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The biology of trilobites

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LANE, P. (1981). The biology of trilobites. *Proceedings of the Shropshire Geological Society*, **1**, 9-12. Trilobites have two main types of eye: where the individual lenses are in contact and a compound eye, each lens having its own cornea. Each lens is made of a single crystal of calcite and at every moult these would be lost and new ones developed with the next shell. The problem of double refraction was overcome by orienting the lens along the C axis.

The shell of a trilobite is composed of 91% calcite which becomes replaced by pyrite. Clarkson made calcite lenses with cartesian surfaces. Sisney used the technique of stereoscopic X-rays. There is a tendency for some groups of trilobites to grow convex and smooth, e.g. *Homelanotus*, a smooth *Calymene* from the Welsh borders, a smooth *Olenid* from the Cambrian of Spitzbergen, and the smooth *Asaphids* from the Ordovician of North America. There is also the rather beautiful British fossil trilobite of the genus *Bumastis*.

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In the last few years more information has become available about trilobites as animals. They can no longer be regarded as bits of stone; they were once beautiful, elegant animals with some surprising specialisations. This lecture dealt with their anatomy, physiology and mode of life.

Trilobites are probably second only to dinosaurs in the amateur's interest in fossils. They were a very successful group from the Lower Cambrian to near the top of the Permian, a period of some 350 million years during the first part of which they were the most dominant animal in the oceans, but then they became rare in the faunas. Their remains are often fragmentary, because as arthropods they were segmented animals and broke into pieces when they died. Similarly their moult was easily broken and dispersed. However they are sometimes found in abundance.

The average trilobite has a head, segmented body and tail plate, a raised axis in the middle and two lower side parts, on the cheeks at the side of the head are a pair of eyes, which are better developed in some trilobites than in others. Within this general pattern as a group they are very variable in their morphology.

A specimen from Canada has only a head and a tail, while at the other extreme is a specimen from the Lower Cambrian of Australia which has a small head and tail with a long body composed of 56 segments. Some trilobites are very flat, such as are found in the Welsh Middle Ordovician, others are extremely globose, some are smooth, some very spiny as found at Wrens Nest. These adaptations, such as spines, must have had some function which is not yet understood. Their range of adult sizes is extreme. The smallest known adult is from the Tremadoc rocks of Sheinton Brook and is less than 1.5 mm long, while the biggest is from the Devonian of America and is 600 mm long.

The interpretation of trilobite life styles has been made from studies of exceptionally well preserved specimens.

One of the most striking features of trilobites are their eyes, which range from absent to complex. A small Bohemian trilobite, which also occurs in Wales and Scotland, has a pair of large compound eyes which meet in front of the head so that they occupy approximately 70% of the head area . This is obviously an extreme development for something; one school of thought is that they lived in muddy water and therefore needed to gather as much light as possible, but this is only conjecture.

There are two main types of eye. Firstly one where the individual lenses of the eye are in contact and all the lenses are covered by a single cornea. Not much work has been done on this type of eye, but intensive study has been made of the second type. This is again a compound eye, the individual lenses are an order of magnitude larger and they are arranged in rows, separated from each other by the ordinary shell of the animal; each lens has its own cornea. Each lens is made of a single crystal of calcite and at every moult these would be lost and new ones developed with the next shell. The problem with a calcite lens is that it gives double refraction. Since the image from several hundred of these lenses would be very confused, the trilobite overcame this problem by orienting the lens along the C axis (the long axis), which is the only orientation which does not give double refraction.

The cross section of a lens shows that it is domed on top, with a very thin cornea, the bottom surface has a double curve and there is a sediment filled space. Study of these lenses has been principally by Ewan Clarkson of Edinburgh University. He identified the hemispherical top area, two types of double curved surface and the sediment filled area which contained a different sediment type to that which comprised the rock. When internal moulds are preserved, the lens shape can be viewed in three dimensions. Although the shell and the lens have both gone, what is left is a boss with a furrow all round it, this is the shape of the bottom of the calcite lens.

There are two general shapes, both rather similar, the difference being that in one the curve does not come back on itself and is rather more funnel-shaped at the bottom of the lens. The reason for this shape was a puzzle until Enricho Levisetti, a Chicago physicist at the Fermi Institute, saw the surfaces and identified them as the surfaces between the two elements of a double lens which is designed to cut down spherical aberations - these are produced because light going through the middle of the lens is focused at a slightly different place from light going through the edges of the lens, giving a zone of focus rather than a sharp point focus. If lenses are made of glasses of two different dispersive powers, spherical aberation is reduced. This type of lens was invented by Descarte in 1673 and a similar shaped lens was invented by Huygens in 1690. The shapes of these two lenses, called cartesian doublets, are very similar to the trilobite's lenses, so trilobites invented them some 600 Ma before Descarte(!) and needed them to concentrate light entering the lens.

To prove the theory, Clarkson made calcite lenses with cartesian surfaces, but the main problem was what had originally filled the now sediment filled area. It seems likely that it was occupied by a fluid with a different diffractive index to make up the doublet. Clarkson made the upper lens of calcite and the lower lens of different types of plastic with different dispersive powers. Eventually he found a combination of calcite and plastic that gave a good focus, therefore knowing the dispersive power of sea water and of calcite, it is obvious that whatever fluid was in the eye had the same refractive index as that particular plastic.

Over the last ten years a lot of work has been carried out on trilobites which are in an exceptional state of preservation, i.e. with appendages. This very exceptional preservation occurs in pyrite. The shell of a trilobite is composed of 91% calcite which becomes replaced by pyrite. The major advantage in having pyrite trilobites is that they do not need preparation or to be developed out. The sample can be placed in an X-ray machine and a radiograph taken of the fossil.

Sisney in the USA has used the technique of stereoscopic X-rays. A picture is taken with the fossil tilted slightly one way, then another is taken with it tilted the other way; this gives a stereo pair which, when viewed through a stereoscopic viewer, gives a three dimensional X-ray view of the trilobite. This gives an outline of the shell, antenae and appendages. Sisney looked at 400-500 pyrite trilobites and did not record a particular feature until it occurred in at least two samples.

From this meticulous work he was able to produce data which supported what had already been thought about trilobites, plus some new revelations. He showed that the mouth was where it had been thought to be, facing backwards behind the hyperstome. He also showed that there was a U-shaped alimentary tract with a stomach and intestine along the axis of the animal. Also the furrows on the glabella were sites of insertion of muscles and hefty sheets of muscle were stretched along the length of the animal, which enabled it to roll up. An unexpected discovery was an internal skeleton as well as the external skeleton of the shell. The internal skeleton consisted of a regular arrangement of calcite bars forming a box girder type structure, to which were attached all the muscles which enabled the trilobite to move, feed, dig, etc.

There was a 'paddle' with strong teeth on it, on the central part of the first segment of opposite pairs of legs, which provided a ripping mechanism, which is found in other arthropods and is called a nathobase. This is the jaw mechanism of the trilobite, but it is not known whether they were predators or scavengers. It has therefore been shown that trilobites could do something else other than the rather unintelligent, mundane things usually attributed to them, such as 'they grubbed in the mud' or 'they used their head as a shovel'.

Sisney was able to use a rock sample containing some 500 pyritised trilobites which represented a community suddenly destroyed by a sudden onrush of sediment and containing larval, juvenile and adult specimens. Sisney measured all 500 trilobites and was satisfied with 360 or so. From these measurements he was able to draw a graph of trilobites of particular lengths against their numbers. This graph shows four separate peaks indicating four different median sizes of trilobite i.e. it is a typical graph of recruitment to a population subject to seasonal, probably annual, breeding. The sample did not contain any of the smallest trilobites and this upholds the theory that the tiniest larvae (0.25 mm to 1 mm) were planktonic and only when they attained a length of 2+ mm did they become benthonic.

Another graph was plotted of length against years, taking the medians, which produced a straight line. This was unexpected, since a sigmoid curve is usually produced from such data, but it indicates a high mortality rate and that trilobites lived at least four years. The adult stage is reached when the last thorassic segment typical of the species is formed, possibly at about 10 months.

There are some 15,000 species of trilobite and the full range of appendages are known in only five. Fortunately these five species are very stratigraphically separated, ranging from Middle Cambrian to Lower Devonian. Appendages are known not only from pyrite preservation but also from the special preservation of the Burgess Shales of Middle Cambrian age in British Columbia, where carbonisation has preserved specimens as well as enabling impressions in the very fine shale.

The appendage has two clear parts, a lower seven-jointed leg and above this a filamentous brush-like structure. The traditional view is that the lower part of the appendage was the walking leg and the upper was a gill. However a researcher in Sweden has produced evidence that it was not a gill, arguing that you do not often get appendages preserved but when you do, you cannot detect a differentiation between the leg and shell. Furthermore, if it was a gill, it should not have an exoskeleton; it should be a delicate membrane capable of exchanging gases.

Therefore, on preservational aspects, it is unlikely to be a gill. The detailed morphology of this filamentous organ is that each element is shaped like the blade of a knife - thin, narrow and long - which is a very bad shape for an exchange mechanism like a gill.

If this structure is not a gill, were there gills and if so where were they situated? Trilobites needed to breathe, but they did not need to have gills. Many trilobites are generally flat and thick in their general morphology, giving them a large surface to volume ratio. There is only one organ of a trilobite that we know nothing about, but it is one it must have had, i.e. a ventral membrane stretched between its outer part of the shell to hold the guts in. Yet it is never known even in delicate preservations, indicating that it must have been extremely fragile. An animal with a large undersurface area such as this may not have needed gills; it would have been possible to exchange gases across such a membrane On the other hand, if they did need gills, they would have been attached to the ventral membrane, protected by the appendages beneath them and the shell above them.

What then is the filamentous structure? It bears similarity to a sediment filter, which would trap food particles and pass them to the appendages at the same time aerating the gills

It is possible to understand something about the mode of life of trilobites from a number of lines of investigation:

1. Overall morphology - why that shape? What was its function?
2. What sediments are they found in?
3. What other fossils are found with it?
4. What is the geographical distribution?
5. Compare the extinct organism with its nearest living relative - a dangerous line.'

The information from these investigations is then used to deduce what trilobites did for a living.

There is a tendency for some groups of trilobites to grow convex and smooth, e.g. *Homelanotus*, a smooth *Calymene* from the Welsh borders, a smooth *Olenid* from the Cambrian of Spitzbergen, and smooth *Asaphids* from the Ordovician of North America.

There is a rather beautiful British fossil trilobite of the genus *Bumastis* which is 12 cm long, very convex and very smooth. The most striking feature is its eye, which is long and parallel-sided - strip like. Therefore if the body was in the 'normal' position, the eye would only look straight up or down but, if the eye is oriented horizontally, the head is up in the air and the tail is on the ground.

This trilobite could have lived in a burrow with its eye horizontal with the surface. This is a good example of how to work out a functional model. This hypothesis is adequately supported by finds of trilobites preserved in their burrows.

There is another type of trilobite with small appendages which would have been useless for swimming, and it is thought that this species probably lived attached to floating algae as part of the epifauna in the surface waters.

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