Charles Darwin was acutely aware of the need to account for the evolution of 'organs of extreme perfection' such as the eye and, in particular, of the importance of demonstrating that numerous gradations in complexity have existed, with each intermediate stage having provided some kind of advantage to its possessor (Darwin 1859). In recent years, there has been remarkable progress in understanding how the eyes of invertebrate and vertebrate animals have evolved, and in this Theme Issue leading figures in the field draw together our current understanding.

Eyes of one kind or another are present in perhaps 95 per cent of all animal species (Land & Nilsson 2002), indicating that imaging vision provides a great advantage in numerous environments. The spatial acuity (or optical resolving power) of these eyes ranges from spectacularly high in the camera-style eyes of vertebrates and cephalopods, through moderate in the compound eyes of arthropods, to very low in the eyes (or eye-spots) of certain 'primitive' invertebrate species.

Indeed, it is a matter of semantics as to what comprises an eye. Common parlance usually adopts a fairly stringent definition, requiring optical imaging capabilities, as, for example, in a camera-style eye or a compound eye. However, in the eye evolution field, a looser definition has often been adopted, encompassing any light-sensitive organ that provides clues to the direction of illumination; an extreme definition would include as an eye a single photoreceptor cell shielded to some degree by dark pigment. The intended meaning is usually clear in context, though ambiguity can be avoided by using terms such as 'imaging eye', 'proto-eye' or 'eye spot'.

The paths by which eyes in different phyla have evolved are steadily becoming clearer, although uncertainties still abound. What is undeniable is that photoreceptor cells employing rhodopsin-like photopigments linked to G-protein cascades had already evolved prior to the divergence of cnidaria (e.g. jellyfish and anemones) from our own bilaterian line, possibly more than 600 Myr ago.

One question that has attracted interest over the last several decades is the number of times that eyes have evolved independently in animals. In their classic survey of photoreceptors and eyes, von Salvini-Plawen & Mayr (1977) concluded that eyes had evolved on at least 40 (and possibly up to 65) separate occasions. However, it is now clear that deep homologies exist between the components of eyes in different phyla. For example, the photoreceptor cells of vertebrates and invertebrates are not as distinct from each other as has sometimes been suggested. Likewise, the opsin photopigments in the photoreceptors of all animal eyes derive from a common ancestral opsin, even though the commonly known animal opsins fall into two distinct groups: rhabdomeric and ciliary. Furthermore, despite the apparent major differences in the structure of photosensitive organs across phyla (for example, compound eyes versus camera-style eyes), the genes that underlie eye development are in most cases quite clearly related.

As a result, determining the number of times that eyes have evolved independently depends to a considerable extent on one's definition of 'independence' in this context and also on the level of comparison—i.e. whether one is comparing molecules, cell types or organs—and at present a clear-cut answer to the question remains elusive. At the molecular level, it has been established that a great many of the components now employed by extant species, either as crucial elements in phototransduction or elsewhere in their eyes (e.g. as screening pigments or optical elements) or as factors controlling the ontogenetic development of their eyes, were already present as precursors in metazoan animals by the time that cnidaria diverged. Accordingly, there can be problems in specifying which of the subsequent specializations of eye construction were genuinely independent of those that occurred in other eyes and which might better be construed as variations on a theme.

In recent years, there has been an enormous increase in the amount of genetic information that is available and relevant to the evolution of photoreceptors and eyes, and this has resulted in a considerable shift in the knowledge base upon which our understanding of eye evolution is currently founded. This genetic emphasis is reflected in the content of many of the articles that follow, as is particularly evident in the breadth of analyses of the phylogeny of opsin genes.

The papers in this Theme Issue cover a wide range of topics in the evolution of phototransduction and eyes, ranging from the origins of light-sensing mechanisms in ancient single-celled organisms, through the acquisition of dedicated photoreceptor cells in early metazoans, to the evolution of proto-eyes and to the subsequent evolution of sophisticated imaging eyes in...
both invertebrates and vertebrates. Our sequence of presentation of the articles follows this general organization.

The Theme Issue opens with a review of the origin of the mechanisms of phototaxis that have evolved in eu-karyotes (Jékely 2009). Organisms first evolved spiral swimming and thereafter acquired photopigments of diverse kinds (often by horizontal transfer from prokaryotes), which were able to modulate ciliary activity. Arendt et al. (2009) present a new model, coined ‘division of labour’, which accounts for the evolution of photoreceptor cells and the various specializations needed to construct ‘proto-eyes’ and visual circuits. Their model is based on the concept that the separate functions of an ancestral multifunctional metazoan cell became distributed between the different members of its descendant cell types. Vopalensky & Kozmik (2009) analyse the finding that only a restricted set of transcription factors (e.g. Pax, Six, Eya, Otx and Mitf) has been deployed in the evolution of disparate eyes across phyla, thereby providing support for the notion that the regulatory controls for essential photoreceptor genes had already been established in the ancestral metazoan photoreceptor cell. Nilsson (2009) next analyses the way in which entire visual systems may have evolved, through the sequential addition of capabilities (i.e. innovations such as efficient photopigments, screening pigments and optics), to produce proto-eyes and thereafter eyes capable of image formation. For instance, the evolution of membrane stacking is seen as a prerequisite for the transition from directional photoreception to the first imaging eyes.

The later articles in the Theme Issue concentrate on the evolution of vertebrate eyes. Peirson et al. (2009) review the recently discovered system of inner retinal photoreceptors in the vertebrate eye, comprising a subset of retinal ganglion cells that express the photopigment melanopsin and that provide the signals for circadian synchronization. Melanopsin is a rhododermic opsin, and vertebrate retinal ganglion cells appear homologous to the rhododermic photoreceptors of protostomes. At the base of the vertebrate lineage, two rounds of whole genome duplication occurred. The remnant signature features of these tetraploidizations, in the paralagon (i.e. quadruplicate) arrangement of genes, are reviewed by Larhammar et al. (2009) for the case of 10 families of genes involved in phototransduction. Shichida & Matsuyama (2009) explore the evolution of opsin photopigments; they concentrate on the opsins of vertebrate cone and rod photoreceptors and they contrast the molecular properties that these alternative proteins contribute to phototransduction.

Kusakabe et al. (2009) examine the evolution of the biochemical pathway for the dark resynthesis of 11-cis-retinal that is unique to vertebrates, and they provide indications for the existence of a proto-RPE65 isomerase in an early chordate ancestor of vertebrates. Next, Lamb (2009) argues that the advent of this biochemical pathway, together with the ability of ciliary opsins to release their all-trans-retinal, provided a selective advantage at the very low light levels encountered in deeper waters, which led not only to the adoption of ciliary rather than rhododermic photoreceptors, but also to the ‘inside-out’ organization of the retina, in the early vertebrate eye. Subsequent stages in the evolution of vertebrate photoreception are addressed by Collin et al. (2009), who describe the emergence of five classes of retinal photoreceptor with cone-like specializations, using five classes of cone opsin, presumably for daylight vision and very possibly underlying colour vision. The final two articles trace the evolution of colour vision in birds and mammals. Birds retain four classes of cone pigment and are generally considered to be tetrachromats; mammals retain only two classes of cone pigment, the short-wavelength-sensitive (SWS1) and long-wavelength-sensitive opsins, and are therefore usually dichromats. Hunt et al. (2009) follow the evolution of spectral tuning of vertebrate visual pigments, paying particular attention to those residues that tune the SWS1 pigments in different groups of both birds and mammals. In the last article, Jacobs (2009) traces the evolution of colour vision in mammals and considers the loss and gain of opsin classes leading to di- and monochromacy, as well as the special case of trichromacy, which is regained in some groups of primates. He also examines the possible role of rods and rhodopsin in colour vision in some species of mammal.

For further reviews of eye evolution aimed at a more general audience, the reader is referred to Gregory (2008) and to the other papers in the same issue of that volume.

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