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# Decapod Crustacean Phylogenetics

edited by

**Joel W. Martin, Keith A. Crandall, and Darryl L. Felder**



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# A Shrimp's Eye View of Evolution: How Useful Are Visual Characters in Decapod Phylogenetics?

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## ABSTRACT

The decapods contain the largest diversity of eye designs and optical types of any group within the Crustacea. This variation has led to debate about the usefulness of visual system characters in the construction of decapod phylogenetic relationships. This debate, however, has not been revisited recently and has never considered the use of molecular aspects of vision. In this paper we review the current understanding of decapod eye anatomy, optics, visual pigments, and evolution. We find that there are many visual system components, including overall optical design and fine structural details, that are potentially useful for reconstructing decapod phylogenetics.

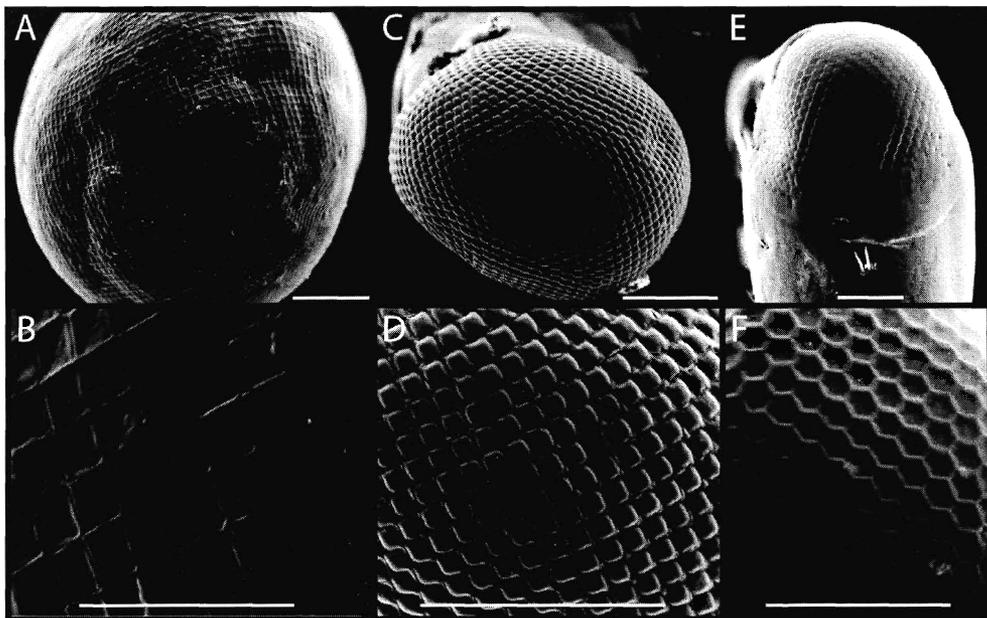
## 1 INTRODUCTION

Within crustaceans, the decapods are unrivalled in species number, morphological diversity, and ecological distribution. Correspondingly, the decapods also exhibit extraordinary variation in the optical design and morphology of their visual systems. This leads to the simple question: 'Does the observed variation in visual systems contain useful information concerning the evolution of the decapods?' The use of visual system characteristics has been debated throughout the history of decapod taxonomic studies, with just as many decapod researchers arguing for the importance of eye characters as cautioning against their use. In this review we will revisit the debate regarding decapod optical design and phylogenetics. Our goal is to move the debate forward by revising the general question posed above to: 'Does the observed variation in visual systems, both morphological and molecular, have anything useful to tell us about decapod phylogenetics?' In order to investigate this question, we will present the current knowledge regarding the taxonomic and phylogenetic distribution of optical designs and the emerging field of molecular studies on visual system evolution within the decapods.

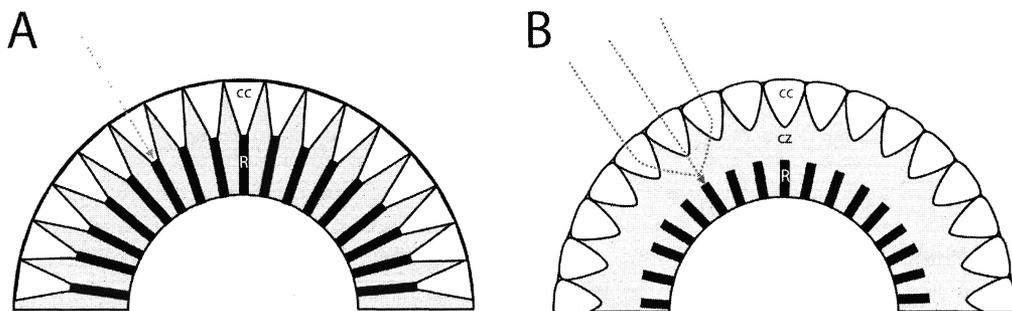
## 2 OVERVIEW OF DECAPOD VISUAL SYSTEMS

### 2.1 *Morphology*

Most Crustacea have compound eyes composed of individual receptive units called ommatidia (Fig. 1). Each ommatidium consists of optical structures (e.g., cornea, lens, crystalline cones) stacked on top of a set of fused retinular cells, which form the photoreceptive rhabdom (Fig. 2). Decapod rhabdoms are formed by eight retinular cells, with seven of these (R1–7) forming the main proximal part of the rhabdom and the eighth (R8), if present, contributing a small distal rhabdomere (Shaw & Stowe 1982). Based on results from a range of methodologies aimed at characterizing visual pigment absorbance and photoreceptor sensitivity (e.g., microspectrophotometry, electrophysiology, intracellular recordings), the spectral characteristics of the R1–7 versus the R8 retinular cells differ. Within the Decapoda, the R1–7 cells of the main rhabdom are sensitive to middle



**Figure 1.** Examples of decapod compound eyes demonstrating different facet shapes. Note that some deformation of the shape of the compound eyes has occurred due to the SEM fixation process. (A, B) *Procambarus* sp., illustrating the square facets characteristic of reflecting superposition optics (scale bars: A = 500  $\mu\text{m}$ , B = 200  $\mu\text{m}$ ). (C, D) *Stenopus hispidus*, which also contains reflecting superposition optics (scale bars = 500  $\mu\text{m}$ ). (E, F) *Clibanarius* sp. (scale bars = 100  $\mu\text{m}$ ). Although the underlying optics of this genus have not been investigated specifically, the hexagonal facets imply that this species does not contain reflecting superposition eyes. Other species within the same family (e.g., *Dardanus* sp., Diogenidae) have refracting superposition optics. (Photos by M.L. Porter.)



**Figure 2.** Schematics of the two basic compound eye optical designs found in decapod crustaceans: (A) apposition optics, (B) superposition optics. Dashed grey lines represent typical light paths through the crystalline cones to the rhabdoms. Abbreviations: cc = crystalline cone; R = rhabdom; cz = clear zone.

(blue-green) to long (red) wavelengths of light (447–570 nm), while the R8 cells are typically sensitive to violet or UV light (360–440 nm, Fig. 3, Johnson et al. 2002; Porter 2005).

As early as the late 1800s (Exner 1891), it was recognized that the compound eye ground plan can be organized into two optical types: apposition and superposition eyes (Fig. 2). Typically optimized for resolution, apposition eyes contain ommatidia that function as individual units, with screening pigments shielding each individual ommatidium from receiving light from neighboring optical components. In contrast, superposition eyes are commonly optimized for sensitivity, with the optical elements of multiple ommatidia focusing light onto a single rhabdom. Within the Crustacea as a whole, most of the visual systems investigated contain apposition optics, with superposition eyes found only in the Eumalacostraca (Nilsson 1983). In comparison, the decapods contain extraordinary variation in eye design within a single order, exhibiting four fundamentally different optical designs that can be observed among species and different life stages. While all decapod larvae use apposition optics, only a few adult decapods retain apposition eyes, including brachyuran, anomalan, and stenopodidean species (Meyer-Rochow & Reid 1994; Eguchi et al. 1997; Gaten 1998, 2007). Within superposition optics, decapods have evolved three mechanisms for focusing light from multiple ommatidial facets onto a single rhabdom: reflection, refraction, and parabolic optics. Refracting superposition eyes have been found in only two other crustacean groups in addition to the decapods, the Mysida and the Euphausiacea, while reflecting and parabolic superposition eyes are not found outside the Decapoda (Nilsson 1988, 1990).

By far the most widespread design in decapod eyes is reflecting superposition optics, found in the adults of all of the major sub- and infraorders, with the possible exception of the Thalassinidea, where eye design has yet to be rigorously investigated (Table 1). First described in crayfish and deep sea shrimp (Land 1976; Vogt 1977), this optical design uses either mirror boxes lined with a reflective surface or complete internal reflection within the crystalline cone to reflect incoming light to a particular rhabdom. In contrast, the remaining two superposition optical variants are found in only a few decapod families. Refracting superposition optics function using refractive gradients in the crystalline cone and have been described in decapods only from species of deep sea shrimp within the Benthescymidae and hermit crab species from the genus *Dardanus*, within the Diogenidae (Nilsson 1990, see Table 1). Parabolic superposition optics utilize a combination of structures including lenses, parabolic mirrors, and light guides, and have been characterized only from brachyuran and anomalan crabs (Nilsson 1988).

**Table 1.** Taxonomic distribution of adult decapod compound eye optical designs. Taxonomic designations follow the scheme of Martin & Davis (2001). Question marks indicate uncertainty about eye type. AP = apposition, RFL = reflecting, RFR = refracting, PB = parabolic.

	AP	Superposition			Reference
		RFL	RFR	PB	
<b>Dendrobranchiata</b>					
Benthescymidae			X		Nilsson 1990
Penaecidae	X				Colin Nicol & Yan 1982; Gaten 1998
Sergestidae	X				Welsh & Chace 1938; Ball et al. 1986
<b>Caridea</b>					
Crangonidae	X				Gaten 1998
Oplophoridae	X				Welsh & Chace 1937; Land 1976; Gaten et al. 1992
Palaemonidae	X				Doughtie & Rao 1984; Fincham 1984; Meyer-Rochow et al. 1992
Pandalidae	X				Gaten 1998
Pasiphaeidae	X				Gaten 1998

**Table 1.** continued.

	AP	Superposition			Reference
		RFL	RFR	PB	
<b>Stenopodidea</b>					
Spongicolidae	X				Gaten 2007
Stenopodidae		X			Richter 2002
<b>Achelata</b>					
Palinuridae		X			Eguchi & Waterman 1966; Meyer-Rochow 1975
<b>Anomala</b>					
<b>Hippoidea</b>					
Hippidae	X				Gaten 1998
<b>Galatheoidea</b>					
Aeglidae	X				Gaten 1998
Chirostylidae		X			Gaten 1998
Galatheidae		X			Kampa 1963; Gaten 1994
Porcellanidae		X			Fincham 1988; Meyer-Rochow et al. 1990
<b>Paguroidea</b>					
Diogenidae			X		Nilsson 1990
Paguridae				X	Nilsson 1988
<b>Astacidea</b>					
Nephropidae		X			Shelton et al. 1981; Gaten 1988
Astacidae		X			Vogt 1975
Cambaridae		X			Tokarski & Hafner 1984
Parastacidae		X			Bryceson 1981
<b>Brachyura</b>					
<b>DROMIACEA</b>					
Dromiidae		X			Gaten 1998
Homolidae		X			Gaten 1998
Latreilliidae		X			Gaten 1998
<b>EUBRACHYURA</b>					
<b>Raninoida</b>					
Raninidae		X			Gaten 1998
<b>Heterotremata</b>					
Geryonidae	X?			X?	Gaten 1998
Hymenosomatidae	X				Meyer-Rochow & Reid 1994
Majidae				X	Nilsson 1988
Portunidae	X?			X	Leggett & Stavenga 1981, Nilsson 1988
Xanthidae				X	Nilsson 1988
<b>Thoracotremata</b>					
Grapsidae	X				Arikawa et al. 1987
Thalassinidea					(undescribed)

On the surface of the eye, either reflecting or parabolic optics can have square ommatidial facets, while apposition, refracting, and parabolic superposition types can all have ommatidial facets ranging from circular to hexagonal. Therefore, the optical design of a visual system cannot be determined without careful investigation of the internal retinal anatomy. As the internal eye structure of only 74

species, representing 32 of ~150 decapod families, has been investigated, the possibility for new discoveries in decapod optical designs still exists.

## 2.2 Evolutionary enigma of eye design

It has been argued that, once evolved, most compound eye designs would not be replaced by another design unless the change rendered a significant optical advantage (Land 1981; Gaten 1998). It is also difficult to conceive how a visual system can move from one eye type to another without going through a near-blind intermediate (Land 1981). This difficulty in moving between states lends support to the stability of eye structure as a phylogenetic character. However, it also makes the evolution of complex eye designs, particularly of superposition optics, an evolutionary enigma.

In comparison with apposition eyes, superposition eyes are optically intricate and a rarity in animal vision (Land 1981). As most crustaceans appear to possess apposition eyes, including all decapod larvae, it is reasonable to postulate that the superposition optics found in adult decapods arose from apposition eyes (Richter 2002). Optically, it is possible to go from apposition to superposition eyes as well, as most decapods make this transition developmentally when changing from larval to adult forms (Meyer-Rochow 1975). In fact, the transparent type of apposition eye found in decapod larvae designed for planktonic life is pre-adapted for superposition optics. Nilsson (1983) showed that the mechanism for superimposing rays is present, but not used, in decapod larval eyes.

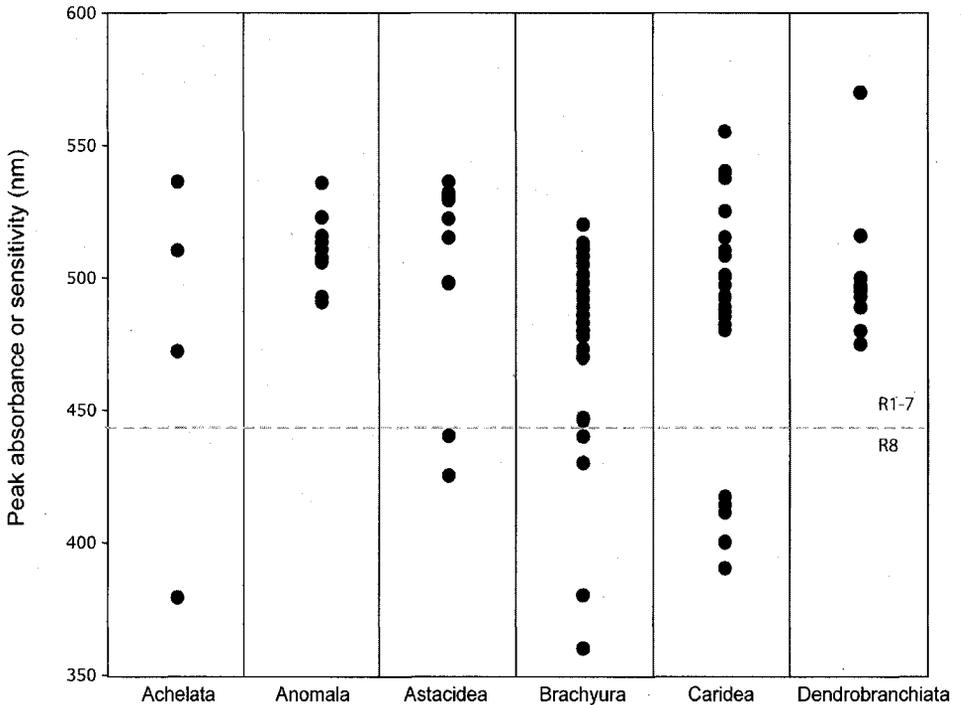
Based on taxonomic (Table 1) and phylogenetic distribution (Fig. 4), it is likely that reflecting superposition optics arose early in decapod evolution. Gaten (1998) suggested that reflecting superposition optics are symplesiomorphic for the Decapoda, having evolved only once, probably in the Devonian; however, it has also been hypothesized that Galatheidae (Anomala) independently acquired reflecting superposition eyes based on the presence of a light guide and the formation of the clear zone via elongation of the distal rhabdom (Gaten 1994). The acquisitions of the remaining eye types in decapods, then, represent transitions between superposition types or the paedomorphic retention of apposition eyes (Gaten 2007).

Because reflecting and refracting superposition eyes have approximately similar qualities and brightnesses of the images they produce (Land 1981), it is difficult to imagine the advantage of switching between eye designs. No functional insight is gained from the ecology of the families where refracting optics have been described: the Benthescymidae, a group of deep-sea shrimp within the Dendrobranchiata, and some species of hermit crabs, e.g., *Dardanus megistos*, found in brightly lit, shallow marine habitats. However, close examination of the structures in these two reflecting eye types indicate different ancestral origins, with the eyes of the Benthescymidae originating from reflecting optics and the eyes of *Dardanus* being derived from parabolic optics (Nilsson 1990). Furthermore, it is theoretically possible to transform from a parabolic into a refracting superposition eye, and various intermediates between the two types have been found (Nilsson 1990; Gaten 1998). Therefore within the anomalan Paguroidea, it is possible that the ancestral optical state is parabolic superposition, with the *Dardanus* refracting eye representing a derived optical state that was an easier transformation than returning to reflecting optics. Regardless of origin, the taxonomic and phylogenetic distributions of both refracting and parabolic superposition eye types imply that there have been multiple independent acquisitions of these eye designs within the Decapoda (Fig. 4).

## 2.3 Molecular aspects of decapod vision

A considerable amount of research has been devoted previously to decapod visual systems (see reviews by Johnson et al. 2002; Cronin 2005). However, most of this research has investigated the morphological structure (Table 1) and physiological function (Fig. 3) of the eye. Very few molecular studies of the decapod visual system have been undertaken, and none has evaluated the phylogenetic signal of the genes involved in vision.

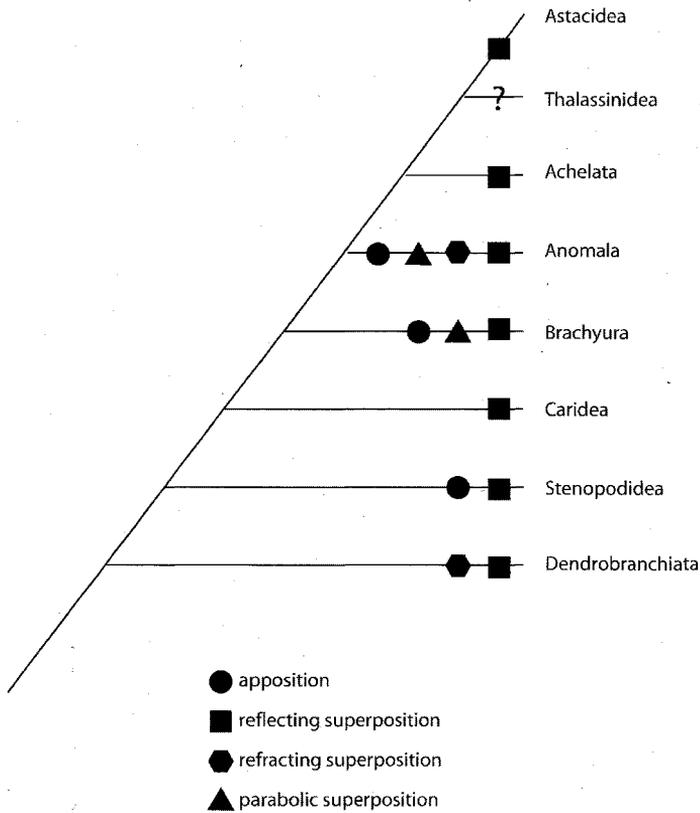
Sensitivity to light in all animal vision is based on visual pigments, which are composed of a chromophore (vitamin A derivative) bound to an integral membrane protein (opsin) and



**Figure 3.** Measurements of spectral maxima ( $\lambda_{max}$ ) of visual pigment absorbance and photoreceptor spectral sensitivities recorded from decapod species, separated by major group (suborder Dendrobranchiata, and infraorders Achelata, Anomala, Astacidea, Brachyura, and Caridea). Data were recorded using a variety of methods, including microspectrophotometry, electroretinography, intracellular recordings, and spectroscopy of pigment extracts (for original sources see Johnson et al. 2002; Porter 2005).

characterized by the wavelength of maximal absorption ( $\lambda_{max}$ ). Although there are a number of morphological and physiological methods of controlling the spectral sensitivity of a photoreceptor, the underlying molecular mechanism is the interaction between the particular amino acid sequence of the opsin protein and the type of chromophore. Two different chromophores have been documented from decapod visual pigments, but one of these, the 3-dehydroretinal form, has been found only in crayfish (Suzuki et al. 1984, 1985; Suzuki & Eguchi 1987). All other decapod species studied utilize retinal as the visual pigment chromophore; therefore, the underlying variation in decapod photoreceptor sensitivity is largely determined by the specific amino acid sequence of the opsin protein.

Currently the only available decapod opsin sequences are from two brachyuran crabs (Sakamoto et al. 1996; Kuballa et al. 2007), ten crayfish species (Hariyama et al. 1993; Crandall & Cronin 1997; Crandall & Hillis 1997), one clawed lobster (Porter et al. 2007), and two penaeid shrimp (GenBank accession: DQ825437 and Lehnert et al. 1999). Opsin sequences are notoriously bad for inferring phylogenetic relationships among species due to the high potential for convergence among gene products of a given spectral sensitivity. Because decapods contain only one or two classes of photoreceptors, each tuned to a fairly narrow portion of the visible spectrum, the problem of convergence may be magnified (Fig. 3). However, even given these constraints there are a few important insights regarding the evolution of decapods that can be gleaned from investigating decapod opsin evolution. First, all of the characterized decapod opsin sequences, with the exception of the brachyurans, cluster with insect long- to middle-wavelength sensitive opsins (Fig. 5). However, the decapod sequences do not cluster together and are scattered throughout the crustacean clade. This,



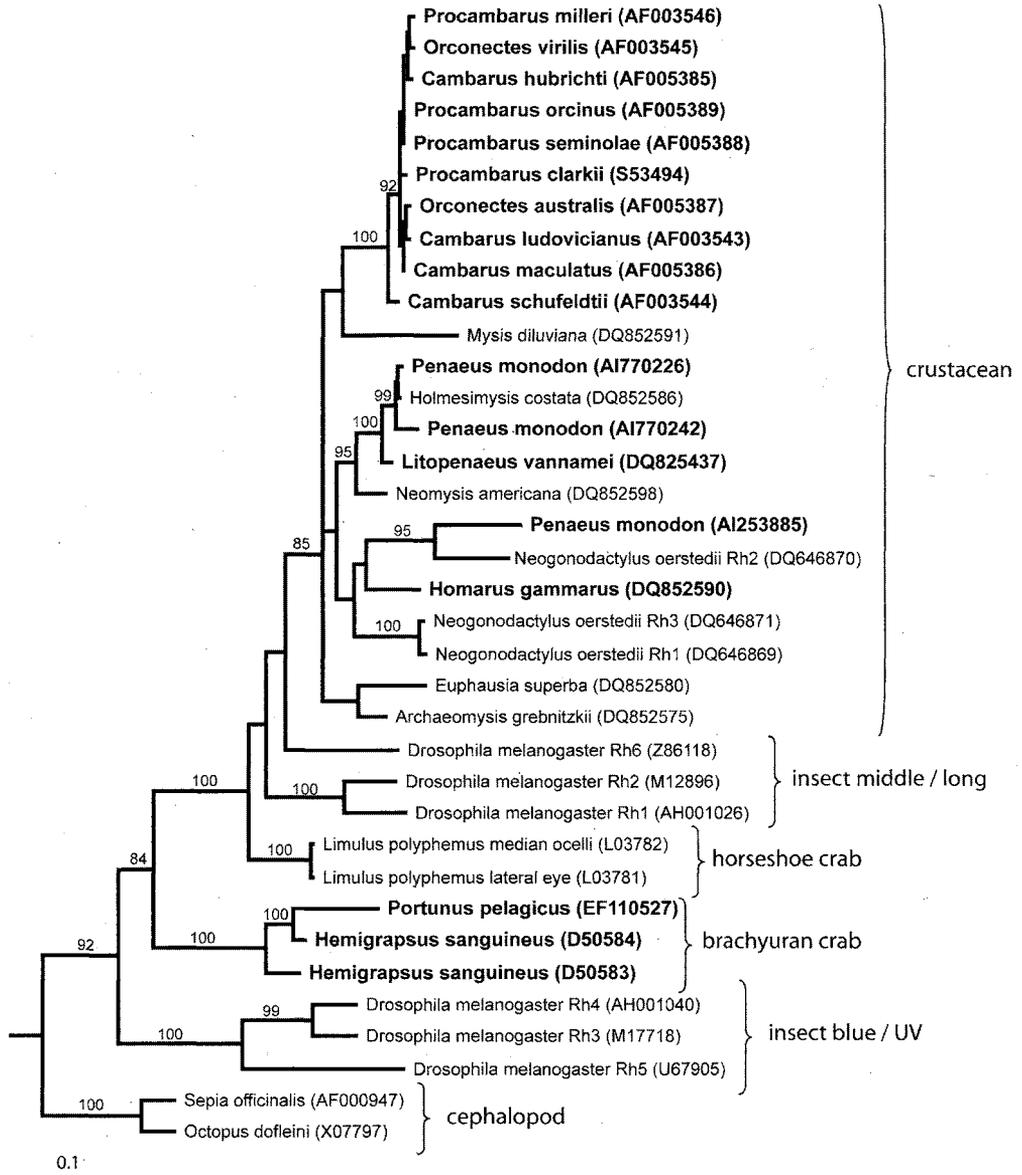
**Figure 4.** Phylogenetic distribution of optical eye designs within the major decapod lineages. Topology of the decapod relationships drawn after Porter et al. (2005).

in conjunction with the identification of three different sequences from a single species (*Penaeus monodon*), implies that opsin gene duplication within the Crustacea has been rampant. Second, the opsin sequences available for brachyuran crabs from *Hemigrapsus sanguinensius* (Sakamoto et al. 1996) and *Portunus pelagicus* (Kuballa et al. 2007) exhibit a distinct phylogenetic placement away from the other decapod sequences. This suggests that in the evolutionary history of opsin gene duplication, diversification, and loss, the brachyuran crabs have co-opted a different copy of the opsin gene from the remaining decapod lineages.

Apart from the admittedly limited information about opsin evolution, little else is known about the network of genes involved in decapod phototransduction. From studies of *Drosophila*, the gene network involved in arthropod phototransduction has been fairly well elucidated (Ranganathan et al. 1991; Zuker 1992, 1996). Few of these interacting genes have been specifically investigated in decapods, and none of the known sequences has been investigated with respect to visual function (Table 2). As opsin is likely to be the most variable gene in the visual signaling cascade due to environmental 'tuning' of the visual pigment spectral absorbance, the remaining genes in the phototransduction network may be more conserved nuclear gene targets for future phylogenetic studies.

### 3 VISUAL SYSTEM COMPONENTS AS PHYLOGENETIC CHARACTERS

Different classification schemes of the decapods have been based on a wide range of characters including behavior (Boas 1880; Borradaile 1907), gill anatomy (Bate 1888; Burkenroad 1963);



**Figure 5.** Phylogeny of decapod and selected invertebrate opsins based on maximum likelihood analyses of amino acid residues. The phylogeny was reconstructed using PHYML (Guindon & Gascuel 2003) and rooted (not shown) using bovine rhodopsin (NC\_007320), chicken pinopsin (U15762), and human melatonin receptor 1A (NM\_005958) and GPCR52 (NM\_005684). The numbers above each branch indicate the bootstrap proportion from 100 replicates (values less than 70% not shown). The major clusters of opsin sequences are indicated by taxonomic group, and, where possible, the visual pigment spectral sensitivity of each cluster is indicated by middle, long, blue, or ultraviolet (UV) sensitive. Decapod sequences are indicated in bold.

**Table 2.** List of decapod genes known to be involved in phototransduction that are available in GenBank.

---

<b>Dendrobranchiata</b>	
Penaeidae	
<i>Penaeus monodon</i>	
	Phospholipase C (PLC): AI253804
<i>Marsupenaeus japonicus</i>	
	Calmodulin: AU175456
<b>Astacidea</b>	
Cambaridae	
<i>Procambarus clarkii</i>	
	Gq-alpha subunit protein: AAB28122
Parastacidae	
<i>Cherax quadricarinatus</i>	
	Calmodulin: DQ847760, DQ847613
Nephropidae	
<i>Homarus americanus</i>	
	Calmodulin: FD467399, EH116795, CN852450
	Inositol triphosphate: FD467309, EW702750
	Phospholipids phospholipase C beta isoform (PLC): AF128539
<b>Brachyura</b>	
Portunidae	
<i>Carcinus maenas</i>	
	Gq/11-alpha subunit protein: DV944278, DV642918

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features of the head, thorax, and carapace (Saint Laurent 1979; Scholtz & Richter 1995); position of the genital openings (Guinot 1978); molecular sequence data (Ahyong & O'Meally 2004; Porter et al. 2005); as well as elements of eye design (Fincham 1980). The utility of visual system components, however, has been debated throughout the history of decapod taxonomic studies. As discussed above (see section 1.1.2), superposition eyes are intricately complex structures, making transitions between different optical types improbable. If this is true, eye structure is a stable character, and therefore the distribution of optical designs in decapods has phylogenetic significance (Fincham 1980; Land 1981; Fincham 1984). Following this line of thinking, elements of the visual system have been used as characters uniting the 'Natantia' or shrimp-like decapods (Fincham 1980) and the 'long bodied' decapods (e.g., shrimp, lobsters, and crayfish) (Land 1981), respectively. In contrast, Nilsson (1983) cautions against the use of visual elements as phylogenetic characters due to repeated, independent gains of similar optical designs.

In fact, visual systems within the decapods exhibit both stable evolutionary characters and independent gains/losses of similar designs. The evolutionary distribution of eye designs within the decapods indicates that the stem lineage most likely contained reflecting superposition optics, at least in adults (Fig. 4, Richter 2002). As the decapods are the only group of crustaceans possessing this unique optical design, reflecting optics serve as a useful character for uniting the decapods. Lineages containing different optical designs, which most assuredly have arisen independently multiple times, may still provide characters for uniting higher-level groups by detailed examination of the optical structures. For example, the refracting optics found in the Benthescymidae differ from the *Dardanus megistos* refracting eye in fine structural details, including the power of the lens and the origin of the light guide crossing the clear zone (Nilsson 1990). With further detailed investigations of decapod eye structure, these types of details may provide additional visual characters containing strong phylogenetic signal. There are also a number of decapod species that live in light-limited

environments (e.g., deep sea, caves, burrows) where eyes are often reduced or lost, and here visual system components may provide little phylogenetic signal (Gaten et al. 1998a, 1998b; Mejia-Ortiz & Hartnoll 2005).

Within decapods, the Anomala and Brachyura contain the greatest diversity of optical designs (Table 1, Fig. 4). This diversity of eye designs has led to multiple interpretations of relationships within the crab infraorders, including removal of the Dromioidea and Homoloidea from the Brachyura based on eye type (Fincham 1980). The validity of the Anomala as a coherent taxon also has been questioned based on the diversity of eye design (Fincham 1980; Gaten 1994). The true evolutionary significance of this variation is still unclear. However, within a phylogenetic context, at least some of the diversity of eye designs found in the crab groups most certainly represents independent acquisitions within specific lineages.

Finally, there are still areas of decapod vision that have not yet been thoroughly investigated, making evaluation of characters for phylogenetic reconstruction difficult. From a molecular perspective, not much is known about the decapod visual system and much work remains. However, the Brachyura appear to use a unique set of opsins not found in other decapods. In some deep sea carideans there is an accessory compound eye on the dorsal margin of the eye (Gaten et al. 1992) that, with further documentation, may provide a useful character within the carideans. Similarly, a number of decapod extraocular photoreceptors have been documented, including intracerebral and caudal photoreceptors (Wilkins & Larimer 1976; Sandeman et al. 1990); investigations of the morphological and molecular components of these extraocular structures also may provide further insight into decapod evolution.

#### 4 SUMMARY

The structure and design of decapod compound eyes reveal their function and are influenced by the behavior, ecology, and evolutionary history of the species (Schiff & Hendrickx 1997; Meyer-Rochow 2001). Here we have reviewed the components of the decapod visual system, both structural and molecular, in the hope of providing information that could lead towards a more synthetic phylogenetic reconstruction of decapod relationships. We also highlight some of the critical information still needed to understand visual system evolution within the decapods. Are the optical designs and molecular pathways involved in vision useful for decapod phylogenetic study? Our review of the current data suggests that there are many phylogenetically useful visual system components. However, much work is needed in decapod vision, including investigations of optical design in understudied groups (e.g., Achelata, Thalassinidea, and Stenopodidea) and studies of the photo-transduction cascade in general. The overall optical eye designs may be useful characters within, but not among, major lineages, and the fine structural details of each visual system may provide further insights.

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