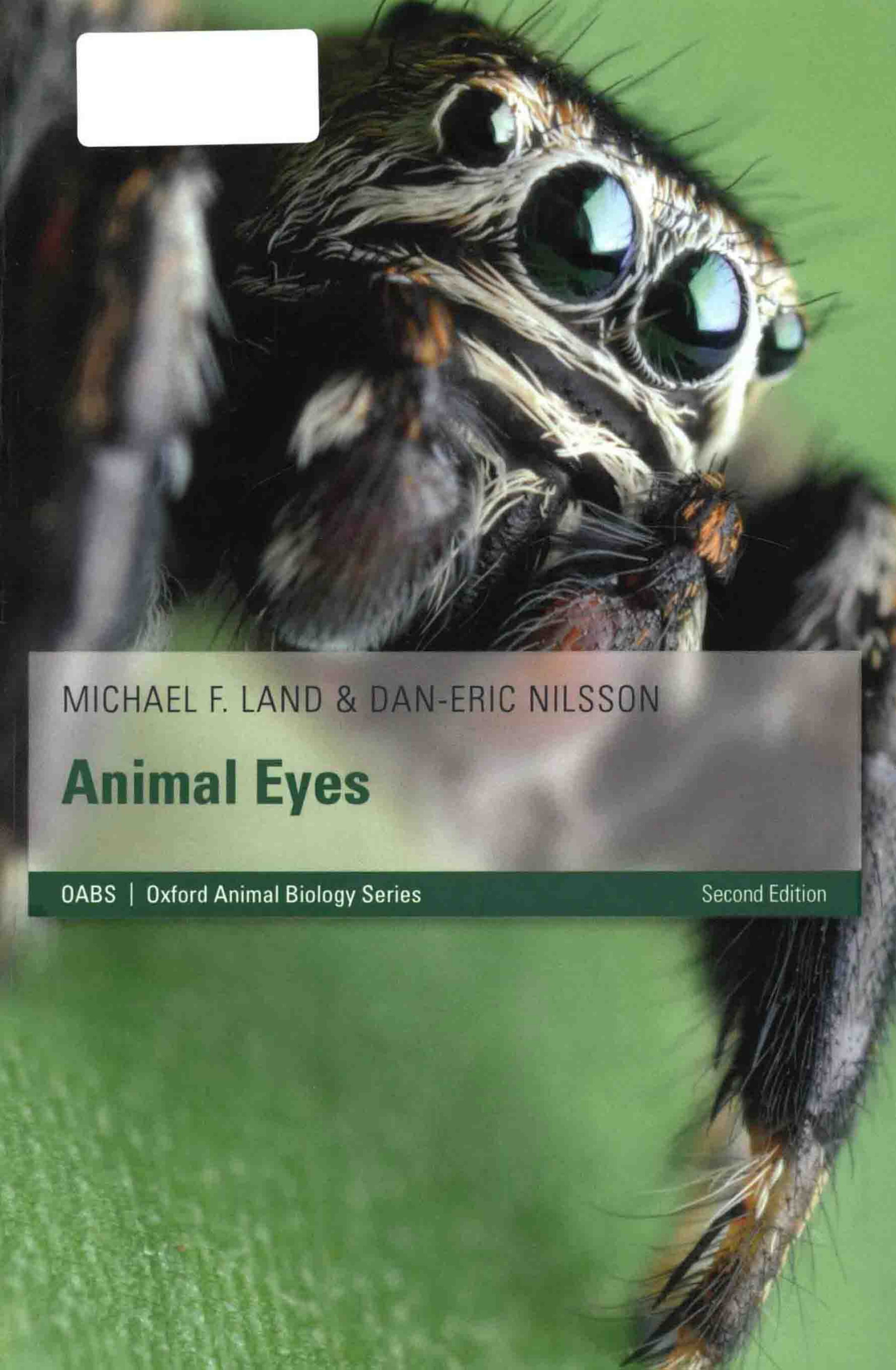

MICHAEL F. LAND & DAN-ERIC NILSSON

Animal Eyes

OABS | Oxford Animal Biology Series

Second Edition

Animal Eyes

Second Edition

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Animal Eyes

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The Oxford Animal Biology Series publishes attractive supplementary textbooks in comparative animal biology for students and professional researchers in the biological sciences, adopting a lively, integrated approach. The series has two distinguishing features: first, book topics address common themes that transcend taxonomy, and are illustrated with examples from throughout the animal kingdom; and second, chapter contents are chosen to match existing and proposed courses and syllabuses, carefully taking into account the depth of coverage required. Further reading sections, consisting mainly of review articles and books, guide the reader into the more detailed research literature. The Series is international in scope, both in terms of the species used as examples and in the references to scientific work.

For Rosemary and Maria

Preface to the second edition

The study of animal eyes is cumulative; old knowledge is rarely superseded, but often added to. This is reflected in the way we have approached this new edition. The chapter layout of the first edition worked well, and we have retained it, along with much of the original text. We have concentrated on advances that have been made in the last decade, and on remedying some of the omissions of the first edition. Chapter 1 has been rewritten, because, thanks largely to the application of molecular genetic techniques, major advances have been made in our understanding of early phylogeny and the molecular origins of photoreception. In Chapter 2 there are new sections on spectral sensitivity and circular polarization; in Chapter 4 new studies on the eyes of cubomedusans are outlined. In Chapter 6 newly described photonic reflecting structures are introduced, and Chapter 9 has new material on the head movements of birds and insect larvae. Other chapters have been similarly updated, but not radically changed. And the last line of the original Preface should now read 80 years rather than 60.

Preface to the first edition

'The eye' to most people means an eye like ours, a single-chambered camera-like structure with a retina in place of the film, or the CCD array. Most know, too, that insects have compound eyes with many lenses, but how many people can answer the question: does the insect see the multitude of images beloved of Hollywood horror films, or a single image similar to our own? We use this example to point out that, even to most biologists, eyes remote from our own are poorly understood and come in only one or two varieties. This hugely underestimates the diversity of eye types: there are at least ten quite distinct ways that eyes form images. Some of these such as pin-holes and lenses are familiar, but others are more exotic. These include concave mirrors, and arrays of lenses, telescopes, and corner reflectors. Some have been known about for centuries (the first demonstration of the inverted image in a mammalian eye was in 1619) but a number are discoveries of the last few decades and have yet to find their way into textbooks of either biology or optics. Some of these eye-types have counterparts in optical technology, but by no means all. Some are still finding applications: for example, the mirror-based optical system of the compound eyes of shrimps and lobsters has recently found a use as the optical basis of wide angle X-ray lenses.

It is our aim in this book to provide a comprehensive account of all known types of eye. We take the diversity of optical mechanisms as a framework, but many other aspects of the structure and function of eyes are also dealt with. Visual ecology—the ways that eyes are specifically adapted to the lifestyles of the animals that bear them—is another important theme. As humans we tend to think of vision as a general-purpose sense, supplying us with any kind of information we require. For most other animals this is not so. Predators and prey, for example, have different visual requirements: foxes and rabbits have different eyes and different visual systems, as have dragonflies and mosquitoes. Similarly, a sedentary clam lives in a different world from a flying insect, and the optical requirements are quite different.

Behind the diversity of eye types is the majesty of the evolutionary process, and this is where we begin the book. The origins of eyes, and the ways in which they reached their present highly developed states has posed an intriguing series of problems from Darwin onwards. The debates still rumble on, particularly about the early origins of eyes before the great Cambrian radiation event gave us most of the eye types we see in animals today. Chapter 1 addresses these questions, and provides a context in which eyes can be seen as different solutions to problems that are, in many respects, similar.

As well as diversity, we are concerned with the 'design philosophy' of eyes. What are the physical constraints on the way an eye performs its functions, and how are these addressed by the different types of eye? To answer this it is necessary first to have some information about the properties of light that are of importance for vision, and this we provide in Chapter 2. We are then able to explore the ways that eyes achieve important aspects of their function, such as good spatial resolution, and (especially for animals that live in dim environments) adequate sensitivity. This is the purpose of Chapter 3, which is devoted to the question 'What makes a good eye?'. This in turn provides a background for assessing the capabilities of the panoply of different eye types, presented in the subsequent five chapters. The ninth and final chapter examines another aspect of the way eyes are used: their movements. Eyes sample the world not only in space but in time, and the movements that they make are as important a part of the process of extracting information as are the optical systems that provide them with spatial resolution.

The book is not aimed at any one readership. It will be of value to undergraduates in Biology and Neuroscience programmes, and to anyone engaged in the study of vision at the post-graduate level. Students and practitioners of ophthalmology and optometry will find it interesting as a background to the study of the human eye, and optical physicists and engineers will find that nature has come up with solutions that they will not have met before.

Aware that many biologists will want the story without too much mathematical detail, we have used Boxes for some of the more complex sections. Equally, however, serious students will want to make use of some of these sections as they contain important 'how to do it' information. For example, Box 5.1 shows how to find the focal length and image position in any optical system of reasonable complexity. We have not provided a complete bibliography justifying every statement in the book, but given references to reviews where the original literature can be found, and to key works, with a bias towards the more recent.

We would like readers to enjoy the book, and share in our enthusiasm for the beauty, intricacy and the logic of animal eyes that has kept us intrigued, and busy, for a total of 60 years.

Acknowledgements

We would like to thank our editors at Oxford University Press. Cathy Kennedy, who edited the first edition, provided encouragement and a great deal of very useful feedback. Helen Eaton, Muhammad Ridwaan and Vijayasankar Natesan have steered us through the editorial and production problems of the second edition with efficiency and skill. We thank all those people who have kindly read and commented upon sections of the book, and who found mistakes in the first edition which we have endeavoured to correct. We are particularly grateful to all those who have contributed original illustrations. Their names appear in the figure captions.

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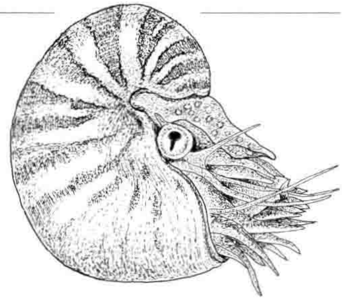

Like no other sensory organs, eyes can provide instantaneous and detailed information about the environment both close up and far away. It is not hard to appreciate the enormous competitive value of a good pair of eyes. In this respect, it may seem a little surprising that within the animal kingdom, only a handful of the more than 30 different phyla have evolved sophisticated eyes. But it does not imply that most animals are blind. In nearly every phylum there are representatives with simple ocelli, and the few groups that have evolved sophisticated eyes, such as vertebrates, arthropods and molluscs, have radiated and diversified to dominate the planet. Evolution has exploited nearly every optical principle known to physics, and produced eyes of many different designs, from camera-type eyes, to compound eyes, and eyes that use mirrors. Having a single pair of eyes located to the head is a common solution, but not the only one (Fig. 1.1). Ragworms typically have two pairs of eyes on the head and spiders have four pairs. In addition to the paired eyes, some lizards and most arthropods have median eyes, and there are numerous examples of eyes on other parts of the body. Clams and mussels have eyes on the mantle edge, chitons have eyes sprinkled all over their back, and starfish have eyes at the tips of their arms. Some jellyfish, having neither a head nor a brain, still have remarkably sophisticated eyes. How did this bewildering diversity evolve?

The first eyes

Although life has existed for several billion years, animals advanced enough to make use of good vision have only been around for little more than half

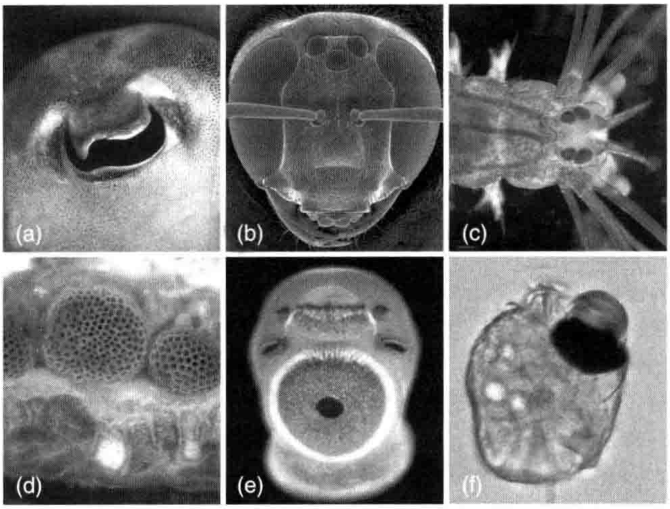

Fig. 1.1 Eye diversity extends far beyond the familiar pattern of vertebrate eyes. The photos illustrate a range of imaging eyes in different organisms. (a) A cuttlefish, *Sepia apama*, with its characteristic pupil, (b) a nocturnal bee, *Megalopta genalis*, with compound eyes and median ocelli, (c) a ragworm, *Platynereis dumerilii*, with two pairs of pigment cup eyes, (d) lens-less compound eyes on the mantle edge of an arc clam, *Barbatia cancellaria*, (e) two lens eyes and two pairs of pigment pit eyes on a sensory club from a box jellyfish, *Chiropsella bronzie*, (f) a dinoflagellate (unicellular green algae, *Erythropsidinium* sp.) with an elaborate eye-spot consisting of a lens and screening pigment. (a, d, e) Photo Dan-E. Nilsson; (b) courtesy Eric Warrant, (c) Detlev Arendt, (f) Mona Hoppenrath.

a billion years. If we trace eyes back through the fossil record, the oldest ones date back to the early Cambrian, about 530 million years ago. Animals from the early Cambrian were not of the same species that exist today, but most of them can be placed into the modern phyla, and many were fully equipped with eyes as far as can be told from the fossils. Only 20 million years earlier, towards the end of the Precambrian, the forms of life seem to have been much simpler, without any large mobile animals that could benefit from good vision. It is even hard to identify any animals at all in the fossil remains of Precambrian organisms. But something remarkable seems to have happened at the interface between the Precambrian and the Cambrian. Within less than 5 million years, a rich fauna of macroscopic animals evolved, and many of them had large eyes. This important evolutionary event is known as the Cambrian explosion.

The Cambrian fossils have been gradually deciphered since 1909 when the palaeontologist Charles Walcott started to analyse the 515-million-year-old rock of the Burgess shale in Canada. What Walcott found was the well-preserved remains of a marine fauna, presumably from shallow water.

The fauna was dominated by arthropods of many different types, but also contained representatives of numerous other phyla. Some of the interpretations of the Burgess shale fossils indicated the appearance of many enigmatic types of animals that did not seem to belong to any of the phyla remaining today. Subsequent and more careful analyses have demonstrated

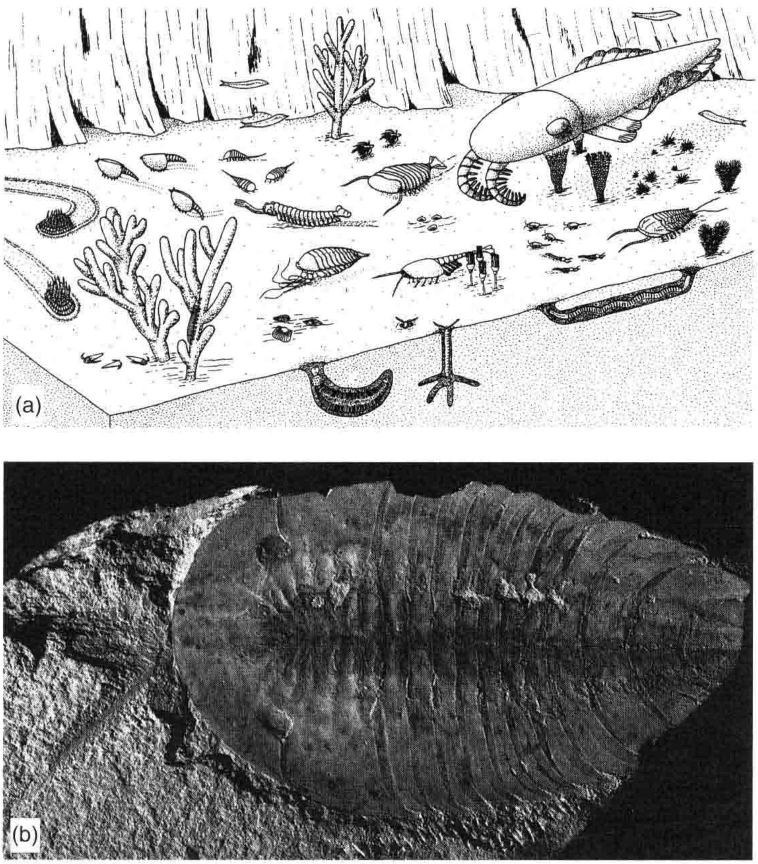

Fig. 1.2 Evidence of the first real eyes comes from Cambrian fossils. The first faunas with large mobile animals appear to have originated at the onset of the Cambrian era, some 540 million years ago, during a rapid evolutionary event called the Cambrian explosion. In the course of a few million years, bilaterally symmetric, macroscopic, and mobile animals evolved from ancestors that were too small or soft bodied to be preserved as fossils. The product of the Cambrian explosion was not just a few species, but an entire fauna (a) including nearly all the animal phyla we know today. The invention of visually-guided predation may have been the trigger for this unsurpassed evolutionary event. Among the very first Cambrian animals, numerous species had prominent eyes. An early example is the arthropod *Xandarella* (b) from Chengjiang, China. Unfortunately, fossils generally reveal very little, if anything about the type or structure of these ancient eyes. (a) from Briggs (1991), originally adapted from Conway-Morris and Whitington (1985), (b) from Xianguang and Bergström (1997), with the authors' permission.

that nearly all of the Cambrian animals were indeed early representatives of modern animal phyla (Conway-Morris 1998). After the discovery of the Burgess shale fauna, even better preserved and earlier Cambrian faunas have been found. These faunas are particularly interesting because they offer a close look at animal life very soon after the Cambrian explosion (Fig. 1.2). Amazingly, these earlier faunas were not very different from those preserved in the Burgess shale. It thus seems that essentially modern types of animals, many with large eyes, evolved within a few million years from ancestors that for some reason were not large or rigid enough to leave many fossil traces.

In the early Cambrian faunas, trilobites and other arthropods were abundant, and they viewed the world through compound eyes that at least superficially resemble those of modern arthropods. In trilobite fossils it is often possible to see the facets of the compound eyes, but in other Cambrian fossils, the eyes are just visible as dark imprints with no detailed structures preserved. Figure 1.2 shows a Cambrian fossil and reconstructed creatures with prominent eyes. From the abundance of eye-bearing species, and from the sizes of their eyes, it seems that vision was no less important in the early Cambrian than it is today. The fossils clearly tell us that, from their first appearance, macroscopic mobile animals were equipped with eyes.

Even vertebrate eyes can be traced back to the early Cambrian. Among the very first vertebrates were animals that resemble the larvae of modern jawless fishes, and these had rather prominent eyes (Fig. 1.3). Later, the Ordovician conodont animals were another group of early vertebrates (Fig. 1.3) that had such large eyes that they must have had better vision than most other animals of their time. Eye evolution is thus largely a story about what happened in the early Cambrian, and thereafter it was only the colonization of land that led to further significant evolutionary events in vision.

As we have seen, the fossil evidence suggests that a large range of visually-guided animals evolved in a very short time during the early Cambrian. Did their eyes evolve from scratch at that time, or might their ancestors already have had some precursor of real eyes? The fossils do not give a clear answer here, but they provide some interesting clues. Fossils formed towards the end of the Precambrian reveal tracks made in the seafloor, and these increase in abundance as the Cambrian explosion approaches. From the size and appearance of these tracks it seems that they were made by small (a few millimetres in length) worm-like animals slowly crawling on the surface of the seafloor. The fact that the actual animals are not fossilized may indicate that they were soft-bodied creatures. If they belong to the