THE CUTICLE OF CRETACEOUS MACRUROUS DECAPODA FROM ALEXANDER AND JAMES ROSS ISLANDS

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ABSTRACT. Remarkably well-preserved cuticles of Cretaceous decapods are described. Similar compositionally to the shell of modern *Lingula*, they were probably phosphatized secondarily, although environmental factors (notably insufficient lime) may have inhibited normal calcification. As the sinuous and fibrillar ribbon-like pore canals have a constant pitch and rotate in phase with the lamellae, these cuticles have a helicoidal molecular structure similar to the Bouligand model. The absence of tegumental ducts suggests that the cuticles were deposited epidermally. Several features, notably the restriction of pore canals to the endocuticle of *Hoploparia stokesi*, are peculiar to certain insect cuticles.

WITH a few notable exceptions (e.g. Scheffen, 1930), the structure of even well-preserved fossil decapod cuticles has been largely neglected by research workers, probably because they have assumed that the fossil cuticles would be virtually homologous with those of living forms which are well documented (e.g. Biedermann, 1903; Cayeux, 1916; Drach, 1939; Richards, 1951; Dennell, 1960).

Although a broad homologous relationship undoubtedly exists, these studies demonstrate some differences, particularly with respect to the occurrence of setal ducts and the vertical extent of the pore canals. The mineralogy of the fossil cuticles has also contributed towards an understanding of the sedimentary environment in which these decapods lived or were buried. In addition, thin sections have demonstrated the presence of a microscopic saprotrophic fungus (Taylor, 1971) similar to the so-called "crayfish plague" fungus (Unestam and Weiss, 1970).

The Antarctic decapods come from the Lower Cretaceous (Upper Neocomian–Upper Aptian) of south-eastern Alexander Island (lat. 69°–72°30′S.) and the Upper Cretaceous (Lower–Middle Campanian) of the James Ross Island area (lat. 63°47′–64°33′S.). The systematics have been described by Taylor (1974) and Ball (1960), respectively. The remarkably well-preserved cuticle of both faunas shows all the major structural sub-divisions as well as the vertical and horizontal components of living decapod cuticles.

Appearance in the hand specimen

Externally, the fossil decapod cuticles are black or more commonly bluish white in colour, the opalescence probably indicating the occurrence of vivianite, a hydrous iron phosphate often associated with phosphatic shells or bone. The vivianite is secondary because unweathered fragments of the same cuticle are brown in both the hand specimen and in thin section. Both black- and opalescent-coloured cuticles are similar mineralogically.

Composition of the cuticle and tests for chitosan

In thin section, the cuticles are amber or pale yellowish green in plane polarized light but isotropic or slightly anisotropic in crossed nicols. Although the mineral or mineraloid is probably collophane, several Campbell–van Wisselingh tests for chitosan were made (Richards, 1951, p. 32–36) on small fragments of cuticle from the cephalothorax of *Glyphea georgiensis* Taylor; the spiny spider crab *Maia squinado* was used as a control. The crab gave good positive reactions at every stage of the tests but the fossil material was rather unsatisfactory even after the KOH had been virtually evaporated, probably because the sample was small and difficult to separate from the matrix.

X-ray analysis

Powder samples from specimens KG.103.14 (a dactylus) and 2.139 (a propodus), and one from *Maia squinado*, were examined by X-ray diffraction with the assistance of L. M. Juckes. As expected from previous analyses (Clarke and Wheeler, 1922, p. 45; Vinogradov, 1953, p. 395), the crab consisted of calcite or manganocalcite $(Ca,Mn)CO_3$, whereas the fossil cuticles

(notably specimen KG.103.14) were practically identical in composition to the shells of two inarticulate brachiopods analysed concurrently by M. R. A. Thomson, i.e. *Discinisca variabilis* Thomson from Waitabit Cliffs, south-eastern Alexander Island (Thomson, 1971) and modern *Lingula*. Both brachiopods contain over 70 per cent of $Ca_3P_2O_8$ (Jope, 1965).

Analyses of *Pemphix sueuri* (Triassic) have shown that this decapod was probably composed originally of chitin and an amorphous or crystalline calcium carbonate. However, Scheffen (1930) suggested that it may be difficult in this and other fossil cuticles to differentiate between primary and secondary mineralization.

Diagenesis of the decapod cuticles

Because these fossil cuticles are so well preserved, the absence of calcite (other than that filling cracks) is problematical. In living decapods, the epicuticle and outer part of the exocuticle are completely calcified concomitantly as part of a hardening process even *before* the endocuticle is fully formed (Lafon, 1943; Dennell, 1947), the calcification resulting from "une injection massive de sels de calcium provenant de l'hémolymphe" (Lafon, 1943, p. 136). Subsequently, large plaques of crystalline calcite also develop in the endocuticle (Fig. 1a).

Thus, the abnormal amount of calcium phosphate (greatly in excess of the 10–15 per cent usually found in the decapod exoskeleton (Vinogradov, 1953)) may be due either to complete decalcification and secondary phosphatization or to inhibiting environmental factors. Secondary phosphatization involving minimal modifications to the primary structural features may have occurred in the pod shrimp *Ceratiocaris papilio* (Rolfe, 1962, p. 35) and in a dicotyledonous wood dredged from the Pacific Ocean (Goldberg and Parker, 1960).

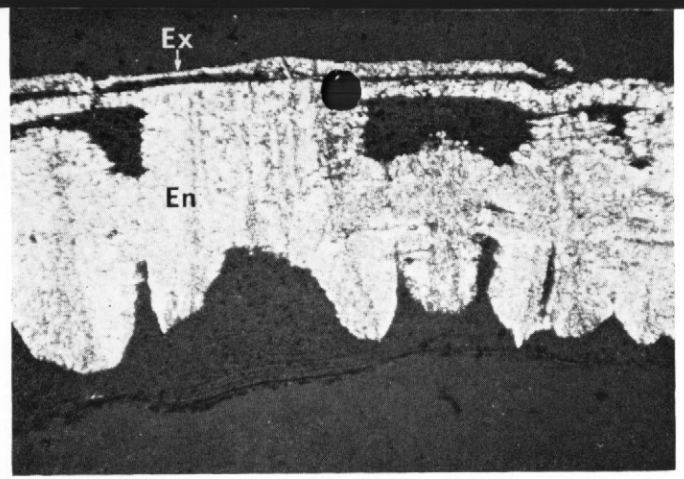
Alternatively, observations and experiments with living Crustacea (including *Carcinus maenas*) suggest that many crustaceans are calcified electrochemically (and in the presence of sufficient lime) by the outward diffusion of salt through their proteinous cuticles which contain semi-conducting complexes (notably quinone or polyphenol). In this process, the cuticle acts as a cathode between a relatively alkaline zone immediately outside the crab cuticle and relatively acidified tissues underlying the permeable cuticle (Digby, 1967, 1968).

Because of an insufficiency of lime, the Antarctic decapods may have been unable to deposit calcite in this way. In the Alexander Island area, during at least part of the Lower Cretaceous, the non-occurrence of limestones (apart from calcareous concretions) compared with the localized abundance of nodular and disseminated iron pyrites suggests that toxic conditions may have existed periodically at or just below the water/sediment interface (Horne and Taylor, 1969; Taylor, 1971). Nevertheless, the decapods may have sclerotized their cuticles with an orthoquinone that tanned the protein constituents (Dennell, 1947). Insects and arachnids, which contain more protein than Crustacea, are hardened in this way rather than by calcification, which in the hermit crab *Eupagurus* depends not on the quantity but on the *type* of protein present (Lafon, 1943, p. 139).

Thin-section material

Seven thin sections were made from the partly exposed carapace of an opalescent glypheid *Glyphea alexandri* Taylor from locality K, three (KG.18.43c, e and g) normal to the carpus or manus of the first pereiopod and three (KG.18.43a, b and d) normal to different parts of the cephalothorax. A seventh thin section (KG.18.43f) was made approximately parallel to the cuticular surface of the carpus or manus. Ten thin sections were made from two black-shelled specimens of *Palaeastacus foersteri* Taylor (KG.50.5 and 6) collected from locality N. Of the five thin sections from specimen KG.50.5, three (a, b and c) were cut normal to the cephalothorax and two (d and e) normal to the abdomen. One section was also prepared from a black-shelled glypheid cheliped (KG.19.34) from locality D and a thin-shelled (?) mecochirid (KG.5.18) from locality G. Three cellulose peels were also prepared from a black-shelled specimen (KG.103.134) of *Palaeastacus* cf. *sussexiensis* from the northern part of Waitabit Cliffs.

For comparison, five thin sections were made from part of the antennal region of *Hoploparia stokesi* (D.3120.5) from the Upper Cretaceous at Dagger Peak, James Ross Island (Bibby, 1966, p. 25). Most of the thin sections had a thickness of 30 μm.



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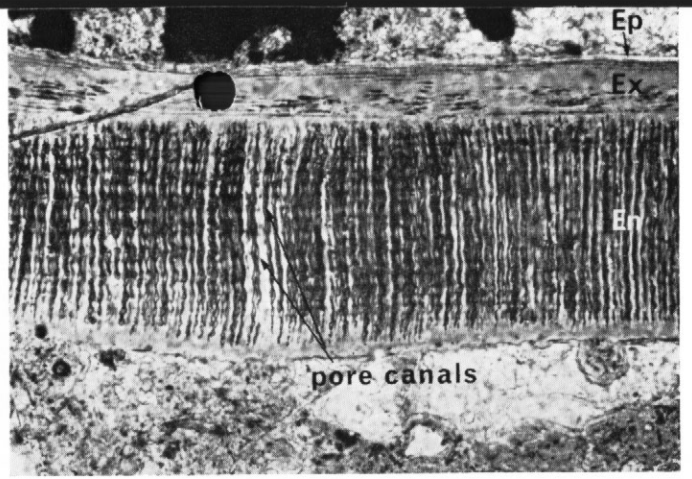

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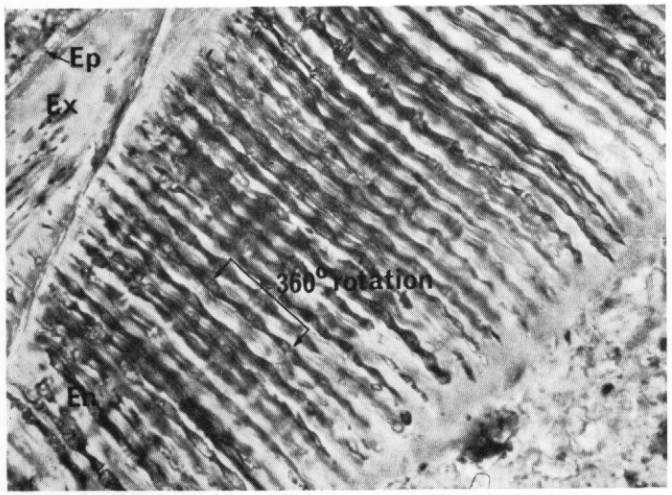

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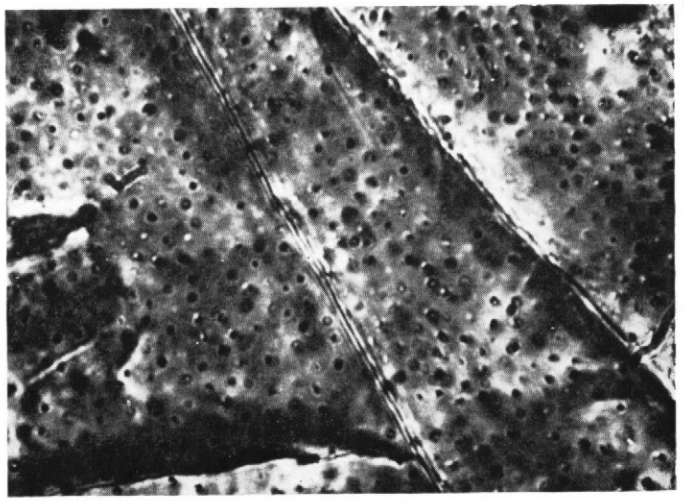

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Fig. 1. a. Normal section through a pereiopod of *Maia squinado* showing the extent of primary calcification (white) compared with the areas of organic material; X-nicols; ×450. Ex, exocuticle; En, endocuticle.

b. Section normal to the cuticle of *Hoploparia stokesi* Weller (D.3120.5d) showing the principal sub-divisions and the slightly sinuous pore canals which terminate abruptly beneath the lower boundary of the exocuticle; ordinary light; ×350. Ep, epicuticle.

c. Pore canals resembling twisted ribbons in phase with the lamellae in *H. stokesi* (D.3120.5d); viewed between crossed polaroids with a first-order red compensating plate. In crossed polaroids, the light lamellae approximately correspond to the broad faces of the ribbon-like pore canals; ×640.

d. Transverse section through the carpus or manus of *Glyphea alexandri* (KG.18.43f) showing the pore canals either as dark pits surrounded by lighter-coloured aureoles or as brightly illuminated spots encircled by darker aureoles; ordinary light; ×1,600.

Micro-structure of the Fossil Decapod Cuticles

Major sub-divisions

The fossil decapod cuticles vary in thickness between individual specimens and between different parts of the same exoskeleton, the cuticle of *G. alexandri* ranging between 0·028 and 0·46 mm. Junctions between major sub-divisions are usually well defined (Fig. 1b).

In *H. stokesi* and several thin sections of *G. alexandri* (e.g. KG.18.43g), the epicuticle is 6·5–7·5 μm. thick and often colourless. Several fine "lamellae" occur but these may be Becke effects as epicuticles of extant Decapoda are unlamellated. The exocuticle is much darker, somewhat granular, 17–31 μm. thick and composed of horizontal lamellae which are particularly conspicuous under crossed nicols. The endocuticle, an even more prominent lamellar layer, is 108–370 μm. thick and characterized by numerous pore canals which seem to terminate abruptly beneath the exocuticle. Beneath the endocuticle is a 12–16 μm. thick layer of closely spaced lamellae. This sub-division, which is often less highly coloured and certainly more difficult to define than the others, probably represents the membranous layer or non-calcified part of the endocuticle.

Coloration and colour banding

All unweathered cuticles are coloured amber, the colour density increasing with the thickness of the thin section. Because the endocuticle of extant decapods is colourless, the coloration of these fossil endocuticles is probably due to collophane which is normally dark brown or yellowish brown in ordinary light. However, some of the pigmentation of the exocuticle, which is slightly darker than the other layers, may indicate the presence of an original tanning such as quinone. In *Gigantoscorpio willsi*, amber-coloured exocuticle is distinguished from colourless endocuticle (Størmer, 1963, p. 17).

Besides this overall coloration, the endocuticles of all the decapods from Alexander Island are characterized by light and dark amber bands, one fragment consisting of 15 such bands. These bands, which usually conform to the shape of the cuticular fragment, represent either successive phases of recrystallization or interference phenomena. Certainly, the masking of lamellae by colour bands in all but the outermost, weathered (and probably bleached) parts of the cuticle of *G. alexandri* suggests that iridescence from the lamellae is apparent only when light is not absorbed by excessively dark pigment.

Pore canals

In thin sections perpendicular or nearly perpendicular to the cuticle, there are numerous spindle-like structures (Fig. 1b and c), possibly filled with air, which are less pronounced in oblique sections. Although no definite canal walls or cytoplasmic membranes occur, it is evident that these structures are pore canals composed of several fibrils or filaments. Fibrils may represent an important component in the three-dimensional framework of cuticle (Neville, 1965*a*, p. 273). Similar pore canals occur in lobsters (where the sheaved fibrils occupy the axis of each canal (Drach, 1953)), *Hydrocyrius* and *Belostoma* (waterbugs), *Tenebrio* (mealworm beetles), *Carausius* (stick insects) (Neville and Luke, 1969*b*, p. 698, fig. 15) and *Sarcophaga* (flesh fly) (Dennell, 1946). In other arthropods (notably the locust), the single filament is axially located and separated from the canal walls or cytoplasmic membranes by an annulus containing cell contents (Neville and Luke, 1969*a*, fig. 4). In rhinoceros beetles, a fasciculated effect similar to Fig. 2 is simulated by the bunching of several pore canals which are moulded into ribbons by the surrounding microfibrils as they pass through layers of preferred microfibrillar orientation (Neville and others, 1969, fig. 2).

In *H. stokesi*, the canals (0·65–2 μm. in diameter) appear either as sinuous tubes with two or three filaments and apparently little or no helical coiling (such as in the post-ecdysial endocuticle of *Limulus polyphemus* (Neville and others, 1969, figs. 10 and 11)) or as broader and more conspicuously coiled twisted ribbons (Figs. 1c and 2) composed of at least six parallel and slightly undulose filaments, some of which appear to be axial in position as in *Locusta migratoria* (Neville and Luke, 1969*b*, fig. 4). Occasionally, these filaments are quite undulose and irregular, particularly between internodes as is emphasized by the crenulated

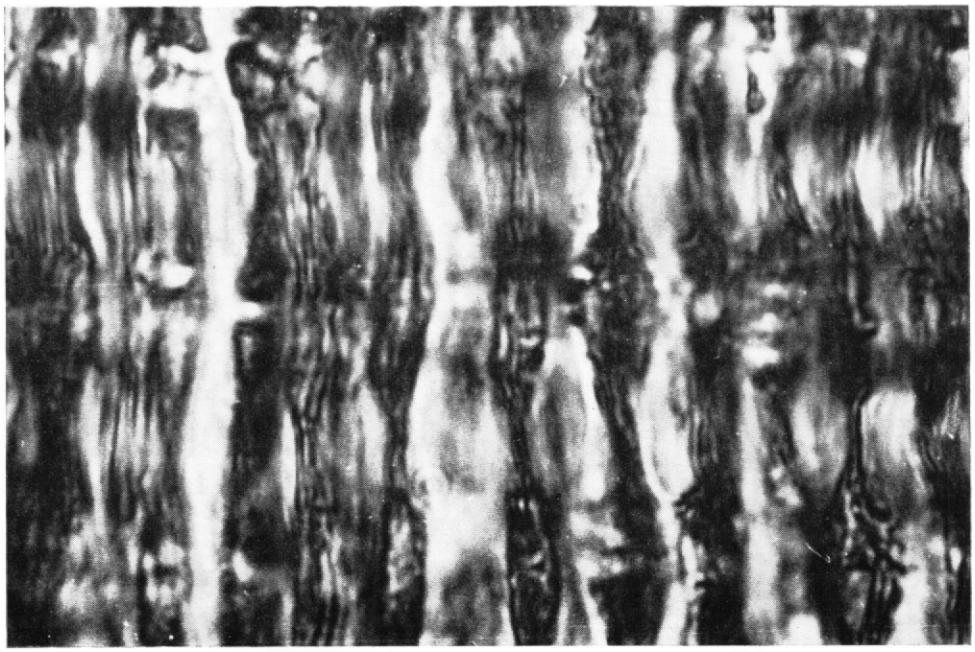


Fig. 2. An enlargement of part of Fig. 1c showing some of the broader and more conspicuously coiled twisted pore canals. These are composed of several undulose filaments. The crenulation of the canals at their "nodes" is also shown; ×3,100.

outer margin of several pore canals (Fig. 2). To date, attempts to examine the arrangement of the filaments using an electron scanning microscope have been unsuccessful.

The pitch of the anti-clockwise sinuosity of both types of canal is constant (11 μm. in 180°) and in phase with other canals in the same thin section. The sinuosity is also in register with the birefringent lamellae although the rotation rate is slow, the ribbons rotating 360° for every third light lamella or for every two and a half lamella couplets so that the broad faces of the twisted pore canals more or less coincide with the lighter lamellae. As the pore canals rotate at the same frequency as the layers of chitin-protein microfibrils (p. 98), they conform to the twisted ribbon model rather than to the helicoidal model as defined by Neville and others (1969, p. 186) and Neville and Luke (1969*a*, p. 356).

The rotation rate in *H. stokesi* is comparable with that of *Hypoderma bovis* (Diptera) (Kennaugh, 1965) but slower than that in *Carcinus maenas* and *Cancer pagurus* where the canals rotate 360° per lamella (Drach, 1939, p. 280). In *Astacus fluviatilis*, the pore canals rotate 180° in 20 μm., i.e. between lamellae (Neville and others, 1969, p. 193). In the fossil decapod *Pemphix sueuri*, the spiral and optically uniaxial pore canals (described as fine fibrils) are said to have a constant pitch and direction of coiling throughout the endocuticle (Scheffen, 1930).

As some lamellae may have been interpolated (p. 96), the canals can only be in phase with them if they represent an earlier structural feature (as in *Sarcophaga* (Dennell, 1946, (p. 356) subsequently modified (probably by crystallization) after the deposition of all the lamellae and the complete expansion of the endocuticle. The secondary distortion of the canals is in agreement with the observations of Dennell (1946) and of Neville and others (1969, p. 193).

Immediately beneath the exocuticle, several canals have a beaded or granular appearance reminiscent of the "vertical rows of granules" described by Travis (1963) as a phase in the calcification of these structures. However, as these canals appear to be uncalcified, they may be more helicoidal beneath this boundary.

In sections parallel to the cuticle surface of *H. stokesi*, the twisted ribbon-like pore canals appear as circular pores of comparable diameters and as more irregular comma-shaped pores.

However, in tangential sections, the pores are not arranged in well-defined parabolae as illustrated by Drach (1939) and illustrated and described by Neville and others (1969, fig. 14), Neville and Luke (1969*a*, figs. 6 and 7, *b*, fig. 4) and Neville and Berg (1971, figs. 1 and 2).

In sections parallel to the cuticle surface of *G. alexandri* (KG.18.43f), the pore canals are circular in cross-section and occur either as dark pits surrounded by lighter-coloured aureoles or as brightly illuminated spots encircled by darker aureoles (Fig. 1d). The pores are regularly arranged only where they occur at the corners of lozenge-shaped fields. Larger, more irregularly shaped pores with dark cores and fairly pronounced margins are also found in another glypheid (KG.19.34) (Fig. 3a).

The light and dark aureoles either represent optical effects or intermediate stages in the calcification of the walls of the pore canals. Although no crystalline calcite has been observed in these fossil decapods, micro-radiographs of crayfish cuticle show pore canals surrounded by lighter aureoles composed of calcite (Travis, 1963, figs. 42 and 43). Compared with the crayfish and cockroach (4,000,000 and 1,200,000/mm.^{2}, respectively), the number of pores in specimen KG.18.43f (235,000) is small.

Lamellae

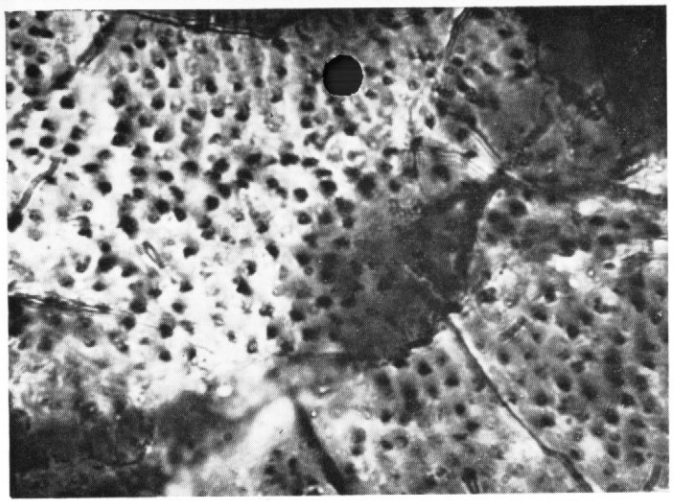
Alternating light- and dark-coloured lamellae are characteristic of cuticle growth in arthropods. Although lamellae are best seen in *Hoploparia stokesi* (D.3120,5a, c and d) (Fig. 3b, c and d), they also occur in the weathered and almost colourless parts of the cuticle of *Glyphea alexandri* (KG.18.43a, b and e) and in at least one slide (KG.50.6a) of *Palaeastacus foersteri*. In all but two of the thin sections (D.3120.5a and KG.50.6a), the lamellae of the endocuticle are visible only under crossed nicols, whereas in the exocuticle, finer lamellae are visible in both plane and crossed polarized light. A non-lamellated band approximately 5 μm. wide occurs between the exocuticle and endocuticle in specimen D.3120.5d (Fig. 3c).

The lamellae of the endocuticle are approximately 5 μm. thick and follow the general configuration of the cuticle, although some are slightly undulose. Near the junction with the exocuticle, a few light and dark lamellae wedge out against a non-lamellated band (Fig. 3b and c). The occurrence of finer and less regular lamellae at the inner margin of the endocuticle suggests that the membranous or non-calcified layer was either being deposited (i.e. post-moult stage C_3) or resorbed by moulting fluid prior to ecdysis and the deposition of new epicuticle (stage D_2 of Drach's pre-moult cycle) (Fig. 3b).

The 5 μm. thick non-lamellated band in *H. stokesi* (Fig. 3c) between the exocuticle and endocuticle is similar to a band of comparable thickness in other arthropods. In the locust, it represents a pause in development (involving six "postimarginal" lamellae) and a change in chitin orientation prior to the emergence of the adult (Neville, 1967*a*, fig. 28, p. 254). A metabolic timing device at emergence is thought to be involved. In *Carcinus maenas*, a comparable zone stains intensely blue with Mallory's triple stain (Krishnan, 1951, p. 336), whereas in the crayfish a "heavy band of calcification" develops at the same interface on the second day following moult (stage B) (Travis, 1965, pl. XVI, fig. 44).

The origin of the lamellae in fossil and extant arthropods has invoked several interpretations. In extant decapods, they have been thought to represent epidermal secretions (Drach, 1939, p. 276), whereas in extant insects (Richards and Anderson, 1942) and in the fossil decapod *P. sueuri* (Scheffen, 1930) they have been interpreted as recrystallization phenomena. In *P. sueuri*, the lamellae have no preferred direction and actually transgress one another (Scheffen, 1930, p. 15).

However, in the Antarctic fossil decapods, the birefringent lamellae are assumed to be primary in origin (even though decalcification may have taken place) because the cuticles exhibit many of the vertical and horizontal components of living decapods. Because the rotation rate of the pore canals indicates that brightly birefringent lamellae repeat every 180° (and that troughs of minimum birefringence occur at the intermediate angles), the molecular structure of these decapods conforms to the so-called Bouligand model (Bouligand, 1965). As such, the lamellae represent birefringent phenomena, each lamella being composed of numerous layers of sub-microscopic and horizontally arranged chitin-protein microfibrils which progressively change in orientation helically through 360°. Thus, in any one section cut normal



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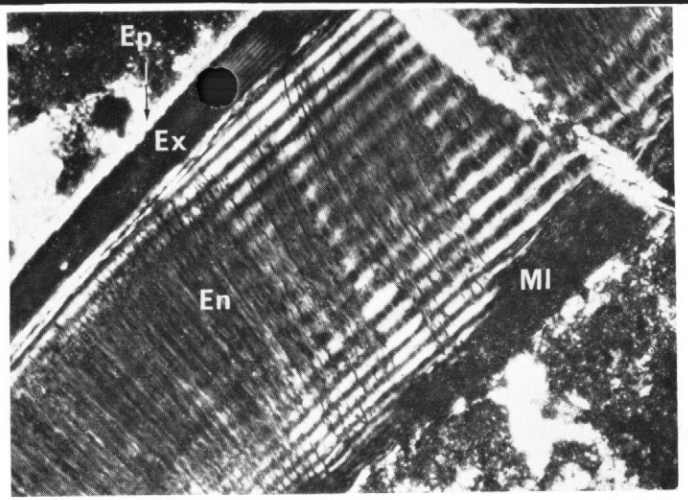

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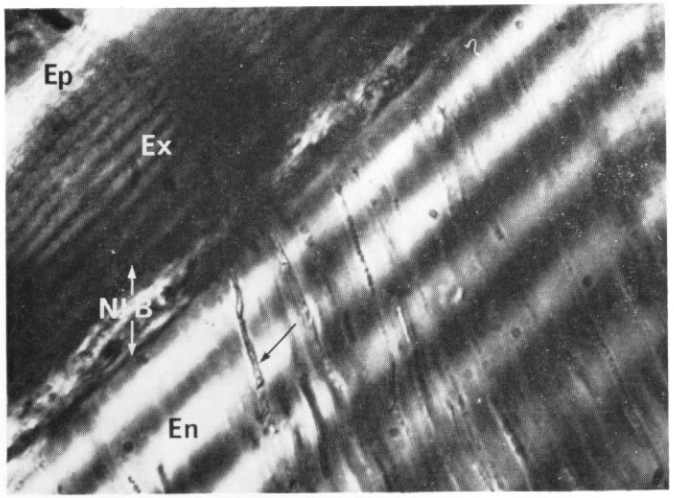

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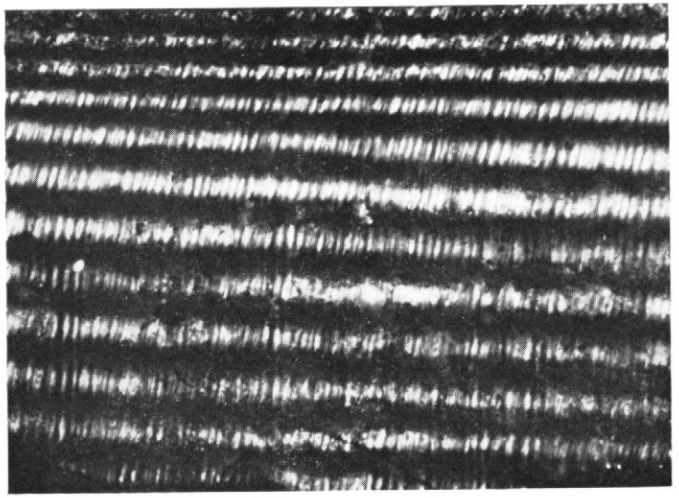

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Fig. 3. a. Transverse section through a glypheid cheliped (KG.19.34) showing more irregularly shaped pores; ordinary light; ×1,400.
b. Section normal to the cuticle of *H. stokesi* (D.3120.5d) showing major structural sub-divisions (including the (?) membranous layer (M1)), pore canals, and lamellae alternately at maximum and minimum birefringence; X-nicols; ×340.
c. An enlargement of part of Fig. 3b showing the lamellate structure of the exocuticle, the non-lamellated band (NlB) and the beaded appearance of the coiled pore canals (at arrow); X-nicols; ×1,800.
d. Part of the endocuticle of *H. stokesi* (D.3120.5c) with lamellae at maximum and minimum birefringence alternately illuminating and masking the pore canals; X-nicols; ×600.

to the cuticular surface, the microfibrils will be alternately at maximum and minimum birefringence for each 90° of the helicoid. To date, the Bouligand model has been demonstrated in several different extant arthropods (Neville and others, 1969) and in the Jurassic lobster *Eryma stricklandi* from the Oxford Clay (Neville and Berg, 1971, p. 203). In other arthropods, notably the locust, the Bouligand model alternates with a diurnal system of lamellae couplets, the timing of the latter being controlled by a circadian clock. Where both types co-exist, one or other may predominate (Neville and Luke, 1969*a*, p. 363).

In the shore crab, *Gaetice depressus*, the number of lamellae appears to be a function of age as expressed by carapace length (Yano and Kobayashi, 1969; Yano, 1970). Moreover, it can be inferred from the work of Yano and Kobayashi that many lamellae in *G. depressus* are developed by intussusception as in *Sarcophaga* (Dennell, 1946, p. 364) and in the crayfish post-moult epicuticle and exocuticle (Travis, 1965, p. 201). Intussusception seems to be demonstrated by the variation in the number of lamellae of shore crabs at the inter-moult stage C_4, i.e. those with a membranous layer. As tissue growth is effectively completed at this stage and the upper and outer interfaces of the cuticle have been determined, the additional lamellae which make the difference between large shore crabs (with many lamellae) and small shore crabs (with fewer lamellae) must have been intercalated. The rate of intussusception and the vertical expansion of the cuticle appear to correspond approximately with the overall growth of the cuticle (as in *Sarcophaga* (Dennell, 1946, p. 363)) but all these processes (and hence the number of lamellae) may depend ultimately on the rotation rate of the helicoidal system (Neville and Luke, 1969*a*, p. 264).

Although the numbers of lamellae in the fossil decapods may not depend on a circadian rhythm, there are striking similarities between the lamellate structure of the fossil decapods and the diurnal lamellar structure of the locust, which, if not causal, demonstrate a number of remarkable coincidences. However, it must be emphasized that no daily growth layers in *fossil* arthropods have been proved (Neville, 1967*b*, p. 434) and no circadian mechanism seems to be involved in the cuticle structure of arthropods other than insects (Neville and Luke, 1969*a*, p. 363).

The desert locust and the fossil decapods from Antarctica are approximately similar in size. Furthermore, the locusts were reared by Neville in temperatures (25–36° C) not greatly different from the sea temperatures calculated for Cretaceous times in the San Martín area of Patagonia, the nearest locality to the Antarctic Peninsula which has been calibrated in this way (Bowen, 1963).

Although the thickness of the locust lamellae couplets varies with their location in the exoskeleton, it is perhaps significant that the combined thickness of one couplet (10 μm.) is the same in both groups. However, perhaps the most remarkable similarity is shown if it is assumed that each lamellae couplet in the fossil decapods is homologous with the diurnal couplet in the locust. Thus, in *H. stokesi* (D.3120.5d), the maximum number of couplets in the exocuticle (nine) and endocuticle (19) indicate a "growth period" for the whole procuticle of approximately 1 month.

Under favourable conditions, the desert locust deposits endocuticle day and night for approximately the same period (19 days) after the final moult (Neville, 1965*b*, p. 315) and the spiny lobster *Panulirus argus* secretes its endocuticle in approximately 20 days, although the amount of cuticle (38 μm.) estimated by Travis (1957, p. 458) to have been deposited daily is four times that in the locust and the fossil decapods. However, the endocuticle of the spiny lobster examined by Travis is approximately four times as thick as that of *H. stokesi* and the locust.

Comparisons with living and other fossil decapod cuticles

Because the fossil decapod cuticles discussed here have no tegumental ducts, the epicuticle and procuticle were presumably deposited epidermally as in *Sarcophaga falculata* (Dennell, 1947). Contrary to Yonge (1932), this suggests that tegumental ducts are not responsible for the deposition of either of these layers (Drach, 1939, p. 288). Moreover, their absence in other fossil decapod cuticles suggests that ducts may represent a comparatively recent feature perhaps associated with cuticle preservation.

The abrupt termination of the pore canals beneath the exocuticle in *H. stokesi* (and their rare occurrence in the exocuticle of the Alexander Island specimens) have analogies amongst the insects, notably certain beetles where pore canals are alleged to be confined to the endocuticle (Eder, 1940). It is also possible that any canals that may have extended into the exocuticle have either been withdrawn into the endocuticle or obscured by recrystallization.

The twisted ribbon appearance of the canals in the fossil decapods and their relationship to the lamellae appears to be consistent with the twisted ribbon model of Neville and others (1969), and is additional evidence supporting the model of rotating chitin-protein layers of microfibrils for the molecular architecture of arthropod cuticle (Bouligand, 1965).

The absence of polygons in the Antarctic material probably implies that the horizontal sections traverse the endocuticle where prisms have not been observed even in Brachyura (Dennell, 1947, p. 496). Alternatively, the polygons may have been fused as in *Homarus* (Yonge, 1932). In *P. sueuri*, polygons claimed to represent the first proof of the outline of cells in fossil crab material are not entirely convincing (Scheffen, 1930, pl. IV, fig. 2).

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