# Chapter 1
# On Distributed Visual Systems

**Michael J. Bok and Elke K. Buschbeck**

**Abstract** Many vision scientists have been drawn to study the remarkable diversity of animal eyes, ranging from very simple light sensors to highly sophisticated image-forming eyes with specializations for color or polarization vision among others. However, relatively few studies exist that specifically draw attention to how multi-eyed visual systems (having three or more eyes) are structured, evolved, and function. Such systems, nearly all of them found among invertebrates, may be centralized, whereas others are completely distributed, spanning across most of the body. Some distributed systems consist of a set of sophisticated visual sensors, providing input to the animal's primary visual system. Other systems consist of very simple organs that, in some cases, are auxiliary to their primary visual system. In this chapter, we provide a theoretical framework on the limits and benefits of distributing vision into multiple organs. We first discuss limitations, as well as benefits, of different organizations in a set of imaginary organisms and then summarize how specific distributed systems are actually organized and how they function throughout major invertebrate groups. This summary includes highlights of the many insightful chapters that authors have contributed to this volume.

**Keywords** Eye evolution · Vision · Visual ecology · Optics · Visually guided behaviors · Eye design · Distributed vision

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## 1.1 Introduction

There are many books on the amazing diversity of visual systems invertebrate eyes exhibit (Land 1981; Cronin et al. 2014; Land and Nilsson 2012), but few are devoted to an in-depth exploration of the most unusual groups with distributed visual systems. These include several taxa that are presumably independently evolved visual systems that sample the world through many sensors, which are often distributed broadly over the body, and can be characterized by the absence of a clear anterior-posterior polarity. Others do have such polarity but rely on multiple eyes that acquire different kinds of information from different directions. Before delving into the details of such systems, it seems fruitful to put some thought into a conceptual framework that explores benefits and constraints of different ways to sample light from the environment.

In principle, there are two ways in which visual systems can increase the information content from sampling the environment. The first relates to the level of sophistication that is reached by each individual eye, and the second results from the number of eyes that are present as well as from the way in which they are positioned on the organism and oriented relative to the environment. These principal arrangements can affect many different aspects of vision, including spatial resolution, which is arguably the most important property that defines a high-functioning visual system. Other visual parameters that would be affected by the way eyes are positioned include motion vision, sensitivity at low-light levels (Warrant 2017), the discrimination of colors (van der Kooi et al. 2021) and polarization (Marshall and Cronin 2011; Horváth 2014), as well as depth perception, for example, through stereopsis (Nityananda et al. 2016). The necessary evolutionary steps that allow for the transition from a simple light sensor to a highly advanced image-forming eye already have been well-defined as arising through an evolutionary cascade generating ever-increasing information content that may drive increasingly sophisticated visually guided behaviors in a surprisingly short space of time (Nilsson 2009, 2013) (Fig. 1.1a).

## 1.2 From a Simple Light Sensor to a Sophisticated Eye

Considering a single light detecting structure, the simplest visual task is nondirectional light detection (referred to as Class I visual behavior by Nilsson (2013, 2021)) (Fig. 1.1b). Such simple light detection can provide information about the time of day and even guide simple behavioral responses by comparing light intensity from different time periods. If screening pigment is added to a photoreceptor, or the animal's body itself limits the directions from which light can be detected, then the light sensing structure is considered to be capable of directional photoreception, or Class II visual behaviors. Such animals (as our imaginary organism illustrates in Fig. 1.2a) thus have a light detector that can facilitate simple phototactic light

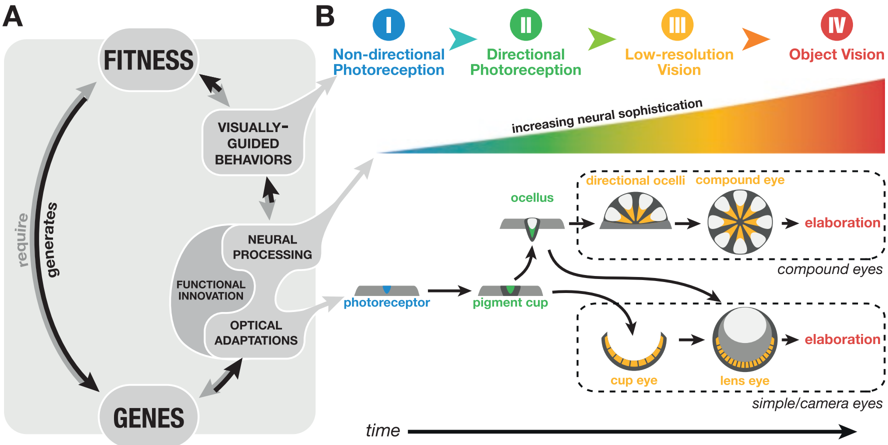

**Fig. 1.1** The evolution of complexity in visual systems and visually guided behaviors. (**a**) Selection based on behavioral success drives the evolution of all sensory systems that acquire external information. Therefore, eye evolution must be driven by the fitness generated by visually aided behaviors, with existing visual systems being harnessed, integrated, and elaborated to support emergent visual tasks. Thus, there is necessarily an optical, neural, and behavioral continuity underpinning the advancement from simple to sophisticated visual behaviors (**b**). Classes I–IV of visually guided behaviors are described in the text and have been adapted from Nilsson (2013, 2021). Coloration refers to the required functional advancements (optical innovations and neural processing) that are necessary to support the classes of visual behaviors at the top

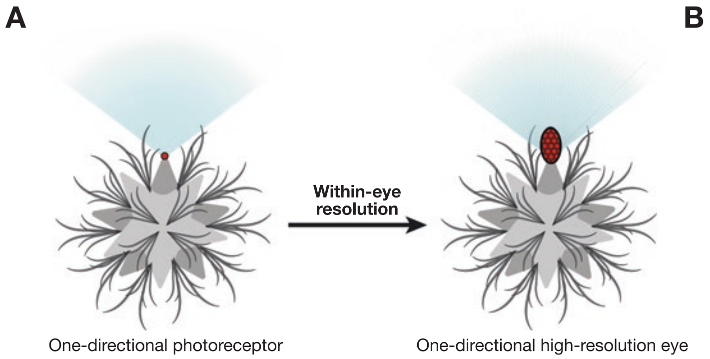

**Fig. 1.2** One way to evolve an eye is through the acquisition of spatial resolution within a light sensor. (**a**) Hypothetical organism with a simple sensor that monitors light from a general angle. (**b**) By adding resolution, details can be resolved within that space; however, unless the animals were to be transparent, a single sensor could not facilitate all-around vision

responses, such as moving toward or moving away from a light source. If only one such receptor exists, however, it continues to remain necessary to compare light reception between different time points. A good example of this mechanism is found in marine zooplankton. For example, in *Platynereis dumerilii*, it has been demonstrated that such light-guided behavior is mediated by the coupling of a simple pigment cup sensor with ciliary motor control (Jékely et al. 2008; Nilsson 2013).

The next step toward sophisticated eyes involves the addition of multiple sample points within the light sensor, hence introducing within-eye resolution and advancement to Class III, low-resolution visual behaviors (Nilsson 2013; Nilsson and Bok 2017). Depending on the level of resolution, such eyes can mediate a variety of more sophisticated behaviors as they allow animals to monitor important features such as self-motion and orientation and even help in the identification of suitable habitats. The final advancement to Class IV visual behavior, or object vision, is accompanied by a further increase in spatial resolution (as exemplified in Fig. 1.2b). This level of resolution is the basis for many more advanced visually guided behaviors. These include navigation in more complex habitats, predation, predator avoidance, and communication with conspecifics. Sophisticated Class IV visual systems are also often elaborated to emphasize specialized visual behaviors, allowing for trade-offs between spatial resolution, temporal resolution, vision at low-light sensitivity, polarization vision, and color vision (Meece et al. 2021).

No matter how sophisticated the optics, there are limitations to vision with a single eye. In part, such limitations depend on the eye type. For example, single-chamber eyes are limited in their maximum field of view. The presence of a single lens typically restricts the visual field to a cone-shaped region of space in front of the eye. Photographers who work with wide-field lenses are well aware of ever-increasing distortions that result from increasing the visual field of a single image, with a general limitation of 180°. Compound eyes, on the other hand, are good at sampling many different directions, a remarkable attribute that has even inspired engineering designs for systems that can overcome the angular limitations of single lenses (Keum et al. 2018; Sanders 1997). However, such an organization needs to maintain a minimum size, as there are optical limitations in regard to how small individual lenses can be, based on diffraction (Land and Nilsson 2012). This, in turn, limits how many individual lenses can be positioned on the surface of an eye of a certain size. Due to these optical constraints, and certainly also influenced by developmental and underlying neurological arrangements, many of the more complex bilaterian visual systems have opted for a pair of eyes on the, usually forward facing and forward moving, head end. However, across Metazoa, there are many fascinating examples of animals that have evolved sophisticated visual systems incorporating three or many more eyes, sometimes distributed broadly across the body.

## 1.3 Sophisticated Vision Through a Distributed Visual System

In a distributed light detecting system, expanded directionality of light detection also may be accomplished by multiple sensors that are oriented toward different directions in space (Fig. 1.3). For multicellular organisms, it is usually the case that

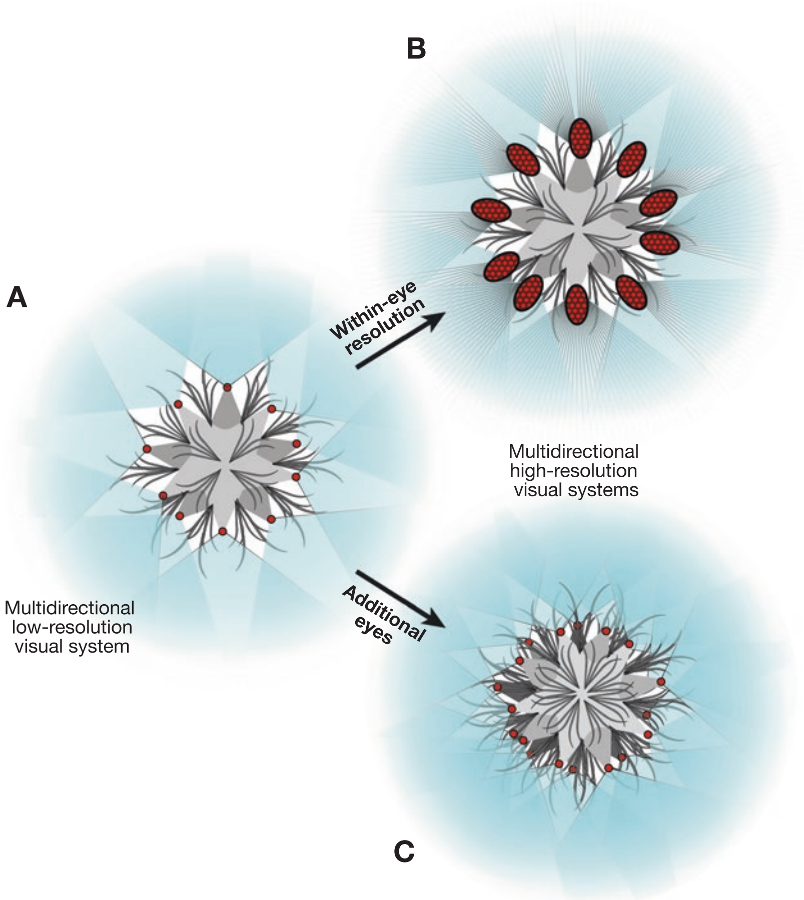

**Fig. 1.3** In principle, a distributed visual system can gain resolution in two different ways. (**a**) Distributed system with relatively low resolution. (**b**) One way to improve the visual system is to increase the within-eye resolution so that the resulting total visual resolution is contributed by a combination of within unit and in-between unit inputs. (**c**) The second way is to increase the number of sampling units

their body occludes certain directions, and hence for comprehensive sampling, it becomes necessary for the organism to distribute sensors strategically to sample different directions. In the simplest case, the number of points that can be depicted would be equal to the number of individual Class II directional light sensing structures. Hence, even the simpler distributed systems functionally are more equivalent to Class III visual systems as defined by Nilsson (2013). At least this is the case if the necessary neural substrate exists to integrate information between those units or at a minimum to allow for comparisons between individual sample points. Simple distributed light sensing systems are relatively common, and even organisms with relatively sophisticated visual systems have been found to have additional extraocular photoreceptors in various regions of the body (for examples, see (Kasai and Oshima 2006) regarding fish, (Kingston et al. 2015) regarding cephalopods, and (Kingston and Cronin 2015) regarding crayfish). In many cases, it remains elusive if and to what degree there is communication between such light sensing structures. In fact, there is evidence that some of them are important for localized regulation of the circadian clock and other nonvisual tasks, rather than a contribution to vision (Cronin and Johnsen 2016).

Following an evolutionary pathway toward visual sophistication, another way to improve spatial resolution is to increase the spatial resolution within each of the component eyes, thus increasing the overall resolution that emerges from the combined distributed system (Fig. 1.3b). As will become apparent from some of the contributions of this book, this approach can generate an impressive degree of spatial resolution. An alternative way to enhance resolution is the addition of further low-resolution eyes, which then work synergistically with other units to jointly facilitate increased levels of resolution (Fig. 1.3c). Interestingly, there are also distributed systems that are composed of both low- and high-resolution eyes. Another important consideration in distributed visual systems with numerous multicomponent eyes is the level to which information in each eye is processed at various levels of the nervous system. Is information processed locally and only a summary sent for higher processing? If resolving visual information is communicated to higher processing regions, how is overlapping redundancy and conflicting spatial information from each eye processed and interpreted? Are there higher processing levels or does vision in these eyes only cause local effects?

## 1.4 Pros and Cons of Distributed Vision (Or "To Evolve a Centralized or Distributed Visual System")

Conceptually, there are pros and cons of distributing visual sampling throughout the organism. One of the advantages includes a high level of directional flexibility. For any multicellular organism, unless it were completely transparent, the only way to truly see into all directions is to break up from where vision is being sampled and to distribute sensors over the surface or at least to some strategic locations. The field of view of each sensor may then be adjusted to fit the spacing so that seamless surround vision can be achieved, and considerable computation and integration is necessary to combine the information. Alternatively, it may be acceptable to have some gaps in a surrounding visual field, especially if combined with eye, head, or whole-body movement. However, if such computational resources are in place, an animal that samples equally well from all directions can then monitor its surroundings without moving. This would be beneficial for predation, allowing ambush of the prey without having to give away position through eye, head, or body readjustment prior to striking. This strategy also can help to facilitate rapid escape responses, for example, if an organism can detect a threat equally well from all directions. Thus, many sessile animals utilize distributed eyes to govern alarm responses that see them withdrawing into a protective tube or shell (Chap. 5). For motile animals, detecting a predator is just the first step in a successful escape, and if vision is omnidirectional, it also would be beneficial to have the necessary motor control to directly move away from the detected danger without first having to turn, a strategy that indeed is implemented in starfish (see Chap. 4).

Another advantage of such distributed systems is that there is some level of redundancy in these relatively delicate systems. Depending on the level of overlap, losing one of the units may lead to relatively minor deficiencies, as appears to be the case in chitons (Chap. 6), in which the eyes constantly decay, while new ones are formed and added (Sigwart and Sumner-Rooney 2021). For these strategies to work, the kinds of samples that are taken from different directions need to be similar in nature.

A further strategy for organisms with distributed systems is to use sensors that are placed at different locations to specialize for different visual functions. For example, some of the sensors may be specialized for orientation, while others are tuned to detect shadows, moving objects, specific colors, or even polarization, as observed among the most sophisticated distributed systems. As beautifully summarized in Chap. 10 on spiders and Chap. 2 on cnidarians, in such sophisticated visual systems, the field of view of individual eyes varies greatly according to the task at hand.

Given such advantages, why have distributed visual systems not evolved in more organisms? In reality, few organisms exist that do not have at least some level of distributed visual systems. In fact, having two eyes as most animals do (Fig. 1.4a) could be considered to constitute a distributed system. A rare example of an exceptionally centralized system is the minute larvae of ascidians, which have a single ocellus. If it is ablated, then these larvae lose the ability for phototaxis (Tsuda et al. 2003). Closer examination of the tunicate *Ciona* reveals that their visual repertoire includes the ability to escape from looming responses in addition to phototaxis and that these behaviors are mediated by distinct photoreceptors (Salas et al. 2018). These data suggest that remarkable complexity already exists in this very simple cyclopic eye that also has served as inspiration for biorobotics (Long et al. 2004).

There also are distinct benefits to having a centralized visual system. To achieve sophisticated eyes that are fully distributed, there needs to be a relatively sophisticated neural substrate that allows for the integration of the many different sources of visual information into one coherent system. Such computation might be easier where neural substrate accumulates, because there are shorter distances between inputs and processing units. Furthermore, vision often needs to be a high-speed sensory modality, so a short distance between photoreceptors and their processing substrate minimizes latency in behavioral responses. It has been argued that centralization also could have been driven by an iterative process (Martinez and Sprecher 2020). For example, if receptors were present in certain areas of an animal, then the processing of acquired information could have resulted in the addition of necessary neural substrate, the presence of which then could have favored the accumulation of additional receptors in that area.

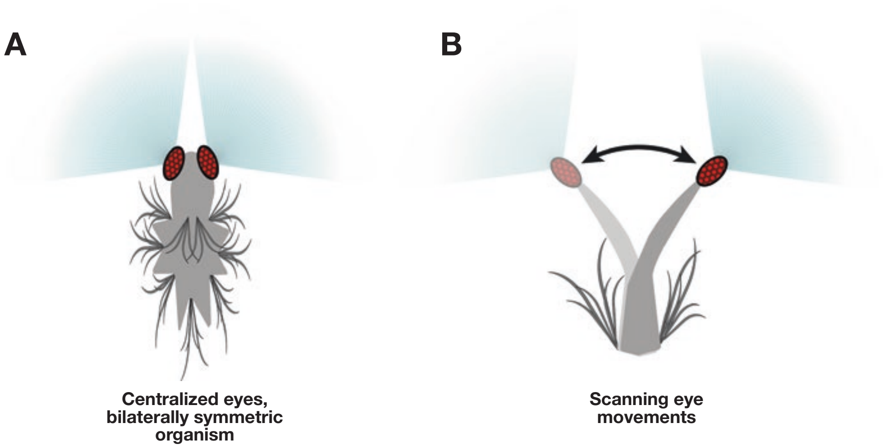

**Fig. 1.4** (**a**) Cephalization and the presence of two relatively well-developed eyes are a common strategy among bilaterally symmetric organisms. (**b**) Another way to expand the visual field or obtain directional visual information is to perform scanning, saccadic, or other eye movements

Evidence for the benefit of centralization of neural computation comes from the evolution of centralization in metazoan brains, which is thought to have emerged independently at least four times, originating from distributed systems (Northcutt 2012). Here the transition involved the formation of ganglia, which are aggregations of neural cell bodies that already bring together neural substrates. There are likely economic reasons that favor the evolution of at least some level of aggregation for the process of vision. Well-ordered centralized eyes can cover a visual area at a high resolution with a minimum of photoreceptor and optical resources. Keeping input receptors together furthermore enables retinotopic mapping and processing in centralized visual systems which is less costly and requires less processing to compensate for ambiguities or overlapping fields of view.

Many organisms do not confine themselves to either a centralized or a distributed system, but their visual system contains components of both, or may transition between dominant centralized and distributed systems at different life stages. In part, this relates to light detecting systems that were likely very common relatively early during evolution, possibly even long before they served the function of vision, perhaps to help avoid light-induced stress (Swafford and Oakley 2019). The diversity of ways in which light is being sampled is also apparent from the presence of many different types of photopigment (such as the c- or r-type opsins) and related components (such as g-proteins) that are found in animals (Nilsson 2004; Porter et al. 2012). In addition to eyelike structures, opsins also may be found on the skin or in deeper parts of the nervous system (Porter et al. 2012; Ramirez et al. 2011) as described for echinoderms (Chap. 3). Among the simplest versions of eyelike structures is the combination of a photoreceptor cell and a pigment cell (Arendt 2003). Evidence exists for multiple independent origins of distributed visual systems, presumably from such substrates. As a corollary, there are interesting points of convergence in the types of cells used and the structures of the eyes in some cases. This suggests that there are some optimal configurations that evolution tends to move toward with its available toolkit, in each respective phylum. In fact, as we hope to capture in this volume, distributed visual systems are quite common in a diverse group of different animals.

Comparing the many different systems, it becomes clear that the distribution of visual sensors often relates to the body symmetry – the radial symmetry of echinoderms and cnidarians, for example, facilitates sampling of many different directions. However, the bilateral symmetry of many other organisms includes the evolution of a body axis that is well-defined by a series of homeobox genes (McGinnis and Krumlauf 1992). This leads to organisms with distinct heads and tails and visual systems that are relatively symmetrically distributed on the two sides of the body. Another important pattern that emerges relates to the animal's ability to locomote. Many of the sessile creatures, in the absence of the ability to adjust their body position, sample approximately equally from the different directions (see Chap. 5 and Bok et al. 2016). When locomotion is directed primarily in one direction, having the visual system primarily on the head end allows the animal to detect what lies ahead and plan appropriate action during locomotion (Fig. 1.4a). Regardless of the level to which a visual system is distributed, additional spatial resolution and/or an expanded visual field can also be gained through eye movements (Land (2019) and Fig. 1.4b).

## 1.5 Survey of Diverse Distributed Visual Systems

In this volume, we seek to gather information on a wide variety of unusual visual systems that, to some extent, emphasize the properties of distributed visual systems described above (Fig. 1.5). In organizing the volume, we endeavored to include examples from most major animal phyla with an emphasis on some of the most dramatic instances of distributed and alternative visual systems. We provide a brief introduction to the various creatures and visual systems discussed in this volume. Generally, these visual systems consist of three or more eyes, sometimes positioned on a head but in many cases more widely dispersed over the body, especially in organisms that lack a head. These visual systems arose separately across a rich tapestry of independent evolutionary trajectories, culminating in unique optical innovations and neuronal processing strategies that influence visually guided behaviors.

### *1.5.1 Cnidarians*

Cnidarians are one of the earliest branching phyla of animals and are of great interest in exploring the early stages in the evolution of vision. A number of unique opsins and photoreceptors have been identified in the group, and the box jellies

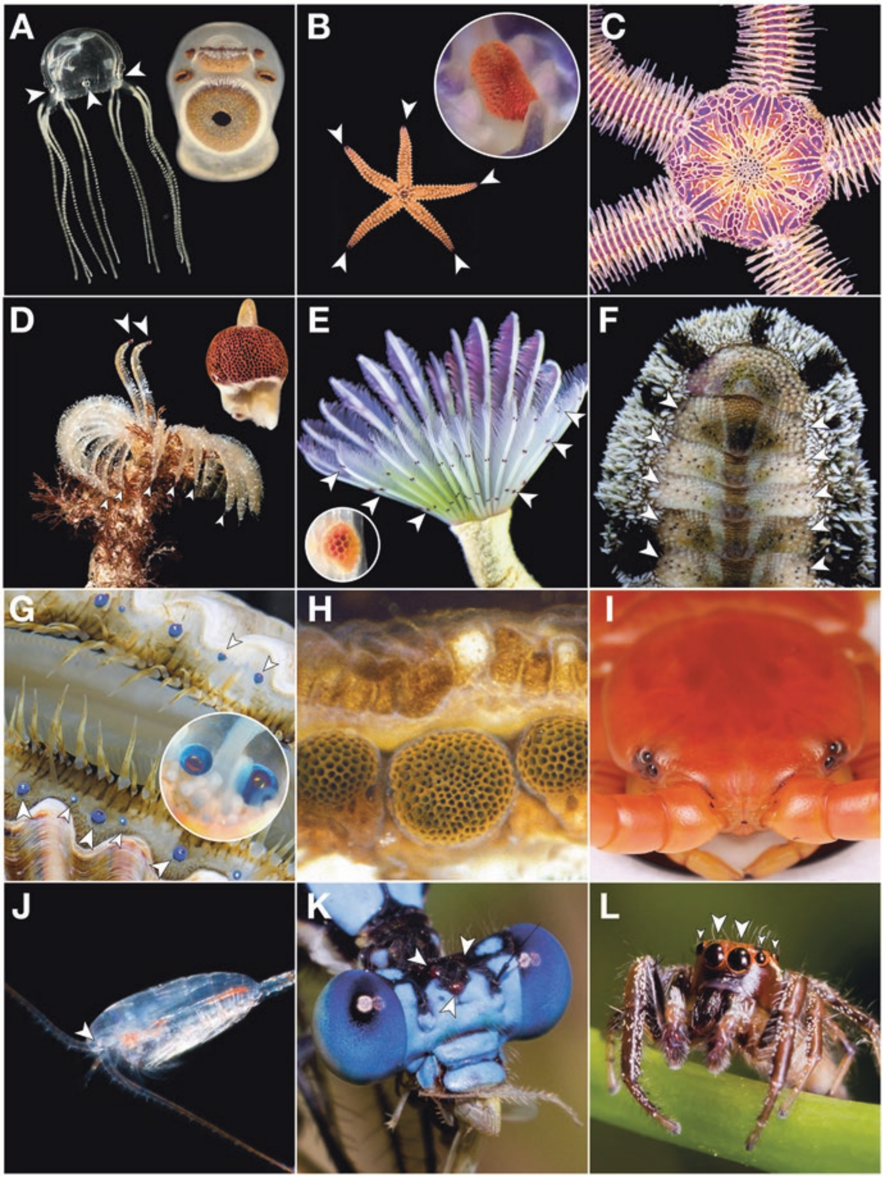

**Fig. 1.5** Distributed and multi-eyed visual systems in animals discussed in this volume. Arrowheads indicate the position of the eyes. In panels **a**, **b**, **d**, **e**, and **g**, magnified views of the eyes are inset. (**a**) Box jellyfish have four rhopalia, each containing multiple simple lens eyes and pigment cups, set around the circumference of their bell. (**b**) Starfish, such as *Marthasterias glacialis*, have compound eyes at the tips of their arms. (**c**) Brittle stars, like *Macrophiothrix nereidina*, have dispersed photoreceptors positioned along the plates that cover their arms. (**d**, **e**) Sabellid fan worms, *Acromegalomma vesiculosum* (**d**) and *Bispira* sp. (**e**), have compound eyes on their radioles. While *Bispira* has dozens of small eyes along each radiole, *Acromegalomma* has a pair of

(continued)

(Cubozoa) in particular possess a surprising diversity of strange but sophisticated eyes (Fig. 1.5a). In Chap. 2, by Sydney Birch, Natasha Picciani, Todd Oakley, and David Plachetzki, the diversity of eyes and photoreceptive systems in the cnidarians is reviewed, and their place in our understanding of eye evolution is considered. Their radially symmetric body plans and decentralized neural processing naturally lend themselves to developing a distributed visual system. However, even within this context, their eyes are quite unusual, some including multiple lens and pigment cup eyes clustered together into the same rhopalium structures (Nilsson et al. 2005). Cnidarians have a polyp stage that is most likely derived from the ancestral lifestyle of these creatures. As is the case for many sessile animals, distributed visual systems serve them well for surveying the environment for threats and initiating a startle response. Interestingly, however, the function of these eyes in cubomedusa appears to include higher-level orientation and navigation tasks, such as maneuvering around obstacles and for maintaining position in mangrove habitats through Snell's window. Here, we see a parallel to another group of radially symmetrical organisms, the echinoderms (described in the next section), in that both groups of animals can use their distributed photoreceptor networks for relatively complex navigation through their habitats. This contrasts with many distributed visual systems that have simpler roles related to alarm responses or posture control. Perhaps the lack of a cranial centralization of neural resources in these groups has led to the development of distributed eyes specifically for these more complicated tasks, rather than evolving a centralized visual system.

### *1.5.2 Echinoderms (Deuterostomes)*

Besides in echinoderms, elaborate distributed visual systems are rare in deuterostomes, perhaps owing to the large size and active lifestyles of many craniates, which have developed sophisticated paired cephalic eyes to drive high-resolution visual tasks like predation and communication. Exceptions to this are the medial pineal and parietal photoreceptive organs (Dodt 1973; Eakin and Westfall 1960). These are usually simple luminance detectors buried in the chordate brain but can

**Fig. 1.5** (continued) enlarged eyes on the tips of the dorsal-most radioles in addition to smaller eyes on the tips of several lateral radioles (small arrowheads). (**f**) Chitons, such as *Acanthopleura granulata*, have clusters of ocelli along their shell plates. (**g**, **h**) Bivalves have eyes distributed along their mantles. While scallops have simple eyes with mirror optics (**g**, *Argopecten irradians*), arc clams have compound eyes (**h**, *Barbatia cancellaria*). (**i**) Myriapods, like the centipede *Scolopendra heros*, have clusters of lateral ommatidia with various degrees of complexity. (**j**, **k**) Crustaceans and insects have diverse tripartite eyes. In copepods like *Calanus finmarchicus*, these are the primary visual system (**j**), while in insects like the damselfly *Argia apicalis* (**k**), the dorsal ocelli perform secondary visual tasks alongside the compound eyes. (**l**) Spiders have an array of eight eyes with various specializations. This is perhaps most dramatically demonstrated in jumping spiders (Salticidae). (Photo credits: **a** Jan Bielecki, Dan-Eric Nilsson (inset); **b** Camilla Elinor Kosvig-Nielsen; **c**–**e** Michael Bok; **f** Alexandra Nahm Kingston; **g** Sönke Johnsen, Dan-Eric Nilsson (inset); **h** Dan-Eric Nilsson; **i** Ted C. MacRae; **j**–**l** Michael Bok) be more elaborate in some taxa. Especially notable is the well-developed parietal eye of some lizards. However, likely due to their radial symmetry, echinoderms are a particularly interesting group of animals in the exploration of distributed systems. Accordingly, there are two chapters that are devoted to this peculiar group of animals in this book. Chapter 3, authored by Lauren Sumner-Rooney and Ullrich Lüter, provides a good overview of the relatively limited information that thus far exists on extraocular vision of some of its members, most notably sea urchins and brittle stars (Fig. 1.5c). These are characterized by a multitude of different visual organs and even have intrinsically photoreceptive nerves. Visual organs possess r-opsin and c-opsin containing visual structures, as demonstrated in a series of immunohistochemical studies that are summarized in the chapter. In some cases, known signal transduction genes are present, and pax6, a deeply conserved gene that in many species can act as a switch for eye development, has also been found in several echinoderms. In both sea urchins and brittle stars, c-opsins and r-opsins are found in part in relatively close proximity, and in part at different locations, which raises interesting questions on the synergy of these different types of visual senses.

A detailed analysis of the dispersed visual system of starfish is provided in Chap. 4 by Anders Garm, Ditte Sunberg, and Camilla Elinor Kosvig-Nielsen. While starfish vary in regard to how many arms they process, they are commonly characterized by small compound eyes on their terminal tube feet, some of which are capable of image formation, albeit at relatively low spatial frequencies, and enable low-pass filtering (Fig. 1.5b). These visual structures presumably function synergistically with extraocular structures, which are less well understood. One of the most peculiar features of starfish, and perhaps echinoderms more generally, is that the different regions appear to have relatively even contribution to gaining visual input and to using that input in their guidance of behavior. For example, as is explored further in Chap. 4, it has been observed that as starfish move, they can do so by using different arms to lead into specific directions (Pearse et al. 1987). Components of the visual system are connected to a nerve ring, which appears to play an important role in the integration of the animal's visual input and behavioral responses. If the nerve ring is bisected, the two halves appear to attempt to take independent paths. These are fascinating findings that also highlight the power of this relatively simple invertebrate system to inform our queries on how distributed information can contribute to a relatively complex decision-making process.

### *1.5.3 Polychaetes (Annelida)*

The annelids have a number of distributed and many-eyed visual systems. These include the lateral cerebral eyes on the head, which often number four in total in errant species like *Platynereis dumerilii*, while others have only two. Beyond the cerebral eyes, many polychaetes also have simple segmental ocelli along the length of the body that may function in exposure avoidance (Backfisch et al. 2013), or pygidial ocelli on the terminal segment, with murkier functionality (Ermak and

Eakin 1976). However, perhaps the most fascinating distributed eyes are found on the feeding tentacles, called radioles, of the sedentary families, Serpulidae and Sabellidae reviewed in Bok et al. (2016, 2017). Commonly referred to as fan worms, these animals project a crown of radioles from their mouths up out of their protective tubes into the water column. Since this is the only part of the animal with a view to the outside world, fan worms have evolved a number of strange ocelli on the radioles that are used in order to govern a startle response that initiates a rapid withdrawal of the crown into their tube. The ocelli are formed by a ciliary photoreceptor cell and various complements of lens and pigment cup cells, depending on the genus, and can be scattered broadly across the lengths of the radioles or consolidated into dozens of compound eyes (Fig. 1.5d, e). Interestingly, these eyes demonstrate fine gradations in the structural evolution of compound eyes in extant species, making them a great target to explore the evolution of complexity in visual systems and their neural processing.

Perhaps uniquely among distributed visual systems, certain genera of fan worms (*Acromegalomma* and *Spirobranchus*) seem to have secondarily evolved consolidated visual systems out of their distributed radiolar eyes. In both cases, there is a single pair of greatly enlarged compound eyes, with over a thousand facets each, positioned prominently on the dorsal-most pair of radioles. It could be that these eyes simply represent a more economical consolidation of visual resources, with less redundant overlap, or they could confer additional visual capabilities due to their increased organization and higher spatial resolution potential.

### *1.5.4 Bivalvia (Mollusks)*

Like the fan worms, many bivalves use distributed eyes as a burglar alarm to detect threats and initiate an alarm response. In Chap. 5, Daniel Speiser, Daniel Chappell, Jorge Audino, Alexandra Kingston, and Jeanne Serb present a thorough review of these eyes in bivalves, with a particular focus on pteriomorphs, including the spectacularly odd mirror eyes of scallops (Fig. 1.5g). Like fan worms, the eyes of bivalves are quite diverse in complexity, arrangement, and positioning. However, they exceed the fan worms in optical diversity, photoreceptor cell type, and neural integration. In this group, we see both compound (Fig. 1.5h) and simple eyes (Fig. 1.5g), including the aforementioned mirror optics of scallops. Moreover, the photoreceptors in the eyes are ciliary in some cases and rhabdomeric in others, and sometimes both photoreceptor origins are found in separate retinas within the same eyes! This lends the bivalves to explorations of parallel photoreceptor specializations in the same eyes, perhaps akin to vertebrate retinas where there are visual ciliary photoreceptors parallel to rhabdomeric-derived, melanopsin-expressing, photosensitive ganglion cells. Furthermore, in regard to function, some species may use their eyes for more than detecting threats and initiating a startle response. There is some evidence that scallops can detect particle density in the water and possibly even navigate to better habitats while swimming.

### *1.5.5 Chitons (Mollusks)*

A diverse set of distributed visual systems, from simple eye spots to image-forming organs, are found in chitons as reviewed in Chap. 6 by Daniel Chappell, Daniel Speiser, Doug Eernisse, and Alexandra Kingston. With a bilaterally symmetric body plan, this group of animals has a well-defined front end, with a cerebral nervous system. These slow-moving mollusks stand out for their variety of different types of distributed systems, which range from a system of simple aesthetes with a cluster of photoreceptors and pigment cells to shell eyes, visual structures with lenses that are made of aragonitic material (Fig. 1.5f). Over time, these lenses deteriorate, but new lenses are formed at the base of the shell plates, albeit in a less regular fashion. This unorthodox organization poses a challenge of ever-changing contributors to this distributed visual system of chitons. As discussed in the chapter, some evidence points to their ability to detect shadows cast by a potential predator, even if they are unable to locate objects in relation to their own position. Such observations stress the need for neural integration. However, how exactly do these very different visual system components contribute to the overall level of integration? One possible answer may lie in their peculiar nervous system organization, where most of the neurons are part of a medullary center rather than the more typical ganglia that are found in other organisms.

### *1.5.6 Myriapoda (Arthropoda)*

A group with particularly diverse eye organizations, and many examples of somewhat different distributed systems, are the Arthropoda. They are generally divided into the Chelicerata and Mandibulata (for a review, see Giribet and Edgecombe 2019), the latter including the insects and crustaceans (also referred to as Pancrustacea). At the base of the Mandibulata are the Myriapoda, which makes them an important group to understand regarding the ancestral state of the Pancrustacea, which have become particularly specious within the terrestrial (insects) and marine environments (crustacea). Myriapods themselves represent a remarkably diverse group with four major subgroups, one potential relationship of which has been suggested through molecular studies (Miyazawa et al. 2014) but remains subject to debate (Szucsich et al. 2020). While most myriapods have a pair of lateral eyes, the diversity in organization mirrors the diversity of the group as a whole, with substantial differences in their sophistication (Fig. 1.5i).

In Chap. 7 by Andy Sombke and Carsten Müller dives deeply into the structural organization of the different eye types that are found in myriapods. As is the case for insects, eyes can typically be found bilaterally, on the side of the head, situated medially. Structurally some of the myriapod eyes are reminiscent of insect ommatidia, with remarkable conservation regarding the number and position of some of the photoreceptor and support cells, as well as the presence of a crystallin cone and cuticular lens. In contrast, some chilopods have much more sophisticated eye units with over 1000 photoreceptor (retinula) cells. Particularly notable is a layering organization of photoreceptors, which in some of the more sophisticated eye units become elaborate. Millipede eyes also have interesting modes of eye growth, with additional eye units being added from a peripheral proliferation zone during molts, a pattern that is reminiscent of what has been found in some groups of insects (Buschbeck and Friedrich 2008).

### *1.5.7 Pancrustacea (Arthropoda)*

The most dominant type of eyes for both insects and crustaceans are the laterally located compound eyes, which may contain up to thousands of small ommatidia, as exemplified in dragonflies (Sherk 1978). Much variation exists in the way they are organized (Cronin et al. 2014; Land and Nilsson 2012; Meece et al. 2021), and some represent a distributed system within an eye through dramatic regional specialization. Good examples of this are the many differently functioning regions of ommatidia in the eyes of mantis shrimp (Marshall et al. 2007; Cronin et al. 2022), the polarization sensitive dorsal rim area of insects (Labhart and Meyer 1999), or the female-spotting sex zones in several species of fly (Land 1997; Land and Eckert 1985). In addition, a variety of different types of lateral eyes, typically referred to as stemmata, exist in the larval form or holometabolous insects (Gilbert 1994). These are particularly interesting as they have evolved from a compound eye ancestor and can manifest as anything from a compound eyelike organization to distributed ommatidial-like structures or sets of highly complex image-forming camera eyes (Buschbeck 2014). For example, in Lepidoptera and Trichoptera, stemmata typically are relatively simple (Paulus 1979; Paulus and Schmidt 2009), following the cellular organization of insect ommatidia. However, in contrast to ommatidia that are part of a compound eye, these visual units have drifted apart from each other, each sampling a different area, and hence they have evolved into a distributed system of stemmata rather than manifesting one cohesive eye. In other groups, such as Coleoptera, some insects have evolved stemmata that are greatly enlarged and comprise extended retinas, as exemplified by tiger beetle larvae (Toh and Okamura 2007) and diving beetle larvae (Mandapaka et al. 2006). The latter include stemmata that are particularly well suited for underwater prey capture, with complex optics and multiple retinas (Stowasser and Buschbeck 2014).

Yet another type of eye found among Pancrustacea is medial, tripartite eye structures that are thought to be homologous to the anterior-median eyes of spiders (Paulus 1979; Friedrich 2006; Morehouse et al. 2017). These are the naupliar eyes in crustaceans (Fig. 1.5j) and dorsal ocelli in insects (Fig. 1.5k). In crustaceans, most larval forms have a naupliar eye (also called frontal eyes) located adjacent to the brain, which persists into adulthood in many cases (Elofsson 2006; Cronin et al. 2017), while the dorsal ocelli in insects are mainly associated with adult forms. The dorsal ocelli and naupliar eyes are both composed of three pigment cup photoreceptors oriented in a manner to potentially aid in stabilization or orientation in flight or in open water, respectively. In their most simplistic forms, these visual systems may not mediate any visual behavior more complex than this role as an optical statocyst. However, in both cases, there are examples where these eyes are expanded significantly in size and complexity, suggesting more advanced functional roles, and, in the case of the naupliar eyes in copepods, even function as the primary visual system. The dorsal ocelli of insects are discussed in detail here in Chap. 8 by Baird and Yilmaz, while the extraordinary elaboration of the naupliar eyes of copepods is discussed in Chap. 9 by Mireille Steck, Kristina Theam, and Megan Porter.

### *1.5.8 Arachnida (Arthropoda)*

Some of the most sophisticated, high-functioning distributed systems are found among the Chelicerata. Ancient visual systems, as exhibited by horseshoe crabs (*Limulus*), have laterally situated compound eyes and relatively simple median eyes. This method of distributing visual organs is reminiscent of the Pancrustacea, despite major structural differences (Barlow 2009; Battelle 2006; Fahrenbach 1968). Divergence from this organization, however, is apparent in many of the other chelicerate groups, notably Arachnida. For example, in scorpions, the lateral eyes are composed of groups of single-chamber lens eyes that vary in number and position (Miether and Dunlop 2016). Arguably the most sophisticated distributed systems here are the eyes of spiders (Fig. 1.5l). Following the amazing diversity of spiders themselves, there is considerable diversity as well in the layout and function of specific eyes, as synthesized neatly in Chap. 10 by Alex Windsor, Nathan Morehouse, and Elizabeth Jakob. These findings are particularly interesting as most of the spider eyes have evolved from compound eyes whereas the anterior-median eyes share their developmental origin with those of insect ocelli (Morehouse et al. 2017).

In many cases, the details as to how the visual system functions relate to the many different hunting strategies that are being employed, but the general layout most likely follows a relatively conserved developmental plan (Morehouse et al. 2017). Particularly elaborate are the visual systems of salticids, jumping spiders, which have high-resolution anterior-median eyes that scan their prey with variously sophisticated color vision. As reviewed in the chapter, these spiders exhibit an elaborate division of labor among their different eyes. Specifically, it has been established with the help of a sophisticated eye tracker that their anterior-lateral eyes, which have a relatively large visual field, precisely direct the boomerang-shaped retina of the high-resolution anterior-median eyes (Land 1969, 1985), onto particularly important parts of the visual field. If a female spider faces a male, this includes specific aspects of his beautifully iridescently colored body parts, as he performs an elaborate courtship dance in front of her.

## 1.6 Summary/Conclusions

As we have begun to summarize in this chapter, examples of distributed and many-eyed visual systems are extremely diverse in nature. Distributing the acquisition of information to different organs has various advantages, and a diverse set of impressive solutions have emerged in the animal kingdom in response to a variety of environmental, developmental, and ecological pressures faced by the animals that use them. Upcoming chapters in this volume provide up-to-date reviews on some of the most prominent examples of such distributed systems. They differ from consolidated visual systems in significant ways and offer unique benefits and challenges.

Distributed visual systems may be useful in the rapidly growing fields of bioinspired distributed sensing and processing applications. For example, what can nature teach us about how resilient distributed systems deal with redundancy, overlap, and conflicting information in order to generate an accurate picture of the environment? How is that picture or internalized view of the outside world used to drive the behavior of an animal, or, for our uses, the environmental monitoring system, or perhaps a swarm of autonomous robots?

Despite the wealth of fascinating research detailed in this volume, distributed visual systems historically have been relatively poorly understood, and we hope that this book will illustrate to our readers that there is great potential in continuing to unravel their secrets.

## References

Arendt D (2003) Evolution of eyes and photoreceptor cell types. Int J Dev Biol 47:563–571

Backfisch B, Veedin Rajan VB, Fischer RM et al (2013) Stable transgenesis in the marine annelid Platynereis dumerilii sheds new light on photoreceptor evolution. Proc Natl Acad Sci U S A 110:193–198

Barlow RB (2009) Vision in horseshoe crabs. In: Tanacredi JT, Botton ML, Smith D (eds) Biology and conservation of horseshoe crabs. Springer, Boston, pp 223–235

Battelle B-A (2006) The eyes of Limulus polyphemus (Xiphosura, Chelicerata) and their afferent and efferent projections. Arthropod Struct Dev 35:261–274

Bok MJ, Capa M, Nilsson D-E (2016) Here, there and everywhere: the radiolar eyes of fan worms (Annelida, Sabellidae). Integr Comp Biol 56:784–795

Bok MJ, Porter ML, Ten Hove HA et al (2017) Radiolar eyes of serpulid worms (Annelida, Serpulidae): structures, function, and phototransduction. Biol Bull 233:39–57

Buschbeck EK (2014) Escaping compound eye ancestry: the evolution of single-chamber eyes in holometabolous larvae. J Exp Biol 217:2818–2824

Buschbeck EK, Friedrich M (2008) Evolution of insect eyes: tales of ancient heritage, deconstruction, reconstruction, remodeling, and recycling. Evol: Educ Outreach 1:448–462

Cronin TW, Johnsen S (2016) Extraocular, non-visual, and simple photoreceptors: an introduction to the symposium. Integr Comp Biol 56:758–763

Cronin TW, Johnsen S, Justin Marshall N, Warrant EJ (2014) Visual ecology

Cronin TW, Bok MJ, Lin C (2017) Crustacean larvae – vision in the plankton. Integr Comp Biol 57:1139–1150

Cronin TW, Porter ML, Bok MJ, Caldwell R, Marshall J (2022) Color vision in stomatopod crustaceans. Phil Trans R Soc. In press

Dodt E (1973) The parietal eye (pineal and parietal organs) of lower vertebrates. In: Berlucchi G, Brindley GS, Brooks B et al (eds) Visual centers in the brain. Springer Berlin Heidelberg, Berlin/Heidelberg, pp 113–140

Eakin RM, Westfall JA (1960) Further observations on the fine structure of the parietal eye of lizards. J Biophys Biochem Cytol 8:483–499

Elofsson R (2006) The frontal eyes of crustaceans. Arthropod Struct Dev 35:275–291

Ermak TH, Eakin RM (1976) Fine structure of the cerebral and pygidial ocelli in Chone ecaudata (Polychaeta: Sabellidae). J Ultrastruct Res 54:243–260

Fahrenbach WH (1968) The morphology of the eyes of limulus. Z Zellforsch Mikrosk Anat 93:451–483

Friedrich M (2006) Ancient mechanisms of visual sense organ development based on comparison of the gene networks controlling larval eye, ocellus, and compound eye specification in Drosophila. Arthropod Struct Dev 35:357–378

Gilbert C (1994) Form and function of stemmata in larvae of holometabolous insects. Annu Rev Entomol 39:323–349

Giribet G, Edgecombe GD (2019) The phylogeny and evolutionary history of arthropods. Curr Biol 29:R592–R602

Horváth G (2014) Polarized light and polarization vision in animal sciences. Springer. https://doi.org/10.1007/978-3-642-54718-8

Jékely G, Colombelli J, Hausen H et al (2008) Mechanism of phototaxis in marine zooplankton. Nature 456:395–399

Kasai A, Oshima N (2006) Light-sensitive motile iridophores and visual pigments in the neon tetra, Paracheirodon innesi. Zool Sci 23:815–819

Keum D, Jang K-W, Jeon DS et al (2018) Xenos peckii vision inspires an ultrathin digital camera. Light Sci Appl 7:80

Kingston ACN, Cronin TW (2015) Short- and long-wavelength-sensitive opsins are involved in photoreception both in the retina and throughout the central nervous system of crayfish. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 201:1137–1145

Kingston ACN, Kuzirian AM, Hanlon RT, Cronin TW (2015) Visual phototransduction components in cephalopod chromatophores suggest dermal photoreception. J Exp Biol 218:1596–1602

Labhart T, Meyer EP (1999) Detectors for polarized skylight in insects: a survey of ommatidial specializations in the dorsal rim area of the compound eye. Microsc Res Tech 47:368–379

Land MF (1969) Structure of the retinae of the principal eyes of jumping spiders (Salticidae: dendryphantinae) in relation to visual optics. J Exp Biol 51:443–470

Land MF (1981) Optics and vision in invertebrates. In: Handbook of sensory physiology, vol VII/6B, pp 471–592

Land MF (1985) The morphology and optics of spider eyes. In: Barth FG (ed) Neurobiology of arachnids. Springer Berlin Heidelberg, Berlin/Heidelberg, pp 53–78

Land MF (1997) Visual acuity in insects. Annu Rev Entomol 42:147–177

Land M (2019) Eye movements in man and other animals. Vis Res 162:1–7

Land MF, Eckert H (1985) Maps of the acute zones of fly eyes. J Comp Physiol A 156:525–538

Land MF, Nilsson D-E (2012) Animal eyes

Long JH, Lammert AC, Pell CA et al (2004) A navigational primitive: biorobotic implementation of cycloptic helical klinotaxis in planar motion. IEEE J Ocean Eng 29:795–806

Mandapaka K, Morgan RC, Buschbeck EK (2006) Twenty-eight retinas but only twelve eyes: an anatomical analysis of the larval visual system of the diving beetle Thermonectus marmoratus (Coleoptera: Dytiscidae). J Comp Neurol 497:166–181

Marshall J, Cronin TW (2011) Polarisation vision. Curr Biol 21:R101–R105

Marshall J, Cronin TW, Kleinlogel S (2007) Stomatopod eye structure and function: a review. Arthropod Struct Dev 36:420–448

Martinez P, Sprecher SG (2020) Of circuits and brains: the origin and diversification of neural architectures. Front Ecol Evol 8:82

McGinnis W, Krumlauf R (1992) Homeobox genes and axial patterning. Cell 68:283–302

Meece M, Rathore S, Buschbeck EK (2021) Stark trade-offs and elegant solutions in arthropod visual systems. J Exp Biol 224. https://doi.org/10.1242/jeb.215541

Miether ST, Dunlop JA (2016) Lateral eye evolution in the arachnids. Arachnology 17:103–119

Miyazawa H, Ueda C, Yahata K, Su Z-H (2014) Molecular phylogeny of Myriapoda provides insights into evolutionary patterns of the mode in post-embryonic development. Sci Rep 4:4127

Morehouse NI, Buschbeck EK, Zurek DB et al (2017) Molecular evolution of spider vision: new opportunities, familiar players. Biol Bull 233:21–38

Nilsson D-E (2004) Eye evolution: a question of genetic promiscuity. Curr Opin Neurobiol 14:407–414

Nilsson D-E (2009) The evolution of eyes and visually guided behaviour. Philos Trans R Soc Lond Ser B Biol Sci 364:2833–2847

Nilsson D-E (2013) Eye evolution and its functional basis. Vis Neurosci 30:5–20

Nilsson D-E (2021) The diversity of eyes and vision. Annu Rev Vis Sci 7:19–21

Nilsson D-E, Bok MJ (2017) Low-resolution vision – at the hub of eye evolution. Integr Comp Biol 57:1066–1070

Nilsson D-E, Gislén L, Coates MM et al (2005) Advanced optics in a jellyfish eye. Nature 435:201–205

Nityananda V, Tarawneh G, Rosner R et al (2016) Insect stereopsis demonstrated using a 3D insect cinema. Sci Rep 6:18718

Northcutt RG (2012) Evolution of centralized nervous systems: two schools of evolutionary thought. Proc Natl Acad Sci U S A 109(Suppl 1):10626–10633

Paulus HF (1979) Eye structure and the monophyly of the Arthropoda. In: Gupta AP (ed) Arthropod phylogeny. Van Nostrand Reinhold, New York, pp 299–383

Paulus VHF, Schmidt M (2009) Evolutionswege zum Larvalauge der Insekten: Die Stemmata der Trichoptera und Lepidoptera. J Zool Syst Evol Res 16:188–216

Pearse V, Pearse J, Buchsbaum M, Buchsbaum R (1987) Living invertebrates

Porter ML, Blasic JR, Bok MJ et al (2012) Shedding new light on opsin evolution. Proc Biol Sci 279:3–14

Ramirez MD, Speiser DI, Pankey MS, Oakley TH (2011) Understanding the dermal light sense in the context of integrative photoreceptor cell biology. Vis Neurosci 28:265–279

Salas P, Vinaithirthan V, Newman-Smith E et al (2018) Photoreceptor specialization and the visuo-motor repertoire of the primitive chordate Ciona. J Exp Biol 221(7):jeb177972

Sanders JS (1997) Ultrawide-field-of-view imaging optical system designs based on arthropod vision systems. In: Acquisition, tracking, and pointing XI

Sherk TE (1978) Development of the compound eyes of dragonflies (Odonata). III. Adult compound eyes. J Exp Zool 203:61–80

Sigwart JD, Sumner-Rooney L (2021) Continuous and regular expansion of a distributed visual system in the eyed chiton *Tonicia lebruni*. Biol Bull 240:23–33

Stowasser A, Buschbeck EK (2014) How aquatic water-beetle larvae with small chambered eyes overcome challenges of hunting under water. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 200:911–922

Swafford AJM, Oakley TH (2019) Light-induced stress as a primary evolutionary driver of eye origins. Integr Comp Biol 59:739–750

Szucsich NU, Bartel D, Blanke A et al (2020) Four myriapod relatives – but who are sisters? No end to debates on relationships among the four major myriapod subgroups. BMC Evol Biol 20:144

Toh Y, Okamura J-Y (2007) Morphological and optical properties of the corneal lens and retinal structure in the posterior large stemma of the tiger beetle larva. Vis Res 47:1756–1768

Tsuda M, Sakurai D, Goda M (2003) Direct evidence for the role of pigment cells in the brain of ascidian larvae by laser ablation. J Exp Biol 206:1409–1417

van der Kooi CJ, Stavenga DG, Arikawa K et al (2021) Evolution of insect color vision: from spectral sensitivity to visual ecology. Annu Rev Entomol 66:435–461

Warrant EJ (2017) The remarkable visual capacities of nocturnal insects: vision at the limits with small eyes and tiny brains. Philos Trans R Soc Lond Ser B Biol Sci 372:20160063