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A FURONGIAN POLYMERID PLANKTONIC TRILOBITE

Brigitte Schoenemann [1], Euan N.K. Clarkson [2], Per Ahlberg [3]
and M. Eugenia Dies Álvarez [4]

[1] Paläontologisches Institut der Universität Bonn, Nussallee 8,D-53115 Bonn, Germany.
bschoenem@t-online.de
[2] Grant Institute of Earth Sciences, School of Geosciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW, Scotland, UK. Euan.Clarkson@ed.ac.uk
[3] Centrum för GeoBiosfärsvetenskap, Avdelningen för Berggrundsgeologi, Sölvegatan 12, S-223 62 Lund, Sweden.
Per.Ahlberg@geol.lu.se
[4] Área de Paleontología, Dpto Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, E-50009 Zaragoza, Spain.
medies@unizar.es

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The invasion of the planktonic realm by adult polymerids was rare and sporadic during Cambrian times, although their juvenile stages may well have inhabited the plankton. Even pelagic Cambrian trilobites were uncommon, a recent convincing record before the Ordovician is *Beishanella* (Fortey and Rushton, 2007). Opinion is still divided as to whether the miomerids, with few thoracic segments (the agnostoids and eodiscoids) were planktonic (Robison, 1972), but accumulating evidence suggests that they were benthic too (Whittington, 1997; Chatterton and Speyer, 1997). A few Cambrian polymerids have beem thought to be planktonic, for example the tiny corynexochid *Thoracocare* (Robison and Campbell, 1974) and the burlingiids (e.g. Ebbestad and Budd, 2002), but such a habit was never claimed as certain. Other small arthropods inhabited the plankton from Lower Cambrian onwards (Butterfield, 2001). Here we report upon a miniaturised Furongian (upper Cambrian) olenid from Sweden, one of the smallest trilobites known, which we interpret as possibly the earliest unequivocally planktonic trilobite. The evidence for this mode of life comes from two sources, the optics of the visual system, and the extreme spinosity of the tiny body.

Ctenopyge ceciliae (Clarkson and Ahlberg, 2002) occurs in great numbers, at one locality only, in calcareous concretions found in a stream bed at Röstånga, in Skåne, Sweden. From the associated fauna it belongs to the *Peltura scarabaeoides* Zone. It is known only from disarticulated sclerites, and probably had no more than a few thoracic segments; here it is reconstructed with three, and although provisional, this restoration seems functionally realistic (Fig. 1). This miniature form was probably derived by progenesis from a normal-sized representative of the genus; even the earliest ontogenetic stages are exceptionally small, and the whole ontogeny is much compressed.

The mature *Ctenopyge ceciliae* has well-preserved reniform and holochroal compound eyes with about 150 calcitic lenses, the smallest juvenile eye has only about 10 and various intermediate stages of eye development are known (Fig. 2). Since the adult is tiny, the eyes are also exceptionally small, which raises the question of how they functioned. The application of the known laws of optics has considerable potential for addressing this vital question, even though only the lens array is preserved, and not the

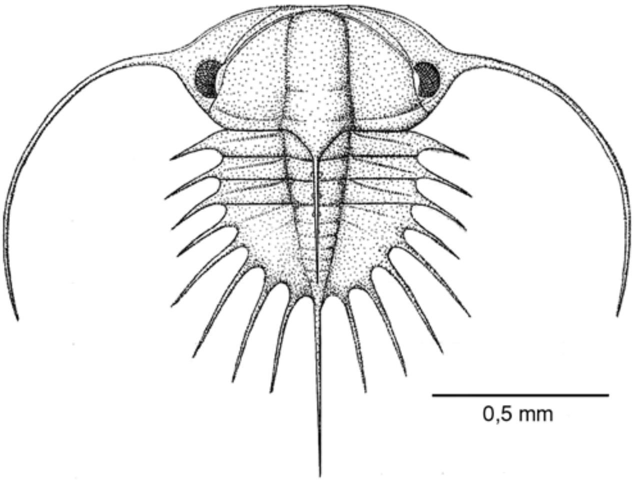

Figure 1. *Ctenopyge ceciliae* (Clarkson and Ahlberg, 2002), adult.

underlying structure. SEM photography has revealed that the lenses, some 21.33 +/- 2.39 µm in diameter (D), do not increase with growth and are much the same size in the smallest eyes as they are in the adult (Fig. 3a) Yet they are larger than they might be, for many arthropods have smaller lenses, as for example in the midge *Culex pipiens* (Linné, 1758) where the diameter is no more than 16µm. This indicates that the eyes of *Ctenopyge ceciliae*, even in the juveniles, are constructed to see; the visual system is not reduced in any way and remains a true compound eye. Since the material is largely undistorted it has proved possible to estimate the interommatidial angle $\Delta\varphi$ for various growth stages even though the packing of the lenses on the visual surface is not perfectly regular.

The thin, biconvex lenses, with the upper surface more convex than the lower, have a high refractive index (n=1.66 for calcite) and are functional in sea water, which a chitinous lens would not be. In Recent marine arthropods, the 'lenses' have planar surfaces and are never biconvex. With growth $\Delta\varphi$ decreases (Fig. 3b) and whereas the number of 'pixels', (represented by the lenses) increases, acuity improves only to a limited degree in the mature trilobite. This indicates that an optimal sensitivity was already established in the juvenile eye, which was not improved on with growth. As in all kinds of eyes, there is a trade-off between acuity and the brightness of the image, and the eyes of *Ctenopyge ceciliae* would only function in a well-lit environment, in other words in the uppermost waters of the sea. In the juvenile stages, they were not image formers, but worked as light detectors. The convex visual surface subtends a broad field of view, and even in the early stages the eye could detect the direction of light, of an object and its related movement, and would enable its bearer to stay within the photic zone. A somewhat improved acuity in the later stages of development would have enabled a better discrimination of the environment, and the recognition of social partners and other patterns.

Miniaturisation (*sensu* Fortey and Owens, 1990) would be in many instances a useful prerequisite for colonising the planktonic realm. Previously (Clarkson and Ahlberg, 2002), this minute trilobite was interpreted as planktonic on account of the very long spines, where the viscosity of the water relative to the dimensions of the animal is high. Study of the optical system greatly strengthens this interpretation: *Ctenopyge ceciliae* was a planktonic filter-feeder, and possibly the earliest known of all trilobites to

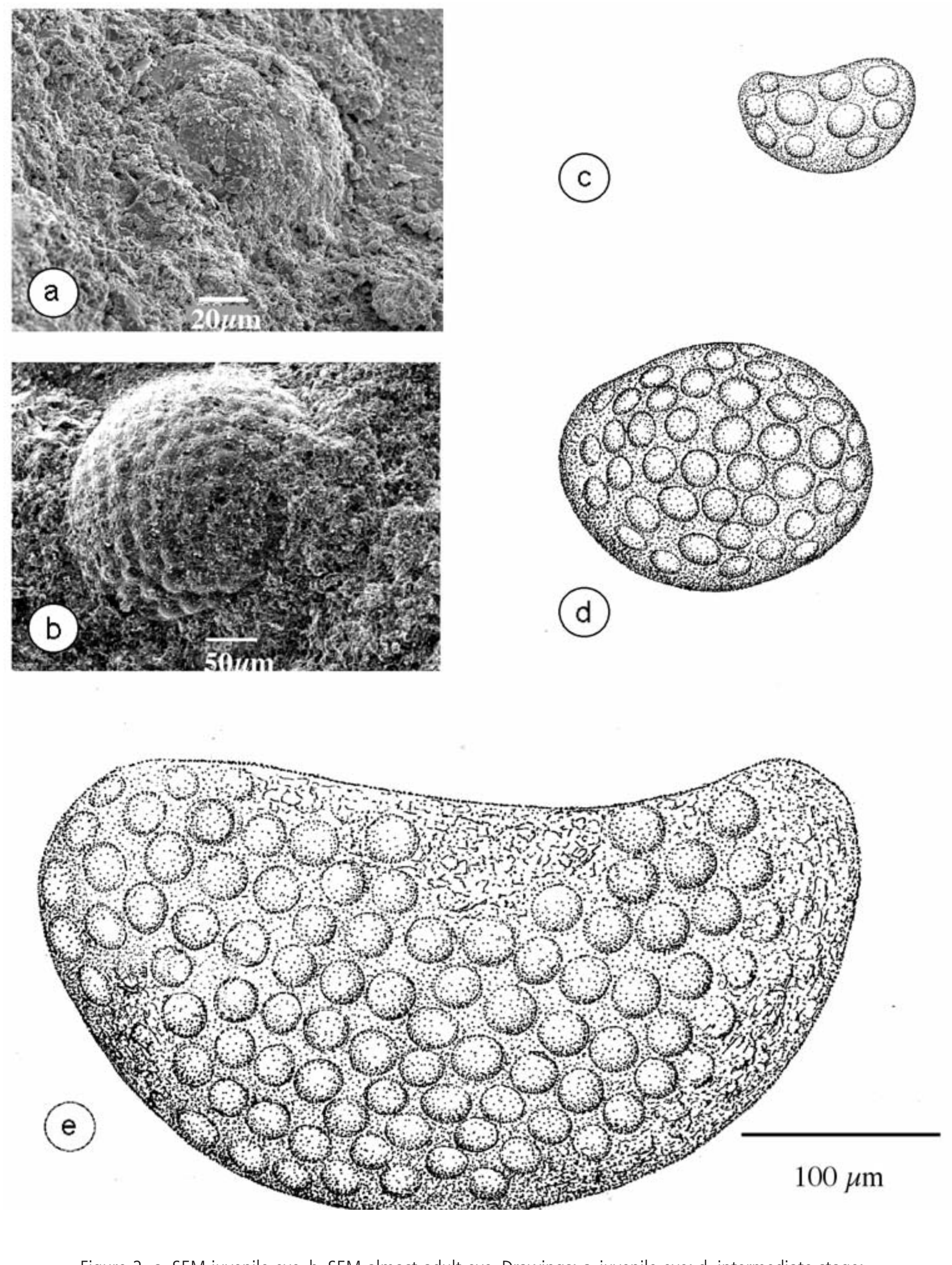

Figure 2. a, SEM juvenile eye. b, SEM almost adult eye. Drawings: c, juvenile eye; d, intermediate stage; e, adult eye (all drawings are at same scale).

colonise this niche. Planktonic life forms are normally widely distributed, but this species occurs at one locality only. It seems, however, to have been a short-lived species, and in any case individuals are very delicate and likely to be preserved only in rare and unusual conditions. Following its extinction, further colonisation did not take place until the great diversification of the Ordovician.

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