



# Colour in Burgess Shale animals and the effect of light on evolution in the Cambrian

Andrew R. Parker

Division of Invertebrate Zoology, Australian Museum, 6 College Street, Sydney, NSW 2000, Australia  
(arparker@laurel.ocs.mq.edu.au)

Diffraction gratings are reported from external surfaces of the hard, protective parts of *Wiwaxia corrugata*, *Canadia spinosa* and *Marrella splendens* from the Burgess Shale (Middle Cambrian (515 million years), British Columbia). As a consequence, the above animals would have displayed iridescence in their natural environment; Cambrian animals have previously been accurately reconstructed in black and white only. A diversity of extant marine animals inhabiting a similar depth to the Burgess Shale fauna possess functional diffraction gratings. The Cambrian is a unique period in the history of animal life where predatory lifestyles and eyes capable of producing visual images were evolving rapidly. The discovery of colour in Cambrian animals prompts a new hypothesis on the initiation of the 'Big Bang' in animal evolution which occurred during the Cambrian: light was introduced into the behavioural systems of metazoan animals for the first time. This introduction, of what was to become generally the most powerful stimulus in metazoan behavioural systems, would have consequently triggered turbulence in metazoan evolution.

**Keywords:** Burgess Shale; Cambrian explosion; diffraction gratings; fossil colours; evolution; vision

## 1. INTRODUCTION: DIFFRACTION GRATINGS, THE BURGESS SHALE AND THE CAMBRIAN EXPLOSION

Recent studies show that diffraction gratings provide an extensive means of displaying light/colour from the hard parts of extant marine invertebrates (Parker 1995, 1998). Diffraction gratings, in their linear form, are surface structures consisting of a series of parallel ridges or grooves (Hutley 1982). They split incident light into its component wavelengths under unidirectional beams, and the reflected coloured rays reform the incident spectrum in each direction when the incident source is diffuse. Although light is more diffuse in water than in air, in marine sunlit environments down to a depth of about 500 m, light is never totally diffuse owing to absorption (Tyler 1960; Lythgoe 1979), and a grating in such an environment would at least appear silvery with flashes of metallic colours when in motion. Gratings occur commonly on the setae, scales and spines of extant crustaceans and polychaetes (Parker 1998). In all the gratings of extant marine invertebrates examined (Parker 1995, 1998), the same iridescent effect from a species is observed in living and preserved specimens when viewed in seawater.

Iridescence is a powerful tool, considerably more reflective (although more directional) than colour pigments. Consequently, iridescence must carry disadvantages. For example, a light that is used to attract a mate may also attract an enemy. Extant marine invertebrates living under relatively high light levels generally expend considerable energy to ecologically adapt their visual appearance. This adaptation in response to light results, in a major part, in reduced predation on the host.

Three-dimensional diffraction gratings, which can be considered as multilayer reflectors, have been identified in Devonian fossils, notably in pholidostrophiid brachiopods (Towe & Harper 1966). Two-dimensional (linear) gratings are known in Eocene flies, where they perform an anti-reflection function (Parker *et al.* 1998a). Diffraction gratings, however, have not previously been reported from the Cambrian in any form. Cambrian animals have been accurately interpreted only in black and white. Among the best-preserved Cambrian animals are those from the Burgess Shale (515 million years (Ma), British Columbia). These animals were preserved in an extremely fine mud and, as a consequence, show remarkable detail, entailing hard and soft parts (e.g. see Gould 1989). Reconstructions of some Burgess Shale fossils, such as *Wiwaxia corrugata*, show somewhat parallel lines along the length of scales, hairs or spines (e.g. see Gould 1989). Although these lines are not periodic, and the smallest spacings are too large to indicate diffraction gratings, it was thought that they could represent particularly well-preserved ridges in irregularly preserved surfaces. The principal aim of this study is to test for the presence of diffraction gratings in some Burgess Shale fossils.

Any new information on the biology of animals from the Cambrian may increase our understanding of the explosion in evolution of metazoan animal phyla which occurred near the beginning of this period (see Irwin *et al.* 1997). It is generally believed that the body plans of all extant animals (i.e. phyla) evolved during a relatively short period in geological history, of about 5–9 Ma, commencing around 543 Ma, at the beginning of the Cambrian (Bowring *et al.* 1993; Isachsen *et al.* 1994). In context of the 3500 Ma history of life on Earth, this is a pronounced event. The Burgess Shale organisms were

present approximately 19–23 Ma after the end of this ‘Cambrian explosion’, again a relatively short period in the history of evolution. They therefore may be taken to represent the metazoans that resulted directly from the Cambrian explosion (a similar fauna to that of the Burgess Shale is known from Chengjiang, China, which followed the Cambrian explosion by about 9–13 Ma). Hard skeletal parts were acquired simultaneously in different phyla during the onset of widespread biomineralization at the Cambrian–Ediacaran boundary (around 543 Ma). The only known Precambrian animal-like forms appeared relatively close to the Cambrian explosion (around 565 Ma). These are the Ediacaran organisms, which were soft-bodied and either form a separate lineage off the evolutionary tree leading to extant phyla (e.g. Bergström 1993) or belong to extant metazoan taxa, particularly the coelenterates, a group near the base of the metazoan evolutionary tree (see Conway Morris 1993).

Various reasons for the cause of the Cambrian explosion have been suggested. These include an enhanced availability of food (particularly phytoplankton) related to a major event of oceanic upwelling (Rhodes & Bloxam 1968); the attainment of a critical atmospheric oxygen level (Cloud 1968) or a decrease in the concentration of atmospheric carbon dioxide (Walker 1977); the acquisition of collagen (Towe 1970); the expansion of shelf areas as a result of worldwide marine transgression (Matthews & Cowie 1979); a sustained period of phosphogenesis, which reached a maximum in the Early Cambrian (Cook & Shergold 1984); and breakthroughs in trophic strategy to fill all available niches (McMenamin & Schulte McMenamin 1990). However, because there is evidence against most if not all of the above explanations, the factors that caused the Cambrian explosion are considered by most workers to be unknown. ‘The trigger of the Cambrian explosion is still uncertain’ (Irwin *et al.* 1997). ‘Why was there a radiation in the Cambrian? Our most sincere answer is that we do not know’ (Bergström 1993). The secondary aim of this study, therefore, is to put any new information found regarding Cambrian animals into an evolutionary context, and in particular identify factors that may have been involved in the initiation of the Cambrian explosion.

## 2. MATERIALS AND METHODS

*Wiwaxia corrugata* and *Canadia spinosa*, probable polychaetes (Butterfield 1990), and *Marrella splendens*, an arthropod (Whittington 1971), from the Burgess Shale were selected for examination because they may have closely related extant relatives and/or show closely spaced parallel lines in their reconstructions. These species were studied for surface structures that would cause coloration. This was achieved by examining (i) the complete fossils under a reflected light microscope; (ii) isolated sclerites/setae (by acid maceration of the rock matrix (Butterfield 1990)) of *W. corrugata* and *C. spinosa* under a transmitted light microscope; (iii) the complete fossils under a confocal laser microscope; and (iv) gold-coated acetate casts of the fossils in a scanning electron microscope (acetate casts show exceptionally fine detail). Five specimens of each of *W. corrugata*, *C. spinosa* and *M. splendens* were examined.

Theoretical calculations of the reflectivity of diffraction gratings were made using the grating formula  $\sin \theta_N = (N\lambda/d) - \sin \theta$ ,

where  $d$  is the periodicity of the grating,  $\lambda$  is the wavelength of light,  $N$  is the order of the reflected wave,  $\theta$  is the angle subtended by the incident light wave and the grating normal, and  $\theta_N$  is the angle subtended by the reflected light wave (in the  $N$ th order) and the grating normal. Calculations were made for light of wavelengths 0.45  $\mu\text{m}$  (blue) and 0.65  $\mu\text{m}$  (red) to show the approximate angular range of the reflected spectra. The orders  $-2$ ,  $-1$ ,  $0$ ,  $1$  and  $2$  were used. Sunlight was considered to be incident vertically. However, the angle of incident light was calculated at  $0^\circ$  (normal),  $30^\circ$  and  $60^\circ$  for *W. corrugata* and *C. spinosa*, and  $0^\circ$  and  $20^\circ$  for *M. splendens*, to show the reflection from a range of parts of each animal examined (reconstructions of these animals show the parts that possess diffraction gratings, see below, orientated over a range of angles relative to the vertical).

To confirm that the reflection of colours actually takes place, complete surfaces with the designs and dimensions of the preserved areas (bearing gratings, see below) on the surface of each of the above fossils, which form a mosaic pattern, were constructed using holographic techniques according to the method of Mello *et al.* (1995).

## 3. RESULTS

On the surface of the scale- and spine-like sclerites of *W. corrugata* (figure 1a–c), and the neuro- and notosetae of *C. spinosa* (figure 1d), areas of longitudinal grooves are present with a constant periodicity of 0.9  $\mu\text{m}$ . These grooves are evident on the surface of the unprocessed fossils and in transmitted light micrographs of isolated parts (e.g. figure 1a–c). Similar grooves are present on the outermost prolongations of the head shield of *M. splendens* (figure 1e), but with a constant periodicity of 0.6  $\mu\text{m}$  and orientated at  $45^\circ$  to, and either side of, a central longitudinal ridge, forming chevron patterns in dorsal view. In each area where these grooves occur, the orientation, periodicity and approximate depth are consistent for each species. Neither body parts other than the above regions nor the surrounding rock matrix exhibit such patterns. No organic material was found to cover any part of the grooves in all species. The evidence suggests that the grooved surfaces occurred externally in the living animals, as is the case with probable extant relatives (see below) (figure 1f; Parker 1995, 1998).

The reflectivity from the parts bearing gratings as they appear on reconstructed models of *W. corrugata*, *C. spinosa* and *M. splendens* when sunlight is incident vertically is shown in figure 2. These results probably show a high degree of error because of uncertainty in the angles used in the animal reconstructions. The results show, however, that a large degree of error is permissible for the reflection of spectra, or metallic colours, in the water above and to the side of the animals. The orientation of the animal and/or the direction of sunlight may also vary considerably while a similar result is achieved. The animal iridescence is not particularly angle-dependent because of the broad range of orientations of the iridescent parts on the whole animal and the wide angular range of the reflected spectra. The first-order spectrum ( $N = -1$  and  $1$ ) would appear brightest.

Manufactured replicas of the surfaces which contain gratings in all of the above animals produce an efficient reflection of all spectral colours in seawater under unidirectional white light, and appear silver with

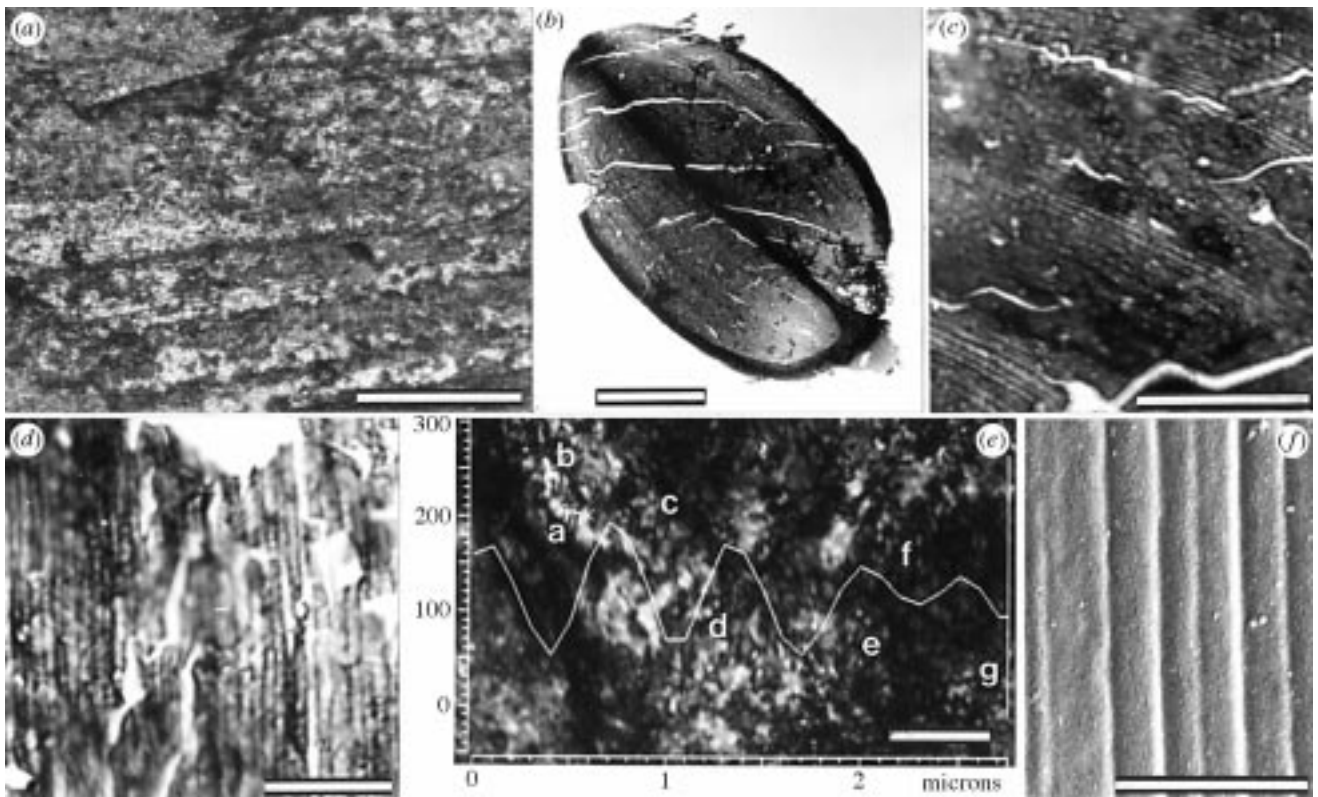


Figure 1. Diffraction gratings. (a) Reflected light micrograph, (b–d) transmitted light micrograph, (e) confocal laser micrograph, (f) scanning electron micrograph. (a–c) *Wiwaxia corrugata*: (a) surface of a spine-like sclerite, basal region, of an unprocessed fossil (USNM 198669), grooves running longitudinally; (b, c) scale-like sclerites, isolated by acid maceration of rock matrix (Butterfield 1990), grooves running longitudinally; (b) MCZ 102118, (c) MCZ 102131. (d) *Canadia spinosa* (USNM 202335) palea, isolated by acid maceration of rock matrix (Butterfield 1990), central region, grooves running longitudinally. (e) *Marrella splendens* (AM F38262), surface of right outermost prolongation of head shield, ‘corner’ region, near edge, sum of 14 sections parallel to the surface. Points ‘a’–‘g’ represent regions with equal topographies where all grooves are parallel; the curve represents an enlarged cross-section of the grating at point ‘a’ taken perpendicular to grooves; vertical axis = pixel intensity, horizontal axis = distance along section (scale bar relates to the actual micrograph, not the curve). (f) *Aphrodita australis* (Polychaeta: Aphroditidae) from 55 m depth, surface of notoseta. USNM = United States National Museum; MCZ = Museum of Comparative Zoology, Harvard University; AM = Australian Museum. Bars: (a, b) = 50  $\mu\text{m}$ ; (c) = 25  $\mu\text{m}$ ; (d, e) = 10  $\mu\text{m}$ ; (f) = 5  $\mu\text{m}$ .

flashes of colour when in motion under near-diffuse white light.

#### 4. DISCUSSION: COLOUR IN *WIWAXIA*, *CANADIA* AND *MARRELLA*

When a surface has the mathematical dimensions of a diffraction grating (Hutley 1982), it must function as such under incident light, regardless of its archetypal function. For example, even if the original function of the grooved surface was to provide maximum strength using minimum material, like a corrugated sheet, it would still produce coloration in a light regime, albeit as an epiphenomenon (incidental) (Parker 1998). Indeed, animal diffraction gratings that display light externally may be incidental in deep-water species, but become either functional or abandoned in shallow-water relatives via selection (Parker 1995, 1998). I conclude, therefore, that the sclerites of *W. corrugata*, the setae of *C. spinosa*, and the outermost prolongations of the head shield of *M. splendens* bore diffraction gratings on their external surfaces. The first-order spectra shown in figure 2 should be considered most important in regarding the behavioural implications of the gratings because they contain the brightest colours.

In addition, some of the wavelengths shown, particularly at the red end of the spectrum, may not have been present in the Burgess Shale animals’ original environment.

Most Burgess Shale reconstructions depict the fossil (Phyllopod) bed at the base of the Cathedral Escarpment, and the estimated water depth of the original site is 70 m (Fritz 1971) or shallower (Walcott 1919). Some extant animals can detect light at about 1000 m (Denton 1990). The Burgess Shale ecosystem must have contained light because of the presence of benthic algae (Walcott 1919), which require light to support their physiology. Although buried in mud slumps (Fritz 1971), the Burgess Shale fauna lived in relatively calm water, and this condition must have been continuous for some time (Walcott 1919). There would have been a relatively high ratio of absorption to scattering of light and, therefore, the ambient light would have had a significant unidirectional component (Lythgoe 1979). Consequently, the gratings of the benthic animals *W. corrugata* and *C. spinosa* would have appeared iridescent (this reflection would have become silvery, but still conspicuous, if conditions became turbid). When the sun was in the zenith and incident vertically on *W. corrugata* or *C. spinosa*, first-order blue light would have been reflected at angles around 30–35° to the vertical (figure 2). At

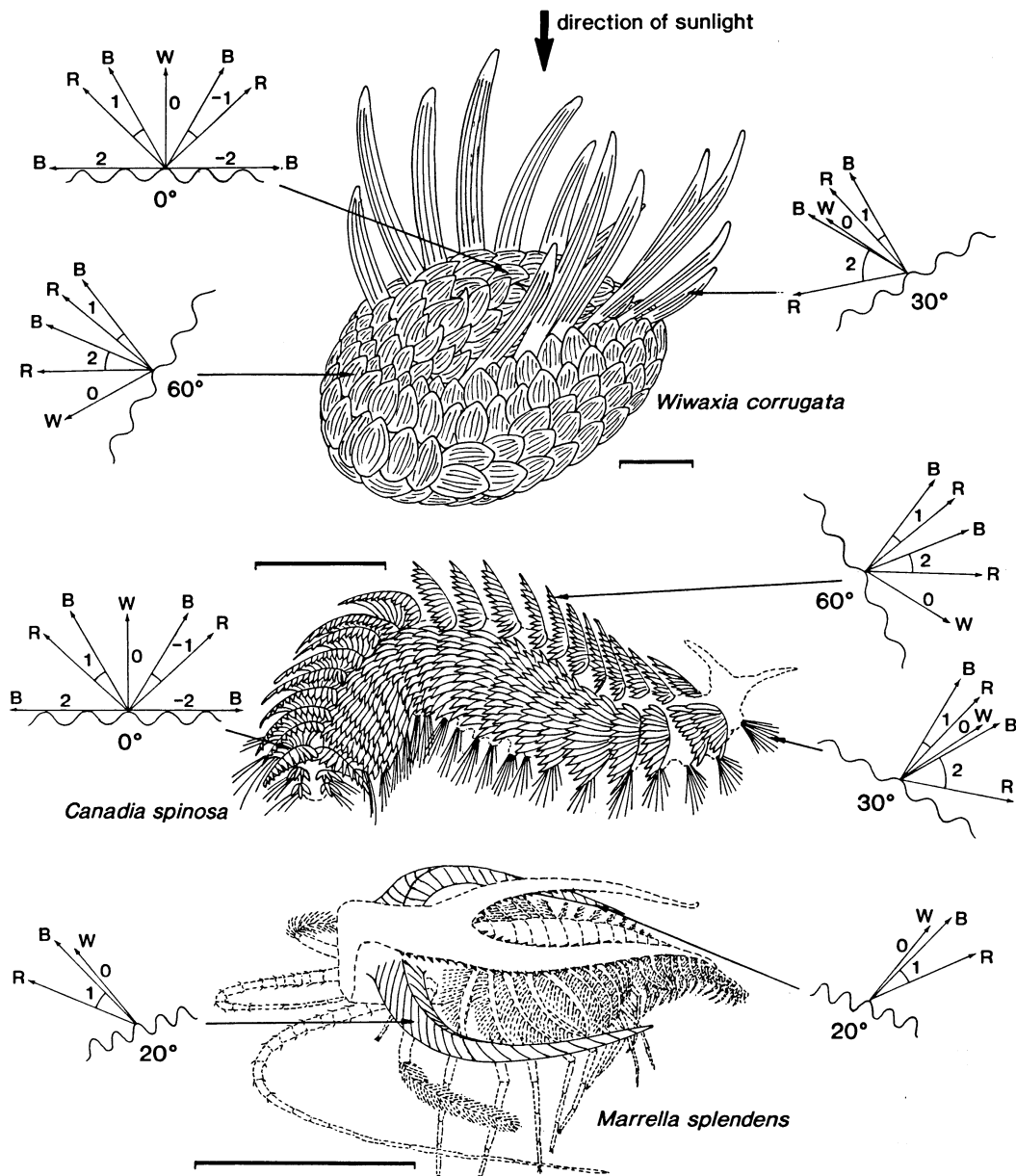


Figure 2. Reconstructions of Burgess Shale animals (modified from Gould (1989), with permission from the author) showing the positions of diffraction gratings on *Wiwaxia corrugata*, *Canada spinosa* and *Marrella splendens*. Parts bearing diffraction gratings are shown with solid outlines; some ridges of the gratings are shown to indicate grating orientations (except in *C. spinosa*, where ridges run longitudinally along the setae). The directions of blue (B), red (R), and white (W) reflections from the gratings at various orientations, as they occur on the animals, are illustrated when sunlight is incident vertically. The zero (0), first-order (-1 and 1) and second-order (-2 and 2) spectra are shown where they occur. Bar = 10 mm.

slightly larger angles, green, and then yellow light would be reflected (figure 2). If the position of the sun changed, iridescent colours would still be reflected at similar angles from *W. corrugata* and *C. spinosa*, owing to the considerable range of orientations of their iridescent parts.

At a depth of about 70 m, the effects of colour pigments are very reduced, but diffraction gratings, with a much higher reflectance in specific directions, appear conspicuous owing to a high contrast against a dark, pigmented background. For example, *Aphrodita australis* (Polychaeta: Aphroditidae), a probable relative of *W. corrugata* and *C. spinosa* (Butterfield 1990) known to live at depths of 70 m and shallower, appears highly iridescent from its setae under low-intensity unidirectional light as a result of diffraction gratings (figure 1f). This iridescence probably

functions to deter predators. *Marrella splendens*, however, was capable of swimming and may have reached very shallow waters (Tiegs & Manton 1958). Here, sunlight would have been highly unidirectional (Lythgoe 1979) and, therefore, the outermost prolongation of the head shield of *M. splendens* would have appeared highly iridescent. This is similar to the iridescence of some ostracods and copepods (also arthropods living at depths of 70 m and shallower), which is known to have a role in the behaviour of its host (Parker 1995, 1998). In the shallowest water, all colours of the white light spectrum would have been present and consequently appeared in iridescent displays, whereas at about 70 m, sunlight, and therefore iridescence, would lack a red component (Lythgoe 1979). When the sun was in the zenith and

incident vertically on *M. splendens*, blue light would have been reflected from the head shield at 45° to the vertical and red light at 70°, with green, yellow and orange between (figure 2). If sunlight was incident at 20° to the vertical, then blue light would have been reflected from the head shield at 30° and 70° to the vertical, and green at 48° and 98°.

## 5. IMPLICATIONS: THE ROLE OF LIGHT IN THE CAMBRIAN EXPLOSION

At depths down to at least 70 m in modern ecosystems, light is sufficiently powerful that any reflected light is important in behavioural recognition to cohabiters with eyes (Parker 1998; Parker *et al.* 1998b). It is also known that light has been the major stimulus in the post-Cambrian evolution of two groups of Crustacea (Parker 1995; Parker *et al.* 1998b).

Eye-bearing arthropods from the Burgess Shale, such as *Anomalocaris canadensis* (Collins 1996) and *Opabinia regalis* (Budd 1996), were probably predators of *W. corrugata*, *C. spinosa* and *M. splendens*. For example, predation on *W. corrugata* is inferred from broken spines (Conway Morris 1985). The coloration of *W. corrugata*, *C. spinosa* and *M. splendens* was probably aposematic (provided a visual warning of their 'spines'): this is suggested by the occurrence of gratings on defensive parts or 'armour', as in *Aphrodita australis*. The armour, including 'spines', of these animals would have appeared as changing, iridescent colours to predators approaching laterally in the water column (the majority of their predators). A changing colour, or flashing light, is more conspicuous than a steady light (e.g. Haamedi & Djamgoz 1996), and so the visual warning would have been optimized. For example, the spine-like sclerites of *W. corrugata* served a defensive role (Conway Morris 1985), and their threatening morphological appearance may have been emphasized by their bright, changing coloration, as in *A. australis*. All the wavelengths of sunlight present in the environment were reflected; Cambrian eyes must have used at least some of these wavelengths to achieve vision. Some Cambrian trilobites possessed eyes capable of producing visual images (Fordyce & Cronin 1989), and the eyes of certain Burgess Shale animals may have been as sophisticated as some of those found in extant animals (e.g. figure 3). It is considered that light display was as important in the Burgess Shale ecosystem as in modern ecosystems at a comparable depth. However, the Burgess Shale fauna is particularly interesting with regard to visual systems because the Cambrian represents a unique period when predatory lifestyles and eyes capable of producing visual images were evolving 'rapidly' (the first report of predation was in the Upper Ediacaran (Bengston & Zhao 1992)).

McMenamin & Schulte McMenamin (1990) used feeding modes, including predation, to explain the cause of the Cambrian explosion. The finding of diffraction gratings in Cambrian animals prompted my consideration of a link between the evolution of predators and eyes in determining the driving forces behind this event. The evolution of eyes would have effectively 'turned on the lights' for metazoan animals by adding an extra, and generally the most important, stimulus to metazoan behavioural systems: light. Consequently, the introduction of predators using vision provided a new and major selection pressure

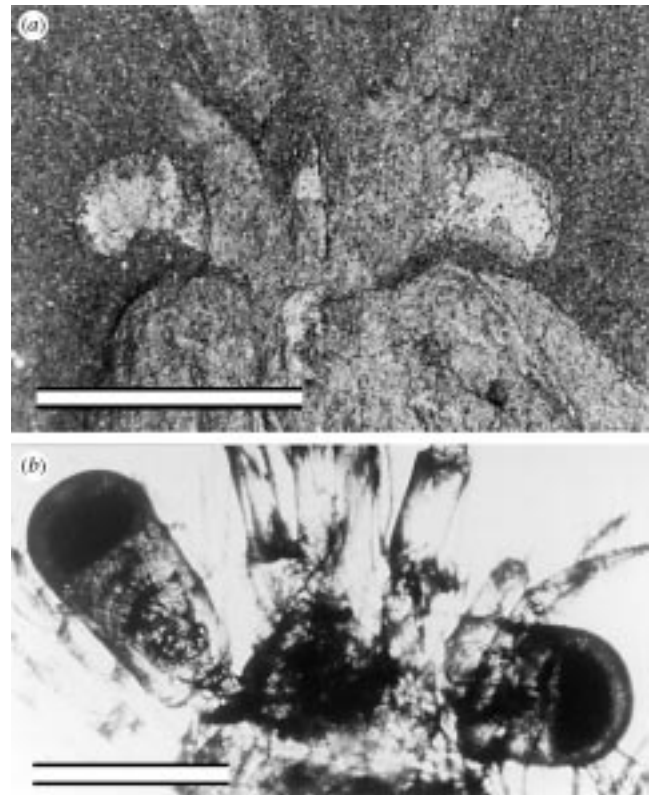


Figure 3. Eyes of extinct and extant arthropods. (a) Head region of *Waptia fieldensis* (United States National Museum 83948j) from the Burgess Shale. (b) Head region of an extant mysid crustacean showing refracting superposition compound eyes (Nilsson & Modlin 1994). Although it is not known to which class of Crustacea *Waptia* belongs, the strong morphological similarities (i.e. relative sizes of internal parts) that exist between these eyes suggest that *W. fieldensis* was capable of producing visual images. Bars: (a) = 2 mm; (b) = 0.5 mm.

for metazoan evolution. Animals were visually exposed to predators for the first time and their evolution responded dramatically. For example, the most parsimonious lifestyle for the first soft-bodied metazoans was moving slowly and freely along the sea-floor. However, with the introduction of predators with eyes, burrowing in the sediment, hiding in rock crevices or the evolution of hard, protective parts was more appropriate, as in today's shallow marine environments. Thus, much of the Cambrian explosion may be explained by the introduction of predators and eyes, that is, the effective introduction of light to metazoan animal behavioural systems.

Light is only one of a suite of environmental stimuli. Light entering the metazoan behavioural system would have been the catalyst for other stimuli to enter. Chemical and mechanical sensations were probably also major driving forces in the Cambrian explosion, although this is more difficult to test. We know that eyes evolved approximately simultaneously with the Cambrian explosion, but the often minute chemo- and mechanoreceptors are difficult to identify in Cambrian fossils. Although defensive spines that appeared during the Cambrian explosion could have targeted mechanoreceptors, they are more likely a visual warning: this suggestion is supported by the iridescence data.

I thank Simon Conway Morris, Jim Lowry, Greg Edgecombe, Derek Briggs, Dan Osorio, Peter Herring, Ken Towe and David Horne for valuable comments on the manuscript. I thank also Douglas Erwin and Frederick Collier for providing Burgess Shale material. This project was supported by Australian Research Council, Australian Museum and Smithsonian Institution grants.

## REFERENCES

- Bengston, S. & Zhao, Y. 1992 Predatorial borings in Late Precambrian mineralized exoskeletons. *Science* **257**, 367–369.
- Bergström, J. 1993 The Cambrian radiation and its explanation. In *Deciphering the natural world and the role of collections and museums* (ed. E. Hoch & A. K. Brantsen), pp. 27–30. Copenhagen: Geologisk Museum Press.
- Bowring, S. A., Grotzinger, J. P., Isachsen, C. E., Knoll, A. H., Pelechaty, S. M. & Kolosov, P. 1993 Calibrating rates of early Cambrian evolution. *Science* **261**, 1293–1298.
- Budd, G. E. 1996 The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. *Lethaia* **29**, 1–14.
- Butterfield, N. J. 1990 A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology* **16**, 287–303.
- Clood, P. E. 1968 Atmospheric and hydrospheric evolution on the primitive Earth. *Science* **160**, 729–736.
- Collins, D. 1996 The 'evolution' of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodontia (nov.). *J. Paleont.* **70**, 280–293.
- Conway Morris, S. 1985 The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. *Phil. Trans. R. Soc. Lond.* **B307**, 507–582.
- Conway Morris, S. 1993 The fossil record and the early evolution of the Metazoa. *Nature* **361**, 219–225.
- Cook, P. J. & Shergold, J. H. 1984 Phosphorus, phosphorites and skeletal evolution at the Precambrian–Cambrian boundary. *Nature* **308**, 231–236.
- Denton, E. J. 1990 Light and vision at depths greater than 200 m. In *Light and life in the sea* (ed. P. J. Herring, A. K. Campbell, M. Whitfield & L. Maddock), pp. 127–148. Cambridge University Press.
- Fordyce, D. & Cronin, T. W. 1989 Comparison of fossilized schizochroal compound eyes of phacopid trilobites with eyes of modern marine crustaceans and other arthropods. *J. Crust. Biol.* **9**, 554–569.
- Fritz, W. H. 1971 Geological setting of the Burgess Shale. In *Proc. North Am. Paleont. Conv., Chicago, 1969* (ed. E. L. Yochelson) vol. 1, pp. 1155–1170. Lawrence, KS: Allen Press.
- Gould, S. J. 1989 *Wonderful life: the Burgess Shale and the nature of history*. New York: W. W. Norton & Co.
- Haamedi, S. N. & Djamgoz, M. B. A. 1996 Effects of different patterns of light adaptation on cellular and synaptic plasticity in teleost retina: comparison of flickering and steady lights. *Neurosci. Lett.* **206**, 93–96.
- Hutley, M. C. 1982 *Diffraction gratings*. London: Academic Press.
- Irwin, D., Valentine, J. & Jablonski, D. 1997 The origin of animal body plans. *Am. Sci.* **85**, 126–137.
- Isachsen, C. E., Bowring, S. A., Landing, E. & Samson, S. D. 1994 New constraint on the division of Cambrian time. *Geology* **22**, 496–498.
- Lythgoe, J. N. 1979 *The ecology of vision*. Oxford: Clarendon Press.
- Matthews, S. C. & Cowie, J. W. 1979 Early Cambrian transgression. *J. Geol. Soc. Lond.* **136**, 133–135.
- McMenamin, M. A. S. & Schulte McMenamin, D. L. 1990 *The emergence of animals*. New York: Columbia University Press.
- Mello, B. de A., da Costa, I. F., Lima, C. R. A. & Cescato, L. 1995 Developed profile of holographically exposed photoresist gratings. *Appl. Opt.* **34**, 597–603.
- Nilsson, D.-E. & Modlin, R. F. 1994 A mysid shrimp carrying a pair of binoculars. *J. Exp. Biol.* **189**, 213–236.
- Parker, A. R. 1995 Discovery of functional iridescence and its coevolution with eyes in the phylogeny of Ostracoda (Crustacea). *Proc. R. Soc. Lond.* **B262**, 349–355.
- Parker, A. R. 1998 Invertebrate structural colours. In *Functional morphology of the invertebrate skeleton* (ed. E. Savazzi). New York: Wiley. (In the press.)
- Parker, A. R., Hegedus, Z. & Watts, R. A. 1998a Solar absorber antireflector on the eye of an Eocene fly (45 Ma). *Proc. R. Soc. Lond.* **B265**, 811–815.
- Parker, A. R., McKenzie, D. R. & Ah Yong, S. T. 1998b A unique form of light reflector and the evolution of signalling in *Ovalipes* (Crustacea: Decapoda: Portunidae). *Proc. R. Soc. Lond.* **B265**, 861–867.
- Rhodes, F. H. T. & Bloxam, T. W. 1968 Phosphatic organisms in the Paleozoic and their evolutionary significance. In *Proc. North Am. Paleont. Conv.*, part K (ed. E. L. Yochelson), pp. 1485–1513. Lawrence, KS: Allen.
- Tiegs, O. W. & Manton, S. M. 1958 The evolution of the Arthropoda. *Biol. Rev. Camb. Phil. Soc.* **33**, 255–337.
- Towe, K. M. 1970 Oxygen-collagen priority and the early metazoan fossil record. *Proc. Natn. Acad. Sci. USA* **65**, 781–788.
- Towe, K. M. & Harper, C. W. Jr 1966 Pholidostrophiid brachiopods: origin of the nacreous luster. *Science* **154**, 153–155.
- Tyler, J. E. 1960 Radiance distribution as a function of depth in an underwater environment. *Bull. Scripps Instn Biol. Res.* **7**, 363–412.
- Walcott, C. D. 1919 Middle Cambrian algae. *Smithson. Misc. Collns* **67**, 217–260.
- Walker, J. C. G. 1977 *Evolution of the atmosphere*. New York: Macmillan.
- Whittington, H. B. 1971 Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia. *Bull. Geol. Surv. Can.* **209**, 1–24.