as one non-visual neuropsin. The tissue of this specimen included half a head and some body segments, and due to the lack of eyes, it is likely that neither of these opsins is used in image-forming processes.

(c) Class Cephalocarida

(i) Brachypoda

The order Brachypoda consists of only 12 species, which live in sediment-rich intertidal habitats. We recovered three LWS opsins from a transcriptome of the species *Lightiella incisia*, although members of this order are eyeless, and previous work by Elofsson & Hessler [79] found no vestigial eye structures. Because only portions of the sequences were recovered, we were not able to verify the existence of the terminal lysine residue in the seventh transmembrane helix necessary for retinal binding. Further investigation is needed to determine if these opsins could be functional in vision. No non-visual opsins were found.

(d) Class Branchiopoda

(i) Anostraca

Members of the order Anostraca have stalked compound eyes and live in hypersaline lakes and temporary vernal pools. MWS and SWS/UVS opsins from this group have been previously characterized using PCR [23]. From this and three additional transcriptomic datasets, we identified three to nine LWS, two to five MWS2, and up to four SWS/UVS opsins, with the highest numbers coming from the species *Eubranchipus grubii*. We saw evidence of duplication in the LWS and MWS clades (3–9 copies) as well as the SWS/UVS (1–4 copies). All non-visual opsin groups (except neuropsins) were identified, with evidence of species-specific duplication in the Rh7 and pteropsins.

(ii) Notostraca

The order Notostraca contains fewer than 20 species that live in the benthos of shallow lakes and vernal pools [80] and possess sessile, dorsally oriented, compound eyes [81]. Kashiyama *et al*. [23] found evidence of MWS and SWS/UVS opsins in this order. Our analysis, including three additional transcriptomic datasets, resulted in one (*Triops longicaudatus*) to four LWS opsins; one MWS1 opsin in all species, except *Triops newberryi* (none) and *Lepidurus cryptus* (two); and up to two SWS/UVS opsins (*L. cryptus*). Non-visual Rh7 and neuropsins were identified, although the former was only found in one species, *T. newberryi*. No non-visual opsins were identified from eye- and ocelli-only transcriptomes.

(iii) Subclass Diplostraca; Orders Anomopoda, Cyclestherida and Spinicaudata

Species in the subclass Diplostraca are found in freshwater, brackish and marine habitats. Members of this subclass possess a sessile compound eye [82]. Early work by Smith & Baylor [83] showed behavioural responses to different wavelengths of light in several species of Diplostraca and further work has shown evidence for short, middle and long wavelength spectral classes of photoreceptors in the eye of *Daphnia magna* (Anomopoda) [25]. The previously published genome of *Daphnia pulex* (Anomopoda) showed evidence of all classes of opsins aside from peropsins [31,84]. From this and three transcriptomic datasets, we identified one to eight LWS opsins across orders as well as three to five MWS1 opsins from the order Anomopoda. No MWS opsins were found in the other orders surveyed, each represented by a single species. One or two SWS/UVS opsins were found in all species analysed with the exception of *Cyclestheria hislopi*, a member of the order Cyclestherida, which lacked an SWS/UVS opsin. Non-visual opsin diversity was highest in the Anomopoda with two Rh7, seven arthropsins, eight pteropsins and one neuropsin identified from *D. pulex*. A Rh7 and an arthropsin were identified from *Eoleptestheria* cf. *ticinensis* (Spinicaudata) and no non-visual opsins were found in Cyclestherida.

(e) Class Hexanauplia

(i) Subclass Thecostraca; Orders Lepadiformes, Scalpelliformes and Sessilia

The subclass Thecostraca consists of the barnacles; here we analysed data from three orders: Sessilia, Lepadiformes and Scalpelliformes. All six species analysed are marine and sessile with simple eyes as adults, though the larvae of these species are motile and free-living. Microspectrophotometry data of *Amphibalanus* sp. (Sessilia) indicated the presence of a single bistable blue visual opsin (492–495 nm and 510–532 nm) [52]. One commonality shared by the marine barnacles analysed here was the conservation of two types of visual opsins: one thecostracan visual opsin and one SWS/UVS. The thecostracan clade of visual opsins may have been duplicated in the order Sessilia, with two copies identified both from a transcriptome (*Semibalanus balanoides*) and a genome (*Amphibalanus amphitrite*). All types of non-visual opsins were identified, except for pteropsins. The highest non-visual opsin diversity in one species was expressed from the sessile barnacle *S. balanoides*. Three neuropsins and one of each non-visual opsin (except pteropsin) were found. Both genome predictions and transcriptomes were analysed for this group, though the genomes did not contain the extensive non-visual opsin diversity of *S. balanoides*, possibly due to limitations in 454 pyrosequencing throughput as compared to Illumina.

(ii) Subclass Copepoda; Orders Calanoida, Cyclopoida, Harpacticoida and Siphonostomatoida

The crustacean subclass Copepoda is ecologically diverse, with more than 14 000 species distributed across ten orders found in almost every known habitat. Correspondingly, the diversity of eye morphologies among the ten orders of copepods is immense [32,45]. Based on analyses of transcriptomes from four species representing four of the ten copepod orders, copepods are unique among crustaceans in that they only use MWS2 visual opsins. These results were similar to a larger study by Steck *et al*. [32] that characterized the transcriptomes from 29 species across the same four copepod orders. Despite having comparatively simple eyes and the expression of a single type of visual opsin, all of the species included had evidence of duplication, with all species, even the parasitic *Lepeophtheirus salmonis*, expressing three or more copies of MWS2 opsins. Species in this group also expressed a range of non-visual opsins, including Rh7, neuropsin, peropsin and pteropsin transcripts; of these, the pteropsins seemed to have varying degrees of duplication across species, with anywhere from 1 transcript in *L. salmonis* to 8 in *Calanus finmarchicus*.

(f) Class Malacostraca

(i) Leptostraca

The Leptostraca are small, filter-feeding, epibenthic marine crustaceans that are often placed as the most basal lineage within the Malacostraca [85]. Studies of *Nebalia* characterized scotopic apposition compound eyes that provide a round-about view from the convex corneal facets [86]. A single LWS visual opsin was found in the transcriptome of *Nebalia bipes* and no non-visual opsins were identified.

(ii) Superorder Syncarida; Orders Anaspidacea and Bathynellacea

The two extant orders within Syncarida consist of exclusively fresh and brackish water crustaceans, which most often live in interstitial groundwater [87]. Previous transcriptomic analysis of the subterranean, interstitial filter feeder *Allobathynella bangokenisis* (Bathynellacea) found no opsins [88]. However, we identified five visual opsins (four LWS one SWS/UVS) from a transcriptome of the species *Anaspides tasmaniae* (Anaspidacea), which lives in moving streams, is carnivorous, and has a caridoid escape response [89]. No non-visual opsins were found.

(iii) Stomatopoda

The stomatopods are an order of predatory crustaceans that have been well-studied for their unusual visual systems. This order is globally distributed, with the majority of species surveyed found in shallow subtropical waters. Stomatopods have stalked compound eyes, each of which is divided into three parts, allowing for trinocular vision and depth perception in a single eye [90]. The existence of colour vision, including the perception of UV light, has been demonstrated behaviourally in this order [91,92] and up to 33 visual opsin sequences have been characterized from retinal tissues, many with unique expression patterns [56]. The five species included in our dataset have a large number of LWS (up to 19), one to eight MWS1, one to five MWS2 and up to three spectrally confirmed UVS opsins [24,55,56,93,94]. There is evidence for extensive duplication of LWS and MWS opsins in this order, potentially to facilitate a unique form of colour vision [92]. No non-visual opsins were found in stomatopods, possibly due to all data coming from retinal tissues.

(iv) Decapoda

The decapods are a speciose and ecologically diverse order containing over 10 000 extant species that span all major habitat types. Accordingly, decapods have a diverse range of visual systems potentially shaped by these differing habitats and ecologies. Compound eyes of all described optical types are found in this order. One LWS opsin and an SWS opsin from crayfish [12,49] as well as MWS opsins from several species [13,50,95] have been previously confirmed using antibody and PCR methods. Additional localization and spectral sensitivity work has shown opsin expression and light sensitivity both in the visual system and extraocular regions [20,38,96]. From 22 transcriptomic datasets, and additional PCR-based published data spanning seven infraorders, we found representatives of every type of crustacean non-visual and visual opsin (with the exception of theocostracan opsins) in the decapod lineage. Putative visual opsin diversity within the decapods was highly variable among species and infraorders (table 1). In general, prawns, shrimp, lobsters and anomuran crabs had higher visual opsin diversity (often more than 8), while crayfish and true crabs expressed fewer opsins (fewer than 5). This could be an indication that high opsin diversity was the ancestral state for the decapods. Approximately one third of the species examined had at least one copy of each visual opsin, more than three quarters had SWS/UVS opsins, and brachyurans lacked evidence of both LWS and MWS2 opsins. There is evidence of rampant gene duplication in decapod LWS opsins, which we observed in at least one species from every infraorder investigated here. Evidence of opsin gene duplication is also present in the MWS clades to a lesser degree, with species expressing up to three transcripts of both MWS1 (Dendrobranchiata, Astacidea, Anomura and Brachyura) and MWS2 (Achelata and Dendrobranchiata). Decapod SWS/UVS opsins appear to duplicate at lower rates, however we found two SWS/UVS opsin copies in *Panulirus ornatus*, as well as several Dendrobranchiata and Caridea species. Additionally, deep sea, burrowing or cave-inhabiting decapods had decreased visual opsin diversity as compared to other species within their infraorder, including a lack of expressed SWS/UVS opsins. Crayfish, prawns and shrimp mostly lacked evidence of any non-visual opsins. The newly named non-visual Rc opsin was not identified from the infraorder Achelata but it did occur in every other infraorder investigated. Due to the differences in tissue types and sequencing depth, the variation seen in non-visual opsins is more likely due to limits in detection rather than biological absence, as evidenced by transcriptome data from eyestalk tissue producing the most types of non-visual opsins.

Table 1. Decapod infraorders with associated common names, and the range of visual opsins found in each group.

infraorder	superfamily	common name	visual opsins
Dendrobranchiata		prawn	2–19
Caridea		shrimp	1–13
Achelata		spiny lobster	2–9
Astacidea	Astacoidea	crayfish	1–3
Astacidea	Nephropoidea	clawed lobster	3–5
Anomura		anomurid crab	0–8
Brachyura		true crab	2–4

(v) Euphausiacea

The order Euphausiacea comprises fewer than 100 species [97] that are exclusive to ocean basins. Euphausiids have stalked superposition compound eyes which, in some species, display adaptations depending on their position in the water column [98,99]. Previous work indicated that one MWS1 opsin was expressed both in the eye and the abdomen of *Euphausia superba*, suggesting a possible application in modulating bioluminescence [29]. Based on RT-PCR data from one species and transcriptomic data from an additional two species, one LWS and four to eleven MWS1 visual opsins were identified, with evidence of at least three duplication events occurring in the MWS1 clade (with multiple duplications occurring in *Meganyctiphanes norvegica*). Two opsins from the novel Rc clade as well as a non-visual pteropsin and two peropsins were identified.

(vi) Lophogastrida

Members of the order Lophogastrida are pelagic, mostly inhabiting deep marine waters, and often use bioluminescence in predator defense [100]. The only study of opsins in the group identified two LWS opsins in both juveniles and adults from the species *Neognathophausia ingens* using targeted PCR, although only a single visual pigment absorbance peak was characterized from their photoreceptors [43]. RNAseq studies in this group are needed to generate better estimates of opsin diversity for more detailed studies of the relationships between opsin diversity, photoreceptor physiology and bioluminescence in open water habitats.

(vii) Mysida

The order Mysida consists of over 1000 described species, with more than 90% found exclusively in marine habitats and the remaining species living in either coastal habitats with direct marine connections or fully freshwater environments [101]. Although mysids display considerable diversity in eye morphology, the variation is based on stalked superposition compound eyes [102,103]. Based on transcriptome data from two species distributed in brackish coastal habitats, visual systems in the order use multiple MWS1 opsins (nine in *Praunus flexuosus* and four in *Neomysis awatschensis*) and one SWS/UVS opsin. Additionally, two non-visual opsins (Rh7 and peropsin) were identified.

(viii) Amphipoda

The order Amphipoda comprises an estimated 10 000 described species found in marine, freshwater and subterranean environments. Amphipod visual systems generally consist of apposition compound eyes and range from no eyes in some deep sea species to large distributed retinas in the mesopelagic species *Paraphronima gracilis* [104]. Previous estimates indicate that amphipods typically have a low number of visual opsins (1–5), with most duplications occurring in the LWS clade [53]. Using transcriptomic data from nine species representing six families, we found one well-supported clade of LWS visual opsins in all species with an apparent duplication of this opsin evident in most species. Evidence of an evolutionarily distinct LWS was also found in *Marinogammarus marinus*, *Gammarus pulex* and *Hyalella azteca*. One MWS1 opsin was identified in all marine species (plus the freshwater species *Gammarus fossarum*). Non-visual neuropsins were found in four species, as well as a pteropsin in *Talitrus saltator*.

(ix) Tanaidacea

Although this cosmopolitan group of small (generally less than 2 mm) crustaceans can be found in freshwater, brackish and marine habitats, most of the 1200+ species are found at depths greater than 200 m where they can be the most abundant fauna present [105]. The few tanaidacean visual systems that have been studied range from well-developed apposition compound eyes in shallow-water species to complete eye loss in species from deep waters [106]. In the one shallow-water species investigated here (*Leptochelia* sp.), four visual opsins (two LWS, one MWS1 and one SWS/UVS) were identified, but no non-visual opsins were found.

(x) Cumacea

The order Cumacea consists of over 1500 species, all of which inhabit soft-bottomed, mostly marine, aquatic environments. Little is known about the visual capabilities of this order, although lensed eyes have been observed [107]. A single low-quality transcriptome from *Cumella* sp. produced one LWS visual opsin and no non-visual opsins.

(xi) Isopoda

The isopods are an ecologically diverse order, with species inhabiting all major habitat types. The three species included here represent some of this ecological diversity, including the semi-terrestrial species *Ligia exotica*, the marine *Idotea balthica* and the freshwater species *Asellus aquaticus*, with both surface and cave populations. Isopods have sessile apposition compound eyes [108], although these can vary from non-existent, to small and simple, to large composite eyes [109]. Based on the opsins identified in these species, isopods utilize up to two LWS, MWS (MWS1 and/or MWS2) and SWS/UVS opsins for vision. The *A. aquaticus* cave population, however, has reduced eyes and correspondingly reduced numbers of visual opsins expressed, including the absence of any MWS opsins, compared to the other two species investigated. A non-visual peropsin was identified from two transcriptomic datasets.

5. Overarching themes in crustacean opsin evolution

By taking a broad approach in our survey of crustacean opsin diversity and including RNAseq data that was not previously used for this purpose, we have identified common evolutionary features, as well as areas that merit further investigation. Unsurprisingly, given the diversity represented within the crustaceans, we found that the opsin repertoire expressed in different orders, and even within orders, is highly variable. While we can only speculate about orders for which no data are available, we can assume that more interesting vision-related stories will surely emerge from this group.

The results of our analysis, which represents the most comprehensive sampling of opsin diversity in the crustaceans at this time, align with the hypothesized visual opsin repertoire of the ancestral pancrustacean proposed by Henze & Oakley [18]. Given the fact that our study focused on opsin diversity within the crustaceans, we are not able to make further conclusions about the diversification events that gave rise to these major opsin clades. However, we see diversification in many crustacean orders, with the number of opsins found often exceeding expectations in both visual and non-visual opsin clades. Some orders, such as those within the class Hexanauplia, appear to have specialized in one or two types of visual opsins. Others, such as orders within the Malacostraca, possess sequences from all major opsin clades but with large amounts of duplication in either the LWS or MWS.

Though there are many studies that use physiological evidence to deduce spectral sensitivity of crustacean photoreceptors [20,25,110,111], the specific wavelength absorbances of most crustacean visual pigments, particularly MWS, remain unknown. Thus, designations of wavelength sensitivity for crustacean opsins remain theoretical. SWS/UVS opsins with a lysine residue at bovine rhodopsin position 90 are predicted to correspond to a shift from blue (characterized by the presence of an asparagine or glutamate residue) to ultraviolet spectral tuning in arthropods [28]. However, this lysine residue was present in all crayfish SWS/UVS opsins despite microspectrophotomic and electrophysiological data from *P. clarkii* measuring violet sensitivity from the R8 cells (440 nm; [26]). Nearly, all SWS/UVS sequences included in our analysis (57 of 64) contained this lysine residue, with the exception of six partial opsin sequences for which the relevant portion of the sequence was missing, and one opsin from the arguloid *A. foliaceus*, which has a valine residue at this position. While traditional wavelength sensitivity designations seem to hold true for insect opsins, our analysis does not provide a clear designation between SW- and UV-sensitive clades in crustaceans, suggesting the existence of additional unidentified tuning sites in crustacean SWS/UVS opsins.

Duplication of visual opsins within LWS and MWS clades was common in crustacean lineages. Up to 19 LWS opsins were identified from a single species (*Pseudosquilla ciliata*) and in MWS clades up to 11 MWS1 and 7 MWS2, were found (*A. siamensis* and *M. norvegica*). Duplication was less common in the SWS/UVS clade, with the most found in *E. grubii* (four). Opsin duplication can arise from several proximal causes, including tandem, segmental or whole genome duplications, though genomic data are often needed to determine the cause of duplication [19]. In order to learn more about the evolutionary mechanisms that have produced these broad patterns of opsin diversification, more crustacean genomes are needed.

From our datasets, by far the largest single clade in our phylogeny was the LWS clade. This is likely the result of early work focused on LWS opsins [12,14] allowing for the development of PCR-based methods [112,113] as well as large amounts of duplication in some orders (e.g. within the Malacostraca). Interestingly, the LWS clade also contained the only Remipede visual opsin from this study, potentially pointing to extraocular function in some groups. Several crustacean classes included in this study did not show evidence of LWS opsins, despite the addition of RNAseq data (e.g. Hexanauplia as well as the order Myodocopida).

Our analysis produced two distinct clades of MWS opsins, which corresponded to Henze & Oakley's schematic [18], with an intermediary clade of thecostracan opsins. The MWS1 clade contains only branchiopod and malacostracan opsins: within this clade, spectral data from brachyuran crabs (480–500 nm) and stomatopod midband ommatidia (400–500 nm) have spectral sensitivities corresponding to the predicted spectral range for the clade [20,56]. Similarly, MWS2 is composed of sequences from a wide variety of crustacean groups, with the only measured spectral data coming from stomatopod midband rows (450–500 nm; [56]). While the spectral sensitivities associated with MWS clades are unlikely to remain consistent between crustacean orders, it is clear that some groups have specialized by using or duplicating a particular MWS opsin (i.e. MWS1 in brachyuran crabs, crayfish, Amphipoda, Mysida, Anomopoda and Notostraca; MWS2 in Myodocopida, Copepoda and Anostraca; and Thecostraca-specific opsins). While these data suggest that MWS opsins are responsible for violet sensitivity in crustaceans, SWS/UVS may also extend to the violet range in some groups (i.e. crayfish).

Despite being relatively rare, potential duplication of SWS/UVS opsins was observed in species of the class Branchiopoda, as well as orders Arguloida, Decapoda, Stomatopoda and one isopod species: *Ligia exotica* (electronic supplementary material, table S1). The bright, relatively shallow aquatic or terrestrial environments that unify these groups may be a factor in their increased number of SWS/UVS opsins. SWS/UVS opsins appeared to have been lost in a majority of crustacean groups, including copepods, amphipods, brachypods, ostracods, cumaceans, mystacocarids and remipedes. For classes without compound eyes such as the Copepoda and Remipeda, this may be due to a lack of R8 cells, where SWS/UVS opsins are expected to be localized. More work is needed in this area to understand the evolutionary and ecological forces that lead some groups to diversify their SWS/UVS opsins while others have lost them altogether.

The putative non-visual opsins identified here resulted in six distinct opsin types in crustaceans: R-type Rh7, arthropsin, and a novel, putatively crustacean-specific, clade (Rc); tetraopsins included peropsin and neuropsin; and C-type pteropsins. Non-visual opsins were missing from some orders included in our analysis, but we do not believe this precludes their eventual discovery. As their name suggests, non-visual opsins are often expressed extraocularly and therefore could have been missed in datasets generated from eye-specific tissue. Additionally, non-visual opsins that are not highly expressed were probably not detected in whole-organism RNAseq datasets. We saw less duplication in the non-visual opsins compared to the more abundant visual opsins. This may be a consequence of the detection issues discussed above but may also suggest evolutionary mechanisms acting against proliferation of certain types of opsins.

The predicted non-visual R-type opsins, Rc, Rh7 and arthropsin, can be found in nearly all crustacean orders (with the exception of taxa with low representation, i.e. Mystacocarida, Nectiopoda and Cephalocarida). Our analysis produced a novel clade of opsin sequences that contain a chromophore binding site and sits at the base of the visual opsin clade. Based on its position outside of the traditional arthropod visual opsins, we believe that this group contains non-visual opsins and have tentatively termed it 'non-visual crustacean opsins' (Rc). Rc-type opsins were found in four orders: Euphausiacea, Decapoda, Sessilia and Anostraca. There is low bootstrap support (44%) for this group, indicating a need for more data and analysis to determine its validity. The next group of predicted non-visual R-type opsins, Rh7, are often found in photoreceptors and may be associated with circadian maintenance [34,114]. This group is found in nearly all crustacean lineages with very few duplications, aside from the decapod Rh7 opsins, which appeared to be polyphyletic. The final group, arthropsins, were found in relatively few transcriptomes, including the orders Anomopoda, Spinicaudata, Anostraca, Lepadiformes, Sessilia and Decapoda (brachyuran crabs only). The low prevalence of this opsin group is likely due to low expression, potentially in non-eye tissue. No labelling or spectral characterization for this group has been done, leaving its function to be determined.

The non-visual opsins known as tetraopsins were divided into two clades: peropsins and neuropsins, with peropsins being expressed in non-visual cells of the eye and neuropsins being expressed in neural tissue [18,31,115]. Our results suggest that crustacean groups are using one or the other of these opsins with very few duplications. Peropsins were present in Euphausiacea, Mysida, Lepadiformes, Anostraca, Calanoida, Arguloida and Isopoda. Neuropsins were present in Amphipoda, Notostraca, Anomopoda, Nectiopoda, Harpacticoida and Podocopia. Orders where both peropsins and neuropsins were found were Cyclopoida, Sessilia and Decapoda. Decapods expressed both peropsins and neuropsins in the infraorders Brachyura, Achelata and Astacidea, while Caridea and Anomura expressed only peropsins (Dendrobranchiata tetraopsins were not found). At this time, it is impossible to determine whether the absence of either opsin type is biological, due to low expression, or because of the tissue type used for generating transcriptomes.

The final group of non-visual opsins found in crustaceans is the C-type pteropsin. These vertebrate-like opsins have been found in the brain of non-crustacean arthropods and are thought to play a role in circadian rhythm entrainment [33]. Though these opsins are not well characterized in crustaceans, previous work suggests that insect pteropsins have absorption maxima ranging from blue to green wavelengths [37]. This opsin group was identified from the orders Arguloida, Decapoda, Euphausiacea, Amphipoda, Anostraca and Anomopoda as well as the class Hexanauplia, with evidence of duplication in the latter three.

The past 50 years of research have revealed surprising morphological and physiological diversity among crustacean visual systems, and this review on molecular opsin diversity offers no exception. It appears that life in an aquatic environment can sometimes result in large levels of opsin duplication, with examples found throughout the orders sampled; this is particularly apparent in the stomatopods and decapods. The evolutionary mechanisms responsible for such an overabundance of opsins in some crustacean species remain unknown, as other species can function with far fewer. Investigating the molecular components provides a basis for further studies on crustacean vision, but more work is needed to tie opsin diversity and abundance to function and ultimately inform research on crustacean ecology and behaviour.

Data accessibility. Opsin sequences identified from publicly available datasets are available as part of the aligned dataset (electronic supplementary material) [116]. Individual nucleotide and protein sequences are also accessible in electronic supplementary material, table S2.

Authors' contributions. S.P.: conceptualization, data curation, formal analysis, methodology, project administration, writing—original draft, writing—review and editing; T.I.: conceptualization, data curation, writing—original draft, writing—review and editing; M.S.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft, writing—review and editing; M.L.P.: conceptualization, formal analysis, project administration, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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