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Cover image: Mating blue-tailed damselflies (*Ischnura elegans*). Insects like these damselflies are derived crustaceans, but they have been historically ranked as different taxonomic classes within arthropods and studied separately. In this issue, articles from the symposium "Linking Insects with Crustacea: Comparative Physiology of the Pancrustacea" develop synergies based on our new evolutionary understanding of the group. Photo by Miriam J. Henze.

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SYMPOSIUM

The Dynamic Evolutionary History of Pancrustacean Eyes and Opsins

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From the symposium "Linking Insects with Crustacea: Comparative Physiology of the Pancrustacea" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2015 at West Palm Beach, Florida.

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Synopsis Pancrustacea (Hexapoda plus Crustacea) display an enormous diversity of eye designs, including multiple types of compound eyes and single-chambered eyes, often with color vision and/or polarization vision. Although the eyes of some pancrustaceans are well-studied, there is still much to learn about the evolutionary paths to this amazing visual diversity. Here, we examine the evolutionary history of eyes and opsins across the principle groups of Pancrustacea. First, we review the distribution of lateral and median eyes, which are found in all major pancrustacean clades (Oligostraca, Multicrustacea, and Allotriocarida). At the same time, each of those three clades has taxa that lack lateral and/or median eyes. We then compile data on the expression of visual r-opsins (rhabdomeric opsins) in lateral and median eyes across Pancrustacea and find no evidence for ancient opsin clades expressed in only one type of eye. Instead, opsin clades with eye-specific expression are products of recent gene duplications, indicating a dynamic past, during which opsins often changed expression from one type of eye to another. We also investigate the evolutionary history of peropsins and r-opsins, which are both known to be expressed in eyes of arthropods. By searching published transcriptomes, we discover for the first time crustacean peropsins and suggest that previously reported odonate opsins may also be peropsins. Finally, from analyzing a reconciled, phylogenetic tree of arthropod r-opsins, we infer that the ancestral pancrustacean had four visual opsin genes, which we call LW2, MW1, MW2, and SW. These are the progenitors of opsin clades that later were variously duplicated or lost during pancrustacean evolution. Together, our results reveal a particularly dynamic history, with losses of eyes, duplication and loss of opsin genes, and changes in opsin expression between types of eyes.

Introduction

With color vision, polarization vision, multiple types of eyes, and more optical diversity than in any other phylum (Land and Nilsson 2012), pancrustacean eyes are of particular interest to evolutionary biologists. How the diversity and exquisite functionality of those eyes evolved are enduring questions. While some species, like *Drosophila*, are well studied (Buschbeck and Friedrich 2008; Wernet et al. 2015), we know far less about groups other than winged insects. In recent years, new information on the phylogenetic relationships of Pancrustacea (Misof et al. 2014; Oakley et al. 2013) and genomic and transcriptomic datasets for a wider range of taxa have become available. This offers great potential to gain a better understanding of the evolutionary history of pancrustacean eyes and their components. Here, we review the presence and absence of the two main types of arthropod eyes across major pancrustacean groups, we summarize data on gene expression in those eyes, and we infer phylogenetic histories of two kinds of pancrustacean opsins, visual r-opsins (rhabdomeric opsins) and peropsins.

From their last common ancestor, pancrustaceans inherited two fundamentally different types of cephalic visual organs (Paulus 1979, 2000; Bitsch and Bitsch 2005; Nilsson and Kelber 2007): lateral and median eyes. Lateral eyes typically are compound eyes; they consist of up to several thousand ommatidia, individual photoreceptive units, and form a convex retina with an overall erect image. In contrast, median eyes, called nauplius eyes in crustaceans and median ocelli in insects, are usually single-chambered eyes, which possess a concave retina and produce an inverted image (Land and Nilsson 2012).

All animal eyes (with a probable exception in a sponge; Rivera et al. 2012) express opsins to form functional visual pigments sensitive to light. Arthropods rely on r-opsins for vision, with different genes specialized for sensitivity to different wavelengths (Briscoe and Chittka 2001; Arikawa and Stavenga 2014; Cronin and Porter 2014). Previous research suggests that the ancestral arthropod had at least three (Koyanagi et al. 2008) or four (Kashiyama et al. 2009) r-opsins. However, those analyses were based on limited sampling of taxa.

Apart from r-opsins, arthropods have other opsins, including c-opsins (ciliary opsins/pteropsins) expressed in brains (Velarde et al. 2005; Eriksson et al. 2013), arthropsins of unknown function (Colbourne et al. 2011), and peropsins/retinal G-protein-coupled receptors (RGRs) of unknown function, but known to be expressed in eyes, at least in *Limulus*, the spiders *Hasarius adansoni* and *Cupiennius salei*, and possibly in dragonflies (Nagata et al. 2010; Eriksson et al. 2013; Battelle et al. 2015; Futahashi et al. 2015). While searching for r-opsins in transcriptomes, we also found candidate peropsins from multiple pancrustacean groups, indicating that these genes are more common than previously appreciated.

The picture that emerges from our analyses is that visual evolution in Pancrustacea was amazingly dynamic. Eyes were lost many times, opsins changed expression from one type of eye to another, and opsins of ancient families re-duplicated or were fully lost in different patterns across the expanse of pancrustacean history.

Methods

Occurrence of lateral and median eyes

We compiled literature on the presence and absence of lateral and median eyes in major pancrustacean taxa (Supplementary Table S1) and displayed the results on two recently published arthropod phylogenies (Oakley et al. 2013; Misof et al. 2014; Fig. 1).

Visual r-opsins

Sampling of taxa/genes

Focusing primarily on pancrustacean species with characterized opsin expression, we downloaded amino-acid sequences of panarthropod r-opsins from GenBank (Supplementary Table S2). In addition, we searched genomes or transcriptomes from exemplars of major taxonomic groups and key species such as basal-branching hexapods (Supplementary Table S3). Unless predicted proteomes were available, we used ORF-Finder to detect open reading frames larger than 100 amino acids in length. These sequences were analyzed by phylogenetically informed annotation (PIA; Speiser et al. 2014), which employs BLASTP to find opsin-like genes and subsequently applies an evolutionary placement algorithm (Berger and Stamatakis 2011) to determine the most likely placement of a gene on a pre-calculated phylogeny of opsins. To our dataset from GenBank, we added sequences from genomes and transcriptomes that PIA placed within the arthropod r-opsin clade (Supplementary Table S4). For all opsins in our list, we revised the available literature on expression in lateral and/or median eyes (Supplementary Tables S2 and S4; Supplementary Figs. S1 and S2).

Phylogenetic analyses

We conducted phylogenetic maximum-likelihood analyses in SATé-II (simultaneous alignment and tree estimation; Liu et al. 2012) using onychophoran opsins (onychopsins) to root the visual r-opsin tree of arthropods (Hering et al. 2012). Within SATé-II we adopted VT, the best-fit model chosen by ProtTest (Darriba et al. 2011), and applied RAxML (Stamatakis 2006) for co-alignment and simultaneous topology search. Afterward, we generated 100 bootstrap pseudoreplicates using RAxML alone. To infer the evolutionary history of r-opsin genes, we next assumed a phylogeny of arthropod species (Figs. 1 and 2) based on recently published phylogenomic analyses (Oakley et al. 2013; Misof et al. 2014) and reconciled our r-opsin tree (Supplementary Figs. S1 and S2) with the species tree in NOTUNG (Durand et al. 2006). Nodes with <90% support in the r-opsin tree were allowed to be rearranged to minimize duplications and losses, with duplications being penalized four times more than losses (Fig. 2; Supplementary Fig. S3).

Panarthropod peropsin-like genes

We attempted to resolve the phylogenetic placement of arthropod peropsin/RGR (Battelle et al. 2015) and RGR-like genes (Futahashi et al. 2015) along with related sequences we discovered in GenBank and in published transcriptomes. Therefore we analyzed almost 500 opsins, gathered as follows: The Uniref90 database (Magrane and Consortium 2011) was searched twice with BLASTP, first using *Limulus* peropsin (AIT75833) and then human RGR (NP_001012738) as queries. For each search, we retained the 250 most similar hits. Odonate RGR-like sequences were not yet incorporated into Uniref90,

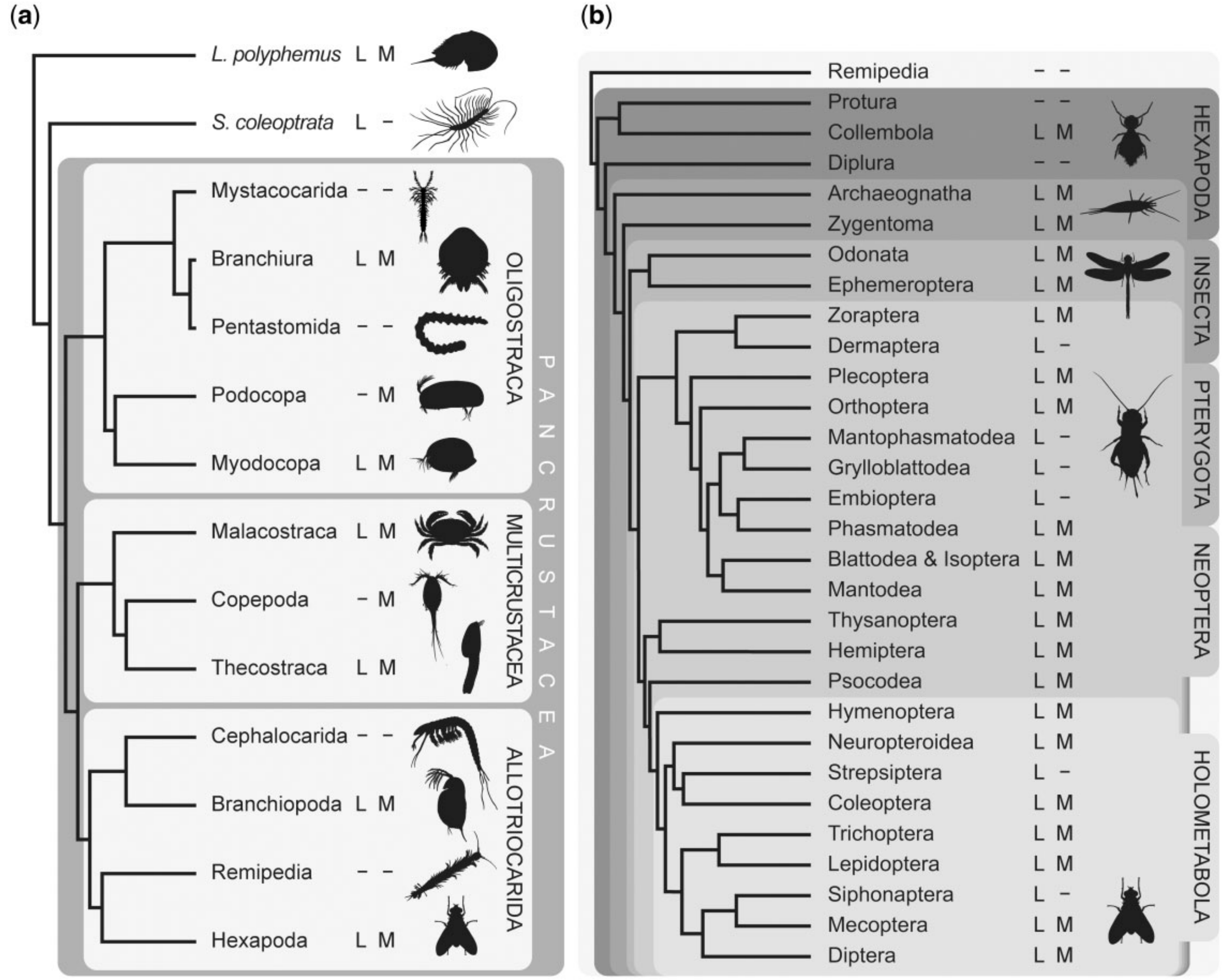

Fig. 1 Occurrence of lateral (L) and median (M) eyes in Pancrustacea. Median eyes refer to nauplius eyes in Crustacea *sensu stricto* as defined by Elofsson (2006) and to median ocelli in Insecta. Lateral eyes denote compound eyes or modifications thereof with lateral connections to the protocerebrum. '-' indicates that no eyes of the respective type have been found in any developmental stage, sex, or morph of a living species. *Limulus polyphemus* (Chelicerata; Battelle 2006) and *Scutigera coleoptrata* (Myriapoda; Müller et al. 2003) are added as representatives of non-pancrustacean arthropods. The phylogeny in (a) and (b) is based on Oakley et al. (2013) and Misof et al. (2014), respectively. For further references see Supplementary Table S1.

so we conducted a third BLAST search looking for matches to a *Bombyx* peropsin-like gene (XP_004930922) on GenBank and kept all 18 top ecdysozoan hits. Finally, we added 27 sequences of the RGR/peropsin (=RPE/peropsin) clade of Hering and Mayer (2014). We combined these datasets and removed duplicates found in multiple searches, as well as three long-branch opsins, which were unstable in their phylogenetic position in informal, preliminary analyses. The amino-acid sequences of the remaining 494 opsins were analyzed using SATé-II fast settings (Liu et al. 2012) with a maximum subproblem size of 200, blind-mode stopping rule, and iteration limit of 1. SATé-II ran FastTree (Price et al. 2010) for approximate maximum-likelihood phylogenetic analysis (we assumed a WAG+G20 model), MAFFT (Katoh and Standley 2013) for alignment and MUSCLE (Edgar 2004) for merging (Fig. 3; Supplementary Fig. S4).

Results

Occurrence of lateral and median eyes

In each of the three major pancrustacean clades proposed by Oakley et al. (2013), namely Oligostraca, Multicrustacea, and Allotriocarida, entire classes or subclasses are missing one type of eye or both (Fig. 1a). Within Oligostraca, eyes are completely unknown in Mystacocarida and Pentastomida (Osche 1963; Elofsson 1966; Elofsson and Hessler 2005;

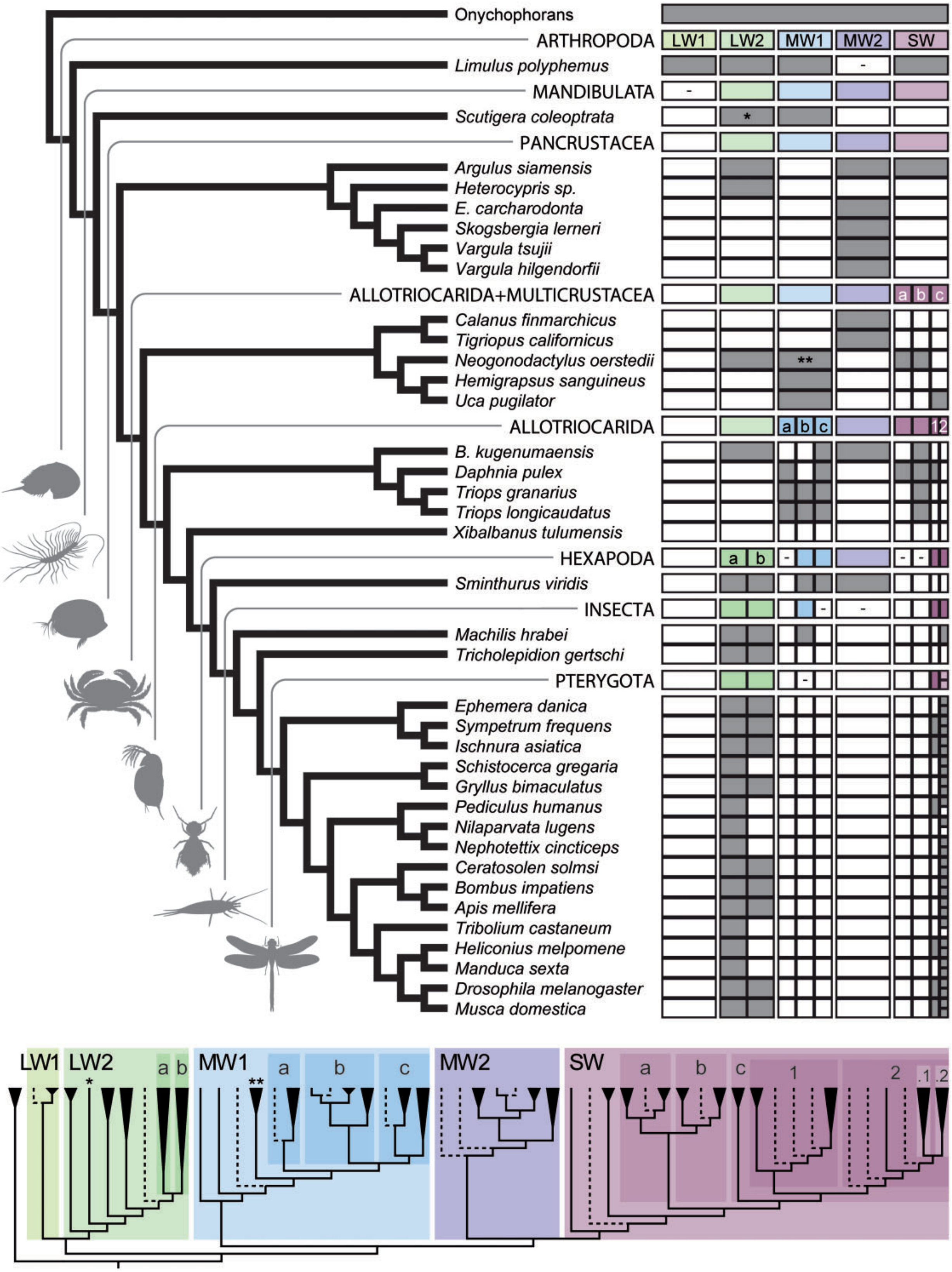

Fig. 2 Evolutionary history of visual r-opsins in Pancrustacea. We adopted the illustrated phylogeny of arthropod species (top left) from Misof et al. (2014) and Oakley et al. (2013). For each species, amino-acid sequences of r-opsins were downloaded from GenBank (Supplementary Table S2), or identified in published genomes or transcriptomes (Supplementary Tables S3 and S4) and subjected to phylogenetic maximum-likelihood analyses using RAxML and SATé-II (Supplementary Figs. S1 and S2). We reconciled the opsin tree with the species tree in NOTUNG (condensed result below, detailed tree in Supplementary Fig. S3) to assess the number of opsin

(continued)

Brenneis and Richter 2010). Lateral eyes are absent in podocopan ostracods, whereas their median (nauplius) eyes can be highly developed (Tanaka 2005; Elofsson 2006). Within Multicrustacea, copepods also lack lateral eyes, but have sophisticated median eyes (Elofsson 2006). Cephalocarida and Remipedia, two classes within Allotriocarida, are eyeless altogether (Elofsson and Hessler 1990; Fanenbruck et al. 2004; Fanenbruck and Harzsch 2005; Koenemann et al. 2009).

Below the level of class and subclass, there is considerable variation in the distribution of eyes as well. Within myodocopan ostracods, all halocyprids lack eyes, but myodocopids have both lateral and median eyes (Oakley and Cunningham 2002). Thecostraca are quite diverse in whether eyes are present or

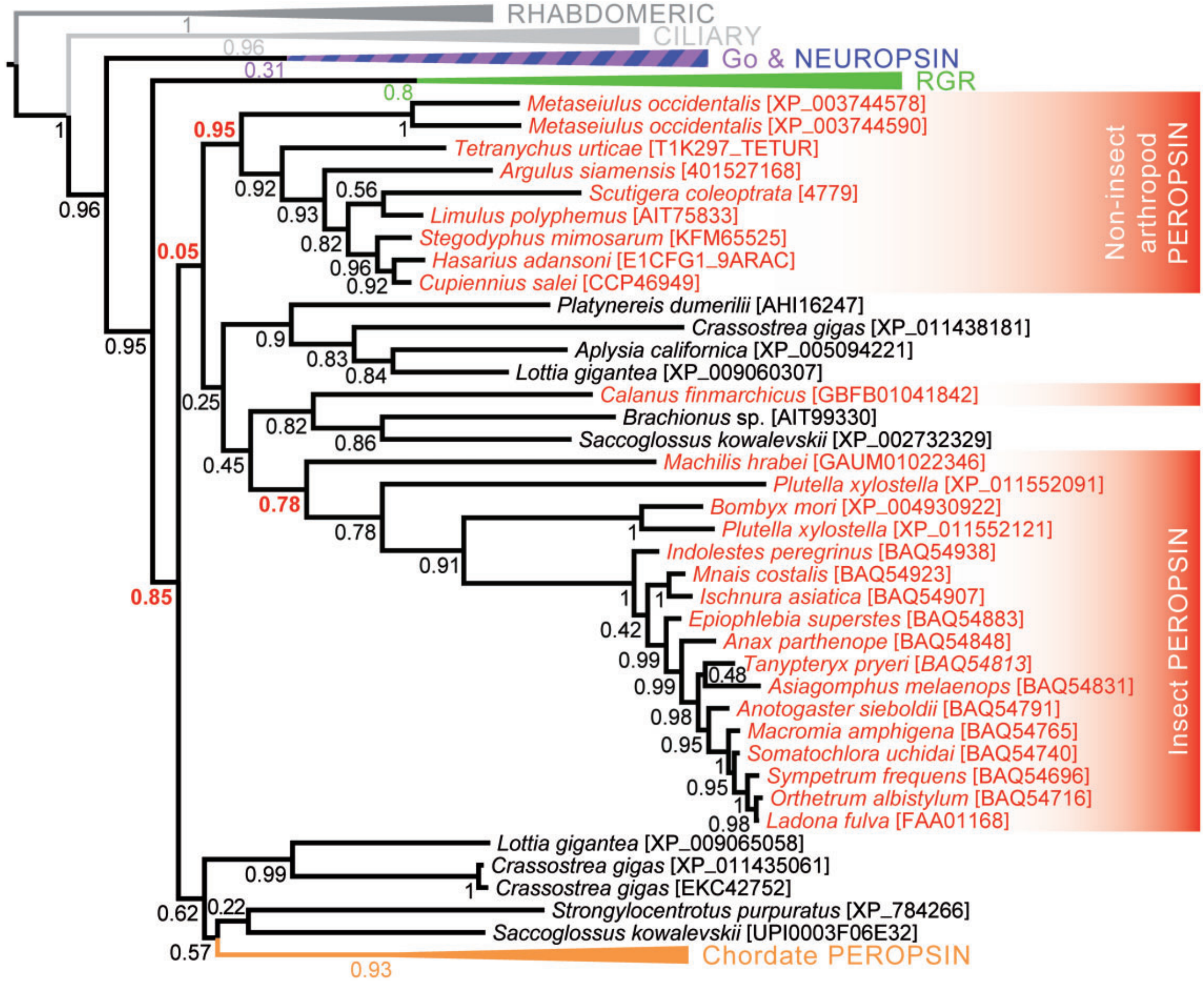

Fig. 3 Phylogeny of pancrustacean peropsins. The tree summarizes the results of our SATé-II analyses of the amino-acid sequences of 494 opsins, focusing on group-4 opsins. Support values mentioned in the text and arthropod taxa are highlighted. For a detailed tree, see Supplementary Fig. S4. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

Fig. 2 Continued
genes in the ancestral arthropod (named LW1, LW2, MW1, MW2, SW) and to estimate the timing of duplications (indicated by lowercase letters and numbers) and losses (broken lines). Our main results are summarized next to the species tree (top right), with boxes representing opsin genes and duplications as subdivisions. The unnamed upper and lower compartment of SWc2 in Pterygota illustrates SWc2.1 and SWc2.2, previously known as the insect UV and blue clade, respectively. Inferred loss of an opsin gene is indicated by '-', blank boxes represent genes that were lost earlier in evolution. The LW2 sequence of *Scutigera* (*) is very short, and only present in the sequence read archive (SRA), not in the final assembly of the transcriptome. Three r-opsin sequences of *Neogonodactylus* that belong to the MW1 clade (**) are not yet deposited in GenBank, but reported in a thesis (Bok 2013). *B.*: *Branchinella*, *E.*: *Euphilomedes*. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

absent (Pérez-Losada et al. 2012). Several neopteran insect orders possess only lateral and no median eyes (median ocelli) (Fig. 1b; references in Supplementary Table S1). Even members of the same pancrustacean family, genus, or species (age-related, sexual, and/or caste polymorphism) can differ by missing one type of eye or both (Kalmus 1945; Parry 1947; Buschbeck et al. 2003; Speiser et al. 2013).

Expression of visual r-opsins in lateral and median eyes

The expression of r-opsins has only been investigated in very few Pancrustacea, even if different techniques to confirm or exclude their existence at the transcriptional, translational, and physiological level (proof of mRNA, protein, and function) are taken into account (Supplementary Figs. S1 and S2). All ultraviolet (UV) opsins identified in median eyes to date are expressed in lateral eyes as well (*Apis mellifera* UV, *Bombus impatiens* UV, *Triops granarius* RhC; Spaethe and Briscoe 2005; Velarde et al. 2005; Kashiyama et al. 2009) with one possible exception (*Gryllus bimaculatus*; Henze et al. 2012). Similarly, *Limulus*, a chelicerate with lateral compound and median eyes, relies on the same UV opsin in both types of eyes (Battelle et al. 2014). Opsins that tune the visual pigment to longer wavelengths, however, are differentially expressed in *Limulus* (Battelle et al. 2015) and in most pancrustaceans investigated so far: eye-specific opsin paralogs have been found in myodocopid ostracods (Oakley and Huber 2004), dragonflies (Odonata; Futahashi et al. 2015), crickets (Orthoptera; Henze et al. 2012), flies (Diptera; Pollock and Benzer 1988), and bees (Hymenoptera; Velarde et al. 2005). Exceptions are the branchiopod *Triops granarius* and the hemipteran insect *Nilaparvata lugens*, which express all or a subset of their lateral-eye opsins in median eyes (Kashiyama et al. 2009; Matsumoto et al. 2014).

The duplications that gave rise to eye-specific opsin paralogs are phylogenetically much younger than are arthropods or pancrustaceans as taxa. A relaxed molecular-clock analysis of lateral- and median-eye opsins of ostracods suggests that they originated within Myodocopida about 200 million years ago (mya) (Oakley et al. 2007). In insects, at least three evolutionary lines exist, based on the presence and absence of genes and their phylogeny. While the LW1-LW2 paralogs of Hymenoptera and GreenA-GreenB paralogs of Orthoptera might go back to an early duplication of a long-wavelength (LW) opsin gene in hexapods (Fig. 2; Supplementary Fig. S3) more than 450 mya (Misof et al. 2014), eye-specific opsin paralogs of dragonflies and flies arose in Odonata and Diptera, respectively (Supplementary Figs. S1 and S3). The RhLWD opsin that is typically expressed in the median eyes of adult dragonflies (Futahashi et al. 2015) is nested within other odonate LW sequences and is neither known in Ephemeroptera nor in Neoptera. However, since RhLWD orthologs are found in Zygoptera as well as in Anisoptera (damselflies like *Ischnura* and true dragonflies like *Sympetrum*), their origin must coincide with or predate the last common ancestor of all living odonate species about 250 mya (Misof et al. 2014). The gene duplication that resulted in the eye-specific Rh1-Rh2 paralogs of flies like *Musca* and *Drosophila* is probably at least 100 million years younger and happened within the dipteran lineage. Rh1 and Rh2 orthologs have not been identified in non-dipteran insects, and are absent from the genome of the mosquitoes *Anopheles gambiae* (Velarde et al. 2005) and *Aedes aegypti* (Nene et al. 2007), early-branching Diptera.

Phylogeny of visual r-opsins

We have analyzed the phylogeny of visual r-opsins from representatives of all major pancrustacean clades proposed by Oakley et al. (2013), including new data on key taxa such as early-branching hexapods, for which no opsin sequences were known. Our results (Fig. 2; Supplementary Figs. S1–S3) suggest that the ancestral pancrustacean likely had four opsins that we call arthropod LW2, MW1, MW2, and SW (long-, middle-, and short-wavelength), based on the maximal spectral sensitivity (where known) of visual pigments formed by opsins of the respective clade in living species. Mandibulata, including pancrustaceans, may have lost a fifth opsin (LW1) present in the ancestral arthropod, but known so far only from *Limulus polyphemus*. We also infer additional r-opsin gene duplications. SW underwent two duplications before the ancestor of Allotriocarida plus Multicrustacea, resulting in SWa, SWb, and SWc. Before the ancestor of Allotriocarida, MW1 duplicated, yielding MW1a, MW1b, and MW1c, and SWc duplicated, yielding SWc1 and SWc2. Finally, LW2 duplicated before the ancestor of Hexapoda, yielding LW2a and LW2b, and SWc2 duplicated before the ancestor of Pterygota, yielding SWc2.1 and SWc2.2.

We failed to detect MW1a, SWa, or SWb in any hexapod, suggesting that those opsin genes were lost before the hexapod ancestor. While our data show that MW1c and MW2 are still present in *Sminthurus viridis* (Collembola), a basal-branching hexapod, they have not been identified in any insect species so far, and were thus probably lost before the ancestor of insects. We found MW1b in *Sminthurus* and in *Machilis hrabei* (Archaeognatha), but not in the transcriptome of *Tricholepidion gertschi* (Zygentoma). Because genes of the MW1b clade are also unknown from the comparatively well-investigated Pterygota, we assume that MW1b was lost early in insect evolution, either before the ancestor of Dicondylia (Zygentoma and Pterygota) or before the ancestor of Pterygota, implying that none of the MW clades was retained in winged insects.

The amino-acid sequences of the opsins in our arthropod SW clade (Supplementary Fig. S3) and physiological data (Supplementary Fig. S2; for references see Supplementary Tables S2 and S4) suggest that the SW opsin of the ancestral arthropod probably formed a UV-sensitive visual pigment. Most of the opsins in our SW clade, including *Limulus* UVOps, have a lysine residue (K) at, or next to, the position corresponding to glycine 90 in bovine rhodopsin (shifts by one amino acid occurred depending on the alignment), which was identified as the basis for UV vision in invertebrates (Salcedo et al. 2003).

Of the three subclades of UV opsins present in Multicrustacea and Allotriocarida (SWa, SWb, and SWc), Hexapoda only retained SWc. SWc1 comprises a clade of poorly characterized opsins known as *Drosophila* Rh7-like sequences, some of which might have undergone neo-functionalization (Izutsu et al. 2012; Kistenpfennig 2012; Hu et al. 2014). SWc2, in contrast, gave rise to the subclades SWc2.1 and SWc2.2, which are well-known as the insect UV- and blue-opsin clades. Interestingly, a lysine residue at the spectral tuning site suggests that some of the odonate sequences in the insect 'blue' clade might actually be UV opsins (Supplementary Fig. S3). It is therefore possible that UV sensitivity was lost several times independently in the SWc2.2 clade of Pterygota. This assumption is supported by different amino-acid residues that substitute lysine in Ephemeroptera (glutamine), Odonata (histidine), and other insect species (asparagine, glutamic acid, or methionine), but leaves unanswered the question why no such changes ever occurred in the SWc1.2 clade.

Peropsins

From the following arthropod species, we identified 11 new sequences that are similar to previously described peropsin/RGR-like genes: *Argulus siamensis* and *Calanus finmarchicus* (Crustacea); *Scutigera coleoptrata* (Myriapoda); *Metaseiulus occidentalis* (two sequences) and *Stigodyphys mimosarum* (Arachnida); *Machilis hrabei*, *Plutella xylostella* (three sequences) and *Bombyx mori* (Insecta).

The phylogenetic results of our peropsin/RGR analyses are sensitive to which genes are sampled and to assumptions of the model. Nevertheless, certain consistencies emerge. We find two reasonably supported clades of arthropod 'peropsins', one of non-insects, the other of insects (Fig. 3; Supplementary Fig. S4). Like previous authors (Hering and Mayer 2014; Battelle et al. 2015), we obtained consistent and strong support (0.952) for a clade of peropsins from non-insects, including opsins from *Limulus*, spiders, and the mite *Tetranychus*. Our current analyses add to this clade another spider opsin (*Stegodyphus*), two more mite opsins (*Metaseiulus*), and opsins from a crustacean (*Argulus*), and a myriapod (*Scutigera*). We also report insect 'peropsins'. Our new insect opsins (from *Plutella*, *Bombyx*, and *Machilis*) form a clade (moderate support of 0.775) with odonate RGR-like sequences (Futahashi et al. 2015). The arthropod non-insect and insect peropsin clades are part of a larger clade (with very weak support of 0.046) that comprises opsins from mollusks, an annelid (*Platynereis*), a rotifer (*Brachionus*), an acorn worm (*Saccoglossus*), and a crustacean (*Calanus*). We provisionally refer to these opsins as 'peropsins', because they form a rather well-supported clade (0.848) with chordate peropsins.

Discussion

Relation between visual r-opsin and type of eye

Developmental and morphological evidence suggests that the median eyes of Pancrustacea and *Limulus* are homologous with onychophoran eyes (Mayer 2006). The last common ancestor of arthropods presumably inherited a similar pair of ocellus-like organs, which were lost in Myriapoda and modified by duplication and fusion in the other euarthropod lineages (Paulus 2000; Bitsch and Bitsch 2005; Lehmann et al. 2012). Lateral compound eyes, in contrast, appeared in the arthropod stem group more than 500 mya (Paterson et al. 2011) and exist today in representatives of Chelicerata (e.g., *Limulus*), Myriapoda (e.g., *Scutigera*), and Panarthropoda (Paulus 2000; Bitsch and Bitsch 2005). Even though compound eyes were transformed in many taxa and might have evolved from a simple progenitor along several independent lineages (Nilsson and Kelber 2007), the lateral eyes of all euarthropods and in particular those of pancrustaceans are considered homologous, based on developmental data (Harzsch and Hafner 2006) and comparative studies of the nervous system (Harzsch et al. 2005).

Our phylogeny of r-opsins expressed in arthropod photoreceptors (Supplementary Figs. S1–S3) does not reflect a separate evolutionary history of opsins in median versus lateral eyes from the early Cambrian onwards, that is, for the time span during which the organs presumably diverged. Opsins in living species often are shared between both types of eyes, which is especially (though not exclusively) true for UV opsins. Eye-specific opsin paralogs exist, but originate from comparatively young duplications that occurred independently in different taxa.

Furthermore, there is evidence that opsin expression switched between types of eyes more than once. In other words, opsins expressed in median eyes were recruited from opsins expressed in lateral eyes and vice versa. All r-opsins identified as part of visual pigments in photoreceptors of arthropods (together with the enigmatic ingroup SWc1, which comprises the *Drosophila* Rh7-like sequences of unknown function) form a monophyletic sister clade to onychophoran visual r-opsins (Hering et al. 2012; Eriksson et al. 2013; Beckmann et al. 2015). Thus, the opsins of arthropod lateral eyes originally must have been co-opted from median eyes. The opposite scenario has also taken place. RhLWD opsins, for example, are preferentially expressed in the median eyes of adult dragonflies and nested within odonate opsins (Supplementary Figs. S1 and S3) primarily expressed in the larvae or in the compound eyes of adults (Futahashi et al. 2015). In some odonate species, particularly in those that lost the RhLWD ortholog, LW opsins of group E (compound eyes of adults) or C (larvae) became specific to the median eyes of the adult. This demonstrates that the involved regulatory mechanisms are quite flexible.

Is there a general pattern, in which opsin expression switches between types of eyes? Losing the gene for the major opsin in one type of eye is a plausible explanation for why a change in the expression pattern of another opsin gene might be evolutionarily advantageous. However, the scenario that both events coincide (loss of gene A and change in expression pattern of gene B) is less likely than the preceding expansion of gene B expression to photoreceptors that express gene A. This might be the case in *Ischnura asiatica*, in which an LW opsin of group E is preferentially expressed in the median eyes of adults together with the typical RhLWD (Supplementary Fig. S1; Futahashi et al. 2015). Studying the reasons and mechanisms of opsin co-expression, which is not uncommon in photoreceptors of arthropods (Arikawa et al. 2003; Jackowska et al. 2007; Mazzoni et al. 2008; Rajkumar et al. 2010; Schmeling et al. 2014; Battelle et al. 2015), could therefore help to understand switches of opsins between median and lateral eyes.

The most obvious cause for the co-option of opsins from the other type of eye would be the loss and regain of the whole visual organ, as proposed for the compound eyes of myodocopid ostracods (Parker 1995; Oakley and Cunningham 2002; Oakley 2003). Myodocopida (subclass Myodocopa) are nested phylogenetically within ostracod groups that have no eyes or only median eyes. Other pancrustacean taxa, such as some Rhizocephala (Thecostraca; Pérez-Losada et al. 2012) and all insects (Hexapoda), are in a similar position. Remipedia, the putative sister group to Hexapoda, lack eyes (Fig. 1a; Fanenbruck et al. 2004), and we have not found visual r-opsins in the transcriptome of the remiped *Xibalbanus (Speleonectes) tulumensis* (Fig. 2). Protura and Diplura, two of the three basal-branching hexapod orders, are also blind (Fig. 1b; Bitsch and Bitsch 2000).

Since the reduction of visual organs is a recurrent feature in the phylogeny of Pancrustacea (Fig. 1), and evidence for an independent origin of some lateral as well as median eyes has been presented (Oakley and Cunningham 2002; Elofsson 2006), ingroups and outgroups of those taxa, that lack one or both types of eyes, are interesting targets for investigations of r-opsin expression. Species, in which a type of eye is missing in part of the population, as in many insects with winged and wingless morphs, could also help to gain insight into changes that occur, when eyes are reduced. In the fig wasp *Ceratosolen solmsi*, for example, only females bear median eyes, but, surprisingly, the LW2 ortholog, which is specific for median eyes in bees, is the major opsin gene expressed in males (Wang et al. 2013).

The expression pattern of visual r-opsins has been studied in just a few pancrustaceans with a bias toward pterygote insects (Wernet et al. 2015), notably butterflies (Wakakuwa et al. 2007; Briscoe 2008). Median eyes were often neglected in species that possess both types of eyes (Supplementary Figs. S1 and S2). In many cases opsin expression was investigated with mRNA only, which leaves the possibility that translation into protein does not take place and no functional visual pigment exists. Especially results that were obtained by reverse transcription polymerase chain recation (RT-PCR) alone have to be treated with caution, since opsin sequences can be amplified from cDNA libraries of tissue, in which they are neither detectable by *in situ* hybridization nor at the protein level (Battelle et al. 2015). More detailed data on species from a wider range of taxa hopefully will fill many of the gaps that are left in our understanding of the evolutionary history of eyes.

Evolutionary history of visual r-opsins

The evolutionary history of visual r-opsins in Pancrustacea is by no means less dynamic than the evolutionary history of the eyes themselves. Our results suggest that the ancestral pancrustacean inherited four of five opsins that were present in its arthropod ancestor (Fig. 2; Supplementary Figs. S1–S3). We named these opsins arthropod LW2, MW1, MW2, and SW, following the tradition to label visual opsins according to the spectral sensitivity of the visual pigments they form. We are aware that the sensitivities may vary in our clades to an extent that could exceed the spectral range associated with LW, MW, or SW, a common problem of this terminology. In addition, some opsins such as members of the SWc clade might not even form visual pigments. Yet, based on the current data, the selected names represent the best possible guess as to the spectral sensitivities that the visual pigments formed by the different opsins might have had in the ancestral arthropod.

Presumably starting from a set of four opsins, the opsin repertoire of Pancrustacea soon diversified by two duplications in the SW clade, before Multicrustacea and Allotriocarida split, and by one more duplication in the SW clade and two duplications in the MW1 clade, before Branchiopoda and Hexapoda split, amounting to at least nine different opsin clades in pancrustaceans at the time, when the last common ancestor of Allotriocarida lived (one LW, three MW1, one MW2, and four SW opsins). This is a surprising number considering that vertebrates only possess five visual opsin classes, which did not diversify much except in bony fish (Bowmaker 2008).

Unlike in the MW1 and SW clades, we did not find any evidence for duplications in the LW2 clade early in pancrustacean evolution. This is the most diverse visual opsin clade in insects, however, and previous authors have therefore predicted a duplication of the insect LW opsin gene prior to the emergence of Neoptera (Spaethe and Briscoe 2004). Our data support this assumption and move the duplication event back to the last common ancestor of Hexapoda (Fig. 2; Supplementary Fig. S3).

MW opsin sequences, which are diverse in non-hexapod crustaceans, were not known from Hexapoda (Cronin and Porter 2014), but only Pterygota had been investigated. We identified MW1 and MW2 in Collembola, and MW1 in Archaeognatha, whereas we did not find any MW sequences in *Tricholepidion gertschi* (Zygentoma) or *Ephemera danica* (Ephemeroptera). Thus, opsins of both MW clades were present in the ancestral hexapod and obviously were lost stepwise in the evolution of insects.

The lack of MW opsins in Pterygota coincides with the exchange of lysine at the position responsible for UV tuning in opsins of the SWc2.2 clade. This supports the speculation raised by Bok (2013) that it might have been the loss of MW opsins that caused the evolutionary pressure to tune some insect SW opsins to longer wavelengths.

While some of our clades are distinct in our original r-opsin tree (Supplementary Figs. S1 and S2), others are only resolved after reconciliation with the species phylogeny (Fig. 2; Supplementary Fig. S3), which shuffled poorly supported nodes of the gene tree to minimize the implied number of duplications and losses. These inferences could be sensitive to the addition of new data and may thus change.

Apart from r-opsin duplications within higher taxa, we also inferred many duplications in terminal branches of our phylogeny, but we do not document those here, because they could be caused by errors in assembling transcriptomes or annotating genomes. Similarly, we do not describe terminal losses of genes, because we and previous investigators may have simply failed to detect genes in transcriptomes, genomes, or in species that were investigated by RT-PCR. There is good evidence, though, that visual r-opsins diversified extensively in certain lower pancrustacean taxa, such as ostracods, stomatopods, dragonflies, and butterflies (Oakley and Huber 2004; Briscoe 2008; Porter et al. 2009, 2013; Futahashi et al. 2015). Given that only few pancrustacean species are investigated so far, more examples are sure to follow in the future.

Peropsins

Arthropods possess genes similar to chordate peropsins and/or vertebrate RGRs (Eriksson et al. 2013; Hering and Mayer 2014; Battelle et al. 2015; Futahashi et al. 2015). Our analyses indicate that they may be more closely related to peropsins than to RGRs (Fig. 3; Supplementary Fig. S4). Even though this conclusion is sensitive to specific choices about phylogenetic analysis, we provisionally refer to these opsins as arthropod peropsins. Arthropod peropsins are now known from chelicerates, crustaceans, myriapods, and insects, implying that the ancestor of arthropods had at least one peropsin. Presence in a rotifer and several lophotrochozoans suggests that peropsin is as old as the common ancestor of protomstomes, and the existence of the gene in deuterostomes pushes its origin back to the common ancestor of bilaterians. Multiple distantly related genes are found in mollusks like *Lottia*, indicating ancient duplications. However, our current analyses are uncertain enough to make specific assignments of orthology difficult. Furthermore, we did not include related genes from cnidarians (including those called "cnidops"; Plachetzki et al. 2007), because the searches described in the "Methods" section did not recover any of them, and because they are only distantly related to arthropod opsins, the focus of this study. Nevertheless, they could shed more light on the deep history of group-4 opsins.

The functions of peropsins in pancrustaceans are poorly understood. In dragonflies, a peropsin (RGR-like) gene is expressed in the head of larvae and in the compound eyes of adults, though to a much lower extent than genes of most visual r-opsins (Futahashi et al. 2015). There is a little more data outside of pancrustaceans, suggesting some connection to eyes in chelicerate arthropods. Peropsin was detected in eyes of the wandering spider *Cupiennius salei* (Eriksson et al. 2013), in non-visual cells in the retina of the jumping spider *Hasarius adansoni* (Nagata et al. 2010), and in membranes of cells closely associated with photoreceptors in *Limulus polyphemus* (Battelle et al. 2015). A functional study of peropsin from *Hasarius adansoni* indicates molecular properties of a photoisomerase and a bistable nature (Nagata et al. 2010).

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Supplementary data

Supplementary Data available at *ICB* online.

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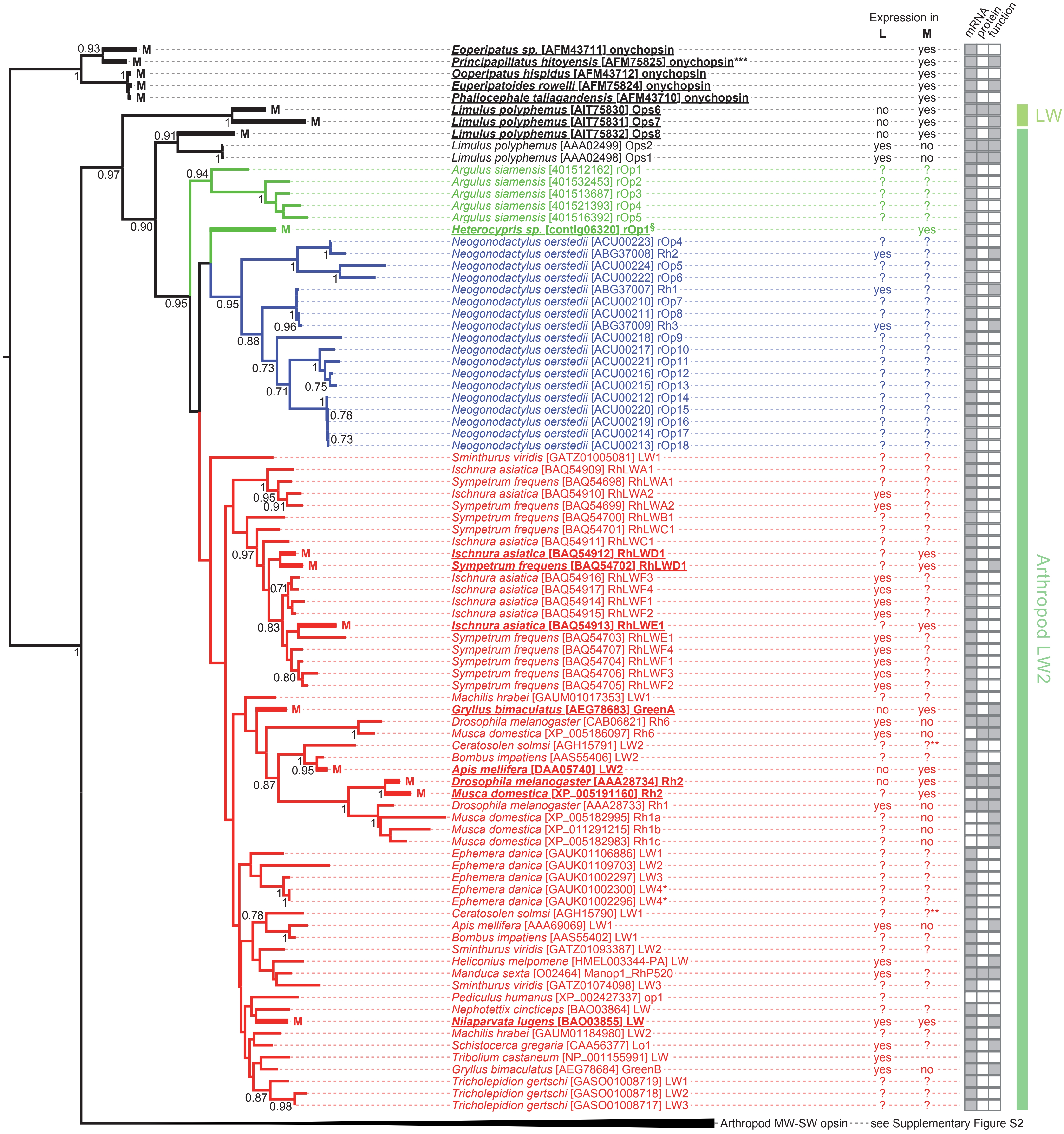


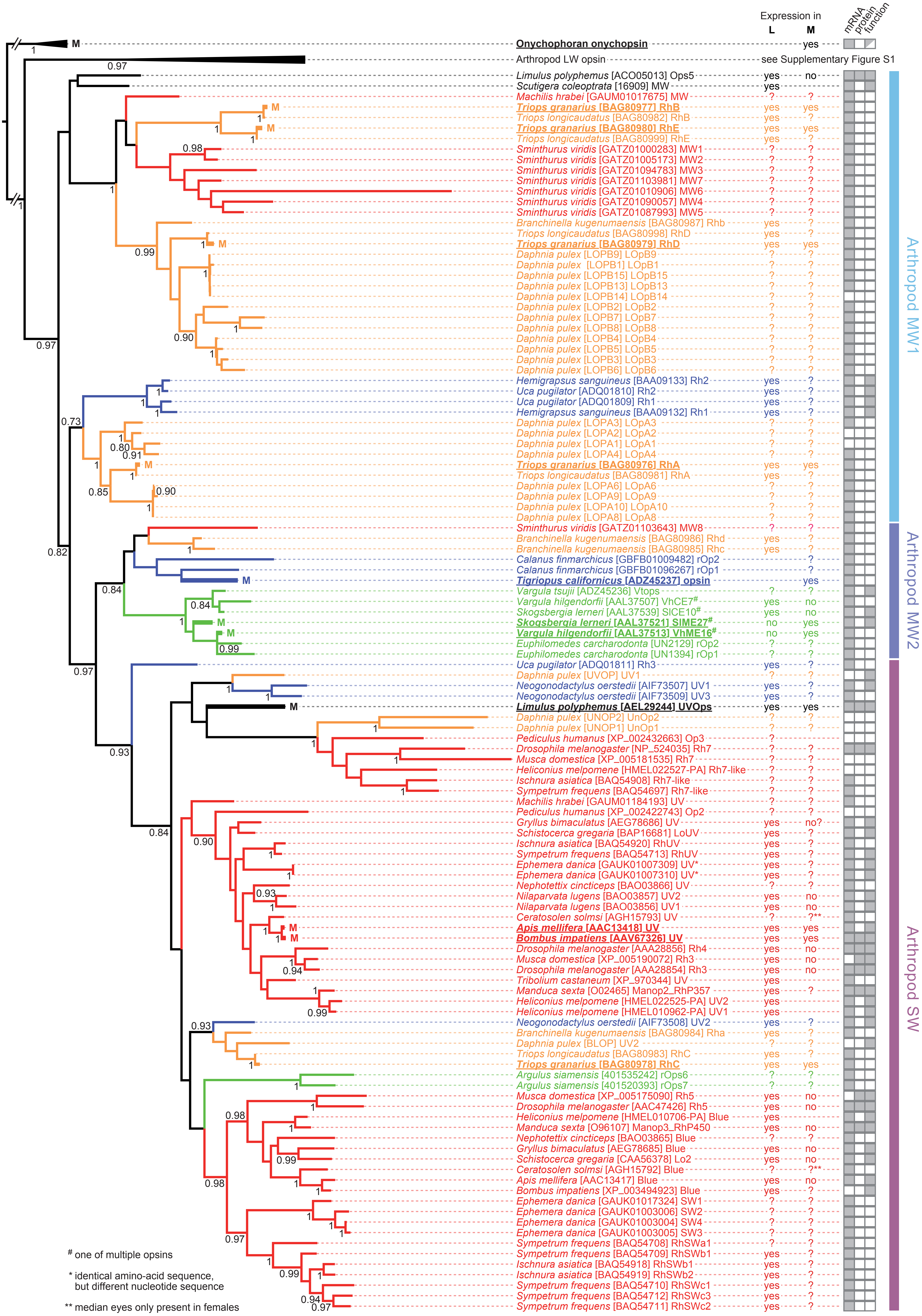
§ one of four, closely related opsins

* identical amino-acid sequence, but different nucleotide sequence

** median eyes only present in females

*** *Principapillatus hitoyensis* is referred to as *Epiperipatus cf. isthmicola* in Hering et al. (2012)

Supplementary Fig. S1 Phylogeny of the amino-acid sequences of pancrustacean LW opsins with onychophoran visual opsins as an outgroup. Branches and branch labels are colored in red, blue, and green for Hexapoda, Multicrustacea, and Oligostraca, respectively. Onychophora and *Limulus* (Chelicerata) are in black. We show only bootstrap values bigger than 0.70. Opsin expression in lateral (L) and median (M) eyes is indicated as follows: verified (yes), excluded (no), unknown or unclear (?). No entry means that the type of eye is missing. Opsins known to be expressed in median eyes are highlighted and marked by a fat final branch and an M at the end of the branch. The quality of evidence is specified by gray boxes as follows: 'mRNA' for transcriptomics, RT-PCR, Northern blot, and *in-situ* hybridization; 'protein' for Western blot and immunohistochemistry; 'function' for spectrophotometry, microspectrophotometry, and electrophysiology. For references see Supplementary Tables S2 and S4.



Supplementary Fig. S2 Phylogeny of the amino-acid sequences of pancrustacean MW-SW opsins with onychophoran visual opsins as an outgroup. Branches and branch labels are colored in red, orange, blue, and green for Hexapoda, Branchiopoda, Multicrustacea, and Oligostraca respectively. Onychophora, *Limulus* (Chelicerata), and *Scutigera* (Myriapoda) are in black. Further details are as described for Supplementary Figure S1.

Supplementary Fig. S3 Arthropod r-opsin phylogeny reconciled with the species tree. Gray branch labels denote losses of genes; otherwise branch labels are formatted as in Supplementary Figures S1 and S2. Major opsin clades are shaded in green, blue, and purple for long-, middle-, and short-wavelength (LW, MW, and SW), respectively. 'K' stands for the gain of a lysine residue at, or next to, the position corresponding to glycine 90 in bovine rhodopsin, 'X' indicates the exchange of lysine by another amino acid, and '?' means that the homologous part of the sequence is missing. In addition to the r-opsins in Supplementary Figures S1 and S2, we have included four sequences that were detected by methods different from those described in the main text. The putative LW sequence of *Scutigera* is very short, and only present in the sequence read archive (SRA). *Neogonodactylus* CRB, CRS and CRV are reported in a thesis (Bok 2013), but not yet deposited in GenBank.

Supplementary Fig. S4 Phylogeny of group-4 opsins. Maximum-likelihood analysis of the amino-acid sequences of 494 opsins from databases and transcriptomes using SATé-II. See "Methods" section of main text for details.

Supplementary Tables

The Dynamic Evolutionary History of Pancrustacean Eyes and Opsins

Miriam J. Henze and Todd H. Oakley

CONTENTS

Table S1 Literature on the occurrence of lateral and median eyes in Pancrustacea as illustrated in Figure 1.

Taxon	References
OLIGOSTRACA	
Mystacocarida	(Elofsson 1966; Elofsson and Hessler 2005; Brenneis and Richter 2010)
Branchiura	(Elofsson 1966; Hallberg 1982; Cronin 1986; Elofsson 2006)
Pentastomida	(Osche 1963)
Podocopa	(Elofsson 1966; Oakley and Cunningham 2002; Oakley 2005; Tanaka 2005; Elofsson 2006; Tsukagoshi et al. 2006)
Myodocopa	(Elofsson 1966; Land and Nilsson 1990; Parker 1995; Oakley and Cunningham 2002; Oakley 2005; Elofsson 2006)
MULTICRUSTACEA	
Malacostraca	(Elofsson 1963, 1965; Paulus 1979; Fincham 1980; Cronin 1986; Elofsson 2006; Cronin and Porter 2008)
Copepoda	(Vaissière 1961; Elofsson 1966, 1992, 2006)
Thecostraca	(Elofsson 1966; Hallberg and Elofsson 1983; Hallberg et al. 1985; Grygier 1987; Elofsson 2006; Glenner et al. 2008; Pérez-Losada et al. 2012)
ALLOTRICARIDA	
Cephalocarida	(Elofsson 1966; Elofsson and Hessler 1990)
Branchiopoda	(Elofsson 1966; Güldner and Wolff 1970; Elofsson and Odselius 1975; Paulus 1979; Cronin 1986; Diersch et al. 1999; Elofsson 2006; Reimann and Richter 2007)
Remipedia	(Fanenbruck et al. 2004; Fanenbruck and Harzsch 2005; Koenemann et al. 2009)
Hexapoda	
Protura	(Tuxen 1931; Bedini and Tongiorgi 1971; Haupt 1972; Bitsch and Bitsch 2000)
Collembola	(Paulus 1972a, 1972b, 1974, 1977, 1979; Bitsch and Bitsch 2000, 2004; Meyer-Rochow et al. 2005)
Diplura	(Bitsch and Bitsch 2000, 2004)
Archaeognatha	(Paulus 1974, 1979; Bitsch and Bitsch 2000)
Zygentoma	(Elofsson 1970; Paulus 1974; Bitsch and Bitsch 2000; Blanke et al. 2014)
Pterygota	(Wigglesworth 1941; Kalmus 1945; Parry 1947; Goodman 1970; To et al. 1971; Dickens and Eaton 1973; Weber and Renner 1976; Wilson 1978; Paulus 1979; Goodman 1981; Hallberg and Hagberg 1986; Mizunami 1994; Grünewald and Wunderer 1996; Insausti and Lazzari 2002; Klass et al. 2002; Buschbeck et al. 2003; Leschen and Beutel 2004; Beutel and Weide 2005; Grimaldi and Engel 2005; Taylor et al. 2005; Warrant et al. 2006; Berry et al. 2007; Nilsson and Kelber 2007; Beutel et al. 2010; Wei and Hua 2011; Wipfler et al. 2011; Gullan and Cranston 2014)

Table S2 Visual r-opsins from GenBank used for phylogenetic analyses, including references on the identification and expression of opsins.

Species	**Accession No.**	**Opsin name**	**Expression in lateral eyes**	**median eyes**	**References**
ONYCHOPHORA (Outgroup)					
Euonychophora					
Peripatidae					
Principapillatus hitoyensis (*Epiperipatus cf. isthmicola*)	AFM75825	onychopsin	not applicable	yes	(Hering et al. 2012; Beckmann et al. 2015)
Eoperipatus sp.	AFM43711	onychopsin	not applicable	yes	(Hering et al. 2012)
Peripatopsidae					
Euperipatoides rowelli	AFM75824	onychopsin	not applicable	yes	(Hering et al. 2012; Beckmann et al. 2015)
Phallocephale tallagandensis	AFM43710	onychopsin	not applicable	yes	(Hering et al. 2012)
Ooperipatus hispidus	AFM43712	onychopsin	not applicable	yes	(Hering et al. 2012)
CHELICERATA (Outgroup)					
Xiphosura					
Xiphosurida					
Limulus polyphemus	AAA02498	Ops1	yes	no	(Nolte and Brown 1970; Smith et al. 1993; Dalal et al. 2003; Katti et al. 2010; Battelle et al. 2014)
Limulus polyphemus	AAA02499	Ops2	yes	no	(Nolte and Brown 1970; Smith et al. 1993; Dalal et al. 2003; Katti et al. 2010; Battelle et al. 2014)
Limulus polyphemus	ACO05013	Ops5	yes	no	(Nolte and Brown 1970; Katti et al. 2010; Battelle et al. 2014)
Limulus polyphemus	AIT75830	Ops6	no	yes	(Nolte and Brown 1970; Battelle et al. 2015)
Limulus polyphemus	AIT75831	Ops7	no	yes	(Nolte and Brown 1970; Battelle et al. 2015)
Limulus polyphemus	AIT75832	Ops8	no	yes	(Nolte and Brown 1970; Battelle et al. 2015)
Limulus polyphemus	AEL29244	UVOps	yes	yes	(Nolte and Brown 1970; Battelle et al. 2014, 2015)

OLIGOSTRACA					
Ostracoda, Myodocopa					
Myodocopida					
Skogsbergia lerneri	AAL37539	SlCE10[#]	yes	no	(Huvard 1993; Oakley and Huber 2004)
Skogsbergia lerneri	AAL37521	SlME27[#]	no	yes	(Huvard 1993; Oakley and Huber 2004)
Vargula hilgendorfii	AAL37507	VhCE7[#]	yes	no	(Oakley and Huber 2004)
Vargula hilgendorfii	AAL37513	VhME16[#]	no	yes	(Oakley and Huber 2004)
Vargula tsujii	ADZ45236	Vtops	unknown	unknown	(Huvard 1993; Colbourne et al. 2011)
MULTICRUSTACEA					
Malacostraca					
Decapoda					
Hemigrapsus sanguineus	BAA09132	Rh1	yes	unknown	(Sakamoto et al. 1996)
Hemigrapsus sanguineus	BAA09133	Rh2	yes	unknown	(Sakamoto et al. 1996)
Uca pugilator	ADQ01809	Rh1	yes	unknown	(Jordão et al. 2007; Rajkumar et al. 2010)
Uca pugilator	ADQ01810	Rh2	yes	unknown	(Jordão et al. 2007; Rajkumar et al. 2010)
Uca pugilator	ADQ01811	Rh3	yes	unknown	(Rajkumar et al. 2010)
Stomatopoda					
Neogonodactylus oerstedii	ACU00223	rOp4	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00224	rOp5	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00222	rOp6	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00210	rOp7	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00211	rOp8	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00218	rOp9	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00217	rOp10	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00221	rOp11	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00216	rOp12	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00215	rOp13	unknown	unknown	(Porter et al. 2009)

[#] one of multiple candidates

Neogonodactylus oerstedii	ACU00212	rOp14	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00220	rOp15	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00219	rOp16	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00214	rOp17	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ACU00213	rOp18	unknown	unknown	(Porter et al. 2009)
Neogonodactylus oerstedii	ABG37007	Rh1	yes	unknown	(Cronin and Marshall 1989; Brown 1996; Cronin et al. 1996; Porter et al. 2007, 2009; Cronin et al. 2010)
Neogonodactylus oerstedii	ABG37008	Rh2	yes	unknown	(Cronin and Marshall 1989; Brown 1996; Cronin et al. 1996; Porter et al. 2007, 2009; Cronin et al. 2010)
Neogonodactylus oerstedii	ABG37009	Rh3	yes	unknown	(Cronin and Marshall 1989; Brown 1996; Cronin et al. 1996; Porter et al. 2007, 2009; Cronin et al. 2010)
Neogonodactylus oerstedii	AIF73507	UV1	yes	unknown	(Marshall and Oberwinkler 1999; Bok 2013; Bok et al. 2014)
Neogonodactylus oerstedii	AIF73508	UV2	yes	unknown	(Marshall and Oberwinkler 1999; Bok 2013; Bok et al. 2014)
Neogonodactylus oerstedii	AIF73509	UV3	yes	unknown	(Bok 2013; Bok et al. 2014)
Copepoda					
Harpacticoida					
Tigriopus californicus	ADZ45237	opsin	not applicable	unknown	(Colbourne et al. 2011)
ALLOTRIOCARIDA					
Branchiopoda					
Anostraca					
Branchinella kugenumaensis	BAG80984	Rha	yes	unknown	(Kashiyama et al. 2009)
Branchinella kugenumaensis	BAG80987	Rhb	yes	unknown	(Kashiyama et al. 2009)
Branchinella kugenumaensis	BAG80985	Rhc	yes	unknown	(Kashiyama et al. 2009)

Branchinella kugenumaensis	BAG80986	Rhd	yes	unknown	(Kashiyama et al. 2009)
Notostraca					
Triops granarius	BAG80976	RhA	yes	yes	(Kashiyama et al. 2009)
Triops granarius	BAG80977	RhB	yes	yes	(Kashiyama et al. 2009)
Triops granarius	BAG80978	RhC	yes	yes	(Kashiyama et al. 2009)
Triops granarius	BAG80979	RhD	yes	yes	(Kashiyama et al. 2009)
Triops granarius	BAG80980	RhE	yes	yes	(Kashiyama et al. 2009)
Triops longicaudatus	BAG80981	RhA	yes	unknown	(Kashiyama et al. 2009)
Triops longicaudatus	BAG80982	RhB	yes	unknown	(Kashiyama et al. 2009)
Triops longicaudatus	BAG80983	RhC	yes	unknown	(Kashiyama et al. 2009)
Triops longicaudatus	BAG80998	RhD	yes	unknown	(Kashiyama et al. 2009)
Triops longicaudatus	BAG80999	RhE	yes	unknown	(Kashiyama et al. 2009)
Insecta					
Odonata, Anisoptera					
Sympetrum frequens	BAQ54698	RhLWA1	unknown	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54699	RhLWA2	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54700	RhLWB1	unknown	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54701	RhLWC1	unknown	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54702	RhLWD1	unknown	yes	*S. frequens* (Futahashi et al. 2015), *S. rubicundulum* (Mobbs et al. 1981)
Sympetrum frequens	BAQ54703	RhLWE1	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54704	RhLWF1	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54705	RhLWF2	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54706	RhLWF3	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54707	RhLWF4	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54708	RhSWa1	unknown	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54709	RhSWb1	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54710	RhSWc1	yes	unknown	(Futahashi et al. 2015)

Sympetrum frequens	BAQ54711	RhSWc2	yes	unknown	(Futahashi et al. 2015)
Sympetrum frequens	BAQ54712	RhSWc2	yes	unknown	Futahashi et al. 2015
Sympetrum frequens	BAQ54713	RhUV	yes	unknown	*S. frequens* (Futahashi et al. 2015), *S. rubicundulum* (Ruck 1965; Mobbs et al. 1981; Meinertzhagen et al. 1983), *S. striolatum* and *S. vulgatum* (Labhart and Nilsson 1995)
Sympetrum frequens	BAQ54697	Rh7-like	unknown	unknown	(Futahashi et al. 2015)
Odonata, Zygoptera					
Ischnura asiatica	BAQ54909	RhLWA1	unknown	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54910	RhLWA2	yes	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54911	RhLWC1	unknown	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54912	RhLWD1	unknown	yes	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54913	RhLWE1	unknown	yes	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54914	RhLWF1	yes	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54915	RhLWF2	yes	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54916	RhLWF3	yes	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54917	RhLWF4	yes	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54918	RhSWb1	yes	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54910	RhSWb2	yes	unknown	(Futahashi et al. 2015)
Ischnura asiatica	BAQ54920	RhUV	yes	unknown	*I. asiatica* (Futahashi et al. 2015), *I. heterosticta* (Huang et al. 2014), *I. elegans* (Henze et al. 2013)
Ischnura asiatica	BAQ54908	Rh7-like	unknown	unknown	(Futahashi et al. 2015)
Orthoptera, Caelifera					
Schistocerca gregaria	CAA56377	Lo1	yes	unknown	(Schmeling et al. 2014)
Schistocerca gregaria	CAA56378	Lo2	yes	no	(Wilson 1978; Schmeling et al. 2014)
Schistocerca gregaria	BAP16681	LoUV	yes	unknown	(Schmeling et al. 2014)
Orthoptera, Ensifera					
Gryllus bimaculatus	AEG78683	GreenA	no	yes	(Henze et al. 2012)
Gryllus bimaculatus	AEG78684	GreenB	yes	no	*G. bimaculatus* (Zufall et al. 1989; Henze et al. 2012; Frolov et al. 2014), *G. campestris* (Labhart et al. 1984)

Gryllus bimaculatus	AEG78685	Blue	yes	no	*G. bimaculatus* (Zufall et al. 1989; Henze et al. 2012; Frolov et al. 2014), *G. campestris* (Labhart et al. 1984; Blum and Labhart 2000)
Gryllus bimaculatus	AEG78686	UV	yes	no?	*G. bimaculatus* (Zufall et al. 1989; Henze et al. 2012; Frolov et al. 2014), *G. campestris* (Labhart et al. 1984)
Hemiptera					
Nephotettix cincticeps	BAO03864	LW	unknown	unknown	(Matsumoto et al. 2014)
Nephotettix cincticeps	BAO03865	Blue	unknown	unknown	(Matsumoto et al. 2014)
Nephotettix cincticeps	BAO03866	UV	unknown	unknown	(Matsumoto et al. 2014)
Nilaparvata lugens	BAO03855	LW	yes	yes	(Matsumoto et al. 2014)
Nilaparvata lugens	BAO03856	UV1	yes	no	(Matsumoto et al. 2014, personal communication February 2015)
Nilaparvata lugens	BAO03857	UV2	yes	no	(Matsumoto et al. 2014, personal communication February 2015)
Psocodea					
Pediculus humanus	XP_002427337	op1	unknown	not applicable	(Kirkness et al. 2010)
Pediculus humanus	XP_002422743	op2	unknown	not applicable	(Kirkness et al. 2010)
Pediculus humanus	XP_002432663	op3	unknown	not applicable	(Kirkness et al. 2010)
Hymenoptera					
Apis mellifera	AAA69069	LW1	yes	no	(Goldsmith 1960; Autrum and v. Zwehl 1964; Menzel and Blakers 1976; Chang et al. 1996; Wakakuwa et al. 2005; Velarde et al. 2005)
Apis mellifera	DAA05740	LW2	no	yes	(Goldsmith and Ruck 1958; Velarde et al. 2005)
Apis mellifera	AAC13417	Blue	yes	no	(Goldsmith and Ruck 1958; Autrum and v. Zwehl 1964; Menzel and Blakers 1976; Townson et al. 1998; Wakakuwa et al. 2005; Velarde et al. 2005)

Apis mellifera	AAC13418	UV	yes	yes	(Goldsmith and Ruck 1958; Goldsmith 1960; Autrum and v. Zwehl 1964; Menzel and Blakers 1976; Townson et al. 1998; Wakakuwa et al. 2005; Velarde et al. 2005)
Bombus impatiens	AAS55402	LW1	unknown	unknown	(Spaethe and Briscoe 2004)
Bombus impatiens	AAS55406	LW2	unknown	unknown	(Spaethe and Briscoe 2004)
Bombus impatiens	XP_003494923	Blue	yes	unknown	(Skorupski and Chittka 2010; Sadd et al. 2015)
Bombus impatiens	AAV67326	UV	yes	yes	(Spaethe and Briscoe 2005; Skorupski and Chittka 2010)
Ceratosolen solmsi	AGH15790	LW1	unknown	females: unknown, males: not applicable	(Wang et al. 2013)
Ceratosolen solmsi	AGH15791	LW2	unknown	females: unknown, males: not applicable	(Wang et al. 2013)
Ceratosolen solmsi	AGH15792	Blue	unknown	females: unknown, males: not applicable	(Wang et al. 2013)
Ceratosolen solmsi	AGH15793	UV	unknown	females: unknown, males: not applicable	(Wang et al. 2013)
Coleoptera					
Tribolium castaneum	NP_001155991	LW	yes	not applicable	(Jackowska et al. 2007; Park et al. 2008; Richards et al. 2008)
Tribolium castaneum	XP_970344	UV	yes	not applicable	(Jackowska et al. 2007; Park et al. 2008; Richards et al. 2008)

Lepidoptera					
Manduca sexta	O02464	Manop1 RhP520	yes	unknown	(Boëthius et al. 1968; Höglund and Struwe 1970; Carlson and Philipson 1972; Pappas and Eaton 1977; White et al. 1983; Cutler et al. 1995; Chase et al. 1997; White et al. 2003)
Manduca sexta	O96107	Manop3 RhP450	yes	no	(Boëthius et al. 1968; Höglund and Struwe 1970; Carlson and Philipson 1972; Pappas and Eaton 1977; White et al. 1983; Cutler et al. 1995; Chase et al. 1997; White et al. 2003)
Manduca sexta	O02465	Manop2 RhP357	yes	unknown	(Boëthius et al. 1968; Höglund and Struwe 1970; Carlson and Philipson 1972; Pappas and Eaton 1977; White et al. 1983; Cutler et al. 1995; Chase et al. 1997; White et al. 2003)
Diptera					
Drosophila melanogaster	AAA28733	Rh1	yes	no	(Harris et al. 1976; Scavarda et al. 1983; Nichols and Pak 1985; O'Tousa et al. 1985; Zuker et al. 1985; Mismer and Rubin 1987; Pollock and Benzer 1988; Zuker et al. 1988; Feiler et al. 1992; Chou et al. 1996)
Drosophila melanogaster	AAA28734	Rh2	no	yes	(Hu et al. 1978; Feiler et al. 1988; Pollock and Benzer 1988; Zuker et al. 1988; Feiler et al. 1992; Chou et al. 1996)
Drosophila melanogaster	CAB06821	Rh6	yes	no	(Huber et al. 1997; Salcedo et al. 1999; Yasuyama and Meinertzhagen 1999; Helfrich-Förster et al. 2002; Malpel et al. 2002; Sprecher et al. 2007; Mazzoni et al. 2008; Sprecher and Desplan 2008)

Drosophila melanogaster	AAC47426	Rh5	yes	no	(Chou et al. 1996; Papatsenko et al. 1997; Salcedo et al. 1999; Malpel et al. 2002; Sprecher et al. 2007; Mazzoni et al. 2008; Sprecher and Desplan 2008)
Drosophila melanogaster	AAA28854	Rh3	yes	no	(Fryxell and Meyerowitz 1987; Zuker et al. 1987; Pollock and Benzer 1988; Feiler et al. 1992; Chou et al. 1996; Mazzoni et al. 2008)
Drosophila melanogaster	AAA28856	Rh4	yes	no	(Montell et al. 1987; Pollock and Benzer 1988; Feiler et al. 1992; Chou et al. 1996; Mazzoni et al. 2008)
Drosophila melanogaster	NP_524035	Rh7	unclear	unclear	(Bleyl 2008; Grebler 2010; Kistenpfennig 2012)
Musca domestica	XP_005182995	Rh1a	unknown	no	(Kirschfeld et al. 1988; Scott et al. 2014)
Musca domestica	XP_011291215	Rh1b	unknown	no	(Kirschfeld et al. 1988; Scott et al. 2014)
Musca domestica	XP_005182983	Rh1c	unknown	no	(Kirschfeld et al. 1988; Scott et al. 2014)
Musca domestica	XP_005191160	Rh2	unknown	yes	(Kirschfeld et al. 1988; Scott et al. 2014)
Musca domestica	XP_005186097	Rh6	yes	no	(Hardie et al. 1979; Hardie 1986; Kirschfeld et al. 1988; Scott et al. 2014), *Calliphora* (Smola and Meffert 1979; Schmitt et al. 2005)
Musca domestica	XP_005175090	Rh5	yes	no	(Hardie 1986; Kirschfeld et al. 1988; Scott et al. 2014), *Calliphora* (Smola and Meffert 1979; Schmitt et al. 2005)
Musca domestica	XP_005190072	Rh3	yes	no	(Hardie et al. 1979; Hardie 1984, 1986; Kirschfeld et al. 1988; Scott et al. 2014), *Calliphora* (Smola and Meffert 1979; Schmitt et al. 2005)
Musca domestica	XP_005181535	Rh7	unknown	unknown	(Scott et al. 2014)

Table S3 Genomes and transcriptomes searched for visual r-opsins and peropsins.

Taxon	Sample	Sequence	References	Accession no.	Visual organs
MYRIAPODA (Outgroup)					
Chilopoda Scutigeromorpha *Scutigera coleoptrata*	generic, head and anterior part of the trunk	transcriptome	(Fernández et al. 2014)	SRX462011 (assembly provided by the authors)	only lateral eyes
OLIGOSTRACA					
Branchiura Arguloida *Argulus siamensis*	whole specimens of both sexes	transcriptome	(Sahoo et al. 2013)	SRA053334	lateral and median eyes
Ostracoda, Podocopa Podocopida *Heterocypris sp.*	median eye	transcriptome	(Oakley et al. 2013)	http://dx.doi.org/10.5061/dryad.tb40v	only median eye
Ostracoda, Myodocopa Myodocopida *Euphilomedes carcharodonta*	whole embryos (males)	transcriptome	(Speiser et al. 2014)	http://dx.doi.org/10.5061/dryad.277g0	lateral and median eyes
MULTICRUSTACEA					
Copepoda Calanoida *Calanus finmarchicus*	six developmental samples of whole individuals: embryo (egg), early and late nauplii, early and late copepodites and adult females	transcriptome	(Lenz et al. 2014)	GAXK00000000.1	only median eye

table continued on next page

Taxon	**Sample**	**Sequence**	**References**	**Accession no.**	**Visual organs**
ALLOTRIOCARIDA					
Branchiopoda Cladocera *Daphnia pulex*	naturally inbred isoclonal isolate	genome	(Colbourne et al. 2011)	ACJG00000000.1	fused lateral eyes and median eye
Remipedia Nectiopoda *Xibalbanus* (*Speleonectes*) *tulumensis*	10 complete specimens	transcriptome	(von Reumont et al. 2014)	GAJM00000000.1	no eyes
Collembola Symphypleona *Sminthurus viridis*	generic, adult	transcriptome	(Misof et al. 2014)	SRX314895	lateral and median eyes
Insecta Zygentoma *Tricholepidion gertschi*	generic	transcriptome	(Misof et al. 2014)	SRX314908	lateral and median eyes
Insecta Archaeognatha *Machilis hrabei*	generic, adult	transcriptome	(Misof et al. 2014)	SRX314868	lateral and median eyes
Insecta Ephemeroptera *Ephemera danica*	generic, adult	transcriptome	(Misof et al. 2014)	SRX314815	lateral and median eyes
Insecta Lepidoptera *Heliconius melpomene*	a single male, inbred five generations of sib mating	genome	(Dasmahapatra et al. 2012)	http://www.butterflygenome.org/ assembly v1.1	only lateral eyes

Table S4 Visual r-opsins identified in the genomes and transcriptomes listed in Supplementary Table S3, and references on the expression of opsins.

			expression in		
Species	**Unique No.**	**Opsin name**	**lateral eyes**	**median eyes**	**References**
MYRIAPODA (Outgroup)					
Chilopoda					
Scutigeromorpha					
Scutigera coleoptrata	16909	MW	yes	not applicable	(Meyer-Rochow et al. 2006), see comment on interpretation of data in Nilsson and Kelber (2007)
OLIGOSTRACA					
Branchiura					
Arguloida					
Argulus siamensis	401512162	rOp1	unknown	unknown	
Argulus siamensis	401532453	rOp2	unknown	unknown	
Argulus siamensis	401513687	rOp3	unknown	unknown	
Argulus siamensis	401520393	rOp4	unknown	unknown	
Argulus siamensis	401516392	rOp5	unknown	unknown	
Argulus siamensis	401535242	rOp6	unknown	unknown	
Argulus siamensis	401521393	rOp7	unknown	unknown	
Ostracoda, Podocopa					
Podocopida					
Heterocypris sp.	contig06320	rOp1§	not applicable	yes	
Ostracoda, Myodocopa					
Myodocopida					
Euphilomedes carcharodonta	UN1394	rOp1	unknown	unknown	
Euphilomedes carcharodonta	UN2129	rOp2	unknown	unknown	
MULTICRUSTACEA					
Copepoda					
Calanoida					
Calanus finmarchicus	GBFB01096267	rOp1	not applicable	unkown	
Calanus finmarchicus	GBFB01009482	rOp2	not applicable	unknown	
ALLOTRIOCARIDA					
Branchiopoda					
Cladocera					
Daphnia pulex	LOPA1	LOpA1	unknown	unknown	
Daphnia pulex	LOPA2	LOpA2	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPA3	LOpA3	unknown	unknown	(Colbourne et al. 2011)

§one of four closely related candidates

Daphnia pulex	LOPA4	LOpA4	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPA6	LOpA6	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPA8	LOpA8	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPA9	LOpA9	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPA10	LOpA10	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB1	LOpB1	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB2	LOpB2	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB3	LOpB3	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB4	LOpB4	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB5	LOpB5	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB6	LOpB6	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB7	LOpB7	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB8	LOpB8	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB9	LOpB9	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB13	LOpB13	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	LOPB14	LOpB14	unknown	unknown	
Daphnia pulex	LOPB15	LOpB15	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	UVOP	UV1	unknown	unknown	(Colbourne et al. 2011), *D. magna* (Smith and Macagno 1990)
Daphnia pulex	BLOP	UV2	unknown	unknown	(Colbourne et al. 2011), *D. magna* (Smith and Macagno 1990)
Daphnia pulex	UNOP1	UnOp1	unknown	unknown	(Colbourne et al. 2011)
Daphnia pulex	UNOP2	UnOp2	unknown	unknown	(Colbourne et al. 2011)
Collembola					
Symphypleona					
Sminthurus viridis	GATZ01005081	LW1	unknown	unknown	
Sminthurus viridis	GATZ01093387	LW2	unknown	unknown	
Sminthurus viridis	GATZ01074098	LW3	unknown	unknown	
Sminthurus viridis	GATZ01000283	MW1	unknown	unknown	
Sminthurus viridis	GATZ01005173	MW2	unknown	unknown	
Sminthurus viridis	GATZ01094783	MW3	unknown	unknown	
Sminthurus viridis	GATZ01090057	MW4	unknown	unknown	
Sminthurus viridis	GATZ01087993	MW5	unknown	unknown	
Sminthurus viridis	GATZ01010906	MW6	unknown	unknown	
Sminthurus viridis	GATZ01103981	MW7	unknown	unknown	
Sminthurus viridis	GATZ01103643	MW8	unknown	unknown	
Insecta					
Archaeognatha					
Machilis hrabei	GAUM01017353	LW1	unknown	unknown	
Machilis hrabei	GAUM01184980	LW2	unknown	unknown	
Machilis hrabei	GAUM01017675	MW	unknown	unknown	
Machilis hrabei	GAUM01184193	UV	unknown	unknown	
Zygentoma					
Tricholepidion gertschi	GASO01008719	LW1	unknown	unknown	

Tricholepidion gertschi	GASO01008718	LW2	unknown	unknown	
Tricholepidion gertschi	GASO01008717	LW3	unknown	unknown	
Ephemeroptera					
Ephemera danica	GAUK01106886	LW1	unknown	unknown	
Ephemera danica	GAUK01109703	LW2	unknown	unknown	
Ephemera danica	GAUK01002297	LW3	unknown	unknown	
Ephemera danica	GAUK01002300	LW4*	unknown	unknown	
Ephemera danica	GAUK01002296	LW4*	unknown	unknown	
Ephemera danica	GAUK01017324	SW1	unknown	unknown	
Ephemera danica	GAUK01003006	SW2	unknown	unknown	
Ephemera danica	GAUK01003005	SW3	unknown	unknown	
Ephemera danica	GAUK01003004	SW4	unknown	unknown	
Ephemera danica	GAUK01007309	UV*	yes	unknown	(Meyer-Rochow 1982)
Ephemera danica	GAUK01007310	UV*	yes	unknown	(Meyer-Rochow 1982)
Lepidoptera					
Heliconius melpomene	HMEL003344-PA	LW	yes	not applicable	*H. erato* (Zaccardi et al. 2006), *H. erato*, *H. numata*, and *H. sara* (Struwe 1972a, b)
Heliconius melpomene	HMEL010706-PA	Blue	yes	not applicable	*H. erato* (Zaccardi et al. 2006), *H. erato*, *H. numata*, and *H. sara* (Struwe 1972a, b)
Heliconius melpomene	HMEL010962-PA	UV1	yes	not applicable	*H. melpomene*, *H. erato* (Briscoe et al. 2010; Bybee et al. 2012), *H. erato* (Zaccardi et al. 2006), *H. erato*, *H. numata*, and *H. sara* (Struwe 1972a, b)
Heliconius melpomene	HMEL022525-PA	UV2	yes	not applicable	*H. melpomene*, *H. erato* (Briscoe et al. 2010; Bybee et al. 2012), *H. erato* (Zaccardi et al. 2006), *H. erato*, *H. numata*, and *H. sara* (Struwe 1972a, b)
Heliconius melpomene	HMEL022527-PA	Rh7-like	unknown	not applicable	

*same amino-acid sequence, differences in nucleotide sequence

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