THE LAMINAE AND CUTICULAR ORGANIZATION OF THE TRILOBITE *ASAPHUS RANICEPS*

by J. E. DALINGWATER *and* J. MILLER

ABSTRACT. The cuticle of *Asaphus raniceps* Dalman has been examined with the scanning electron microscope after preparation by breaking and etching. Three main zones are defined on differences in appearance and dimensions of laminar units. Some details of the fine structure of laminar units are described. The presence of an organic framework within the cuticle is confirmed. The laminae and organization of the cuticle of this species are considered comparable to those of many extant arthropod cuticles.

RECENT work has presented a general picture of the microstructure and composition of the trilobite cuticle (Dalingwater 1973; Teigler and Towe 1975), as well as a consideration of the possible functions of cuticular organs (Miller 1975, 1976). Much of this work was based on optical examination of thin sections; Teigler and Towe (1975) also studied some aspects of the cuticle with the transmission electron microscope (TEM). Recently, we have prepared trilobite cuticles for study with the scanning electron microscope (SEM) by cutting and etching or by fracturing; fracturing followed by etching proved to be a most effective technique.

Laminae are a particularly prominent feature of some well-preserved trilobite cuticles prepared by this method. Most extant arthropod cuticles when viewed in cross-section show a laminar structure, usually visible as sets of alternating dark and light bands (Richards 1951). Whilst laminar units have been recognized in optical microscope preparations of trilobite cuticles by many previous workers (see Rolfe 1962; Dalingwater 1973) generally they are not very clearly visible. They have often been described as narrow bands although occasionally wider laminar units have been recognized, for example by Størmer (1930). Teigler and Towe (1975) recognized a crudely layered aspect to the crystals making up the cuticles of some of the trilobite species which they studied but did not consider it to be true lamination. For this reason, and others discussed below, they concluded that the trilobite cuticle did not have a laminate aspect comparable with that of the majority of extant arthropod cuticles but more strongly resembled the architecture of the calcified ostracod cuticles described by Bate and East (1972).

There has been much recent controversy as to the reality of laminae in extant arthropod cuticles. The view of Bouligand (1965, 1972) and of Neville and his coworkers (1969) that the laminate appearance of cuticles is an artefact resulting from sectioning helicoidally arranged flat sheets of fibres (text-fig. 1) had, until recently, been supremely ascendant over the traditional view of laminae as real structures. Recent papers, notably those of Dennell (1973, 1974) and Mutvei (1974), have re-emphasized the reality of laminae and thereby revived the controversy. Nevertheless, all these authors agree that laminae, real or artefact, at least reflect

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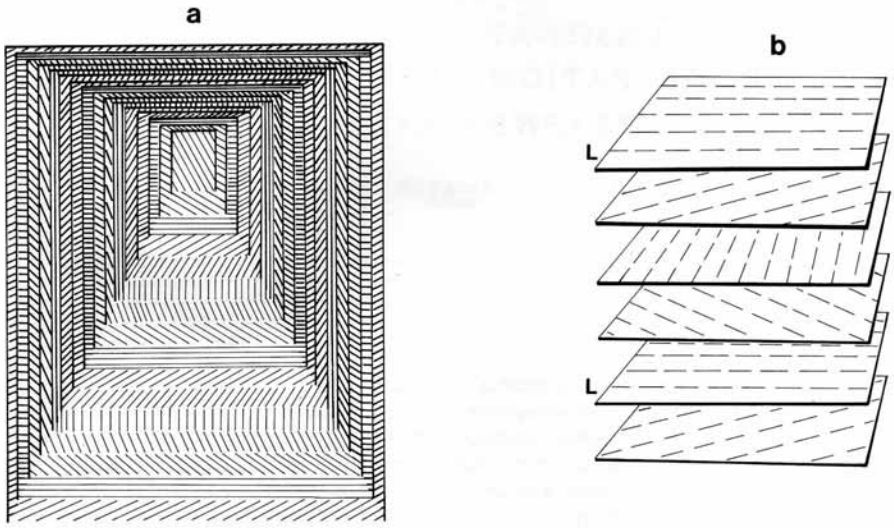

TEXT-FIG. 1. Bouligand helicoidal model (re-drawn, after Bouligand 1965, 1972). *a*, truncated pyramid of cuticle viewed from above. Flat sheets of fibres are arranged in stacks and the fibre orientation changes from one sheet to the next in an anti-clockwise direction. *b*, simplified 'exploded' view of the system. Apparent laminae (L) result when sheets of fibres are sectioned parallel to fibre orientation, i.e. in the plane of the page.

a repetitive layered organization which is a fundamental feature of nearly all arthropod cuticles. Furthermore, important subdivisions of cuticles are often reflected by differences in laminar aspect, for example in the dimensions of laminar units.

In this paper:

We indicate that laminae and canals in some well-preserved trilobite cuticles can be demonstrated particularly well by the technique described.

We define three zones in a trilobite cuticle distinguished by differences in laminar disposition, correlate these with the subdivisions of the cuticle established by Dalingwater (1973) and Teigler and Towe (1975), and compare the subdivisions of the trilobite cuticle with those of extant crustaceans.

We present a case for considering the laminae of the species studied, and by implication those of some other previously described trilobite species, as similar to those of many extant arthropods. Particularly in this respect, we question Teigler and Towe's (1975) interpretation of the trilobite cuticle as more similar to that of some calcified ostracods than to that of the typical arthropod.

We advise caution in adopting Teigler and Towe's (1975) use of the term *pore canal* for all categories of primary ducts through the trilobite cuticle.

MATERIALS AND METHODS

We have examined the cuticles of a variety of trilobite species after preparation by the method described below, including those of:

Illaenus aduncus, lower Ordovician, Öland.
Illaenus sarsi, lower Ordovician, Oslofjord.
Onnia sp., upper Ordovician, Onny River, Salop.
Tretaspis spp., upper Ordovician, Oslo.
Calymene blumenbachii, middle Silurian, Dudley, West Midlands.
Phacops rana subspp., middle Devonian, Ohio.
P. rana africanus, middle Devonian, Rio de Oro, Tifariti.
Harpes macrocephalus, middle Devonian, Gerolstein.

Although laminae and other microstructural features were seen in all the cuticles examined, the most immediately striking results were obtained from the cuticle of *Asaphus raniceps* Dalman *sensu* Angelin (1854) from the lower 'Raniceps' Limestone, Haget, Öland, Sweden (lower Llanvirn—*bifidus* Zone), particularly from specimens with dark chocolate brown exoskeletons collected from bed 'e' of Bohlin (1949). We therefore concentrated our attention on this material.

Fragments of cuticle were removed from various regions of the exoskeleton, rebroken to produce as clean a fracture surface as possible, and then etched for about one hour in a saturated aqueous solution of E.D.T.A. (disodium salt). After rinsing with distilled water, they were then washed in absolute alcohol several times and mounted on stubs. Preparations were gold or gold/palladium coated before examination with the SEM. Fragments of cuticle from a thoracic limb podite of the fossil decapod crustacean *Hoploparia longimana* (Sowerby) from the Cambridge Greensand, figured and discussed below, were prepared in a similar manner to the trilobite material, but etched for about three hours in E.D.T.A. Cuticle from the great chela of the extant decapod crustacean *Austropotamobius pallipes* (Lereboullet) was prepared as described in Dalingwater (1975). All figured preparations are stored in the Department of Zoology, University of Manchester.

TERMINOLOGY

The major textural subdivisions of the trilobite cuticle previously recognized were an outer layer often prismatic, and an inner or principal layer (Dalingwater 1973; Teigler and Towe 1975). Subdivisions of the cuticle described herein, based on differences in appearance and dimensions of laminar units, are termed zones. Correlation between the layers and zones is discussed later.

Following Dennell (1973), we refer to the narrow part of each laminar unit as a lamina and the wider part as an inter-lamina. In some crustacean cuticles laminae appear to consist of sheets of horizontal fibres, and inter-laminae of sheets of fibres which arc between successive laminae (Dalingwater 1975). Dennell (1976) has demonstrated the presence of a lamina membrane in the cuticles of a variety of arthropods, and suggests that it might provide a template for laying down the cuticular fibres.

OBSERVATIONS

Cuticle zonation. The appearance of etched fracture surfaces of *Asaphus raniceps* cuticle varies somewhat in different preparations possibly due to slight differences in the method of preparation (including angle of break) and/or in preservation. There are also slight but consistent differences in the cuticle from different parts of the exoskeleton. Nevertheless, a general outline of the appearance of the cuticle when examined with the SEM can be given. The outermost part of the cuticle is etched back very rapidly and was therefore not often visible in our preparations. Below this, various zones can be defined based on differences in appearance and dimensions of the laminar units:

An outer zone of narrow laminar units (around 5μ thick) comprising up to one-fifth of the total thickness of the cuticle.

A central zone of four or five very prominent wide laminar units (50–70μ) grading inwards through a zone of less prominent wide laminar units into;

a narrow innermost zone of fine laminar units of similar dimensions to those in the outer zone.

The outer finely laminated zone tends to be most readily seen, and is possibly best developed, in preparations of thoracic pleurae (Pl. 9, fig. 1). In contrast, it often seems narrower in preparations of cephalic cuticle (Pl. 10, fig. 1). In some preparations there is apparent discontinuity of laminar units between the dorsal part of the exoskeleton and the doublure (Pl. 10, fig. 1).

Individual calcite crystals are difficult to resolve, but roughly shaped perpendicular plates of calcite are prominent in the wider inter-laminae, in some cases pierced by canal-like elements about 1μ wide (Pl. 9, fig. 2). In angled breaks these plates of material stand out as pillars separated by a network of voids (Pl. 9, fig. 3).

Structure of laminar units. In many preparations the laminae themselves appear as narrow co-planar bands which have been etched inwards more rapidly than the intervening material (Pl. 9, fig. 4). However, in some cases laminae are represented by wider bands of material, crossed by similar fine perpendicular canal-like structures to those in the inter-laminae (Pl. 9, fig. 5). Occasionally, traces of a rough chevron pattern can be perceived at the laminae (Pl. 9, fig. 6), and in one preparation faint

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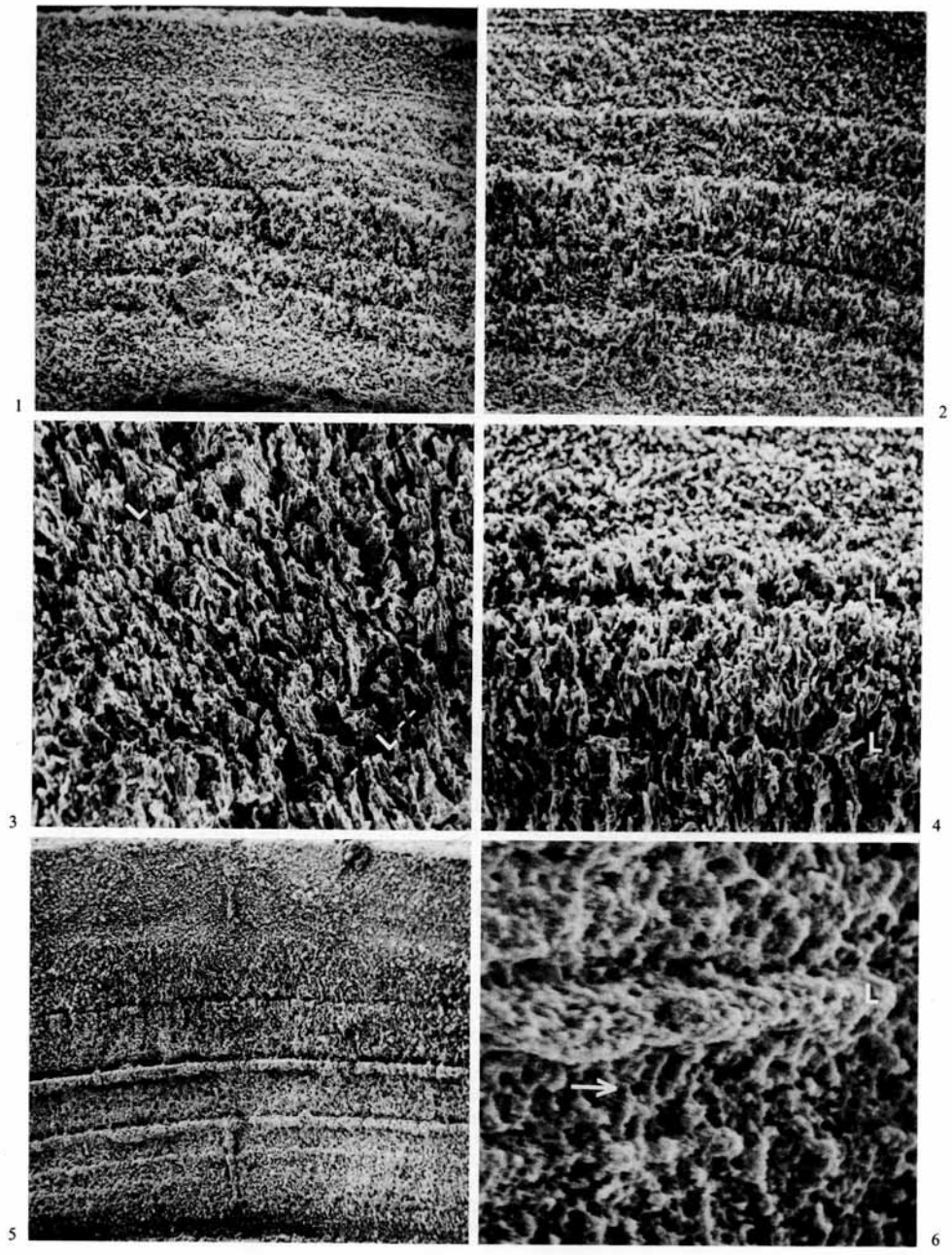
EXPLANATION OF PLATE 9

Figs. 1–6. *Asaphus raniceps* Dalman: scanning electron micrographs of etched fracture surfaces of the cuticle. 1, longitudinal perpendicular break across a thoracic pleura. Outer fine laminate zone clearly visible. Prep. 21375-3. ×170. 2, detail of the central zone from the same preparation, showing perpendicular canal-like elements in the inter-laminae. ×210. 3, tangential angled break across the edge of the cephalon. Central zone. Roughly shaped pillars of calcite stand out, separated by a network of voids. L—lamina. Prep. 11174-1. ×420. 4, transverse perpendicular break of cephalic cuticle. Central zone. Laminae (L) have been etched inwards more rapidly than the intervening material. Prep. 21375-1. ×420. 5, tangential perpendicular break of cephalic cuticle. Some central zone laminae are represented by wider bands of material. The narrow inner laminate zone can just be seen. Prep. 11174-2. ×140. 6, tangential perpendicular break of cephalic cuticle. Faint horizontal fibres (arrowed) just visible below a lamina (L). Prep. 11174-2a. ×820.



DALINGWATER and MILLER, trilobite cuticle

more or less horizontal fibres are visible in the plates of inter-lamina material just below a lamina (Pl. 9, fig. 6).

Decalcification of the cuticle. One exceptional preparation examined and photographed by reflected light microscopy (Pl. 10, fig. 2) deserves mention here. A thoracic pleura was removed from a large specimen of *A. raniceps* and a clean longitudinal perpendicular break achieved. Decalcification was allowed to proceed for five hours and the process observed at regular intervals. Laminae in the central zone of the cuticle were immediately apparent and some perpendicular ducts, about 5μ wide, could just be seen at this stage. After about five hours, much of the inorganic material of the cuticle had been dissolved inwards for some distance from the break surface leaving a layer of brown jelly-like material, with lighter-coloured material standing up through the gel at the laminae. The 5μ ducts could now be seen in depth piercing the brown jelly, their component material apparently unaffected by the E.D.T.A. Dissolution of inorganic material seemed greatest at the outer and inner zones of the cuticle, despite protection of the edges by adhering matrix.

DISCUSSION

Laminae and pore canals. Teigler and Towe (1975) gave a number of reasons why the crudely laminate aspect of the calcite in some of the trilobite cuticles they examined should not be considered similar to the laminae in many extant arthropod cuticles:

1. Using the TEM they found no difference in the texture of the calcitic material at the laminae, only a slight furrowing, and decided that the laminae could have resulted from variation in the concentration of organic material within the cuticle rather than from some basic variation in the nature of the calcite crystals. However, laminae are essentially reflections of the organization of organic material within the cuticle; the essence of the lamina seems to be an organic lamina membrane (Dennell 1976). Miller's (1976) observation of flimsy organic membranes left representing the laminae while etching the cuticle of *Phacops rana*, as well as Teigler and Towe's comments on the distribution of organic material in the cuticles they studied, seem to indicate that in this context the laminae in trilobite cuticles can be seen to resemble those of many extant arthropods. The furrowing at the laminae in the cuticle of the fossil decapod crustacean studied (Pl. 10, fig. 3) strongly resembles

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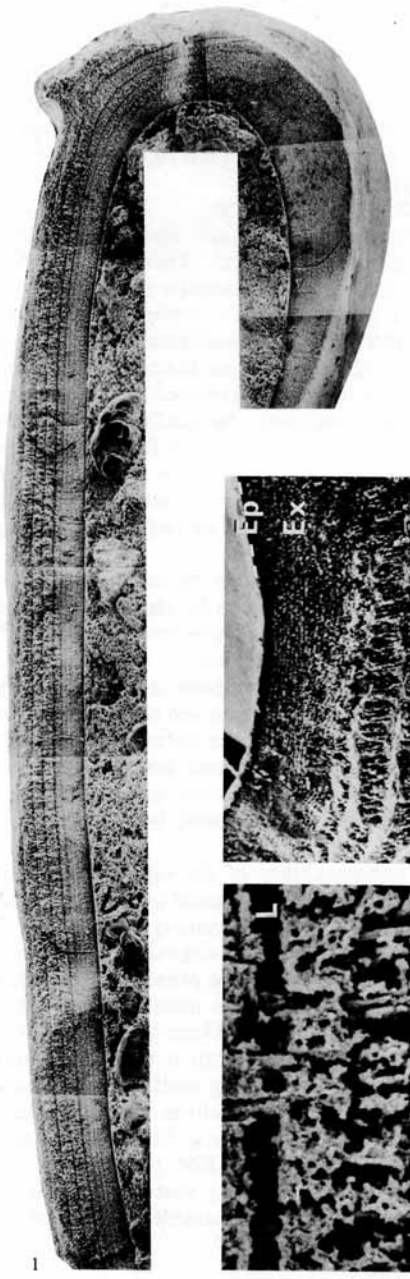
EXPLANATION OF PLATE 10

Figs. 1, 2. *Asaphus raniceps* Dalman. 1, SEM photo-montage of a transverse perpendicular break of cephalic cuticle. The outer laminate zone can just be seen on the left. The wide laminar units of the central zone are prominent along the length of the preparation, except where the cuticle deflects to form the doublure. Prep. 21375-2. ×35. 2, reflected light micrograph of a longitudinal perpendicular break across a thoracic pleura after about five hours decalcification. Prep. 191274-0. ×65.

Fig. 3. *Hoploparia longimana* (Sowerby). Transverse perpendicular break of the cuticle from a thoracic limb podite. Two laminar units in the calcified zone. L—lamina. Prep. H.s. 141175-1a. ×2100.

Fig. 4. *Austropotamobius pallipes* (Lereboullet). Transverse perpendicular break of the complete thickness of the cuticle from a great chela dactylopodite. Ep—epicuticle; Ex—exocuticle; Cz—calcified zone; En—endocuticle. Prep. A.p. 3376-2a. ×280.



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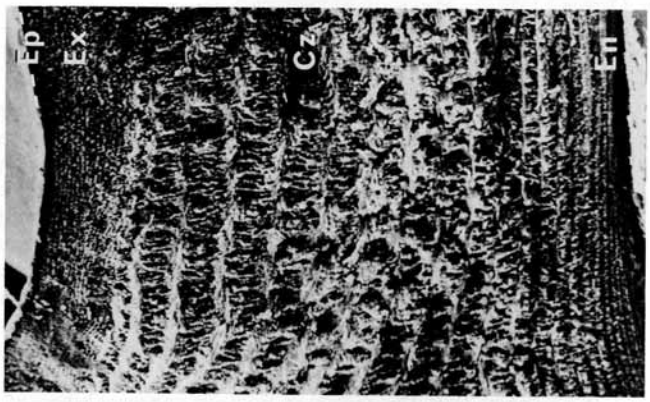

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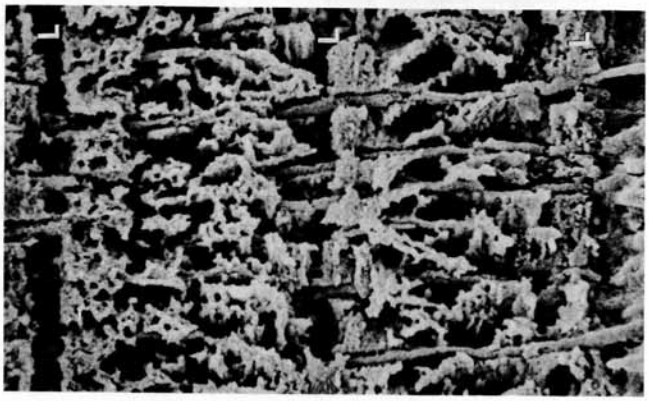

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DALINGWATER and MILLER, arthropod cuticle

that seen in the trilobite cuticle. In both cases the absolute alcohol preparative treatment would remove any concentration of organic material from these furrows, for we have found that the organic residues left after complete decalcification of both trilobite and fossil decapod crustacean cuticles are completely dispersed by absolute alcohol. Incidentally, this might explain why well-preserved brown-coloured trilobite exoskeletons are 'whitened' by alcohol treatment.

2. They decided that the absence of helical pore canals and parabolic patterns also rendered difficult direct comparison with the usual extant arthropod cuticular laminae. However, pore canals are not necessarily helical (Travis 1970; Mutvei 1974), nor need their pattern be related to helicoidal architecture (Kennaugh 1965; Travis 1970; Dalingwater 1975). Even if the pore canals of trilobites were originally helical then this could have been altered in the process of fossilization (see discussion in Osmólska 1975). For example, only a straight contained filament or a straight lining might be preserved, with the canal itself (the lumen) infilled in the latter case. Parabolic patterns are only observed in angled sections (classically 45° sections) of extant cuticles, and only in *some* angled sections according to Drach (1939) and Dennell (1974). Many of Teigler and Towe's figured sections are more or less perpendicular slices; one would not expect parabolic patterns in such sections. Again diagenesis might alter the material and make recognition of parabolae in angled sections difficult.

3. They noted that not all trilobite species, even those from the same locality, show laminae, and concluded that a 'genetic control' appears to be the major factor in their distribution. We suggest that the precise history of preservation (see Miller 1975), and possibly the stage in the moult cycle reached before death in the case of intaglios, may determine whether laminae are prominent or even visible in examples studied. Methods of preparation and examination are clearly important: Dalingwater (1973) made an extensive investigation of the cuticle of *A. raniceps* using specimens from the same locality and horizon as those described above; he included an SEM examination of break surfaces and etched ground slices, but did not observe the distinct laminae that we have demonstrated by the break+etch technique.

We suggest that the evidence favours comparability of the laminae of trilobite cuticles, especially those of *A. raniceps*, with those of the typical arthropod cuticle.

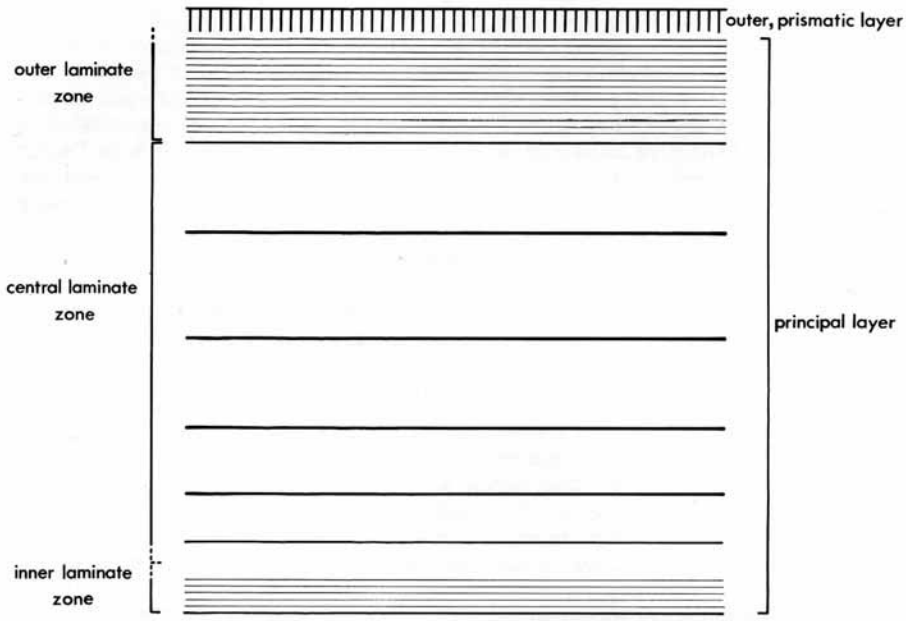
Some of the laminar units in *A. raniceps* cuticle are extremely wide (up to 70μ) compared with those encountered in most extant cuticles, although in the crayfish *Austropotamobius pallipes*, laminar units about 20μ wide are present in the calcified zone (Dalingwater 1975). However, the trilobite cuticle is usually relatively very thick for an arthropod often only a few centimetres long. These laminar units may represent material laid down rapidly after ecdysis (although it must be admitted that no evidence seems to have been presented correlating width of laminar unit with rate of cuticle formation). Finer co-planar structures within very wide laminar units have been reported from light microscope studies (e.g. Størmer 1930), and occasionally similar fine structures are encountered in SEM preparations. It is possible that these reflect the organization of inter-lamina material in low-angle arcs between laminae. The ultrastructural detail just recognizable in some preparations and described above tends to add strength to this view.

Perpendicular canals. Teigler and Towe (1975) termed all primary duct-like processes in trilobite cuticles *pore canals*. Whilst we recognize that it is difficult to decide whether canals of relatively narrow dimension (of the order of 1μ in diameter) are exactly equivalent to the pore canals of extant arthropod cuticles, or are merely unusually narrow tegumental or setal ducts, and that there is some imprecision in the definition of the pore canal even in extant cuticles, we are unhappy with Teigler and Towe's terminology. Canals 75μ and more wide are clearly not comparable with the pore canals of extant arthropod cuticles. Their proposal would place trilobite terminology in step with ostracod cuticle terminology, but out of step with that employed for all other arthropod cuticles. The fine perpendicular canal-like elements present in the inter-laminae of many preparations we have examined are considered similar to the pore canals of extant arthropod cuticles, in that they are relatively narrow (about 1μ in diameter), are very numerous, and have been observed in all regions of the cuticle examined.

Organic material. The presence of brown organic material in trilobite cuticles has long been recognized. Davies (1894) considered it possibly to be a replacement product of the original organic material of the cuticle, Dalingwater (1973) isolated organic material from a trilobite cuticle after decalcification with E.D.T.A., and Teigler and Towe (1975) carried this study further by examining sections of the material with the TEM. Their observation of a delicate meshwork does not eliminate the possibility of the presence of laminae comparable with those of most extant arthropod cuticles, for their sections are apparently more or less horizontal and the pattern figured is not incompatible with the architecture observed in horizontal slices or breaks of extant cuticles (see Travis 1970; Dalingwater 1975). Further work is needed to establish the nature of this relict organic material and to determine its precise relationship with the inorganic component of the trilobite cuticle.

Subdivisions of the cuticle. In our description of the cuticle of *Asaphus raniceps* we define three zones based on the appearance and dimensions of their laminar units. The central and innermost zones apparently correspond with the median and inner subdivisions that Størmer (1930) defined in his classic study of the cuticle of *Tretaspis kiaeri*, although as previously noted (Dalingwater 1973) his pigmented layer is a dense micritic envelope. The term zone is deliberately used in this paper to avoid confusion with the layers of the trilobite cuticle recently defined mainly from light microscope observations (see text-fig. 2). The outer prismatic layer was not always present prior to etching (possibly removed with the overlying matrix), but when it was present at least part of it was etched back very rapidly in E.D.T.A., so the zones defined herein possibly all lie within the principal layer (the central and inner laminate zones certainly do). As the outer layer of the cuticle can show aspects other than prismatic (Teigler and Towe 1975), and as it is quite possible that this part of the cuticle may subsequently be shown also to contain laminae, at present we prefer to reserve judgement on the precise relationship of the outer prismatic layer and our outer laminate zone. Examination of newly formed cuticles may help to solve this problem and work is in progress on the material described by Miller *et al.* (1974).

We are confident that the trilobite cuticle described is similar to those of many extant arthropods in laminar organization and divisibility into zones based on



TEXT-FIG. 2. The major layers and laminate zones of the cuticle of *Asaphus raniceps*. *Right*: the previously defined layers (Dalingwater 1973). *Left*: the laminate zones defined in this paper.

laminar disposition. However, it is difficult to make any precise correlation of the trilobite zones and layers with those of any specific group of extant arthropods, for there is some variability in cuticular subdivisions between the different groups of extant arthropods, and the exact subdivision is based largely on histochemical criteria. Nevertheless, in being impregnated with mineral salts and in its general laminar organization, the trilobite cuticle described here most favourably resembles that of decapod crustaceans (e.g. *Austropotamobius pallipes*, see Pl. 10, fig. 4). We agree with Teigler and Towe (1975) that the trilobite cuticle is unusual in being so heavily impregnated with calcite, but suggest that this enables the production of a relatively very thick and strong cuticle, economic in terms of organic material. However, we would hesitate to attach any phylogenetic significance to this particular feature for other groups of crustaceans as well as the ostracods (e.g. cirripedes) have produced heavily calcitized cuticles in functional response to particular environmental demands. We must also add that in comparing the trilobite cuticle favourably with that of decapod crustaceans, we attach no phylogenetic significance to our analogy.

The epicuticle of many extant decapod crustaceans is calcified (Digby 1967; Welinder 1975) so it is quite possible that traces of a similar layer might be preserved in trilobites; the outermost layer described by Dalingwater (1973) is positionally and

structurally compatible with the extant decapod epicuticle. The prismatic layer and the outer laminate zone can be considered equivalent to the exocuticle, and the central zone to the calcified principal zone, of extant decapods. Comparison of the innermost zone of the trilobite cuticle described herein with the inner region of extant decapod cuticles presents a difficulty, for in the latter this is usually an uncalcified endocuticle refractory to fossilization. However, in some regions of, for example, crayfish cuticle, the uncalcified endocuticle laterally transforms into a region which is calcified, strictly speaking therefore part of the calcified principal zone, but still distinguishable by the relative narrowness of its laminar units (Dr. J. Kennaugh, pers. comm.). A similar situation may exist in the trilobite cuticle. Further investigation of the inner region of the trilobite cuticle is necessary, particularly to determine if there are any differences between the cuticles of intaglios and exuviae. This could reveal whether there is any resorption of material prior to ecdysis.

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J. E. DALINGWATER
Department of Zoology
The University
Manchester M13 9PL

J. MILLER
Department of Educational Studies
The University
Edinburgh EH8 9JT

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