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The Formation of the Epicuticle and Associated Structures in *Oniscus asellus* (Crustacea, Isopoda)

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Summary. The integument of the woodlouse, *Oniscus asellus*, consists of a two-layered epicuticle, a largely lamellate procuticle – itself divided into two regions (pre- and postecdysial cuticles), and the epidermis. At the initiation of new cuticle production the epidermal cells become vacuolated and retract away from the cuticle. Apolysis occurs immediately after the cessation of postecdysial cuticle production. The formation of the epicuticle is unique among the arthropods since material aggregates along the distal epidermal membrane. By indenting, doubling back on itself, and incorporating septa, the epicuticle forms surface structures such as plaques and tricorns.

The innervation, and so the receptive function of the tricorns is confirmed, but since there is no connection between the old and new receptors during premoult, sensory information from these exoreceptors must be severely curtailed. This may explain the biphasic moult in all isopods since it ensures that only half the body experiences this sensory deprivation at any one time. In terrestrial species there is the additional advantage of restricting the area of permeable new cuticle. The frequency of moulting may be due to the need to renew disrupted receptor surfaces.

Tricorns do not appear to be the mechanoreceptors involved in the marked thigmotactic response of woodlice since they do not have the typical internal structure of such receptors; rather, the dendrite – which extends into the lumen of the tricorn – is protected from deformation by the previously unreported combination of a dendritic sheath and a cuticular tube. The modality of tricorns is possibly one of hygro-perception. One of the behavioural responses of woodlice to desiccation is aggregation. The numerical distribution of tricorns over the body surface is admirably suited to assist in the formation and maintenance of such aggregates during desiccation and to their observed dispersal when the relative humidity rises.

A. Introduction

The arthropod cuticle provides both the barrier and the means of communication between the animal and its environment. Studies on its structure in arthropods

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have been concentrated in two main fields, namely the adaptations it possesses for controlling the passage of water and metabolites, and the adaptations of the general structure to the specific requirements of sensory apparati. Although the fine structure of the cuticle of most arthropod groups has been studied in detail (see Neville, 1975 for review) relatively few members of the Crustacea have been subjected to intensive study. This is particularly so with regard to the terrestrial Isopoda – the Oniscoidea, where only the cuticle lining the hindgut (Holdich and Mayes, 1975) and the surface of the exoskeletal epicuticle (Holdich and Lincoln, 1974; Schmalfuss, 1978) have been studied in any detail. This is surprising because the Oniscoidea represent an interesting line of evolution, having made the transition from sea to land via the littoral zone (Edney, 1968). They also possess many of the features shown by present day marine isopods themselves being very successful on land (Sutton, 1972) even though they apparently lack a cuticular waterproofing mechanism, as found in insects. A comparison of the structure of woodlouse cuticle with that of insects would therefore prove very instructive, as would a comparative study of woodlice from different positions on the "terrestriality gradient" (Edney, 1968). Isopods represent a still further interest in that they are unique in moulting in two halves (George and Sheard, 1954), thus one animal can supply both premoult and post-moult cuticle.

One of the most important layers of the cuticle of arthropods is the epicuticle, since it is known to be responsible for the majority of water conservation, in insects at least, and is believed to restrict water loss in Crustacea (Cloudsley-Thompson, 1977). In isopods the epicuticle also forms a number of surface structures such as tricorns and plaques (Holdich and Lincoln, 1974) the origin of which is unclear.

The present work is part of a complete description of the cuticular changes associated with the moult cycle of *Oniscus asellus* L., and describes a unique method of epicuticle formation, the origin of the plaques and tricorns, and discusses possible functions of the innervated tricorns.

B. Materials and Methods

Non-breeding adult male and female *Oniscus asellus* were maintained individually in numbered petri-dishes lined with damp filter paper, and fed regularly with fresh carrot. Each animal was marked on the anterior and posterior dorsal surface with a small spot of enamel paint. Daily observations were made for the onset of the premoult condition (i.e. the appearance of white sternal plates) and the completion of each phase of the biphasic moult (i.e. the disappearance of the paint spots). Samples of the anterior and posterior pereopods were taken at regular intervals from these animals (the protopodite was used in each case), fixed for 2 h in ice-cold 3.5% glutaraldehyde in 0.1 M sodium cacodylate buffer with 0.05% $CaCl_2$ (Clifford and Witkus, 1971), followed by a buffer wash for 1 h and post-fixing for 1 h in ice-cold 1% osmium tetroxide in 0.1 M sodium cacodylate buffer. After a buffer rinse, the sample was block-stained for 1.5 h in 0.5% aqueous uranyl acetate at room temperature, rinsed and slightly decalcified in Cal-Ex (Lane and Nott, 1975), washed, and then dehydrated through a graded series of acetones and embedded in Polaron araldite. Thin sections were cut on a Cambridge ultramicrotome, picked up on uncoated 200 hexagonal Cu/Pd grids, stained with lead citrate and alcoholic uranyl acetate and viewed with a Corinth electron microscope.

Pereopodal tissue was chosen for the present study because, unlike cuticle from the dorsal tergites, the epidermis remains attached to the cuticle during processing. In addition, repeated, similar, small samples of tissue could be obtained from the anterior and posterior parts of the same animal without fatal injury and without inducing precocious moulting (Skinner and Graham, 1972). By sampling once a week, a reasonable span of the moult cycle in one animal could be obtained. By comparing the time of sampling with that recorded for the animal's ecdysis, the moult stage (as revealed by examination of the sections) could be expressed as a number of days before or after ecdysis, and the percentage of the cycle that had elapsed, calculated.

C. Results

It is not possible to find the static situation typical of true intermoult since apolysis (the splitting of the epidermis from the overlying postecdysial cuticle) occurs immediately after the cessation of postecdysial cuticle production (Price and Holdich, in preparation). If apolysis is taken as the beginning of the moult cycle (Jenkin and Hinton, 1966) epicuticle formation in *O. asellus* occurs after 22% of the cycle has elapsed.

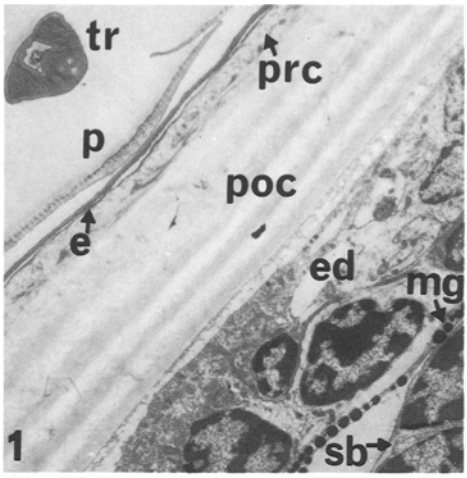
The general structure of the cuticle in a pereopod of *O. asellus* is shown in Fig. 1. The majority of the cuticle is formed by the lamellate postecydysial cuticle (i.e. that region produced after ecdysis) which corresponds roughly with the endocuticle referred to by other workers (e.g. Green and Neff, 1972). The remaining cuticular layers are produced prior to ecdysis and are the pre-ecdysial cuticle and the epicuticle. The epicuticle is itself composed of two main regions, the outer epicuticle (oe) and the inner epicuticle (ie) which are similar in form to those found in the woodlouse hindgut (Holdich and Mayes, 1975).

External to the epicuticle, but nevertheless composed of a type of epicuticle, are surface plaques, and sensory structures such as tricorns (Figs. 1 and 2). In surface view (Fig. 2) the perimeter of each pereopodal plaque appears partially fused with the general epicuticular surface. The connection is seen in Fig. 12. Some tricorns are bordered anteriorly and posteriorly by plaques, the posterior plaque overlapping the proximal part of the tricorn (Fig. 5).

Internal to the postecdysial cuticle lies a layer of epidermal cells proximally bounded by a row of melanin granules (Fig. 1).

Epicuticular sensory structures and plaques are formed beneath the old cuticle prior to the formation of the rest of the new cuticle (Figs. 4 and 5) and before ecdysis. The first stages of new cuticle production are indicated by increased vacuolation of the epidermal cells (cf. Figs. 1 and 4).

During the formation of the new cuticle, the apices of the epidermal cells initially become more apparent as material is laid down, until a distinct layer (which will become outer epicuticle) some 0.03 μm wide is formed (Figs. 4 and 6). At various points this layer indents and extends back along itself so that the two inner faces are juxtaposed (Fig. 6). As this occurs, bars or septa of material which have formed in the path of the advancing layers, become incorporated (Fig. 6). As alternate points of indentation advance in opposite directions, they meet and then fuse to lift a double layer of outer epicuticle and associated septa, clear of a single outer epicuticle layer (Fig. 5). In this manner, plaques are formed; the single outer epicuticle layer now forms either more plaques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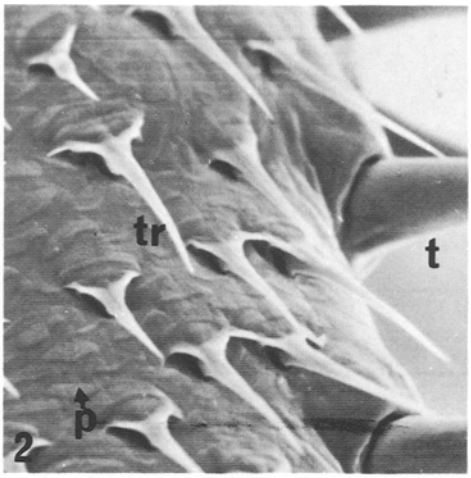
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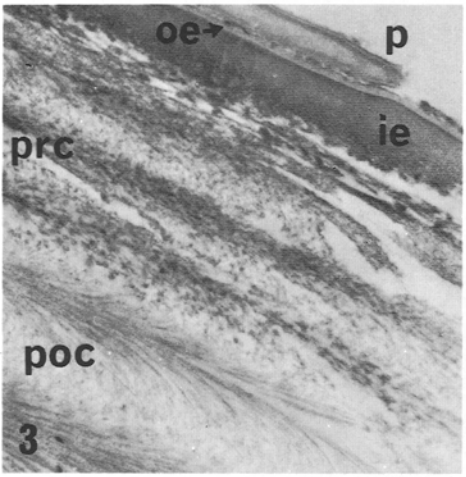
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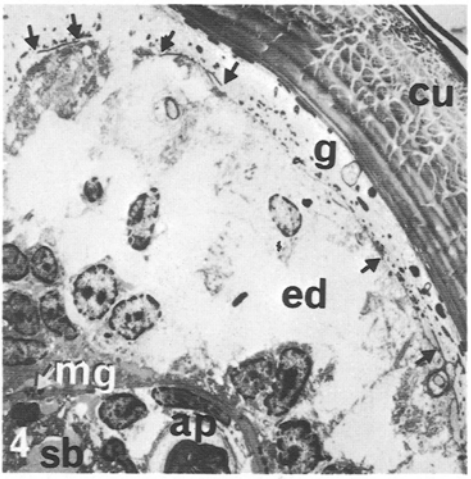
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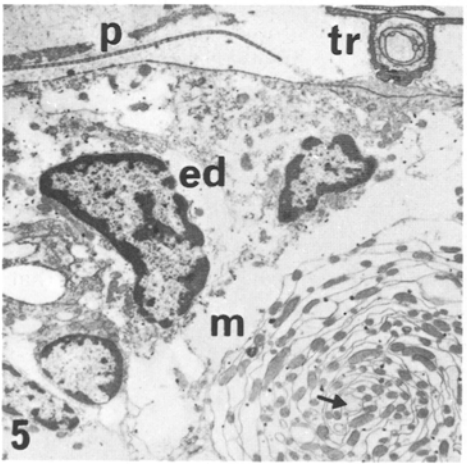
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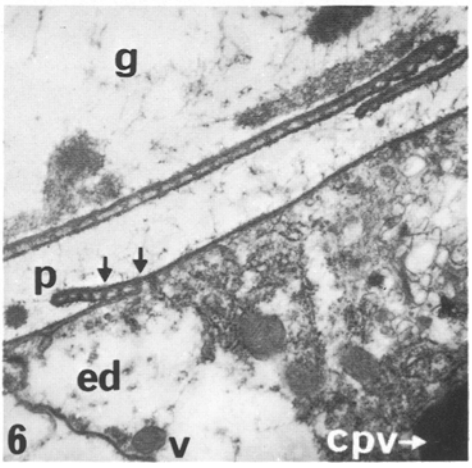
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or becomes the most external layer of the main cuticle (Fig. 1). Large cuticle precursor vesicles associated with main cuticle production and small structured vesicles of unknown function, are present at this time (Fig. 6). Prior to ecdysis, the staining patterns of the new epicuticle (Fig. 10) are the reverse of the old epicuticle thus the outer epicuticle appears more electron dense than the inner epicuticle.

In section, the outer layers of the newly developing tricorn (Fig. 7) appear similar to new plaques (Fig. 6) suggesting that they are formed by a modification of the latter. The separation of the outer epicuticular layers of the new tricorn increases during the rest of the premoult period and the structure becomes innervated (Fig. 8). This nerve, however, does not extend to the tip of the tricorn (Fig. 9). Membrane-bound mitochondria (Fig. 5) are usually found below a developing tricorn and have associated with them a structure which may be a nerve (Fig. 5). About three days prior to ecdysis, the new tricorns are complete save for the cuticular and dendritic sheaths (Fig. 8) which surround the nerve in the fully developed tricorn (Fig. 11); these are, however, present in the base (Fig. 10) and must, therefore, extend into the body of the tricorn in the intervening period prior to ecdysis. Small cuticle precursor vesicles are found which appear intimately associated with pre-ecdysial cuticle production (Fig. 10). The probable relations of the various cuticular layers of a tricorn with those of the main cuticle are illustrated in Fig. 13, seen in longitudinal section and constructed from numerous transverse sections.

For comparative purposes the structure of a pereopodal trichium, with its associated cuticular layers, is shown in Fig. 12. It is clear from this that the whole cuticle is involved, unlike the situation found in tricorns.

Fig. 1. Transmission electron micrograph (*TEM*) of transverse section of posterior pereopod one day after ecdysis to show the basic cuticle structure of *Oniscus asellus;* the lamellate postecdysial cuticle is still being produced. Epicuticle (*e*); epidermal cells (*ed*); epicuticular plaque (*p*); non-lamellate pre-ecdysial cuticle (*prc*); incomplete lamellate postecdysial cuticle (*poc*); melanin strands along proximal epidermal border (*mg*); subepidermal cells (*sb*); epicuticular tricorn (*tr*). ×2,500

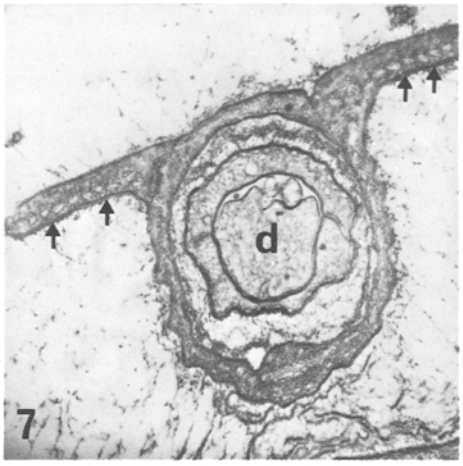
Fig. 2. Stereoscanning electron micrograph of anterior pereopod showing relative size and distribution of tricorns (*tr*), trichia (*t*) and plaques (*p*). ×550

Fig. 3. TEM of pereopod cuticle showing association of plaque (*p*) with bi-layered epicuticle. Note the similarity between the structure of the plaque and main epicuticle, both being composed of outer (*oe*) and inner (*ie*) epicuticle. Pre-ecdysial cuticle (*prc*); postecdysial cuticle (*poc*). ×40,000

Fig. 4. TEM of pereopod during the initial stages of new cuticle production – the highly vacuolated epidermal cells (*ed*) are separated from the old cuticle (*cu*) by the width of the ecdysing gap (*g*). On their distal margins, plaques (*arrows*) are being formed. Melanin granules (*mg*) border the proximal epidermal margin. Apodeme (*ap*); subepidermal cells (*sb*). Note pore canals in old cuticle. ×1,000

Fig. 5. TEM of early stage of epicuticle formation, showing the frequently observed association of whorls of membrane-bound mitochondria (*m*) with the newly formed tricorn (*tr*). Invariably, amongst the membrane-bound mitochondria is a structure (*arrow*) which may be a dendrite. Epidermis (*ed*); newly formed plaque (*p*). ×2,500

Fig. 6. TEM of early stage of plaque (*p*) formation showing the incorporation of septa (*arrows*). Cuticular precursor vesicle (*cpv*); epidermis (*ed*); ecdysing gap (*g*); structured vesicle (*v*). ×15,000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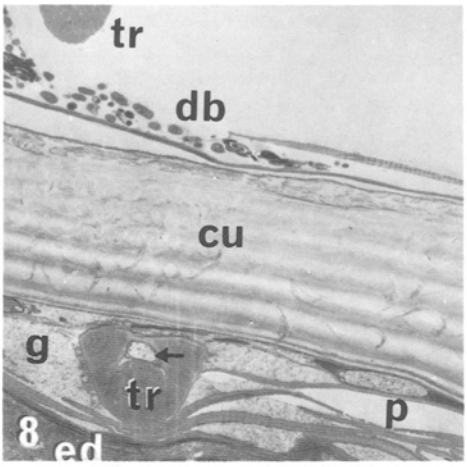
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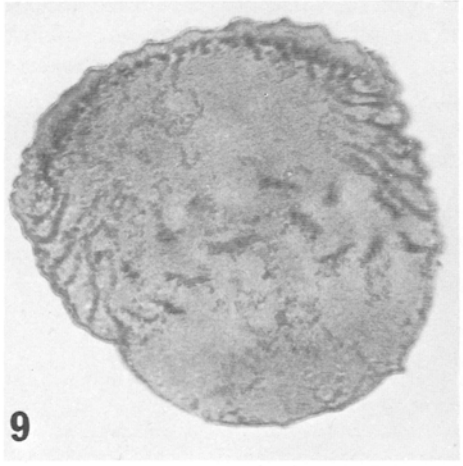
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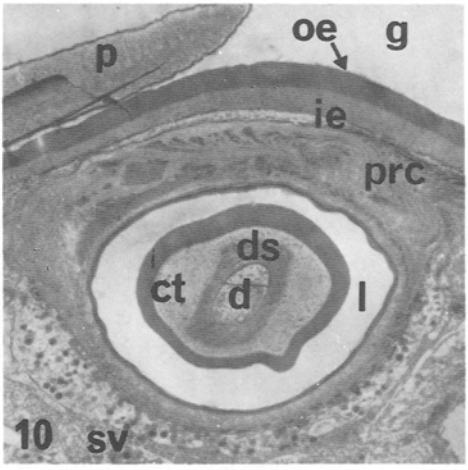
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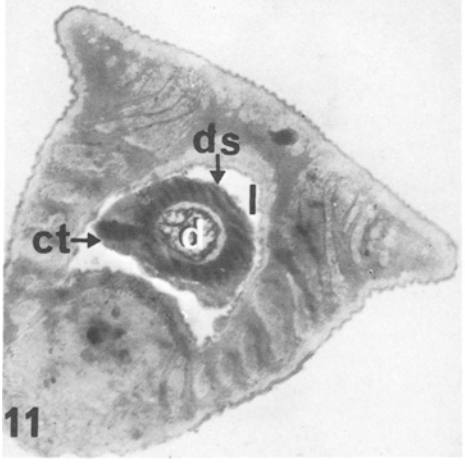
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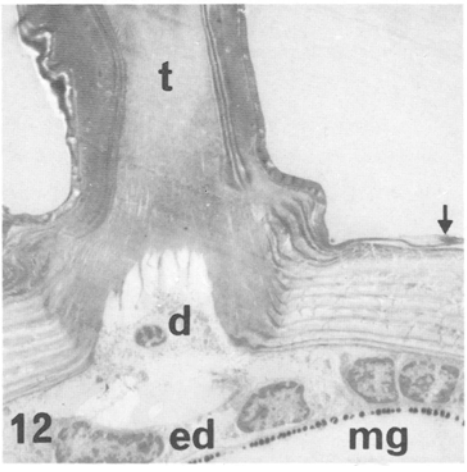
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D. Discussion

The production of new cuticle beneath the old prior to ecdysis, increases the separation of the animal's interior milieu from its external environment by the thickness of the new cuticle and the width of the ecdysing gap. This obviously affects all communication between the animal and the outside world; for example the diffusion path for gases is increased making respiration less efficient (Edney, 1968), which may be one reason why new cuticle remains relatively permeable prior to ecdysis. In addition it is essential that it remains pliable enough to allow for expansion at ecdysis. Once expansion is complete chemical changes occur in the outer and inner epicuticles which reduce permeability and render these layers rigid. These changes are revealed by the alterations in the staining patterns as seen in the present results.

The actual production of epicuticle described here is simple but unique – differing from that of decapod crustaceans (Kawaguti and Ikemoto, 1962; Kummel et al., 1970; Green and Neff, 1972) and insects (Locke, 1969) where the epidermis forms distal microvilli on the tips of which material aggregates, prior to fusing laterally with those of neighbouring microvilli to form a complete layer.

The main bulk of the integument is composed of lamellate (postecdysial) cuticle which is laid down after ecdysis; the lamellate layers produced before ecdysis (pre-ecdysial cuticle) become distorted by the strains imposed on them at this time (Price, 1978). Since apolysis occurs immediately after the cessation of postecdysial cuticle production, there can be no intussusceptive growth in

Fig. 7. TEM of early stage of tricorn formation showing distinct septa (*arrows*) in lateral extensions. Within the lumen is the dendrite (*d*); what appears to be a sheathing cell is wrapped around the dendrite. × 15,000

Fig. 8. TEM of old and new cuticle shortly before ecdysis showing the reduction in the ecdysing gap (*g*) and the crowding of the new surface plaques (*p*). Note the presence of debris (*db*) on the surface of the old cuticle (*cu*) and the juxtaposition of the old and new tricorns (*tr*); the new tricorn's dendrite (*arrow*) lacks a dendritic or cuticular sheath. Epidermis (*ed*). × 2,500

Fig. 9. TEM of tricorn tip at a point where the lateral extensions have been completely reduced and the lumen occluded. × 25,000

Fig. 10. TEM of base of new tricorn prior to ecdysis showing that at this point the dendrite (*d*) lying in the lumen of the tricorn (*l*) is sheathed by both the dendritic sheath (*ds*) and the cuticular tube (*ct*). The continuation of new cuticle production is indicated by the presence of small vesicles (*sv*) in the epidermis beneath the pre-ecdysial cuticle (*prc*). Ecdysing gap (*g*); inner epicuticle (*ie*); outer epicuticle (*oe*); surface plaque (*p*). (Note that at this stage the *oe* is more electron dense than the *ie*, cf. Fig. 3). × 6,000

Fig. 11. TEM of fully formed tricorn at a point where the lateral extensions are beginning to be reduced in size. Cuticular tube (*ct*); dendrite (*d*); dendritic sheath (*ds*); lumen (*l*). × 11,000

Fig. 12. TEM of trichia to show that these mechanoreceptive structures involve the whole cuticle. The junction of a plaque with the main epicuticle is indicated (*arrow*). Dendrite (*d*) restricted to base of trichia (*t*); epidermis (*ed*); melanin granules (*mg*). × 1,000

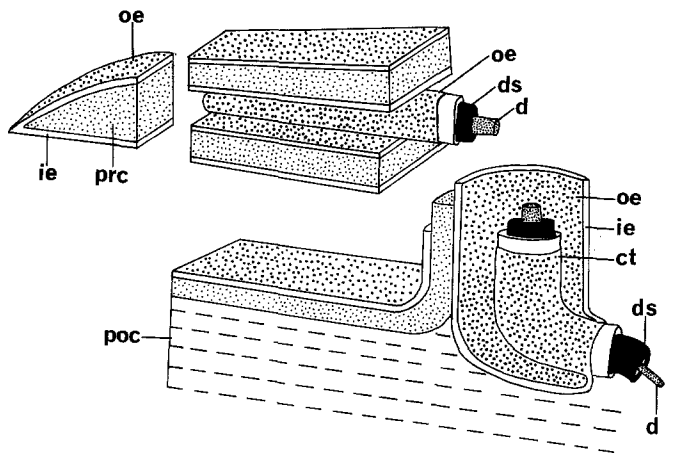

Fig. 13. Diagram of longitudinal section through a tricorn to show the relative positions of the various cuticular layers (not to scale). Cuticular tube (*ct*); dendrite (*d*); dendritic sheath (*ds*); inner epicuticle (*ie*); outer epicuticle (*oe*); postecdysial cuticle (*poc*); pre-ecdysial cuticle (*prc*)

Oniscus asellus (i.e. an increase in cuticle thickness without an increase in the number of lamellae) as has been postulated for decapods (Green and Neff, 1972).

The large cuticle precursor vesicles found in the present study are similar to those reported in other Crustacea (Green and Neff, 1972; Halcrow, 1976) suggesting that they may be a common crustacean feature; but the small vesicles, the presence of which is related to pre-ecdysial cuticle production, and the structured vesicles, whose function is unknown, have not apparently been reported elsewhere.

The vulnerability of arthropods during ecdysis to desiccation and mechanical damage has often been remarked on. However, it has been observed that isopods do not always grow at ecdysis (Price, 1978), indeed there have been reports of size reduction (Tait, 1917). Under these circumstances, the only likely explanation for their risking the dangers inherent in moulting is that it provides the means whereby receptors or receptor surfaces can be renewed. This is borne out by the damaged appearance of many receptors in intermoult woodlice at least compared to ones that have recently moulted (Holdich and Lincoln, 1974; Price, 1978). There is an additional hazard inherent in the arthropod method of growth that has received less attention, namely the effect this process has on the efficiency of exoreceptors (Moran et al., 1976). Exoreceptors are physically and numerically reduced in terrestrial arthropods because of their susceptibility to damage and/or desiccation (Laverack, 1976); nevertheless, if those that still exist are to remain functional during new cuticle production they must maintain some connection with the outside world.

Tricorns are amongst the most widely distributed surface structures of terrestrial isopods (Holdich and Lincoln, 1974; Price, 1978; Schmalfuss, 1978), occuring on the dorsal surface and ventral epimera, as well as on the pereopods (Fig. 2). As the present results show, tricorns are apparently formed by a modification of the basic form of plaque, these structures also being widely distributed over the body surface of woodlice. A variety of morphologically based nomenclatures exist for arthropod surface structures, including one derived especially

for some Crustacea (Cals, 1972). However, many morphologically similar structures serve widely differing functions (Steinbrecht and Muller, 1976). In the present study, the terms trichia (meaning structures involving the whole cuticle) and microtrichia (meaning structures involving only the epicuticle) have been adopted (Richards, 1951). Both tricorns and plaques are, therefore, microtrichia and have been grouped into several types depending on their position (Holdich and Lincoln, 1974; Price, 1978); mechanoreceptors of the sort seen in Figs. 2 and 12 are trichia.

The mechanoreceptive function of tricorns has been previously postulated (Holdich and Lincoln, 1974) since their distribution corresponds approximately with that of the innervated structures described by Jans and Ross (1963) using light microscopy. The present study has demonstrated that tricorns are indeed innervated and so do presumably have a receptive function.

Since the newly developing tricorns in *Oniscus asellus* lack any apparent connection physical, nervous or otherwise with the old ones they differ from the mechanoreceptors of insects such as *Periplaneta* (Moran et al., 1976). This suggests that the information from the tricorns must be severely, if not completely, curtailed at late premoult when the old receptors are totally isolated. If this functional loss was typical of all isopod receptors prior to ecdysis it might well explain the phenomenon of biphasic moulting in both aquatic and terrestrial isopods, since the sensory information from only half the body is lost at any one time. In terrestrial isopods the biphasic moult has the additional advantage of restricting the area of new thin cuticle and consequently also water loss.

Study of the available scanning electron micrographs reveals that tricorns, or very similar structures are present in a wide variety of terrestrial isopods (Holdich and Lincoln, 1974; Schmalfuss, 1975, 1977, 1978; Price, 1978) but are absent from aquatic species (Jones and Fordy, 1971; Jones, 1974; Holdich, 1976; Schmalfuss, 1978).

Tricorns are generally placed so as to receive minimum mechanical stimulation. They lie close to the surface of the woodlouse, the majority on the general body surface pointing backwards; they even occur between the bulging ommatidia of the eye (Holdich and Lincoln, 1974; Price, 1978). They lack an articulated base and have a dendrite which extends within the structure and is protected from mechanical distortion by the unique combination of an extracellular supporting tube and a cuticular tube. The former is quite commonly seen in insect and crustacean receptors and is sometimes called the cuticular sheath (Slifer, 1970; Greenwood and Holdich, 1979) despite the lack of evidence of any cuticular component (Mill and Lowe, 1971). A cuticular tube has been described from *Limulus* chemoreceptors (Hayes, 1971) and, like the supporting tube, is believed to protect the dendrite from distortion.

In view of these facts it is concluded that, despite their shape and wide distribution, tricorns are not the mechanoreceptors responsible for the marked thigmotactic response of isopods (Friedlander, 1964); circumstantial confirmation of this comes from the presence of a thigmotactic response in aquatic isopods (Edney, 1968) which apparently lack tricorns. This reponse, in terrestrial isopods at least, could be mediated by the peg organs and dorsal sensillae

(Holdich and Lincoln, 1974; Price, 1978) which are admirably placed to fulfil this function (Friedlander, 1964). Tricorns are probably involved in another, frequently observed response of terrestrial isopods – aggregation (Allee, 1926). In dry conditions, lateral and vertical grouping of woodlice occurs in order to reduce transpiration (Warburg, 1968); aggregation does not occur in damp conditions, and increasing humidity disperses preformed aggregates (Allee, 1926). If the tricorns modality was hygro-perception, maximal stimulation would be achieved in dry conditions when under an aggregate of transpiring woodlice (between which there is a chemical attraction (Kuenen and Nooteboom, 1963)) or, failing this, under a stone or log (maintenance of this position being reinforced by negative phototaxis). For those woodlice unable to penetrate the base of an aggregate, the next best thing, in terms of stimulation of the hygroperceptive tricorns, would be to crawl on top of the transpiring woodlice, thus stimulating the few ventrally placed tricorns. Woodlice at the base of the aggregate would be maximally stimulated and would, therefore, remain still, thus maintaining the aggregate. An increase in the ambient humidity would mean that the maximum humidity detectable by the uppermost animals (which have the more numerous dorsal tricorns exposed) would no longer be below them, leading to the eventual dispersal of the aggregate as observed by Allee (1926). The implication of tricorns in humidity perception is based on the structure and positioning of the tricorns, and the known behaviour of woodlice. However, without electrophysiological evidence it is impossible to definitely establish this beyond doubt. Indeed the question of whether or not woodlice need external humidity receptors has been open to debate for many years (Cloudsley-Thompson, 1964; Ross and Jans, 1964; Lindqvist, 1968).

Effective sensitivity to humidity can be achieved by measuring a variety of allied parameters as well as by direct measurement of ambient relative humidity or saturation deficit (Warburg, 1968) e.g. detection of the rate of evaporation or the mechanical, thermal or osmotic changes caused by evaporation (Dethier and Schoonhoven, 1968). A single sensillum possessing such multipurpose functions has been demonstrated in insects (Waldow, 1970; Yokohari and Tateda, 1976) and in some cases the dendrites were found to be protected by two walls (Altner et al., 1977) as are those of tricorns. The suggestion that in a hygroreceptor, transduction could be achieved if the receptor was composed of hygroscopic substances deformable by water gain or loss (Pielou, 1940) although possibly applicable to some insects (Yokohari and Tateda, 1976) is an unlikely explanation for the situation in tricorns since the dendrite is so extensively protected from mechanical deformation. It is interesting to note that *Ligia oceanica* uses evaporative cooling for temperature regulation (Edney, 1951), and possesses receptors generally distributed over the body surface which, in section, resemble the tricorns of the more terrestrial species (Price, 1978). These too may be involved in the process of humidity perception as this supralittoral animal spends a large proportion of its time out of water.

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