Explanations of figures

Fig. 1. Basic structure of a trilobite as illustrated by the giant *Paradoxides davidis*, 34 cm long, from Manuels River, Newfoundland. The head (cephalon) has a central swollen part, the glabella, below which lay the stomach. The lines of weakness (facial sutures), which facilitate moulting, are not clearly seen in this specimen (though well shown on Fig. 9); the lateral parts (librigenae) with their long genal spines, break off on moulting, allowing the initially soft–shelled trilobite to escape from the old shell without damage. Behind the glabella is the arched occipital ring, which links with the first segment of the thorax. The thorax has many segments, each with an arched central axis, flanked by a pair of lateral pleura, each with a backwardly curved spine. The tail (pygidium) in this case is small, spinose, and backwardly tapering. (Photo by R.Levi–Setti).

Fig. 2. A generalised camera eye, in which a lens focus light onto a retina, thus stimulating the photoreceptors, which are connected to the brain by an optic nerve. In the human eye the nerves fibres run outside the retina, rather than behind it, and are gathered together to form the optic nerve. (Based on R.Levi–Setti *et al* 1998).

Fig. 3. A compound eye, consisting of very many photoreceptive ommatidia, capable of forming a mosaic image. (Based on R.Levi–Setti *et al.* 1998).

Fig. 4. Simplified geological history of trilobites, showing various eye–types and major historical events. The vertical bars represent Suborders, grouped bundles represent Orders. Following Stein *et al.* (1995) and others, the Agnostina are regarded as close relatives of stem–group crustaceans and are unrelated to the Eodiscina (though up till now traditionally classified together in Order Agnostoida). Symbols are as follows for the higher taxa (Orders and Suborders). AG, Agnostina; EO, Eodiscina; RE, Redlichiida; CO, Corynexochidae; LI, Lichida; PH, Phacopida (including schizochroal–eyed Phacopina); PT, Ptychopariina (including pitted–fringe Harpina (Ha)); AS, Asaphida (including pitted–fringed Trinucleoidea (Tr)); PR, Proetida.

Major events are numbered as follows: 1. Base of the Cambrian System. 2. First appearance of trilobites. 3. Origin of the unique system of a tiny median eye and reduced ventral compound eyes. 4. The cryptic origin of the eodiscid abathochroal eyes. Most trilobites in this taxon, however, are blind. 5. The earliest holochroal eyes in Redlichiida. 6. Extinction event at the end of the Cambrian. 7. Acme of trilobites and proliferation, amongst others, of blind, pitted–fringed taxa (Harpetida (Ha), and Trinucleoidea (Tr), and pelagic groups with enormous holochroal eyes. 8. Origin of schizohroal eyes in Phcopina, as a result of paedomorphosis. 9. End–Ordovician extinction event. 10. Gradual decline and final extinction of many taxa during the Devonian. 11. Loss of eyes in many Phacopina and Proetida. 12. Late Devonian major extinction event. 13. Proetida continue to the latest Permian. 14. Final extinction of trilobites. Genera illustrated are (i) *Machairagnostus*. (ii) *Pagetia*. (iii) *Paedumias*. (iv) *Scutellum*. (v) *Dicranurus*. (vi) *Acaste*. (vii) *Olenus*. (viii) *Pricyclopyge*. (ix) *Trinucleus*. (x) *Paladin*.

Fig 5. Holochroal eyes. *Paladin eichwaldi shunnerensis* (a Middle Carboniferous proetid, Yorkshire, England) (A) adult (scale bar 5 mm) (B) Holochroal right eye of same (scale bar 0. 5 mm). (C) An early developmental stage of the same species (scale bar 0. 5mm). (D, E) Tiny eye of the same specimen, showing that at this stage in development it is schizochroal. (Scale bar for (D) 0.1mm) See also Fig. 14. (F). *Pricyclopyge binodosa* (a very large eye of a pelagic asaphine from the Ordovician of the Czech Republic) (scale bar 2.5 mm). This eye is preserved as a mould of the internal surface, in siltstone. The original calcite has been leached away by percolating acid groundwater. (G, H) *Sphaerophthalmus alatus* (an upper Cambrian olenid from Skåne, Sweden). All these specimens except for (F) retain their original calcite exoskeleton. (C, D, E, G and H) are scanning electron micrographs. (Photos by E.Clarkson).

Fig. 6. Holochroal eye of a corynexochid, *Platyscutellum massai*, from SE Morocco. Note the characteristic lens–packing system of intersecting logarithmic spirals. Length of the eye is 7.5 mm (Photo by R.Levi–Setti).

Fig 7. Holochroal eyes (A) *Paladin eichwaldi shunnerensis* (see Fig. 5A), Middle Carboniferous, Yorkshire, England. Reconstruction of a single lens cut to show radial lamellae and vertical trabecula, fanning out above. (B, C) *Asaphus raniceps* (Lower Ordovician, Sweden). Vertical section through adjacent 'lenses', actually long cylinders, showing thin cornea (black), hemispherical lower terminations, and focal point. (C) Surface view, with the cornea removed at the left hand side to show the radial lamellae. (D, E) *Sphaerophthamus alatus*, Upper Cambrian, Skåne, Sweden (See Figs. 5 G, H). (D) Section through thin biconvex lenses and focal point. (E) Surface view of the lenses, with the cornea removed on the left hand side to show the radial lamellae.

Fig. 8. Schizochroal and abathochroal eyes. (A–F) Schizochroal eyes (A) *Calyptaulax brongniartii* (Upper Ordovician, Girvan, Scotland). A mould in siltstone of the internal surface of this complete phacopid trilobite in side view, showing the large schizochroal eye. The original exoskeleton has been leached away by acid groundwater. Scale bar 10 mm). (B) A right eye of the same species. Here rubber latex solution has been applied to a mould of the external surface of an eye, perfectly replicating the original surface before photographing. (C, D) *Eldredgeops rana rana* (Middle Devonian, Ohio, U.S.A.). Scanning electron micrographs of a right eye (scale bars respectively 1 mm and 0.25 mm). (E) *Eldredgeops rana crassituberculata* (Middle Devonian, Ohio, U.S.A.). Large specimen, right eye (scale bar 1 mm). F. *Denckmannites volborthi*. Silurian, Lochkov, Czech Republic. Left eye, showing reduced lens number. Scanning electron micrograph of the original exoskeleton (scale bar 0.5 mm).

(G, H) Abathochroal eyes of *Neocobboldia chinlinica*. (Lower Cambrian, Henan, China). These eyes are preserved as phosphate films. The original calcite, of which they were made, has been dissolved in solution by acetic acid when freeing the specimens from the limestone matrix. (G) In this case the eye is broken to reveal both the outer and inner surface (scale bar 0.1 mm). (H) The internal structure of the lenses, each showing a central dimple (scale bar 0.1 mm) (Photos by E.Clarkson).

Fig. 9. *Hollardops mesocristata* (Middle Devonian, SE Morocco) An antero–lateral view showing the position of the schizochroal

eye, and the facial suture, which enabled the old exoskeleton to break into pieces during moulting. Length of original specimen is c. 5.4 cm. (Photo by R.Levi–Setti).

Fig. 10. *Hollardops mesocristata* (Middle Devonian, S.E. Morocco) Same specimen as in Figure 9. A fine hexagonal decoration of small tubercles is present on the sclera between the lenses. Length of eye c. 7mm. (Photo by R.Levi–Setti).

Fig. 11. *Eldredgeops milleri* (Middle Devonian, Ohio, U.S.A.). An enrolled specimen showing the position of the schizochroal eye. Length of specimen, as enrolled, c. 15 mm (Photo by R. Levi–Setti).

Fig. 12. *Eldredgeops milleri* (Middle Devonian, Ohio, U.S.A.). Schizochroal eye of same specimen as in Fig. 11. Length of eye c. 2.8 mm. (Photo by R. Levi–Setti).

Fig. 13. Schizochroal eyes. (A) *Phacops fecundus* (Silurian, Czech Republic). Eye cut horizontally showing a single sublensar capsule. The existence of such capsules has recently been confirmed. (B) *Dalmanitina socialis* (Ordovician, Czech Republic). Section through a lens, showing the intralensar bowl, in black. It is not known if a core was present. (C) *Dalmanites*, Silurian, species and locality unknown. Here a core is present though less well defined than in (D). (D) *Eldredgeops rana* (Middle Devonian, Ohio, U.S.A.). A highly convex lens in which the core is well defined and of the same appearance as the bowl. The bowl thins out and vanishes below the core. (E). *Crozonaspis struvei* (Ordovician, Brittany, France) (E) Ray tracing through the lens, after Clarkson & Levi–Setti 1975). If the intralensar bowl (black, left hand side) has a refractive index of 1.63, less than that of calcite, 1.66, light is brought to a perfect focus. If there is no correcting mechanism (right hand side) it will hardly focus properly at all. (F) *Acuticryphops acuticeps* (Upper Devonian, southern France). Cephalon in side view and (below) an enlargement of the reduced eye. The swelling at the bottom centre may be an imperfectly formed lens (simplified from Crônier & Feist 2000).

Fig. 14. *Paladin eichwaldi shunnerensis* (Middle Carboniferous, Yorkshire, England). (A, B) Drawings to illustrate the adult eye from the side and from above, and (C) the eye of an early developmental stage which is schizochroal. The earliest schizochroal phacopid eyes arose by paedomorphosis from the immature eye of a holochroal–eyed ancestor (see also Fig. 5 A–E).

Fig. 15. *Onnia grenieri* (Upper Ordovician, Morocco). A blind trinucleid trilobite, where the head is surrounded by a pitted fringe. This may have been a vibro– or chemo–sensory organ (Photo by R. Levi–Setti).

Finding trilobites

Trilobites occur in many kinds of sedimentary rock, and are best preserved in limestones and calcareous mudstones, but they can be found in siltstones and even sandstones. They occur in most countries in Europe, Scandinavia, Britain, France, Germany and the Czech Republic being classic places for them. But there are also plenty of them in Spain and Portugal, and elsewhere in the Spanish–speaking world, especially Argentina and Bolivia.

In Spain they are abundant in the Toledo Mountains, in the north–east near Zaragoza, the Sierra Morena, and many other places. Magnificent collections are to be found in the Museo Geologico y Minero in Madrid, beautifully displayed, and with valuable information about where they come from. For any student wishing to learn more, this is fine place to start. In Portugal, close to Arouca, there are to be found many kinds of giant trilobites, much larger than usual (up to 80 cm long), but we have no certain knowledge as to how they came to be so enormous.

Many professional palaeontologists, working in universities and museums, and amateurs also, find trilobites irresistibly fascinating. The Fourth International Trilobite Conference on Trilobites was held in Toledo in June 2008, with field excursions to various places, and it was attended by over a hundred delegates from over 20 countries.

The trilobite horizon

Many trilobite workers have interesting stories to tell about finding trilobites in the field. Here are a few from Euan Clarkson.

In the year 1959 I was a second year university student of geology, and on a field trip to south–west Wales we visited a famous locality known as Porth–y–rhaw. This is an inlet of the sea, with vertical walls, and a rough floor of hard back shale, tilted vertically. From here, in the past many large specimens of Paradoxides davidis *had been collected, similar to those illustrated in Figure 1). We were told that these trilobites were only found in a very few thin layers or bands of sediment and that nobody had found any for many years. I inspected the vertical surfaces of rock on my hands and knees. Was that not a fragment, a curving spine of a large trilobite on one of the rock surfaces? I attacked the rock vigorously with my hammer and a long chisel. But by this time the tide was rushing in, our leader called us, and it was time to go. My chisel was irretrievably wedged in the rock, and I could not extract it. A sad day! Five years later, when I was a junior lecturer at Edinburgh University, I revisited Porth–y–rhaw with a keen student party. To my amazement there was my chisel, still in place though very rusty, marking the trilobite horizon! I called the students, many of whom had fine large hammers and strong chisels. They set to work with great vigour, and within an hour we had four almost complete specimens, and many which were more fragmentary. I used these for teaching for many years, and they have now peen presented to the National Museums of Scotland.*

Twenty-seven years after

Another tale concerns the flat topped Carboniferous mountain country of north Yorkshire, in England.

When I was still a research student in Cambridge in the early 1960s, I had seen two or three exquisitely preserved trilobites from a horizon of grey fine limestone which had originated from this area. The trilobites, Paladin eichwaldi shunnerensis, *showed up as black against the limestone and their preservation was extraordinary (Figure 5A–B). The source of these was a thin band of limestone close to the summit of the 716 metre hill of Great Shunner Fell. I first visited this vast hill in the summer of 1964, walking 11 km from Hawes, the village where I was staying, up a long road and over rough moorland. The locality was quite easy to find and proved to be rich in perfectly preserved fossils, including trilobites, though complete specimens are rare. I collected for six hours in a furious wind, so strong that it blew most of my lunchtime sandwiches away. Then I walked another 11km back to the village with 15 kilograms of rock on my back and went up again next day. At the end of the week I had 90 kg of rock, and when I took it back to Edinburgh and started to sort through it, I discovered that many young growth stages were present. I had not seen them in the field because they were pale, the same colour as the rock; it is only the larger ones that were black.*

I returned to Shunner Fell year after year and collected enough material for a really detailed study. We prepared them for study with the scanning electron microscope. Quite unexpectedly, we found that the thin shells of the smallest specimens retained the impressions of the cells from which they had been formed (Figure 5 D and inset drawing). We also found also that the juvenile eye is schizochroal (Figure 5 D, E; see text for explanation). I had so much other work to do in the succeeding years that this information was not finally published until 1991, with my Chinese friend Zhang Xi–guang, twenty–seven years after I first visited Shunner Fell. But I have returned to these golden uplands many times thereafter, and the locality still yields magnificent fossils.

Figure. An early developmental stage of a Carboniferous trilobite, *Paladin eichwaldi shunnerensis*, from north Yorkshire, England. It is so well preserved that the shapes of cells which formed the exoskeleton are visible.

Weather forecast

Usually the weather has been good when I have gone trilobite hunting. When Riccardo Levi–Setti visited me in Scotland some years ago we had a perfect day in the Silurian rocks of the Pentland Hills, close to Edinburgh, where trilobites are abundant. But two days later we visited the classic area of Girvan on the west coast, with another friend who drove *a fast Jaguar. Here the weather was so bad, and the rain so intense that Riccardo contracted acute bronchitis He recovered thanks to the British National Health Service and some very effective medicine. Nowadays he prefers to find trilobites in Morocco, where the weather can be guaranteed to be fine!*

Preparation and photography of trilobites

If you crack open a rock, of the right age and type, using a hammer, you may be fortunate enough to see a trilobite. Sometimes the two halves of the rock will separate cleanly along the surface of the trilobite, which acts as a plane of weakness. This is commonly the case in limestones. But very often only part of the trilobite is exposed, and the rest of the matrix needs to be removed. This can be done by hand, using a fine needle, but is often best effected using an electro–mechanical device (vibrotool) with a vibrating needle. When all the matrix has been removed, and the trilobite is clean and dry it is ready for photography. When there is a good contrast between the fossil and the rock in which it sits, a colour photograph may be the best solution (Figures 1, 10–13). But more details are usually visible using black–and–white photography. The technique here is to whiten the surface with fine powder before photographing Figure 5 A, B, F; 8 A, B, E). There are two main ways to do this. One is to burn a magnesium ribbon underneath the trilobite, so that the surface becomes covered with very fine magnesium oxide. A second technique is to place some ammonium chloride powder in a pipette, on the end of which is a rubber bulb. Gentle heating will cause the ammonium chloride to turn into vapour, and when the bulb is pumped this comes out as a jet from the nozzle of the pipette. It can then be directed at the fossil, and coats the surface with a thin white film as it cools. Either technique reveals details of structure which would be less clearly seen otherwise. The main problem is obtaining an even coating; some people are very skilled at this.

Quite often trilobites are preserved in calcareous siltstone. If the ground–water, percolating through the sediment is slightly acid, it will eventually dissolve the not only the calcareous component of the siltstone, but the trilobite shell as well. What remains are moulds of the internal and external surfaces (Figure 8 A). Although no internal structure remains, these are otherwise very easy to work with. All that is needed is some liquid rubber latex, to which ink can be added. This is poured into the moulds, and built up in layers. The result is a flexible, and usually perfect replica of the original surface which can be whitened and photographed in the usual way.

Many kinds of sedimentary rock, especially limestones, undergo physico–chemical change after deposition, collectively known as diagenesis. This is because sedimentary rocks usually consist of different kinds of particles, including organic material from dead organisms, and bacteria. If there is extra phosphate or silica in the rocks then a thin film of one or other mineral may spread over the surface of a fossil. Such mineral coating is not uncommon, especially on small fossils, such as trilobite larvae. Both outer and inner surfaces may be coated in this way, and the thin mineral coats are surprisingly stable. When the limestone containing these fossils is dissolved in weak acid, the delicate thin films are released, and all parts of them may be studied in detail, using the scanning electron microscope (Figure 8 G, H). Much of our knowledge of early larval stages in trilobite is based on such material.

The scanning electron microscope which first came into general use in the early 1960s has revolutionised the study of trilobites and other fossils (Figure 5 C, D, E, G, H; 8 C, D, F, G, H). This microscope can reveal minute details of their structure, especially of the early stages in development, and has proved to be a phenomenal blessing in every way.

A tiny planktonic trilobite

Most adult trilobites lie within a size range of 2–15 centimetres long. There are some, such as the Ordovician giants from Portugal which are huge (<80 cm) and there is even a Canadian example over a metre long. But there are also tiny miniaturised trilobites, including the one illustrated here, *Ctenopyge ceciliae*; note the scale bar to see how small this tiny and spiny trilobite actually was. They were first found in 1993 in a block of black Upper Cambrian limestone in a stream bed in southern Sweden, and more blocks were discovered later. It was formally described as a new species in 2002. All these blocks were full of these tiny trilobites, and though they were always found as disarticulated fragments (heads, tails, thoracic segments etc.) it was possible to make what seems to be a reasonable reconstruction, as shown here, based on the original scientific description

Ctenopyge ceciliae is one of the smallest trilobites known, and it has a pair of tiny compound eyes. A German scientist, Brigitte Schoenemann, studied the material in Lund University, Sweden, in 2005. She found larval specimens with eyes having no more than 8 lenses; the adult has about 150, and made a range of photographs with the scanning electron microscope. But these lenses in the earliest developmental stages were the same size as those of the adult – 20 ìm. According to Dr Schoenemann's physical calculations, the larval eye could not function as an image former; there were too few lenses. And although the adult eye had better resolution, because it had many more lenses, it still would have formed only a hazy image. These eyes, both in the early developmental stages, and in the adult, functioned only as detectors of direction and intensity of light. They would only have worked in an environment flooded with light, in other words in the upper waters of the sea. The remarkable spinosity of this tiny trilobite would have inhibited sinking; to an animal of such a size the viscosity of the water would have been high. Both line of evidence suggest that *Ctenopyge ceciliae* was a planktonic trilobite, feebly swimming or passively drifting in the upper waters of the sea. Whereas the great majority of Cambrian trilobites were benthic, in other words living on the sea floor, *Ctenopyge ceciliae* had 'escaped' into the plankton, and was probably one of the first trilobite species ever to colonise this ecological niche.

Figure. A tiny, spiny, planktonic trilobite, *Ctenopyge ceciliae*, from the Furongian (Upper Cambrian) of southern Sweden.