THE CUTICLE OF SOME MIDDLE SILURIAN CERATIOCARIDID CRUSTACEA FROM SCOTLAND

by W. D. I. ROLFE

ABSTRACT. Well-preserved specimens of the Scottish Valentian phyllocarid *Ceratiocaris papilio* Salter and a giant form almost 2 feet long have been collected from concretions in the Ree Burn Formation of the Hagshaw Hills inlier. The cuticle of the crustaceans is preserved in collophane, partially replaced by calcite. Moniliform ? pore canals, laminae, Balkenlagen, and prisms can be recognized in preparations of this exoskeletal cuticle, but no major stratifications are preserved. Tubules attributable to aquatic thallophyte perforants penetrate the cuticle, and other microstructures of doubtful origin are described. Reference is made to other fossil arthropod cuticles and reinterpretation of some of the described microstructures is attempted.

GIANT specimens of the pod-shrimp *Ceratiocaris* approaching 2 feet in length have been collected from concretions in the marine Ree Burn Formation of the Hagshaw Hills, suggested to be of uppermost Valentian age (Rolfe 1960, 1962). Smaller individuals associated with the giant forms may be ascribed to *C. papilio* Salter 1859. A statistical study of museum collections of topotype Lesmahagow material shows that *C. papilio* is indistinguishable from *C. stygia* Salter 1860. These species were artificially restricted to medium-sized forms by Jones and Woodward (1888, p. 43), but giant forms, comparable with those from the Hagshaw Hills, and smaller 'species' such as *C. laxa* Jones and Woodward 1886, also occur at Lesmahagow. It seems probable that these forms are instars or moult stages of the single species *C. papilio*, and ontogenetic variation in shape and ornamentation is to be expected (Kesling 1954). I hope to describe the giant Hagshaw specimens after further study of the more abundant Lesmahagow material.

The terminology used for the microanatomy is that of Richards (1951, 1958) and wherever possible reference is made to his 1951 review, rather than to original authorities, unless this is essential. Mean values of measurements are followed by the standard error of the mean, with the number of observations in parentheses.

All preparations and most of the specimens are in the Geology Department, Birmingham University.

Occurrence. A large-scale map showing the location of individual specimens collected for this study is given in the writer's Ph.D. thesis at the University of Birmingham (1960, fig. 15).

The only non-crustacean fossils found in the concretions were rare orthocone fragments, ? plant fragments (concretions 20, 21, 22), syngenetic pyrite organisms, and thelodont denticles (33). Such an 'exclusive' fauna may be deceptive, however, and Gürich (1929, p. 32) and others (Matern 1931, p. 164; Brooks 1957, p. 896) have explained how concentrations of arthropod material can arise at the expense of other elements of a fauna by selective dissolution. It must also be remembered that 'probably the majority of fossil arthropods are represented by empty sloughs' (Størmer 1944, p. 21).

The concretions lie parallel to the bedding and several may occur on the same bedding-plane. Individual crustaceans may be preserved in adjacent concretions. Thus 30Q consists of one concretion preserving the anterior regions of the crustacean and a second

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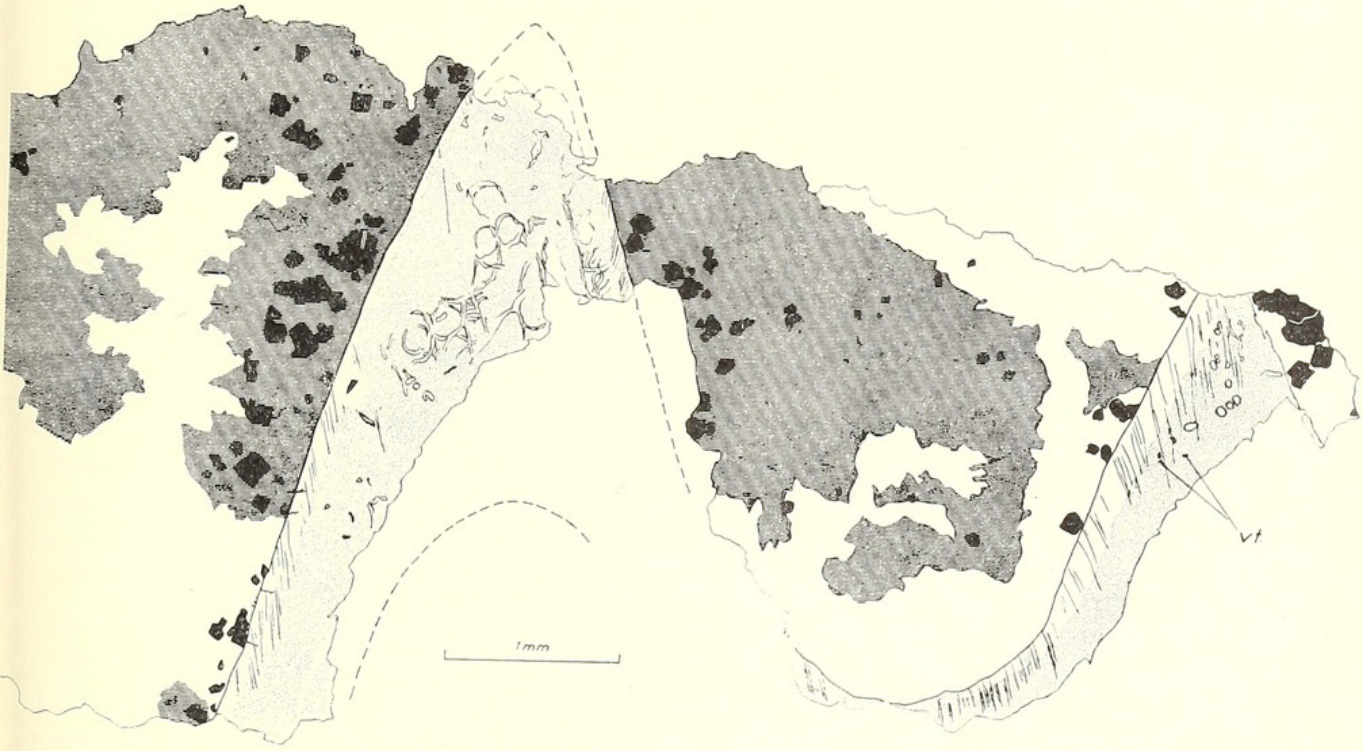
containing the posterior. In only one concretion have fragments attributable to two individuals been found, one far smaller than the other (12A and 12).

Calcite, iron pyrites, quartz, barytes, galena, and zinc blende occur in septarian veins in the concretions. Pyrite commonly invests individual fossils and may also intrude the thickness of the cuticle, or form euhedral cubes. Plate 8, fig. 3 and text-fig. 1 show pyrite (black) concentrated in the area of the dextral mandible from specimen 5. Calcite (white on the figure) replaces the cuticle but also infills what must have been cavities trapped in



TEXT-FIG. 1. Camera lucida drawing of thin section through teeth on dextral mandible of specimen 5. Stippling indicates collophane of the mandible bored by vermiform tubules (vt.). Calcite of the 'pseudo-enamel' and matrix is left unshaded, iron pyrites—black and siltstone by the close ruling (see also Plate 8, fig. 3; compare with Harley 1861, pl. 17, figs. 12*b*, 12*e*).

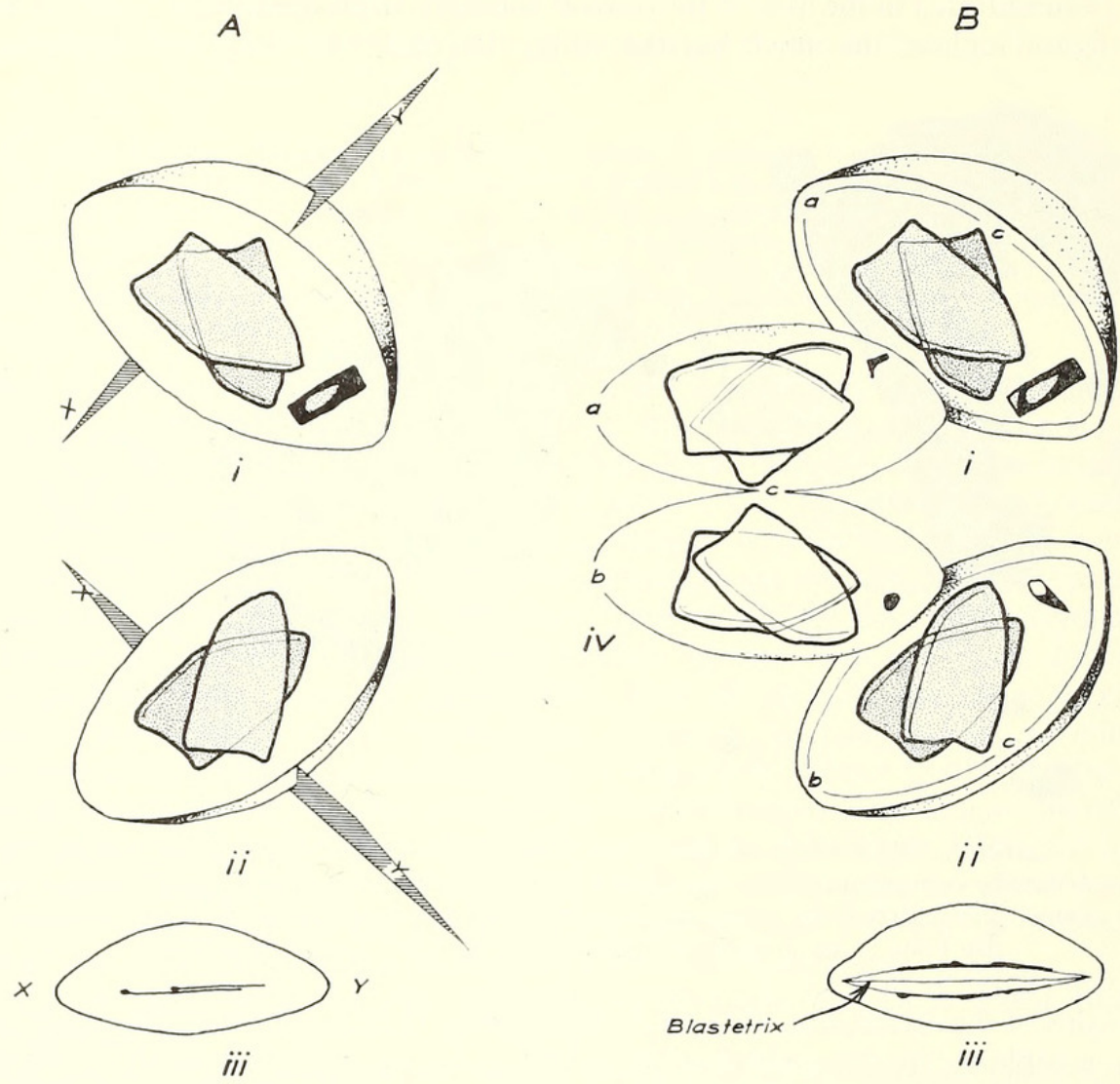
the remains of the crustacean. There have been several periods of calcite diagenesis and it is impossible to decipher whether or not the pyrite antedates the calcite. Certainly, some of the calcite-veining fissures earlier pyrite (e.g. right-hand edge of text-fig. 1). Gocht and Goerlich have recently described syngenetic calcite and pyrite infilling ostracod tests (1958, p. 207). Quartz veinlets cut into a spiral calcite vein in concretion 35 and follow its Blastetrix (Sander, see Ramberg 1952, p. 123) for a short distance, showing that the former postdates the latter.

PRESERVATION

Description of replacement of the cuticle is given in the section on primary microstructures below.

Transfer replication. One feature of the preservation of the fossils caused much confusion in the early stages of the work. At first sight what appeared to be four identical

impressions of, for example, the two slightly displaced valves of the carapace could be exposed by digging down through the concretion. The course of events leading to this appearance is, however, quite straightforward and is explained by text-fig. 2 which shows the history of fossilization of the two valves of an individual or exuvia.



TEXT-FIG. 2. Diagram illustrating process of transfer replication, based on specimen 29K. A before and B after the process. For explanation see text.

The valves, which are slightly displaced before burial, are flattened by compaction before final concretion, and two moulds are formed. These moulds then split apart, each one being clogged by filmy debris of the original test. Text-fig. 2A i–ii shows a concretion split open at this stage, and A iii a section of the unopened concretion taken along the plane X–Y. This is diagrammatic and no attempt has been made to show splitting and transference of the carapace test, as this is better shown by the style fragment in the diagrams. The stipple represents the thin films of collophane left in the moulds; the solid black the thicker cuticle of the style. As a cause or effect of the separation of the two moulds referred to above, a lenticular calcite vein fills in the gap between them,

and replicates or casts them on its surfaces, transferring some of the debris from the moulds at the same time. This calcite septum bearing an upper and lower impression can thus be referred to as the transfer replica. It may be relatively thick: in specimen 29K, on which text-fig. 2 is based, it is 7 mm. thick at the centre of the concretion. Text-fig. 2B i, ii, iv, is an exploded view of the concretion at this replication stage, and B iv shows the transfer replica hinged open along one edge of the Blastetrix. The letters *a*, *b*, *c* serve to locate the feather edge of the transfer replica in its position sandwiched inside the concretion. Text-fig. 2B iii is a section of the unopened concretion taken along a similar plane to that of A iii.

Composition. The test is preserved in a dark brown to black material. Sometimes a thin film of bluish-white vivianite encrusts the surface of this test. In thin section the material varies from dark brown when thick, through amber to colourless when thin (1–2 μ). It is isotropic but locally slightly anisotropic. These distinctive properties suggested the mineraloid collophane. With the aid of Dr. C. C. F. Blake of the Chemistry Department, Birmingham University, X-ray powder photographs were prepared of the material.

Samples were separated under a binocular microscope from the mechanically exposed, transverse-sectioned style of specimen 30Q. The cut and polished surface, from which the samples were dug, had been further prepared by etching with a 0·5 molar triammonium citrate solution. Calcite is 47 times more soluble than apatite in this solvent and hence the collophane crust forming the style was left standing up as a thin wall after several weeks' etching. The acetic acid technique used for macerating the cuticles would probably have been more satisfactory for this purpose as it is faster acting. This wall was then broken off with fine needles and formed sample 1; sample 2 was dug from the infilled core of the style and was thought to be largely calcite. Both samples, each amounting to no more than a few milligrammes, were pulverized and sealed in Lindemann borax glass tubes. Powder photographs were then taken of both samples using a 19-cm. Debye-Scherrer camera and are shown in Plate 8, fig. 5. Table 1 shows the interplanar spacings and intensities measured from these photographs. Comparison with the A.S.T.M. index, combined with optical data from thin sections, shows that collophane, calcite, quartz, pyrite, and dolomite are present in sample 1, but only calcite and dolomite in sample 2.

The collophane lines compare closely with those of hydroxyapatite, and the X-ray photograph can be compared with that illustrated by Thewlis, Glock, and Murray (1939, fig. 1*b*) prepared from a pure synthetic sample. Collophane is 'a generic name for the massive, cryptocrystalline (or microamorphous) form of apatite . . . it commonly is a carbonation, intermediate member of the hydroxylapatite-fluorapatite series' (Dana 1951, p. 885) or metacolloidal apatite (Frondel 1943, p. 220). The absence of fluorapatite lines from the photographs is noteworthy; even in F-poor environments diadochic replacement of the OH ions by F takes place, especially under marine conditions (Goldschmidt 1954, pp. 455, 460; Beevers and McIntyre 1946). Carbonate- and hydroxy-forms of apatite cannot be distinguished using X-ray methods, however (Geiger 1950, pp. 166–7).

Two Campbell–van Wisselingh tests for chitosan (Richards 1951, pp. 32–36) were carried out on fragments of cuticle recovered from the maceration of style 30.3. Integument from an abdominal sternite of *Periplaneta americana* used as a control gave good

TABLE 1

Sample 1

d Å	I (visual)	d Å	I (visual)	d Å	I (visual)	d Å	I (visual)
1. 5·020	vvw	17. 2·419	ls	33. 1·720	mw	49. 1·254	vw
2. 4·476	vvvw	18. 2·275	ms	34. 1·630	ls	50. 1·241	vvw
3. 4·257	vvvw	19. 2·241	ls	35. 1·598	ls	51. 1·230	lw
4. 4·244	mw	20. 2·208	ls	36. 1·558	vvw	52. 1·211	lw
5. 4·034	mw	21. 2·123	vw	37. 1·539	vvvw	53. 1·179	vvw
6. 3·981	m	22. 2·086	ms	38. 1·517	lw	54. 1·150	lw
7. 3·448	ms	23. 2·059	vw	39. 1·500	lw	55. 1·142	vvw
8. 3·343	ms	24. 1·989	vw	40. 1·464	lw	56. 1·129	vvw
9. 3·168	mw	25. 1·931	ms	41. 1·448	lw	57. 1·103	vw
10. 3·117	vw	26. 1·905	ms	42. 1·435	lw	58. 1·094	vw
11. 3·031	vs	27. 1·868	ms	43. 1·417	lw	59. 1·069	vvvw
12. 2·896	vw	28. 1·844	ms	44. 1·370	vvvw	60. 1·041	ls
13. 2·785	s	29. 1·814	vvw	45. 1·352	vvvw	61. 1·031	vw
14. 2·698	ms	30. 1·789	mw	46. 1·333	vvw	62. 1·021	vw
15. 2·622	ls	31. 1·763	mw	47. 1·292	vvw	63. 0·956	vw
16. 2·488	ms	32. 1·742	mw	48. 1·271	vvw		

Sample 2

d Å	I (visual)	d Å	I (visual)	d Å	I (visual)	d Å	I (visual)
1. 3·850	ls	12. 2·017	s	23. 1·468	w	34. 1·139	w
2. 3·723	vvvw	13. 1·926	vw	24. 1·436	ls	35. 1·058	vvw
3. 3·355	vvvw	14. 1·904	s	25. 1·417	vls	36. 1·043	ls
4. 3·027	vs	15. 1·866	s	26. 1·354	w	37. 1·032	vvw
5. 2·897	w	16. 1·788	vvw	27. 1·334	vls	38. 1·009	vls
6. 2·834	w	17. 1·623	w	28. 1·293	ls	39. 0·983	vvvw
7. 2·486	lw	18. 1·600	ls	29. 1·281	vvw	40. 0·974	vvvw
8. 2·398	ls	19. 1·581	vvw	30. 1·243	w	41. 0·948	ls
9. 2·276	vvw	20. 1·554	vvvw	31. 1·232	w	42. 0·944	vvvw
10. 2·193	s	21. 1·520	vls	32. 1·176	vls	43. 0·941	w
11. 2·086	vw	22. 1·506	w	33. 1·150	vls	44. 0·936	vvw

positive reactions but nothing was obtained from the fossil material. This method has been used successfully on graptolites by Kraft, who noticed, however, that some specimens of cuticle had lost their ability to react to the test (1923, p. 288 and Richards 1951, p. 34).

Macerated fragments were found by crushing to be very brittle, and readily disintegrated to a fine powder. Sohn has shown that the residues of decalcified fossil ostracods containing appreciable amounts of original organic material are flexible. Nonflexible residues, such as those obtained from the present material, contain little or none of the organic framework (Sohn 1958, pp. 733–4).

It is impossible to know if the collophane of the fossil material was of primary or secondary origin. The calcification of modern arthropod cuticles is in the form of calcite and vaterite (Richards 1951, p. 101). Unfortunately, the amorphous $CaCO_3$–Ca_3PO_4 calcification does not seem to have been investigated mineralogically, although such compounds occur in many cuticles (Richards 1951, table 7, p. 101). Pérez has noted the presence of crystalline apatite along the articulation lines of the telson in *Galathea* (in

Prenant 1927, p. 836). Prenant, however, has shown that the amorphism is proportional to the P_2O_5 content; when the P_2O_5/CO_2 ratio exceeds 0·105, the crystallization will be amorphous (1927, p. 833). The mineraloid would presumably be co-precipitated as a carbonate-apatite and possess properties similar to those of collophane. Cayeux mentions that cuticles of modern crustacea may show the polarization colours of apatite, and sometimes be isotropic (1916, pp. 445–6), and Needham states that the 'basic phosphate of crustacean skeletons is probably hydroxyapatite' (1954, p. 186). On the other hand, secondary phosphatization may occur quite rapidly, especially at increased depth and low pH (Goldberg and Parker 1960). Such conditions seem likely from the scanty lithological evidence.

The calcite replacement of the collophane probably took place soon after entombment. Thus Etheridge and McCulloch describe dolomite-replaced cuticles in subrecent decapods from nodules (1916, pp. 3–4). Rogers has described similar replacement of collophane by calcite in fossil bone (1924, pp. 549–50).

TECHNIQUES

Three techniques were used to prepare materials for microscopic examination: maceration, thin sectioning, and peeling.

Maceration. The sandwich-filling replacement of the collophane cuticle by calcite described below enables the cuticle to be broken down easily by acid treatment, especially if the fossil has been transfer replicated. The intracuticular calcite occurs at one or more levels in the cuticle (i.e. the sandwich is multiple) and can be etched out using 30 per cent. acetic acid. In practice, preparation of the specimens for study resulted in unavoidable flaking away of the test. These fragments were then etched overnight in the acid, washed, dried, and mounted in Marco or Ceemar resin. The resin has several advantages over normal mountants, as Wills has described (1959, p. 265). A number of slides were made from each etching and labelled; thus 30.3z 3 indicates the third slide made from maceration of fragments of the z segment of specimen 30.3.

If the fragments were sufficiently large they were mounted in Marco resin blocks and etched with acetic acid using the transfer method (Toombs and Rixon 1950, pp. 105–7; Wills 1959, pp. 263–5). Replicated fragments of cuticle were etched in this way and so the final preparation is a double transfer of the original cuticle, from original via replacement to surface of infilling calcite septum; and subsequently by etching from this surface on to the Marco resin block.

Thin sections. These were prepared in the normal way, but had to be taken to about one-sixth of the thickness of the normal petrological slide (to about 5 μ) if they were to give any detail in the microstructures. Sections are labelled by the same convention as the macerations but distinguished by an asterisk.

Peeling. Surfaces were peeled in the usual way (Kesling 1957, pp. 28–31) using Durofix in acetone as the peel solution.

Comparison of methods: Thin-sectioning wastes valuable material: the minimum slice practicable with a thin 6-in. diameter diamond saw is almost 5 mm. wide, two saw cuts are 1·3 mm. wide, and the thickness of the slice 1·4–2·1 mm. Also, grinding the sections

sufficiently thin demands skilled technique; sections only 15 μ thick will not show details of the canals.

Macerations yield fragments down to 1 μ thick and even less. These result from the following: the calcite supporting a feather edge of the unreplaced collophane may be etched away; individual laminae may split off, or, when they have been replaced by calcite, they may be etched out, leaving collophane laminae behind. The main disadvantage of this technique is the small size of the fragments it yields and the consequent difficulty of relating finer structures to the overall structure of the cuticle.

The use of the two methods, however, enables a reconstruction of the fine structures with a reasonable amount of economy. Peels were useful for detail of surface exposures but found to yield little detail from polished and etched surfaces.

Controlled etching. Part of the style of 30.3 was suspended with its inner surface in the acid for a few hours and fragments allowed to fall away for subsequent mounting. Thus, depending on the amount of mineral initially present only the calcite-filled lumen of the hollow style was eaten away in some places, and the style completely corroded away elsewhere. All intermediate sections could then be seen in different parts of the preparation, giving a sagittal view of the whole cuticle.

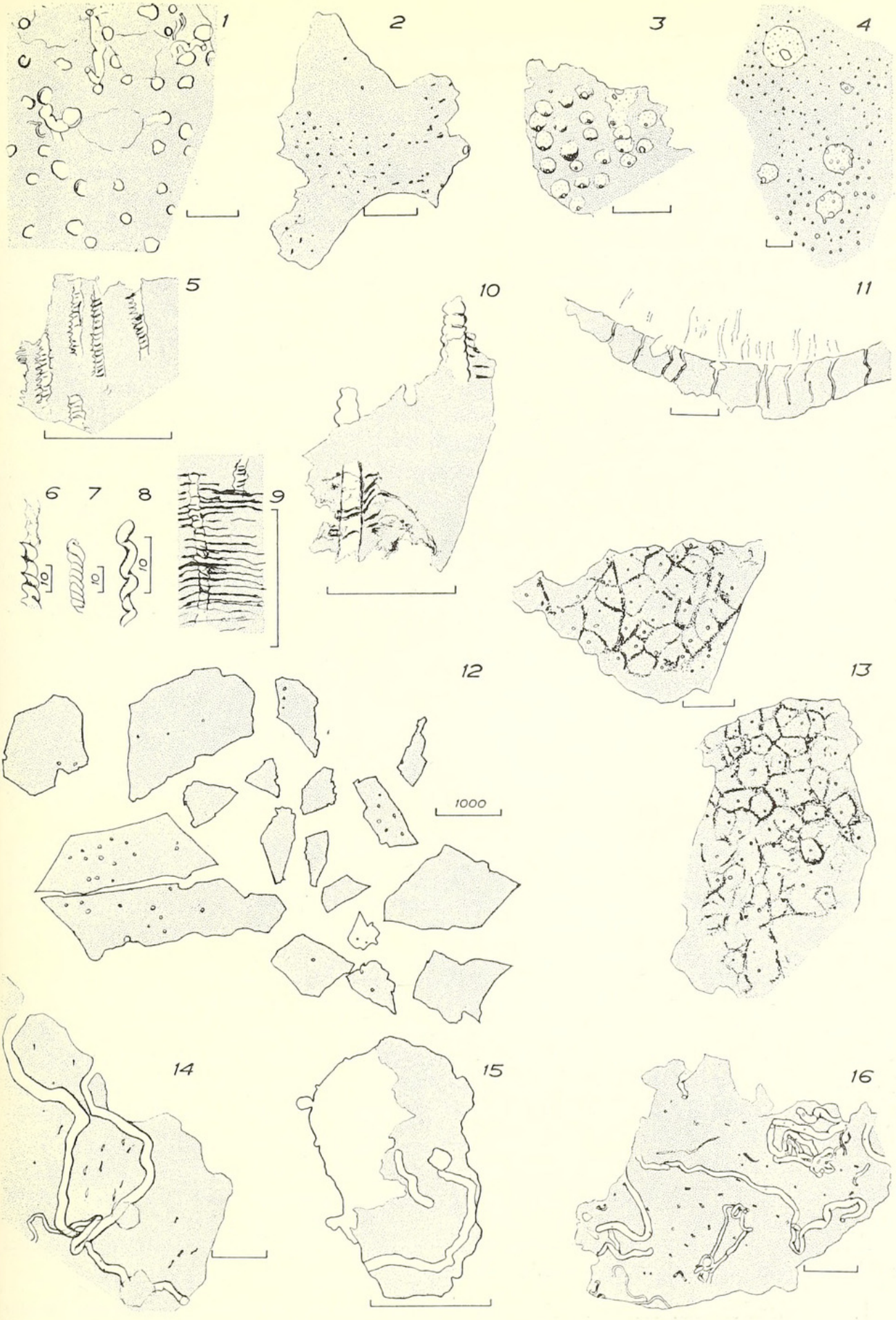
This drastic treatment was entirely justified by its results, as it provided the final key for the integration of a number of features recognizable in the macerated fragments, yet not discerned in the thin sections.

GENERAL MICROANATOMY OF THE CUTICLE

Grosser structure. The thickness of the cuticle varies from 0·03 mm. for the carapace to 0·60 mm. for the style of specimen 30.3. Locally, however, it may be much thicker; for example, the ventral ridge of the z segment of specimen 24 is 0·70 mm. thick, and the tip of the dextral mandible of specimen 30Q is 2·5 mm. thick. Barrande records the cuticle thickness of *Ceratiocaris bohemica* as 'at least 1 mm.' (1872, p. 448), of *Ceratiocaris decipiens*' abdominal segments as $\frac{1}{3}$ mm. thick (p. 450), and of *Ceratiocaris scharyi* as $\frac{1}{4}$ mm. (p. 454).

No major subdivisions of the cuticle can be detected, although replacement may give the cuticle a false appearance of such layering. Barrande records that the test of *Aristozoe*

TEXT-FIG. 3. Camera lucida drawings of cuticular microstructures. The scale represents 50 μ except where otherwise indicated in microns. Stippling indicates collophane, unshaded areas show calcite or etched out regions in the macerated specimens. 1, 5 mandible 1, large and sparse pores; compare with the denser and smaller pores in 2, 30.3z 1. Vermiform tubules are also shown in 1. 3, 30.3v 1, small holes leading to single pores, compare with larger holes enclosing many pores in 4, 30.3 stylet. 5, 30.3 style 8, canal showing incipient splitting apart of laminae (see Plate 7, fig. 2). 6, 7, 8, Variation in spiralling of canals, 6, 30.3 style 8, and 7, 30.3 style 3 are tightly coiled or thickened moniliform canals, but 8, *24 stylet is a loose spiral. 9, 30.3 style 8, laminae (see Plate 7, fig. 4). 10, 30.3Y 1, moniliform canals projecting into mountant (see Plate 7, fig. 3). 11, *24 style 2, undulating canals, one with a swelling, traceable as 'ghosts' through the replacement calcite in the subsurface part of the cuticle (above). 12, 30.3 style 2, 3, 6, 7, and 9, 'cleavage fragments' of cuticular collophane. 13, 30.3 carapace rim 1, two areas of polygons enclosing single pores (see Plate 7, figs. 7, 9), 14, 15, 16, Vermiform tubules produced by ? thallophyte perforants, pores and canals can also be seen in 14 and 16. 14, 5 mandible 2, 15, 30.3 style 6, 16, 29I carapace 1 (see Plate 7, fig. 8).



TEXT-FIG. 3.

regina consists of two layers and is not more than 1 mm. thick (1872, p. 582). Sclerotized recent arthropod cuticles can be split up into three major subdivisions, from the external surface inwards: the epicuticle, the exocuticle, and the endocuticle (Richards 1951, p. 147). The exocuticle and part of the endocuticle may subsequently be calcified and constitute the 'calcified corium' (Williamson 1860, p. 36). In view of this absence of major subdivisions in the fossil material it is impossible to know how much of the original cuticle has been preserved. Thus the thicknesses quoted above are minimal. It seems unlikely that the thin epicuticle is ever preserved, and it is possible that many subdivisions recognized in other fossil cuticles are merely due to replacement. One peculiar feature shown by the mandibles of specimens 5 and 30Q deserves description here. A 'pseudo-enamel' is present over the surface of the teeth in these two individuals. It consists of a layer of calcite 0·02–0·17 mm. thick, extinguishing parallel to the laminae. Some of it is secondary and in optical continuity with calcite in the matrix. It probably reflects a primary difference in this superficial layer (? the exocuticle), since it is absent from an edge of mandible 5 broken off during burial (on extreme right of text-fig. 1). The pseudo-enamel showed a 'root', 0·40 mm. deep into the tip of one of the teeth, which was lost during sectioning.

Some cuticle fragments were flexible at burial as all stages occur from gently curved to highly contorted fragments, and, eventually, ruptured and impacted cuticles. Many specimens show sediment actually within the thickness of the cuticle where laminae have split apart, presumably during burial.

Fragments of cuticle in the macerated preparations often show what appears to be cleavage, as shown on text-fig. 3: 12. The cleavage angles are 35°–75° and 105°–155°; the means of forty-two measurements are 65° and 115°. As the isotropic collophane is cryptocrystalline it can develop no such cleavage, nor do fragments crushed under a cover slip. The most likely explanation is that the fragments have split along the interprismatic boundaries, the basal planes of the fragments being formed by the easily separated laminae.

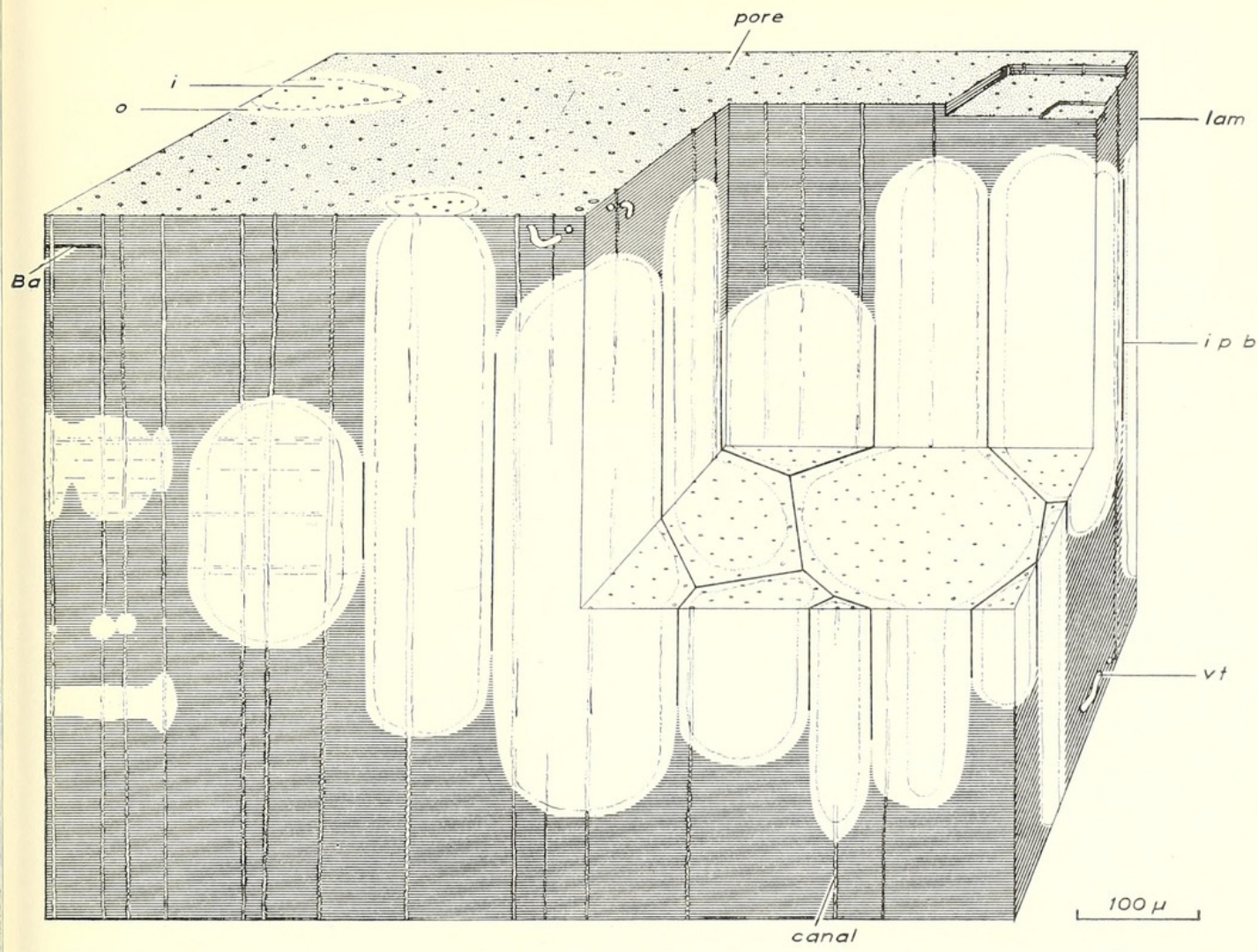
The other possibility is that the cleavage is imposed on the collophane from the replacement calcite. Basal sections of the $10\bar{1}1$ rhombohedral cleavage of calcite would intersect at 60° and 120° and this is fairly close to the calculated mean values of the fragments. This is a less satisfactory explanation than the former which caters for the wide range of variation in the measured angles.

Microstructure. Forty-four slides of macerations from various regions of the exoskeleton of eight individuals, two peels and nineteen thin sections of six individuals were found to be of value, and eight distinct types of microstructure have been recognized in these preparations. Text-fig. 4 is a semi-diagrammatic scale reconstruction of the fossil cuticle showing these features, based on the controlled etch of style 30.3 but with data added from other preparations.

PRIMARY MICROSTRUCTURES

Structures which may be compared with those developed in modern arthropod cuticles and thus 'essential' or 'endogenous' structures.

1. *Pores and canals.* These are the most obvious microstructures of the cuticle. Every



TEXT-FIG. 4. Semi-diagrammatic scale reconstruction of the cuticle of *Ceratiocaris papilio*, based on style 30.3 Replacement calcite is shown white and the close ruling represents laminae in the collophane. *Ba*, Balkenlagen; *o*, outer wall, and *i*, inner pillar of calcite replacing a prism; *lam*, laminae; *ipb*, interprismatic boundary; *vt*, vermiform tubule. Ghost laminae and canals are shown as fainter lines through the replacement calcite (see Plate 8, fig. 6).

region of the cuticle examined is penetrated by these canals, which in transverse section are seen as circular pores, as shown by Plate 7, fig. 1. The canals run through the whole thickness of the collophane cuticle and are generally filled with calcite. They are truncated by the sandwich-filling calcite replaced areas, but can be followed through them with difficulty as 'ghosts' (text-figs. 4, 3: 11). The canals usually run straight through the cuticle, but may rarely pursue a meandering course; text-fig. 3: 11 shows a specimen with an unusual concentration of such undulating canals.

The canals penetrate the cuticle perpendicularly, with only two exceptions: *5 mandible teeth 1 and 30.3 carapace rim. Both these areas are relatively thick, the former exceptionally so. Text-fig. 1, and Plate 8, fig. 3 show the mandibular teeth with the subparallel canals intersecting the surface at angles dependent on the shape of the tooth. This 'oblique relation' was figured by Harley from a vertical section of '*Astacoderma undulatum* var. *compositum*' (1861, pl. 17, fig. 12, pp. 546–8, 550). Harley's assignation

of this particular astacoderm to a phyllocarid can thus be confirmed, but the fragments are of mandibles, not gastric teeth (cf. 1861, pp. 548, 550). As well as those normal to the surface, the carapace rim shows oblique canals intersecting the surface at angles between 38° and 55°.

Under high power the canals appear as moniliform tubes, for example, text-fig. 3: 10, Plate 7, figs. 3, 4, or sometimes as spirals. These spirals are tight: text-fig. 3: 6, 7, or, very rarely, loose: text-fig. 3: 8. With crossed nicols, the highest order interference colours seen in a longitudinal section of the moniliform canals occur at the level of the constrictions. This suggests that the thickest calcite lies not in the swollen areas of the canal as might have been expected, but to one side of them. This can be explained if the moniliform appearance is due to a tightly coiled tube, i.e. one with a low pitch relative to the diameter of the helix. Incidentally, the polarization colours afford a useful check on the thickness of the canal preserved in the section, if Dudich's method is used (1931, pp. 57–59). However, although loosely coiled tubes are easily recognized the commoner moniliform appearance is not due to a straightforward tight coil. All that can be seen in the best-preserved canals is a spiral thread and groove running around the canal walls, forming in engineering terms a knuckle threaded internal screw. Both dextral and sinistral threads and tubes are present. Possibly an originally coiled tube has been completely destroyed during fossilization and all that remains is the threaded external mould. If there was no coiled tube inside, however, it means that two types of canals are present; a wider one with a taenidia-like, tight spiral thickening and a thinner, loosely spiralling tube.

The pitch of the canal spirals varies from 0·8 to 7·2 μ with a mean of $3{\cdot}80 \pm 0{\cdot}079$ (63). This pitch is proportional to the external diameter of the canal, possibly suggesting that the thread is only a mould and not an original thickening. Text-fig. 5 shows the graphical relation between the pitch of the thread and the external diameter of the canal as measured from the preparations. Some of the abnormally low values recorded for the diameter of canals with a similar pitch are probably of the less than maximum diameter seen in an off-centre plane of section. The three lines plotted are the expressions of three types of coiled tube. The centre line is of an ideal helix coiled as tightly as possible. This helix can then be expanded in the two ways shown on the graph by the other lines, either laterally or vertically. The former increases the umbilicus of the helix, the latter exaggerates the pitch.

The pitch commonly coincides with the lamination of the cuticle, and laminae may show incipient splitting apart where they abut against the canal wall—text-fig. 3: 5, 6; Plate 7, fig. 2. Replacement calcite may follow along, or be the cause of this splitting, which may proceed until the canal has the appearance of a Christmas tree, with its

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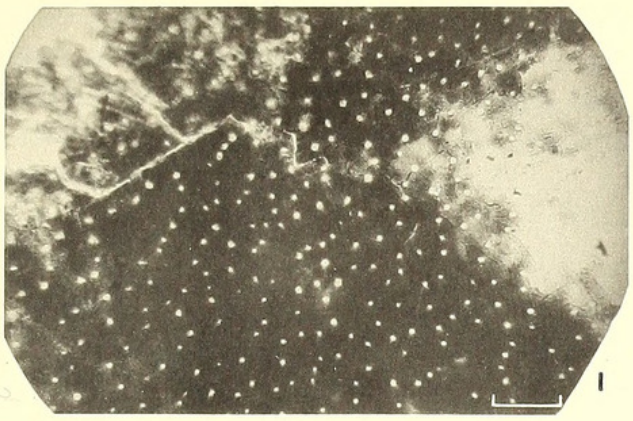
EXPLANATION OF PLATE 7

Microstructures of the cuticle of *Ceratiocaris papilio* Salter. The scale represents 50 μ. Figs. 1–3, Pores and canals. 1, *24 style 5, transverse section of canals (= pores). 2, 30.3 style 8, longitudinal section of canals, showing incipient splitting of laminae. 3, 30.3 Y 1, moniliform canals projecting from collophane (dark) into mountant. Figs. 4, 5. Laminae. 4, 30.3 style 8; 5, *30.3Z ventral process, showing festooned laminae between canals. Fig. 6. 29I carapace right valve, small bumps surrounding individual pores. Figs. 7, 9. Polygons. 7, 30.3 carapace rim 1, two areas of thin collophane showing polygons, separated by thicker collophane (dark). 9, Right edge of fig. 7 at higher magnification, showing single pores in centre of polygons. 8, 29I carapace 1, vermiform tubules produced by ? thallophyte perforants.



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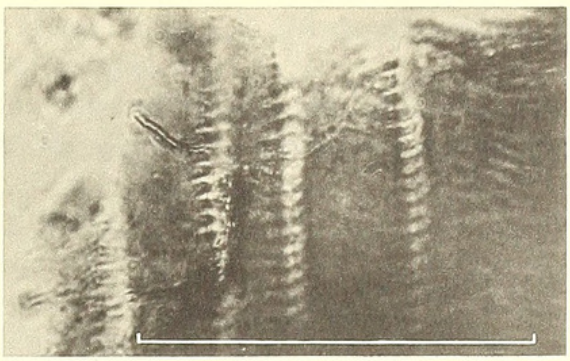

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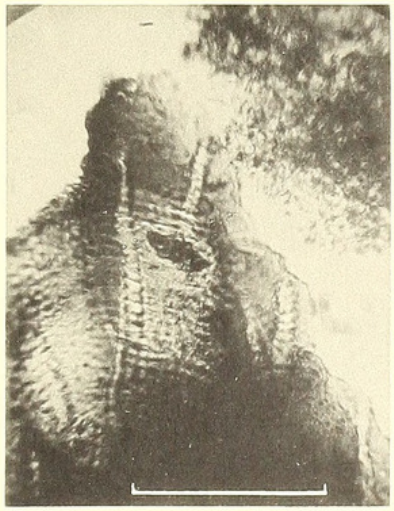

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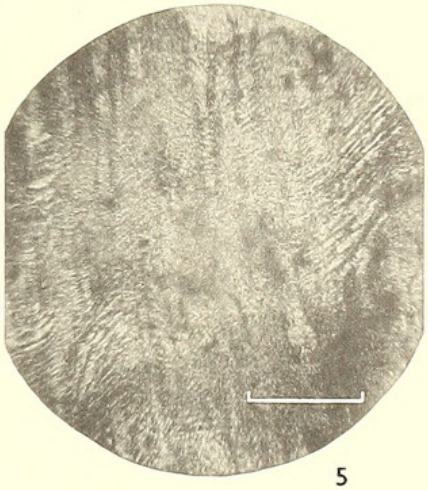

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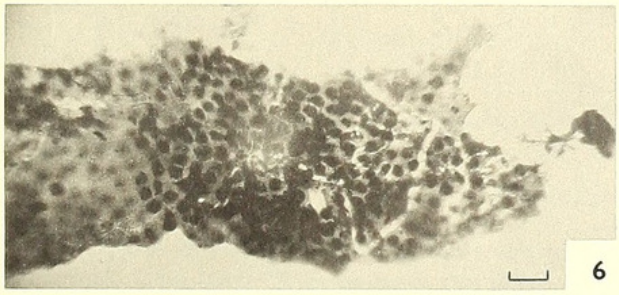

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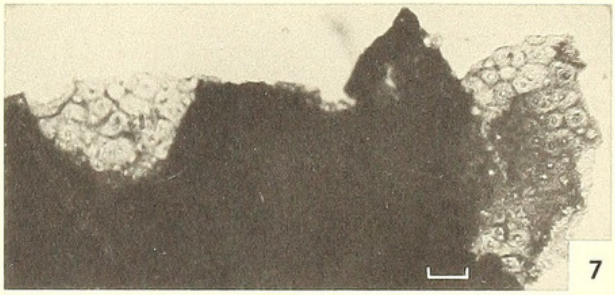

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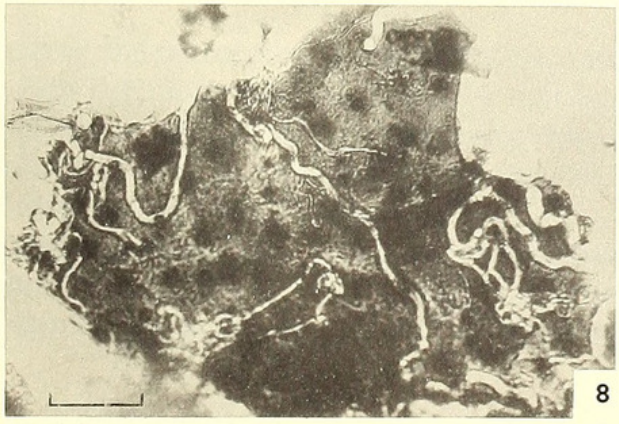

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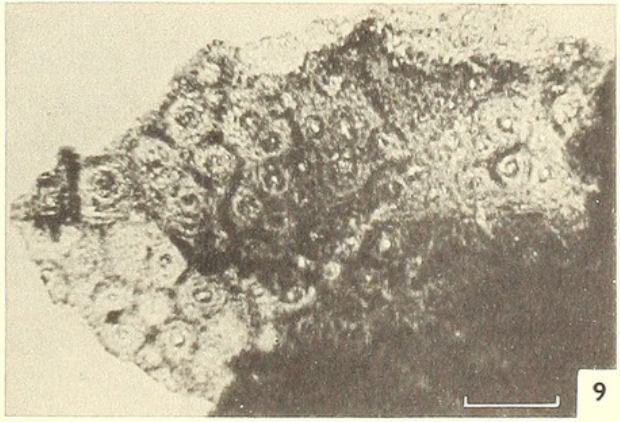

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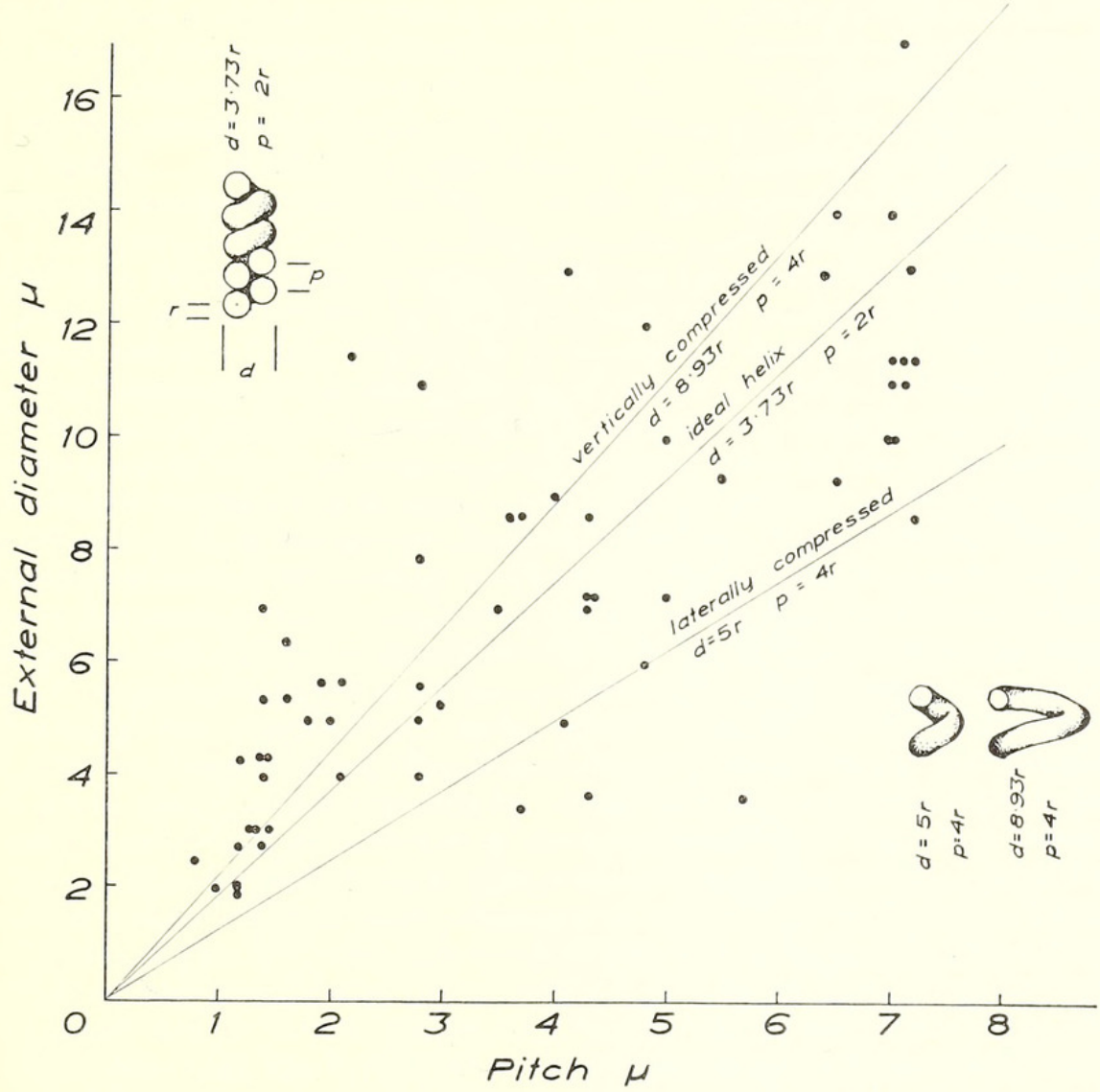
branches represented by calcite replaced laminae (Plate 7, fig. 5). Eventually adjacent branches of the tree will join up and whole laminae be replaced.

The circular pores often show a ragged sector on their otherwise smooth circumference, due to the spiralling down of the canal out of the plane of the section revealed by breaking along a lamina—text-fig. 3: 1.



TEXT-FIG. 5. Graph showing correlation between pitch of canal spirals and external diameter of canals through cuticle. The three lines express the three illustrated types of coiled tubes; *r*, radius; *p*, pitch of tubes; *d*, external diameter of canal.

Canals in the macerated preparations occasionally project from their enclosing collophane into the mountant, as shown by text-fig. 3: 10, Plate 7, fig. 3. As the calcite infilling of the tube has been etched away this must be some form of discrete lining or wall left behind. It is transparent, but may be of collophane which is also transparent at this thickness of only a few microns.

The maximum external diameter of the canals and pores varies from 0·7 to 17·0 μ, the mean diameter is 6·0$\pm$0·178 (121). The thickness of the fossilized cuticle could only be measured accurately in the thin sections and hence there is not adequate data to

enable any statistically reliable correlation between the diameter of the canals and the thickness of the integument they pierce. The wide variation in diameter of canals in the same cuticle further hinders any simple correlation. However, there does appear to be a slight positive correlation between the thickness of the test and the pore diameter.

The density of the pores varies from 1,400/sq. mm. in 5 mandible 1, text-fig. 3: 1, to 4,700/sq. mm. in 30.3 z 1, text-fig. 3: 2. The mean density per sq. mm. is 2,356$\pm$74·4 (28). A minor part of this variation in density is undoubtedly due to the calculation of densities from macerated fragments derived from different levels in the cuticle. The internal surface area of the cuticle of the exoskeleton may be up to about 10 per cent. less than that of its external area. Thus densities of canals measured on fragments from low levels in the cuticle will differ by a corresponding amount from those measured on fragments derived from higher levels.

There is no statistically reliable correlation between pore density and diameter. The pores of smaller diameter are perhaps denser than the larger pores. Peel 5 mandible 3 shows pores 4–11 μ in diameter, with a density of 2,000/sq. mm. in the thin-walled area of the mandible flank. Towards the thicker cutting edge of the mandible, only 6 mm. away, this density increases to 3,300/sq. mm. at the much smaller diameters of 0·7–3·0 μ.

The canals often swell and balloon out along their length due to calcite replacement. These individual blebs of calcite, strung along the canals at irregular intervals like beads on a necklace, increase in size by fusing laterally along the laminae and vertically along the canals. All stages may be seen in this process of replacement, from merely swollen areas of the moniliform canal to completely replaced individual laminae and groups of laminae, until, eventually, whole sections of the cuticular collophane have been replaced. The role of the prisms in this replacement process will be described later. The early stages in this process are shown on the left of the block diagram and Plate 8, fig. 4. This process and its result may be termed sandwich-filling replacement. Schäfer (1951, pp. 235–6, fig. 12) has recently described a section through the cuticle of the recent brachyuran *Portunus* allowed to decompose for two months in sea water. Although Schäfer (1951, p. 236) notes that the pore canals are most resistant to destruction, his figure strikingly resembles sections of an 'early stage' in sandwich-filling replacement of the fossil cuticle. Plate 8, figs. 1–2 show successive sections *24 style 1 and 2, photographed between crossed nicols, with the isotropic collophane sandwiching the calcite-infilled core of the cuticle. It is impossible to decide whether or not some of these swellings on the canals are primary or merely the replacement phenomena described above. Text-fig. 3: 11 shows a cuticle, the external surface down, with a distinct and regular-shaped swelling on the canal. The dilated tips of Diplopod gland ducts are superficially similar (Richards 1951, fig. 32, p. 155).

The canals can best be compared with the pore canals of recent arthropods. The only problem lies in their size; thus Wigglesworth terms the pore canals of *Sarcophaga* larva 'relatively coarse' with a diameter of 1 μ (1950, p. 23), and canals of 0·15 μ diameter at a density of 1,200,000/sq. mm. are recorded for the cockroach (Richards 1951, p. 181). However, some crustacea have larger pore canals (Richards 1951, p. 177). The size of the canals is closer to that of the ducts of tegumental glands or setal ducts, but these are usually of restricted distribution and less dense in number. Similarly neither of those ducts follows a spiral course through the cuticle (R. Dennell, private communication), although gland ducts may have spiral thickenings (Richards 1951, pp. 251, 254). The

distribution of the canals within the prisms as described below is identical to that in modern cuticles (Dennell 1947, 1960). Tegumental gland ducts and setal ducts, having a unicellular or multicellular origin, can never be present in such densities in a single prism, which is the vertical extension of a single epidermal cell. Richards states that pore canals are probably 'a characteristic feature of chitinogenous tissue and transport peripherally various components for cuticle production' (1951, p. 182).

It is strange that the only reference to calcite filling pore canals should be that in which pore canals were first described (Valentin 1837, p. 124). Valentin describes how he etched the calcite away with acid and was then able to see the canals clearly.

The origin of the helices of the pore canals has been explained by radial contraction during cuticle formation (Richards 1951, p. 179). The remarkable hollow, chambered and spiral crystal whiskers, grown in colloidal media, have been cited as having genuine analogies with biological growth processes, and might provide a key to this problem (Nabarro and Jackson 1958, p. 25). The origin of turbination in shells poses analogous mechanical problems (Berner 1956).

Many of the structures described, taken from fossil arthropod cuticles and compared with modern pore canals, are either gland or setal ducts. Not only are they too large and sparse for genuine pore canals, but in several cases they have been described as leading up to the bases of setae. Thus Waterston has shown the 'pore-canals' through the cuticle of the eurypterid *Campylocephalus scouleri* to be bristle bases (1957, p. 279). Eisenack has recently described microstructures of some Silurian eurypterids in detail, but no undoubted pore canals can be discerned (1956). Fuller references to the literature on eurypterid microstructures are given by Størmer (1936, pp. 27–32) and Eisenack (1956).

Canals have been described from several trilobite genera but again may be too large and sparse for pore canals although quantitative data are lacking. Thus Størmer compares canals in *Tretaspis*, which measure 20μ on his plate 12, fig. 2, with Porkanälchen (1930, pp. 98–99). Cayeux recognized the existence of tubes larger than pore canals in the crab and describes 'canaux' from '*Trinucleus goldfussi*' (1916, pp. 444–6). The canals described by Father Rome from *Phacops* are not measurable with any accuracy (1936, p. 3). Evitt and Whittington have described perforations from 0·4 μ to 75 μ in diameter through the exoskeleton of *Flexicalymene* (1953, p. 53). It seems most likely that the smaller canals are genuine pore canals while the larger ones are setal and tegumental gland ducts.

The term pore canal has become entrenched in the literature on the ostracod cuticle, yet many of the canals are relatively large and described as leading to hairs and bristles (Kükenthal and Krumbach 1927, p. 402; Schulze 1926, pp. 7–8). Kesling defines the ostracod pore canal as 'a passage originally connecting sensory hairs to the nerves of the hypodermis' (1951*a*, p. 124), and records that hairs reach through radial canals as well (1951*b*, p. 64). They may also show the dilated tips such as occur in some gland ducts (Sylvester-Bradley 1941; cf. Richards 1951, p. 155). In addition to normal 'pore canals', however, Wagner figures fine punctae in the carapace of *Cytherura gibba* measuring less than 1 μ in diameter and at a density of about 55,000/sq. mm. (1957, p. 74, pl. 33, fig. 1). These are possibly genuine pore canals, which serves to indicate that the majority of so-called canals from ostracods are in fact setal and tegumental gland ducts.

Harley recognized that the microstructure of some of his Astacoderma from the

Welsh Borderland was 'unmistakeably Crustacean' (1861, p. 546). A process of careful elimination, based on thin sections of other fossils, including trilobites, enabled him to refer many Astacoderma to *Ceratiocaris* fragments. His data indicate that canals through the cuticle were 0·6–1·0 μ (1861, p. 546) in diameter suggesting that these are quite normal pore canals, an observation that will require verification. The punctuations of *Dithyrocaris* cuticles figured by Jones and Woodward are of comparable diameters to the canals from the present material, but they have either far lower or higher densities, only reaching 800/sq. mm. according to their figure of *Dithyrocaris insignis* (1898, pl. 25, fig. 5*b*) and yet 15,000/sq. mm. in *D. testudinea* (1899, pl. 29, fig. 11*b*). Further work on these dithyrocaridids would be profitable.

2. *Laminae.* The laminae are seen as extremely fine striations in the collophane, parallel to the surface of the cuticle. They are not always visible, probably for a variety of reasons, such as sections too thick, lighting unsuitable, refractive index of mountant too close to that of specimen (Richards 1951, pp. 174–5). Like the canals, the laminae may be completely obliterated by the replacing calcite, or traceable through it as 'ghosts'. Under high power the amber collophane laminae are seen to be separated by dark bands. When the collophane is so thin as to be transparent, the darker bands contrast strongly with the lighter bands. The dark bands may be equal in thickness to the light bands but are usually much thinner, and often appear to be only an inter-laminar boundary. They are well seen on text-fig. 3: 9, Plate 7, fig. 4. Although the laminae usually run parallel to the curved surface of the cuticle, they may occasionally hang in festoons between the canals (Plate 7, fig. 5). The process of replacement of individual laminae by calcite has already been described, and also how the festooned laminae came to have the appearance of Christmas trees, due to the replacement of alternate collophane laminae by calcite. The laminae are planes of weakness and the cuticle readily flakes off along them, as illustrated on the top right-hand edge of text-fig. 4.

The thickness of individual laminae was measured from one dark band to the next, thus including one dark and one light band. It may be up to 7·2 μ but it is usually far less, and the lower limit is beyond the range of the optical microscope. The thinnest lamina measured was 0·8 μ. The mean thickness of twenty-eight measured laminae is 3·26 μ, but this is too large a figure since thinner laminae could not be measured. The thickness of the laminae commonly coincides with the pitch of the canals. These laminae are identical to those recognizable in modern cuticles (Richards 1951, pp. 174–7), the origin of which is not yet understood, but which have been explained in terms of periodic crystallization and Schiller plane phenomena. The dark bands of the laminae of *Periplaneta* are half the thickness of the light bands (Richards and Anderson 1942, p. 150) and are denser and stronger than them. Modern cuticles also tend to split apart along the laminae, but 'they are chemically similar to one another' (Richards 1951, pp. 124, 175). Dennell has proposed a model in which the lighter bands are composed of loose, vertical, chitin fibrillar crystallites which bend over and are gathered into horizontal masses in the denser bands (1960, p. 459). The replacement of alternate laminae in some areas of the fossil cuticle is thus presumably fortuitous; splitting apart occurs along the lighter bands with calcite growth as a cause or effect.

Laminae have been recognized in other fossil cuticles. Harley has figured 'excessively fine' laminae of ? ceratiocaridid astacoderma (1861, p. 546). Rome records 13 to 19

laminae in the cuticles of *Phacops* (*Ph.*) *accipitrinus* measuring 0·4–0·7 mm. thick (1936, p. 7, pl. 1). Cayeux records that the 'lignes d'accroissement extrèmement fines' (i.e. of the laminae) of '*Trinucleus goldfussi*' were 'souvent interrompues par la fossilisation' (1916, p. 447). In Zittel's textbook Beecher refers to 'thin laminae of carbonaceous and phosphatic compounds of calcium' in trilobites (1900, p. 609). Størmer (1930, p. 98) distinguished 7 to 8 'lamellae' picked out by pyrite grains in the cuticle of *Tretaspis seticornis*, and was able to make out several less well-defined layers between. The difficulty in resolving laminae makes those in modern arthropods appear broader than they are in actual fact (Richards and Anderson 1942, p. 150), and thus the thickness recorded of laminae selectively replaced in fossil cuticle is certainly far greater than that in the original cuticle.

3. *Balkenlagen*. These have only been seen in one macerated specimen, 30.3v 2. They consist of alternating dark and light bars perpendicular to the darker bands of a number of laminae 1·4 μ thick. They are only visible adjacent to one canal, and then only by careful focusing. Three dark and light bars can be measured in a distance of 1·4 μ, giving the total width of one dark plus light bar as 0·48 μ.

These can only be the traces of the oriented micelles or chitin crystallites referred to as Balkenlagen (Richards 1951, pp. 192–4). Although most commonly recognized in beetle cuticles, they have also been recorded from crustacea (Richards 1951, p. 192; Krishnakumaran 1956, pp. 174, fig. 2, p. 176).

4. *Prisms*. These structures were only found by the controlled etch of the style of 30.3. The successive planes of section revealed by etching through the inner colophane of the style, through the calcite sandwich-filling and the outer collophane, show the following features. Where the basal portion of the cuticle adjacent to the originally calcite-filled lumen has been revealed, it is seen to be penetrated by the lumen of a dorsal spine, by the canals and a rare hole. When the internal collophane has been removed and the sandwich-filling of calcite lightly attacked by the acid, differential corrosion picks out a network of straight vertical fissures 1–2 μ wide, bounding more or less regular four-, five-, six-, and seven-sided prisms, varying from 0·052 to 0·27 mm. in maximum diameter, with the mean 0·15 mm. $\pm$0·00312 (67). Each prism is usually composed of two layers; an outer wall (*o* on text-fig. 4) of resistant calcite, 0·01–0·06 mm. thick, surrounded by the fissures; and an inner cylindrical pillar of easily corroded calcite (*i*), usually only visible as a circular well 0·04–0·21 mm. in diameter, filled with dusty-looking calcite. These prisms are riddled with canals, which can only be estimated to have a maximum diameter of 0·007 mm. and which correspond to the canals described above. The number of canals varies from twenty to more than eighty per prism. One pentagonal prism, with a cross-sectional area of 0·035 sq. mm., contains about eighty pores which equal a density of 2,300/sq. mm. These structures are shown on Plate 8, fig. 6.

When the calcite has only just been destroyed, the inner surface of the outer collophane sandwich is seen to be pitted by a number of circular funnels or sockets of variable depth, which are the continuations in depth of the prisms. Most of these sockets terminate bluntly before the external surface is reached, although a few may intersect it to form the holes mentioned earlier. At the calcite/collophane interface the interprismatic fissures are only seen as cleavages in the collophane. Even these cleavages disappear from the collophane outside the interface.

Very little evidence of the prismatic structure can be detected in the thin sections. The outer calcite wall of the prism can sometimes be distinguished by its lack of colour compared with the biscuit-coloured calcite of the inner column (Plate 8, figs. 1–2). It may then be traceable around the end of the column, but although this is shown as being the case on text-fig. 4 it is not always detectable. Nothing can be seen of an interprismatic septum which would etch away to leave the fissure characteristic of the corroded specimen. Areas which must be interprismatic from the shape of the infilling inner and outer calcite consist merely of calcite apparently identical to the outer wall. In the block diagram an interprismatic boundary (*ipb*) has been drawn of the same width as the interprismatic fissure revealed by etching.

The replacement by calcite described under the earlier sections is ultimately governed by the prisms. Calcite replaces laminae and balloons out from canals only within individual prisms; the presence of inner and outer zones of calcite may reflect differences in composition of the original prismatic material.

Apart from their relatively gigantic size the prisms may be compared with those from modern cuticles (Valentin 1837, fig. 23; Drach 1939, pp. 292–8, 374–5; Dennell 1947, pp. 485–503, 1960, pp. 455–64; Richards 1951, pp. 146, 194). Modern hexagonal prisms are thought to correspond to the underlying epidermal-cell outlines and are originally composed of the chitin-protein complex forming the cuticle. In the early stages of cuticle formation each prism is separated from its neighbour by an interprismatic space. The prisms may then fuse by an infilling of the interprismatic spaces with epicuticular lipoproteins, or become calcified; in both cases the prisms usually lose their optical identity. This calcification takes place from the outer surface and proceeds inwards via the interprismatic spaces, spreading out horizontally along the laminae in much the same way as the endoprismatic replacement of collophane by calcite proceeds via the canals and laminae in the fossil cuticles described above. From a study of the pre-moult breakdown of the calcified endoskeletal prisms of decapod crustaceans Drach showed that the centre of each prism disappears first to leave a 'réseau hexagonal' of interprismatic material (i.e. the order of breakdown is the reverse of crystallization). His pl. vii, figs. 35, 36 (1939) show this very well. These soft centres to the prisms probably correspond to the easily corroded pillars, and the resistant mesh of the interprismatic septa to the interprismatic boundaries or fissures of the fossil material. Drach records the diameter of the prisms as 10–15 μ with an interprismatic width of 0·2–2·0 μ.

If the size of the prism does correspond to that of the subjacent epidermal cell, these

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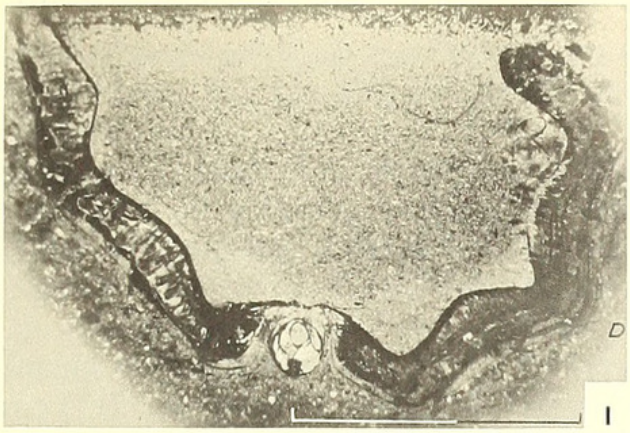
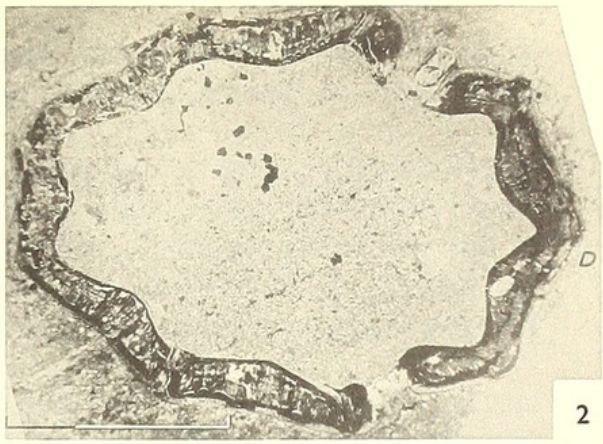
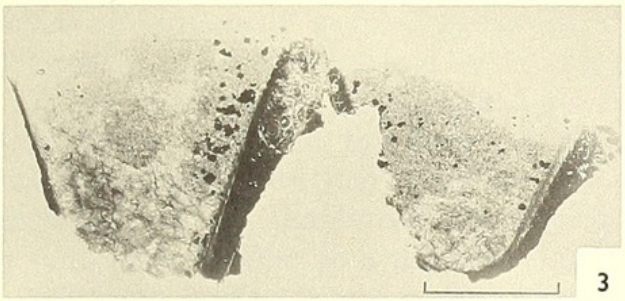
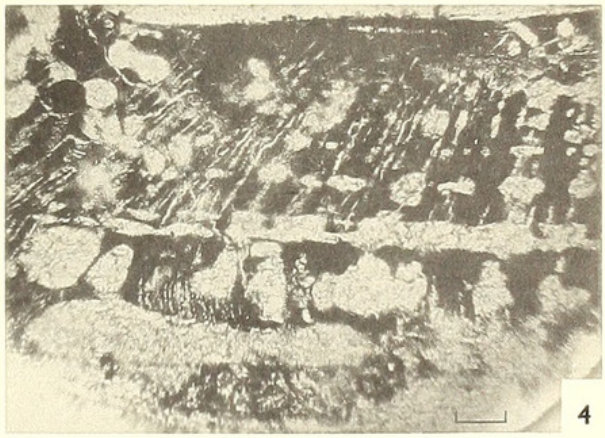
EXPLANATION OF PLATE 8

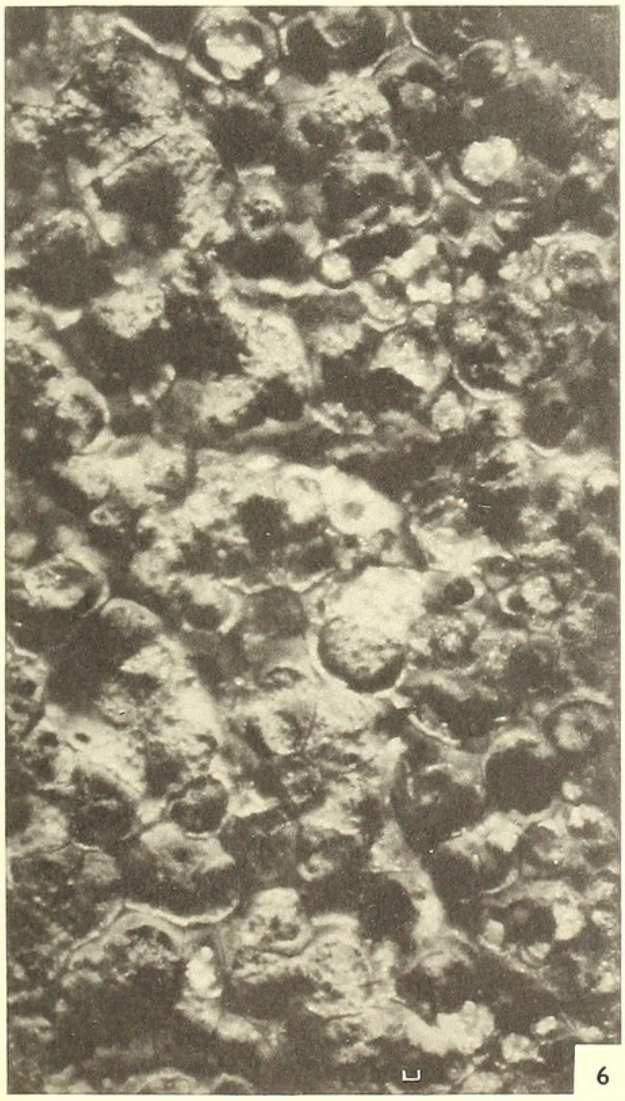
Microstructures and X-ray powder photograph of the cuticle of *Ceratiocaris papilio* Salter. The scale is 2 mm. long except below Figs. 4, 6 where it represents 50 μ. Figs. 1, 2, *24 style 1, 2, transverse sections showing sandwich-filling replacement. Letter D indicates the dorsal ridge I of the style. Crossed nicols; collophane isotropic, replacement calcite grey and white. Fig. 3. *5 mandible teeth 1, showing calcite 'pseudo-enamel' penetrated obliquely by canals. See text-fig. 1 for detail. Fig. 4. *24 stylet 1, transverse section showing early stage of sandwich-filling replacement of collophane (dark) by calcite. Fig. 5. X-ray powder photographs. Sample 1 from cuticle, sample 2 from infilled lumen of style 30Q. The numbered lines refer to Table 1. Fig. 6. Controlled etch of style 30.3. Numerous interprismatic fissures can be seen as straight black lines, bounding the lighter prisms, formed of outer and inner portions. Pores can be seen piercing the inner pillar of a prism just below the centre of the figure.

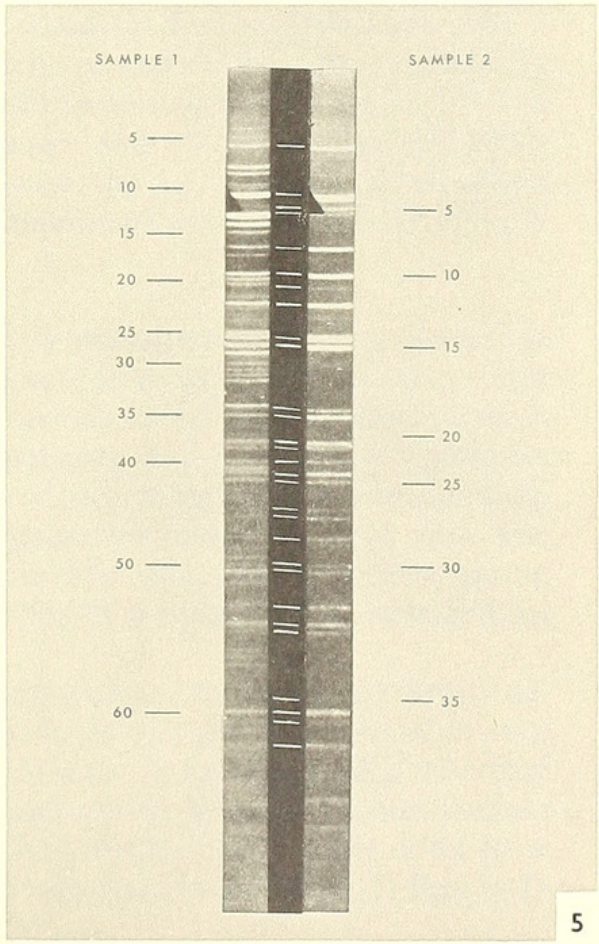












ROLFE, Silurian Crustacea

cells in the *Ceratiocaris* style must have been relatively gigantic (cf. Drach 1939, fig. 5, p. 294; Richards 1951, pp. 204, 211). If this were the case it might also account for the large pore canals.

Prisms do not seem to have been recognized from fossil cuticles before. Cayeux figures some polygonal areas 28–40 μ in diameter with walls 16 μ thick from '*Trinucleus*', each containing one pore with a density of about 230/sq. mm. (1916, pl. 43, fig. 3), and of 'signification inconnue' (p. 447). If these are genuine prisms, as seems likely, his 'canaux' must then be tegumental gland or setal ducts. The reticulation of *Dictyocaris* is possibly of prismatic origin (Salter 1860, p. 161; Packard 1883, p. 446).

Some of the so-called 'ornament' of ostracods is certainly of replacement origin and possibly related to cuticular prisms. Kesling (1954, pp. 17–18) draws attention to the two layers of 'ornament' in fossil ostracods, in which 'the thin outer layer of the shell has one sort of ornamentation and the layer below has another and completely different kind . . . the outer layer is fragile and could easily have been removed by corrosion or abrasion. It is possible that this layer was present in many species, but has disappeared from all specimens before their collection'. He describes two species of *Ctenoloculina*, one of which has fine reticulation and the other granulae and small punctae on their outer layer; both have papillae in a subjacent layer. Elsewhere, Kesling describes structures from *Hibbardia lacrimosa* which were revealed, significantly, by etching and peeling. He describes vertical thin lines which 'do not appear to be pore canals because of their small size', and which run through the 'middle of each element of the reticulation' (1957, p. 33). His excellent plates leave no doubt that the structures described are in fact corroded interprismatic boundaries. The cup-shaped depression surrounded by the walls of each reticulation might well be the equivalent of the intra-prismatic pillars described above. Indeed, his pl. 11, fig. 22 shows these cup-shaped areas apparently roofed over by an uneroded outer layer, which would be consistent with prism-dictated sandwich replacement. The prisms would then measure under 1 mm. in diameter, with interprismatic septa 1 μ wide. If this should be the case, the interpretation of ornament as a character in the specific and generic differentiation of ostracods will need more drastic revision than even Kesling has attempted.

5. *Polygons*. Text-fig. 3: 13, and Plate 7, fig. 7 show polygonal outlines preserved in collophane from 30.3 carapace rim 1. The polygonal fields can only be seen where laminae have split away above the two areas which are about 2 μ thick. Focusing has to be either above or below the section to bring out the denser, amber-coloured boundaries which are 4 μ wide. One pore is present in the centre of each field, but where the interfield boundaries are faint or possibly absent, the polygons contain more than one. The diameter of the polygons is 12–35 μ, but larger ones with more than one pore are up to 65 μ in diameter. Most of the pores are surrounded by a patchy, concentric zoning, or 'granulation'.

The only comparable structures from modern cuticles are the prisms previously described. The presence of only one pore per polygon would then indicate a gland or setal duct origin for all the pores; their density, and relation to the genuine prisms described above, does not favour this, however. They may possibly be the scars of inter-laminar splitting, homologous to the holes and bumps described above. They only differ from these in their fainter and generally more 'organic' appearance (cf. Plate 7, figs. 6–7).