TRILOBITE CUTICLE MICROSTRUCTURE AND COMPOSITION

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ABSTRACT. Previous literature on the microstructure and composition of the trilobite cuticle is reviewed. The microstructure of the cuticle of *Asaphus raniceps* Dalman *sensu* Angelin (1854) is described in detail, and a table outlining the major features of the cuticles of fourteen other trilobite species is included. In *Asaphus raniceps* and some other species, two main regions of the cuticle are consistently present: an outer layer characterized by perpendicular prisms, representing about one-fifteenth of the total thickness of the cuticle and an inner area forming the bulk of the cuticle. In the inner area of many cuticles, characteristic primary microstructures are fine perpendicular canals, a variety of wider canals, and horizontal laminae. Three types of tubercle are distinguished from thin-sections. Inorganic analyses of *Asaphus raniceps* show that the cuticle consists largely of calcite. Decalcification of this cuticle with E.D.T.A. left organic residues.

A LARGE number of incidental observations has been made on the trilobite cuticle, usually during the course of systematic descriptions. However, no author has studied the cuticle of a wide range of trilobite species in the thorough way that Lindström (1901) and latterly Clarkson (1967, 1969) have examined visual organs. Attempts at comparing trilobite cuticles with arachnid or crustacean cuticles have therefore often been based on inadequate evidence, and in some cases recent work on extant arthropod cuticles has been totally disregarded.

PREVIOUS LITERATURE

Subdivisions of the trilobite cuticle. The terms 'chitinous' and 'integument' have frequently been used in descriptions of trilobite exoskeletons. Although chitin is the most characteristic organic component of arthropod cuticles, it comprises only a small fraction of the dry weight of calcified cuticles. The use of the term chitinous to describe dark hard fossil material is particularly inappropriate: pure chitin is colourless, soft, and flexible. The term integument includes the cuticle, the underlying epidermal cells which secrete it, and the basement membrane. In trilobite exoskeletons, therefore, only the cuticle is found preserved.

Harley (1861) was probably the first to examine the trilobite cuticle critically, while attempting to establish the systematic position of various 'Astacoderma' from the Ludlow Bone Bed. Thin-sections through the cuticle of *Calymene* (L. Ludlow) showed that it consisted of an outer fibrous layer and an inner prismatic layer, both pierced by canals. However, Harley doubted whether this was the original structural appearance. In his monograph on the visual organs of trilobites, Lindström (1901) figured sections of the cuticles of many species but made very few comments on their structure. Cayeux (1916) compared the structure of trilobite and crustacean cuticles, and Størmer (1930), who gave a detailed account of the 'shell' structure of some Trinucleidae, recognized four main layers in the cuticle of *Tretaspis* and compared these with the four layers in the cuticle of *Homarus*. The microstructure of the cuticle of *Phacops accipitrinus maretiolensis* R. and E. Richter was described by Rome

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(1936) who distinguished three main regions of the cuticle besides observing many other features. Hupé (1953) considered that three layers in the cuticle might correspond to the epicuticle, pre- and post-exuvial layers of modern cuticles. Harrington (1959) reviewed the work of Størmer (1930), Hupé (1953), and Kielan (1954) and interpreted the three main layers of Størmer and Kielan as corresponding to those of the modern arthropod endocuticle. However, Rolfe (1962) considered that many of the subdivisions apparent in fossil cuticles were due to diagenetic replacement. More recently, Majewske (1969) and Horowitz and Potter (1971) reviewed some of the previous literature on trilobite cuticles, figured some photomicrographs of thin-sections, but made few observations. Bathurst (1971) has given a more comprehensive account of previous work.

Primary microstructures. The term 'primary microstructures' was introduced by Rolfe (1962) to describe all structures found in fossil cuticles comparable with those in modern arthropod cuticles. A brief review of characteristic structures in extant cuticles has been given by Dalingwater (1973).

Pore-canals: Rolfe (1962) reviewed descriptions of structures from fossil cuticles resembling the pore-canals of extant cuticles, and concluded that the various small canals described by Størmer (1930), Rome (1936), and Evitt and Whittington (1953) were perhaps too large and too sparsely distributed to be true pore-canals. However, Harley (1861) had observed that the cuticle of *Calymene* was traversed by many straight tubes 0·5–1·8 μ in diameter, Lindström (1901) figured many sections of cuticles perforated by numerous minute canals, and Balashova (1948) clearly distinguished very fine 'canalicules' from larger canals perforating the carapace of the Asaphidae.

Larger canals: Rolfe (1962) suggested that many of the larger canals in fossil cuticles should be termed gland or setal ducts. In extant arthropods such ducts are generally larger, are more irregularly placed, and occur less frequently than pore-canals. Larger apertures through trilobite cuticles have been described by Lindström (1901), Richter (1914), Cayeux (1916), Raymond (1920), Størmer (1930, 1931), Whittington (1941, 1956, 1962), Ross (1951), Evitt and Whittington (1953), Hupé (1953), Whittington and Evitt (1954), Richter and Richter (1954), and Harrington (1959).

Laminae: Nearly all extant arthropod cuticles are horizontally laminated and individual laminae are 0·2–10 μ thick. Rolfe (1962) reviewed some of the earlier literature on laminae in trilobite cuticles, commenting on the work of Zittel (1900), Cayeux (1916), Størmer (1930), and Rome (1936). However, Harley (1861) had observed obscure indications of a finely laminated structure in the cuticle of *Calymene*, Sorby's (1879) 'lines of growth' are presumably laminae, and Lindström (1901) also figured many finely laminated cuticles.

Tubercles: Tubercles are defined by Harrington, Moore, and Stubblefield (1959) as small knob-like prominences on any part of the exoskeleton, whereas smaller structures are termed granules. However, the term tubercle has been used imprecisely to describe:

(i) Structures involving thinning and doming of the cuticle (Raymond, 1920; Størmer, 1930; Kielan, 1954).

(ii) Domed thickenings differentiated to some extent from the main part of the cuticle (Rome, 1936).
(iii) Discrete structures embedded in cuticle surfaces (Lindström, 1901; Walcott, 1921).

Prisms: The surfaces of many arthropod cuticles are covered by a close polygonal network. Each polygon possibly represents the area of activity of an underlying epidermal cell and is formed by inward extensions of epicuticlar material at the interfaces between adjacent areas of influence (Dennell 1960). Larger, less regular polygonal areas seen in perpendicular sections of calcified cuticles may represent areas of activity of crystallization centres. Cayeux (1916) figured some relatively large polygonal areas from the cuticles of '*Trinucleus goldfussi*' and Hupé (1953) mentioned 'un fin réseau à mailles polygonales' in his account of the trilobite cuticle.

Inorganic chemistry and mineralogy. It has often been stated, without critical examination of the cuticle itself or of the results of previous research, that the trilobite cuticle contains significant amounts of phosphate. For example, Zittel (1887) described alternate thin layers of calcium carbonate and phosphate, but Cayeux (1916) found no trace of these layers and neither did Bøggild (1930) who clearly thought Zittel was mistaken. Richter (1933) estimated that the trilobite exoskeleton contained up to 30% phosphate, whereas Cayeux's (1933) detailed analyses indicated that phosphates were present only in limited quantities. Only Raw (1952) considered that the cuticle was originally aragonitic, subsequently becoming silicified or coarsely crystallized to calcite. Probably the most significant contribution to a study of the original inorganic composition of the trilobite cuticle was made by Stehli (1955). Although he analysed only one trilobite pygidium, the specimen came from the Middle Permian Buckhorn asphalt deposit in which original shell mineralogies seem to have been preserved. X-ray analysis showed that this pygidium was composed entirely of calcite.

Organic chemistry. Abelson (1954) referred to the presence of three amino-acids in an Ordovician *Calymene*, whereas Fujiwara (1963) found no amino-acids in another species of the same genus.

MATERIAL AND METHODS

Thin-sections provided most of the information for this study but material was also prepared by E.D.T.A. decalcification and acetate-peel preparation. A preliminary study, using the Scanning Electron Microscope (S.E.M.), was made on surfaces as well as on broken and etched material. A wide range of trilobites in varying modes of preservation was examined. The most satisfactory specimens for thin-sectioning were those preserved in fine-grained limestones, with part of the exoskeleton enclosed in matrix. The identity and orientation of these specimens could thus be determined, while the matrix formed a most satisfactory natural embedding medium. Where possible, serial sections were made from a single specimen. Random section series were also made from samples crowded with trilobite remains. Sections were finished by hand using 1200 mesh carborundum and then left relatively thick (20–30 μ). Such thick slices offered much detail, but were unfortunately somewhat

difficult to photograph satisfactorily. All preparations are stored in the Department of Zoology, University of Manchester, England.

The cuticle of *Asaphus raniceps* was in addition analysed in a Phillips X-ray diffractometer, and by X-ray powder photography.

THE CUTICLE OF *ASAPHUS RANICEPS*

Specimens of *Asaphus raniceps* Dalman *sensu* Angelin (1854) were collected from the lower 'Raniceps' Limestone, Haget, Öland, Sweden. About 100 longitudinal, transverse, and tangential perpendicular sections were made across all the calcified areas of the exoskeleton. In addition, a preliminary study of the cuticle of this species was made using the S.E.M. The cuticle of this species is the best documented here and serves as a model for detailed description.

The cuticle is relatively thick compared with that of modern arthropods of comparable size but varies considerably from one area of exoskeleton to another. In a ten-slide series made from block Öl.0.1 the following ranges of thickness were measured: cephalon 180–450 μ, hypostome 120–560 μ, thorax 100–300 μ, pygidium 160–300 μ.

Surfaces of the cuticle examined with the S.E.M. show a matrix of calcite prisms with morphological indications of c-axes orientated perpendicular to the cuticle surface (Pl. 107, fig. 1). In thin-sections an outer layer comprising one-tenth to one-fifteenth of the total cuticle thickness is seen, composed of fairly regular perpendicular prisms (Pl. 107, fig. 5). However, under crossed-nicols this layer does not extinguish uniformly (Pl. 107, fig. 6) suggesting that although prisms may be orientated with their c-axes normal to the surface, this orientation is not totally uniform. Broken sections of cuticle examined with the S.E.M. confirm light microscope observations that the outer layer is distinct (Pl. 107, fig. 2) from the main part of the cuticle (hereafter termed the inner area). No individual prisms can be seen in the inner area even when it is examined at a magnification of about $\times 1{,}000$ with the light microscope. Again, total extinction does not occur when particular areas of the cuticle become aligned with the planes of polarization. Under the S.E.M., broken sections of the inner area suggest fibrous crystallites running tangentially to the surface (Pl. 107, fig. 3) but this impression is not confirmed by etched sections (Pl. 107, fig. 4).

The inner area of the cuticle includes fine perpendicular canals approximately 0·1 μ in diameter, and occasionally fine parallel horizontal laminae approximately 1 μ apart can be seen. The cuticle is thicker at the anterior margin of the cephalon, where fine vertical canals are often emphasized by impregnation with pyrite. Wider canals

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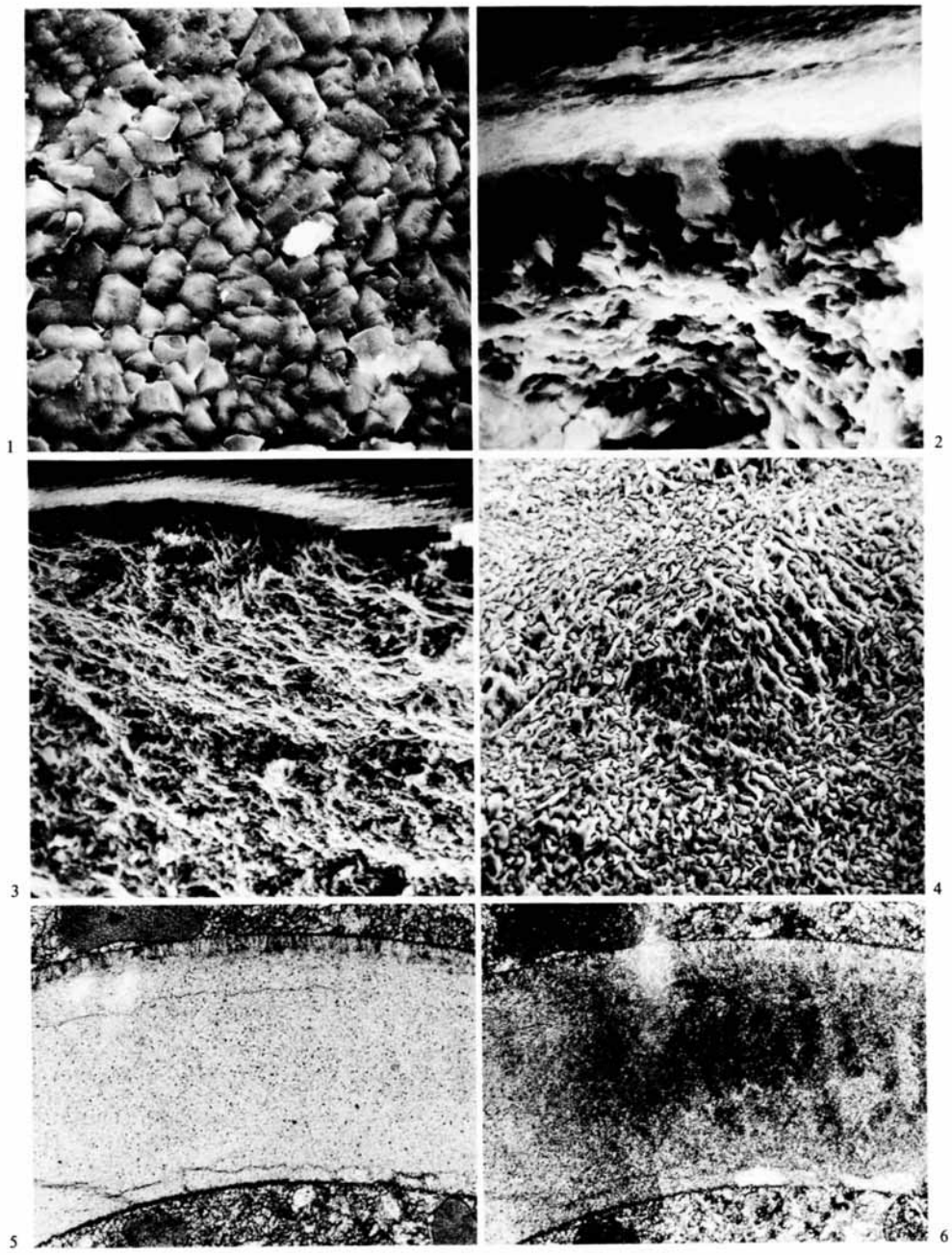
EXPLANATION OF PLATE 107

Figs. 1–4. Scanning electron micrographs of librigenal cuticle of *Asaphus raniceps* Dalman. 1 Upper surface of cuticle, showing fairly regular calcite prisms. $\times 1950$. 2 Broken perpendicular section of cuticle, showing discrete outer layer. $\times 1730$. 3 Broken perpendicular section, showing apparent fibrous crystallites tangential to surface. $\times 420$. 4 Etched perpendicular section of cuticle. $\times 545$.

Figs. 5–6. Longitudinal perpendicular section (L.P.S.) of glabella of *Asaphus raniceps* Dalman showing outer layer and inner area of cuticle. Slice Öl.98.1. 5 Plane-polarized light. 6 Crossed nicols. $\times 125$.



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approx. 4 μ in diameter extend to thorn-like projections representing sections through ridges on the anterior part of the cephalon (Pl. 108, fig. 1). This sculpture is even more pronounced on the cephalic doublure, the forward projecting 'thorns' (= sections of terrace lines) becoming flattened and scale-like with canals opening at their bases. The terrace lines on the pygidium are seen in thin-section as thickened ridges of cuticle, but the outer edge of the pygidial doublure is distinctly corrugated. Sculptured ridges on the hypostome are seen in section to be penetrated by canals approximately 4 μ in diameter.

Several sections were made through the hypostomal maculae where the cuticle is slightly thicker. Here, in contrast to other areas of the hypostomal cuticle, fine perpendicular structures are accentuated by pyrite.

The outer surface of the thoracic cuticle is generally smooth but cuticular sculpturing on the pleural doublure is reflected in thin-sections. Where the cuticle deflects to form the narrow posterior ventral doublure of the thoracic axial rings, the angle is characterized by an area of darker cuticle. This area may represent differentiation of the cuticle to permit flexibility between segments additional to that provided by the soft intersegmental membrane.

Well-preserved material, particularly when freshly broken from the matrix, exhibits a glossy lustre. This possibly represents an extremely thin outermost layer not visible in thin-sections. Isolation of this layer proved difficult but decalcification with a 5% solution of E.D.T.A. (disodium salt) left a residue of brown material with a clear surface layer. In several specimens this surface layer is regularly prismatic in some areas, each prism being 6–7 μ across (Pl. 108, fig. 2). The brown residue is usually amorphous but sometimes contains small twisted tubules about 1 μ in diameter.

X-ray analyses of cuticle from the cephalon, thorax, and pygidium indicated a composition entirely of calcite.

EXPLANATION OF PLATE 108

Figs. 1–2. *Asaphus raniceps* Dalman. 1 L.P.S. anterior of cephalon. Slice Öl.96.1. ×27. 2 E.D.T.A. preparation, showing prismatic surface layer. E.D.T.A. prep. 19. ×360.

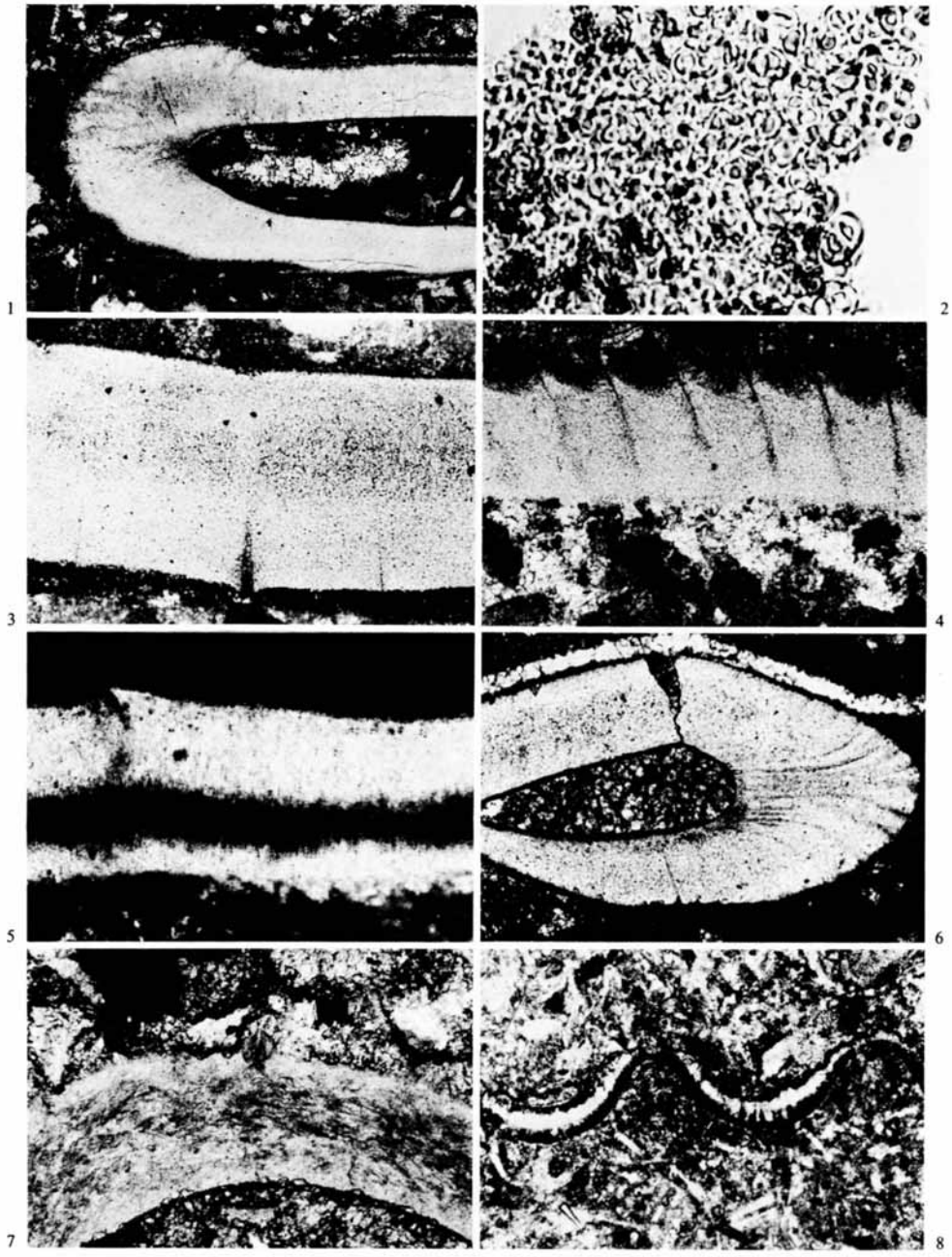
Figs. 3–4. *Illaenus aduncus* Jaanusson. Slice Öl.I.1a.2. 3 Tangential perpendicular section (Tan. P.S.) librigena, perforated by large perpendicular canals. These canals are regularly spaced (50–150 μ) and were observed in all areas of the exoskeleton examined. ×100. 4 Tan. P.S. edge of thoracic pleura, cuticular sculpturing perforated by 'hair-like' structures. ×90.

Fig. 5. *Bumastus barriensis* (Murchison). L.P.S. pygidial doublure, showing tightly helically coiled fine perpendicular canals accentuated by pyrite. Slice Dy.B.1b.2. ×100.

Fig. 6. *Paladin eichwaldi shunnerensis* (King). Transverse perpendicular section (T.P.S.) pygidial margin, showing larger perpendicular canals which are particularly prominent in this region of the cuticle. Slice W.s.1a.1. ×90.

Fig. 7. *Cyrtometopus* sp. L.P.S. glabella lobe, showing irregular undulating laminae which give the cuticle of this genus its characteristic 'cloudy' appearance. Slice C.(FMB)1.2. ×90.

Fig. 8. *Encrinurus punctatus* (Wahlenberg). L.P.S. glabella, showing large tubercles—the cuticle domes and thins. Tubercles of this type are also present in axial regions of the thorax. Small discrete tubercles are present on lateral areas of the cephalon. Slice Dy.E.7.1. ×24.



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THE CUTICLES OF OTHER TRILOBITE SPECIES

Brief descriptions of the cuticles of fourteen trilobite species are deposited with the British Library, Lending Division, Boston Spa, Yorkshire, reference number SUP 14001. These are illustrated in Plates 108 and 109, and Table 1 summarizes their characteristic features.

TABLE 1. Synopsis of the characteristic features of the cuticles of fourteen trilobite species.

	Material examined	Cuticle thickness (μ)	Outer layer	Larger perpendicular canals	Fine perpendicular canals	Laminae	Special features
Agnostus pisiformis (Linnaeus) Middle Cambrian, Öland.	c.,p.	7-30	-	+	-	+	-
Nileus armadillo Dalman 'Raniceps' Limestone, Öland.	c./s.	100-200	-	-	+	-	+
Illaenus aduncus Jaanusson 'Raniceps' Limestone, Öland.	c./s.	180-700	+	+*	+	+	+*
Bumastus barriensis (Murchison) Wenlock Limestone, Dudley.	c.,p.	300-500	-	+	+*	+	-
Cyrtosymbole pusilla (Gürich) Famennian Limestone, Poland.	s.	30-100	+	+	-	-	+
Paladin eichwaldi shunnerensis (King) Shunner Fell Limestone, Yorkshire.	p.	150-200	+	+*	+	+	-
Ampyx nasutus Dalman Expansus & 'Raniceps' Limestones, Öland.	c.	100-200	+	-	+	+	+
Cyrtometopus clavifrons (Dalman) 'Raniceps' Limestone, Öland.	c.	200-340	-	+	-	+	+*
Encrinurus punctatus (Wahlenberg) Wenlock Limestone, Dudley.	c./s.	100-240	+	+	+	+	+*
Calymene blumenbachii Brongniart Wenlock Limestone, Dudley.	c./s.	200-400	+	+	+	+	-
Phacops granulatus (Münster) Famennian Limestone, Poland.	s.	100-600	-	+	-	-	+*
Trimerocephalus caecus (Gürich) Famennian Limestone, Poland.	s.	120-270	-	+	-	-	+*
Acaste downingiae (Murchison) Wenlock Limestone, Dudley.	c.	160-300	+	+	-	-	+*
Boedaspis ensifer Whittington & Bohlin Expansus Limestone, Öland.	p.	200-250	+	-	+	-	+*

KEY c. = cephalon, p. = pygidium, c./s. = complete specimens, s. = slides, + = present, - = not observed, * = figured.

EXPLANATION OF PLATE 109

Fig. 1. *Calymene blumenbachii* Brongniart. L.P.S. glabella lobe, showing a range of perpendicular canals accentuated by pyrite, some of which are similar to the fine canals of other trilobite cuticles. Slice Dy.C.1.2. ×160.

Fig. 2. *Phacops granulatus* (Münster). T.P.S. edge of pygidial axis, showing large tubercle; the cuticle domes and thickens. Slice P.g.(0)1. ×92.

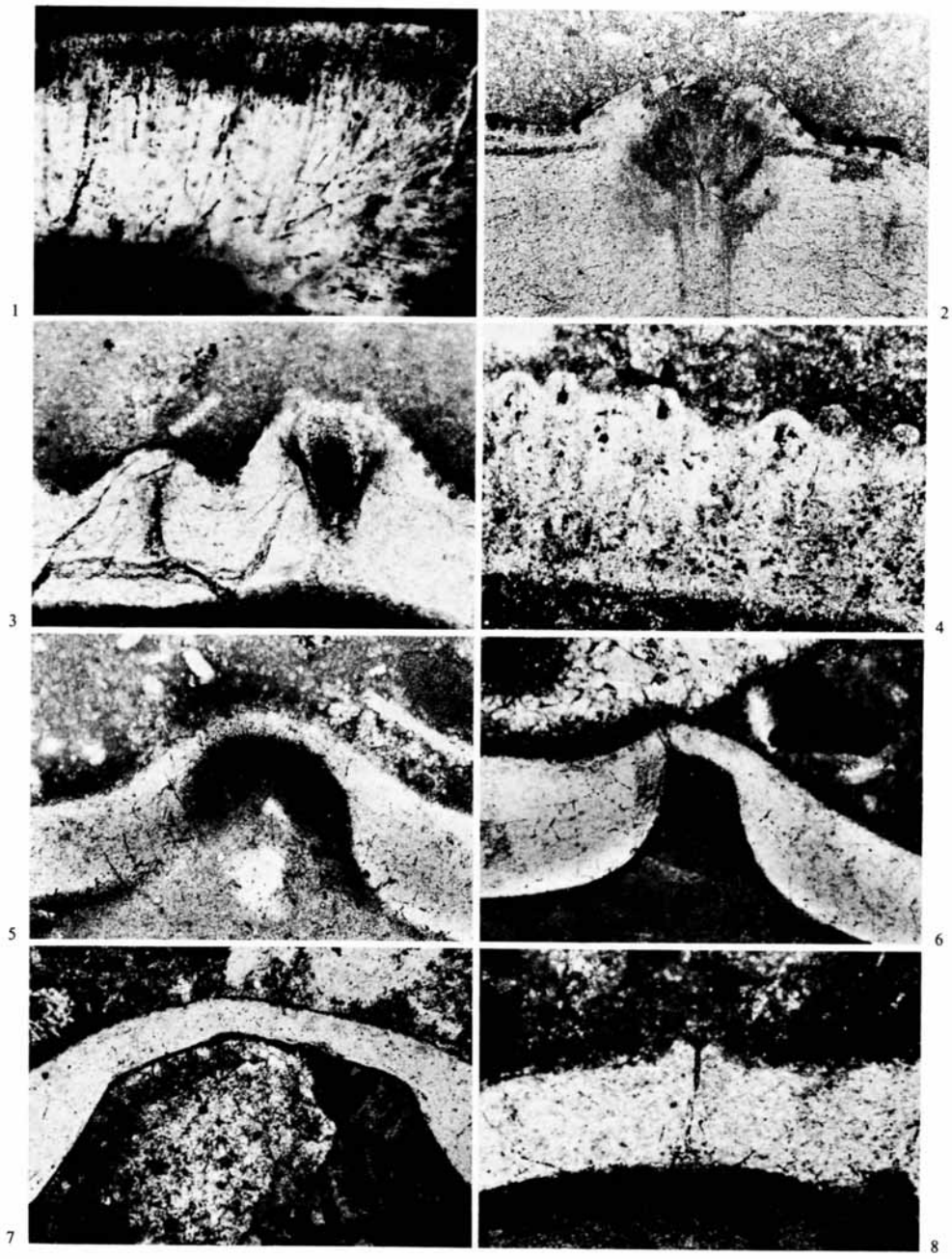
Fig. 3. *Trimerocephalus caecus* (Gürich). T.P.S. large tubercle on edge of librigena. Slice T.c.(O)3. ×92.

Fig. 4. *Acaste downingiae* (Murchison). L.P.S. discrete tubercles on cephalon. Note spine-like structure arising from one tubercle, also canals which may serve the tubercles. Slice Dy.A.d.1.3. ×135.

Figs. 5–8. *Boedaspis ensifer* Whittington and Bohlin.

Figs. 5–7. Tan. P.S. edge of pygidium, showing three types (or aspects?) of tubercle involving doming and thinning of the cuticle. Slice Öl.B.e.1b.2. All ×85.

Fig. 8. Tan. P.S. edge of pygidium, showing discrete tubercle. Slice Öl.B.e.1a.1. ×135.



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DISCUSSION

Subdivisions. The calcitic composition of *A. raniceps* cuticle agrees with the observations of Bøggild (1930), the detailed analyses of Cayeux (1933), and Stehli's (1956) analysis of a pygidium composed entirely of primary calcite. In most trilobite cuticles, replacement and infiltration of the original inorganic material has probably taken place; this may have been partly inhibited by the organic component. Diagenesis of the calcite in the eye-lenses of *A. raniceps* has been described in detail by Clarkson (1973).

Many previous authors including Sorby (1879), Cayeux (1916), and Majewske (1969) have stated that thin-sections of trilobite cuticle extinguish uniformly when viewed with crossed-nicols, but here it is shown that in *A. raniceps* cuticle (and in most other cuticles examined) extinction is not totally uniform. Moreover, examination of thin-sections of cuticle with the light microscope, and broken sections with the S.E.M. indicates that calcite prisms with any definite orientation occur only in the thin outer layer.

Størmer (1930) suggested that the four cuticular layers of *Tretaspis* were directly comparable with the major structural subdivisions in *Homarus*. However, it is difficult to envisage how an inner uncalcified area of endocuticle (equivalent to the inner layer in *Homarus*) might be preserved when the ventral trilobite cuticle is so rarely encountered. Moreover, an outer epicuticle, if present, is unlikely to be seen in thin-sections of trilobite cuticles prepared by conventional petrological methods. Furthermore, Størmer's 'pigmented layer' is a dense micritic envelope (J. Miller, pers. comm.). Although Richards (1951) established that the subdivision of any arthropod cuticle must be based mainly on histochemical distinctions, Hupé (1953) and Harrington (1959) compared the various layers described by previous authors directly with those of extant arthropod cuticles. Harrington's statement that: 'the exoskeleton of trilobites consists of a thin integument that is directly comparable to the chitinous cuticle of other Arthropoda', seems particularly inappropriate. In contrast, Rolfe's (1962) comment that many subdivisions in fossil cuticles are the result of replacement, may be pessimistic. In the present study the only consistent divisions of the trilobite cuticle seen in thin-section are a thin outer prismatic layer and an inner area. The outer layer, comprising one-tenth to one-thirtieth of the total thickness, was not observed in all cuticles studied, possibly because it is easily eroded and the boundary between it and the inner area seems to be a natural plane of weakness. In broken sections of cuticle examined with the S.E.M., the outer layer appears superficially similar to the tanned calcified exocuticle of *Carcinus maenas*, where the prominent perpendicular elements are pore-canals. Clarkson (1973) has described how the outer layer of the trilobite cuticle corresponds with the cornea; in some modern decapods, the tanned calcified exocuticle also laterally merges with the cornea. The appearance of the prismatic network of thin transparent material obtained on decalcification of *A. raniceps* cuticle resembles that of the epicuticle of some extant arthropods. In the latter, the walls of the regular prisms probably reflect the boundaries of the hypodermal cells responsible for secretion of the cuticle (Dennell 1960).

Thus, although there is some evidence for correlating the subdivisions seen in some trilobite cuticles with those of extant decapod cuticles, no precise comparisons can be made in the absence of histochemical data.

The cuticles of some trilobites (e.g. *Agnostus*) are thin, but most species studied have thick cuticles compared with modern arthropods. Although the general cuticle thickness is rarely greater than 500 μ, the cephalic cuticle of some large trilobites sometimes exceeds 1 mm.

Canals. Fine perpendicular canals, usually less than 1 μ in diameter, occur in the majority of cuticles studied. They are a characteristic feature of the cuticle and occur in large numbers closely packed together. In some cuticles, they appear to be helically coiled. Previous workers, notably Cayeux (1916), have compared these fine canals in the trilobite cuticle with those in modern arthropod cuticles. They are more evident in some species or only locally prominent. Larger canals appear to be more prone to pyrite impregnation and are thus accentuated. The prominence of fine canals in certain areas may also be due to preferential pyrite impregnation.

However, it is more difficult to understand why canal-like structures are accentuated in specialized areas of cuticle such as the hypostomal maculae, dark spots, the cuticle surrounding the eyes, and the anterior margin of the cephalon. Raymond (1920) suggested that the maculae and dark spots represent muscle-attachment sites. In contrast, Lindström (1901) thought that the hypostomal maculae were rudimentary optic organs because in many species the marginal areas of the eyes and the maculae have a similar aspect. Furthermore, he observed that small, closely spaced 'lenses' were present on the maculae of some trilobites. Balashova (1948) also noted the similarity of the eye-margins and maculae in the Asaphidae, but disagreed with Lindström's conclusions and suggested instead that both areas were characterized in life by dense concentrations of sensory setae. Harrington (1959) also thought it unlikely that the hypostomal maculae represented areas of muscle-attachment, partly because he supposed that the 'mineralized integument' was thinner at the maculae. In fact, the cuticle *thickens* at the maculae in the Asaphidae, where perpendicular elements are most prominent in this area. It is suggested here that all these areas were sites of muscle-attachment, and that some of the perpendicular elements may represent tonofibrillae (cuticularized muscle fibres). Their frequent occurrence in multiple units may explain the rudimentary lens-like structure inferred by Lindström (1901). In recent arthropod cuticles it is often difficult to distinguish tonofibrillae from pore-canals (Dr. J. H. Kennaugh, pers. comm.).

A variety of wider canals was observed in the trilobite cuticles studied, some of which are remarkably similar to canals in modern cuticles. However, because conclusive evidence such as the remains of sensory hairs is rare, it is difficult to assess whether these wider canals represent tegumentary or setal ducts. Wide canals are often prominent at the extremities of the exoskeleton. In extant decapods similar regions are plentifully supplied with tegumental glands (Dennell 1960), but in trilobites these canals were probably sensory rather than associated with extensive phenolic tanning. Contrary to Evitt and Whittington (1953), wide canals are present even in 'smooth-shelled trilobites'.

Laminae. The fine parallel laminae described from a few trilobite cuticles are possibly comparable with those in extant decapod cuticles. However, microfibrils were not seen even in the best-preserved material, and it seems more likely that examination

of well-preserved eurypterid cuticles will extend studies of cuticle architecture back into the Palaeozoic.

Tubercles. The various types of tubercles described by previous authors have been recognized in the cuticles studied. Although the term 'tubercle' has been used indiscriminately to describe various structures in modern arthropod cuticles, several authors, notably Kennaugh (1968), have used the term more precisely to describe discrete structures embedded in the cuticle of arachnids. However, as it is difficult to determine which type of tubercle is present without sectioning the cuticle, it seems premature to introduce terminology to distinguish these various structures.

Rome (1936) indicated that *Phacops accipitrinus maretiolensis* was immediately identifiable in thin-section but doubted whether other trilobites could be distinguished so satisfactorily. However, certain species have characteristic, perhaps unique, cuticles which might enable specific identification to be made from a small fragment. When the cuticles of many trilobite species have been described in detail (including variations in structure due to different modes of preservation) this information may prove useful, particularly in borehole work.

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