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FINE STRUCTURE OF THE CUTICLE
AND STRUCTURAL CHANGES OCCURRING DURING MOULTING
IN THE MITE TETRANYCHUS URTICAE
I. FINE STRUCTURE OF THE CUTICLE

BY Ursula MOTES-HAGNER* and Karl-August SELTZ*

ABSTRACT: Structure of the cuticle of Tetranychus urticae (Acari, Tetranychidae) is described by means of electron microscopy.

The cuticle is composed of an epicuticle and a lamellated procuticle. The epicuticle exhibits an inner 'dense layer' which shows a weak fibrillar appearance, a cuticulin layer, a wax layer and an outer cement layer. The procuticle can be differentiated in an outer exocuticle which extends to the ridges and lobes, characteristic of the cuticular surface, and an inner lamellated endocuticle. Lamellae are formed of helicoid arranged electron lucent microfibrils embedded in an electron dense matrix. Pores penetrate all cuticular layers.

Structure of the cuticle is compared to published information on the insect cuticle.

INTRODUCTION

Structure of the arthropod cuticle, a multilayered extracellular material, has been investigated and summarized in numerous reviews (ANDERSEN, 1977, 1979; HACKMAN, 1971; HEP-BURN, 1976; LOCKE, 1974; NEVILLE, 1975; RICHARDS, 1951; WIGGLESWORTH, 1948).

The main layers are an outer nonchitinous epicuticle and an inner chitinous procuticle composed mainly of protein and chitin. According to the physical properties, the cuticle may be soft, tanned or sclerotized. Many parallels may be drawn

* Department of Zoology, Philipps University, Lahnberge D-3550 Marburg, Federal Republic of Germany.

between insect and mite cuticles but interpreting arthropod cuticle in terms of what is known of the insect cuticle can be misleading. Especially, the recent reviews of HACKMAN (1982) and HACKMAN and FILSHIE (1982) on tick cuticle show that knowledge on the cuticle of the Acari is limited.

Structure of mite cuticle has been investigated by ALBERTI et al. (1981) according to the taxonomic relationship of mite species. In addition, the cuticle of the spider mite *Tetranychus urticae* has been of special interest (ANWARULLAH, 1963; CROWE, 1975; HENNEBERRY et al., 1963, 1965; GIBBS and MORRISON, 1965; MAYR, 1971) because it is suggested that one factor of resistance of mites towards acaricides is related to special cuticular structures. Although such precise information exists, several points are discussed with some controversy.

The first part of the present paper describes the ultrastructure of the cuticle of *Tetranychus urticae* and compares it with previously published information on mite and insect cuticle.

**Materials and Methods**

The animals were reared by following the method described earlier (MOTHE'S and SEITZ, 1980). Entire animals were fixed in 4% collidine buffered glutaraldehyde followed by osmication for 15 min. After dehydration in graded acetone solutions, polymerization was effected in Spurr's medium (SPURR, 1969). Ultrathin sections were cut with a diamond knife on an LKB ultratome and stained with KMnO₄ and lead citrate (REYNOLDS, 1963), using a method modified from SOLOFF (1973).

**Observations**

In describing the fine structure of the cuticle, the nomenclature used for the layers is that which other authors have used (ANWARULLAH, 1963; GIBBS and MORRISON, 1959; MAYR, 1971; ALBERTI et al., 1981; HACKMAN and FILSHIE, 1982) and is valid also for the insect cuticle (ANDERSEN, 1977; 1979; FILSHIE, 1982). The spider mite cuticle has a thickness of 0.5-2.5 μm. Procuticle thickness varies between 0.25 μm and 2 μm in the different body regions. The cuticle bears typical surface differentiations such as ridges and lobes (MOTHE'S-WAGNER, 1982) which are of taxonomic interest, and is composed of an epicuticle and a procuticle (Fig. 1). The latter can be differentiated into an outer exo- and inner endocuticle (Fig. 3 a). The epicuticle exhibits different layers (Fig. 2 a, b, arrows) : the inner layer is a “dense layer” (MAYR, 1971) which is overlain by an electron dense cuticulin and electron lucent wax layer. The outer layer is an often ruptured cement layer (Fig. 2 a, b). Fibrillar material observed in several tick epicuticles could be clearly demonstrated in the setal cuticle of *T. urticae* (Fig. 2 c) and, with some difficulties, in the body epicuticle (Fig. 2 c). Between epicuticle and endocuticle, the exocuticle with its mostly granular material extends to the ridges (Fig. 2 a). Especially in males, the exocuticle is penetrated by electron dense plaques (Fig. 1), the origin and

![Fig. 1](image1.jpg)

**Fig. 1:** Cross section of the dorsal opisthosomal cuticle of male. The outer layer is an epicuticle (arrow) which forms the taxonomically relevant ridges (RI) and lobes (LO). Epicuticular material extends to the procuticle (X). The inner layer is a lamellated procuticle (PR). Curicular glands (double arrow) and pores (asterisk). Hypodermis (HY) with lipoprotein granules (+) and bacteria (B).

**Fig. 2 a-c : Epicuticle. 2 a-b.** — The epicuticle of the dorsal opisthosome is composed of an outer cement layer (arrow), a wax layer (double arrow), a cuticulin layer (arrow head) and an inner ‘dense layer’ (DL). The exocuticle (EX) with mostly granular material extends to the ridges (RI) and lobes (LO). — 2 c. — The epicuticle of seta shows a fine striation.

**Fig. 3 a, b:** Cross section of lateral opisthosomal cuticle. Below the epicuticle (EP) the granular exocuticle (EN) with fibrillar deposits (+) is situated, followed by an inner endocuticle (EN) with helicoidal arranged fibrils (arrow).

**Fig. 4 a, b:** Cuticular gland apparently functioning in wax secretion (arrow) has contact with membranous structures of the hypodermis (X).

**Fig. 5:** Soft cuticle of joint. Epicuticle (EP) extremely electron dense. Procuticle (PR) thin and electron lucent compared to adjacent cuticle (+).
function of which is unknown. The endocuticle shows a conspicuous lamellation which is due to the helicoïdal arrangement of electron lucent fibrils in an electron dense matrix (Fig. 1, 3a, b). In different body regions, from four to sixteen such lamellae may be seen. In other regions they are lacking (lateral prosoma, ventral cuticle). The cuticle is interspersed with pore canals and cuticular glands (Fig. 1, 4a) which secrete the wax layer (Fig. 4b). The cuticle of the soft joints shows conspicuous alterations. The surface profile is knobbed (MOTHESWAGNER, 1982) and the procuticle is less compact (Fig. 5). Fibrils are easy to detect and may show an altered arrangement.

DISCUSSION

Presented results on the structure of the cuticle of Tetranychus urticae agree with those published by other authors (ANWARULLAH, 1963; GIBBS and MORRISON, 1965; HENNEBERRY et al., 1963, 1965; MAYR, 1971) and can be compared to information on the insect (ANDERSEN, 1977; 1979; FILSHIE, 1982) and tick cuticles (HACKMAN and FILSHIE, 1982).

Epicuticular layers are described in a variety of ways by the above authors, although it appears that the epicuticle is of uniform structure over the whole animal and is the same in larval and nym- phal instars. Existence of a wax layer is universally acknowledged (MAYR, 1971; GIBBS and MORRISON, 1965; BOSTANIAN et al., 1973; ANWARULLAH, 1963; ALBERTI et al., 1981), although the nomenclature may be different (see ALBERTI et al., 1981). Findings on the cement layer, “dense layer”, and the polyphenol-containing cuticulin layer are either discussed with some differences (ALBERTI et al., 1981; MAYR, 1971), or have not been mentioned (ANWARULLAH, 1963; BOSTANIAN et al., 1973). GIBBS and MORRISON (1965) reported a nonchitinous cuticulin layer, which later was refuted by means of biochemical tests (MAYR, 1971). ALBERTI et al. (1981) investigated the cuticles of 71 mite species and described an epicuticle as well as a procuticle which rarely can be differentiated into the two layers of exo- and endocuticle. The procuticle showed mostly a pronounced lamellation of microfibrils while the epicuticle was formed of homogenous material. The epicuticle was covered by a secreted layer of cement and wax and was suggested to be responsible for the special surface differentiation (ALBERTI et al., 1981).

According to the presented results on T. urticae, the epicuticle is composed of four layers: cement, wax, cuticulin and “dense layer”. The latter seems to be composed of lipoproteins (MAYR, 1971) or proteins (HACKMAN and FILSHIE, 1982), according to its staining behaviour. Determination of these materials, however, can only be done on the basis of histochemical reactions. The epicuticle of ticks contains fibrillar structures, none of which have been reported from other arthropod cuticles (HACKMAN, 1982). In Tetranychus urticae too, electron lucent microfibrils can be detected in the “dense layer” and the setal cuticle which is continuous with that of the body. During preliminary investigations on the chitin content of T. urticae, evidence has arisen that the epicuticle contains chitin (MOTHESWAGNER, unpubl.), a condition which is also described for the arachnid Palamneus swammerdami (Scorpionidae) (KRISHNAN et al., 1955). In the absence of definitive histochemical evidence, however, the presence of nonstaining microfibrils in the epicuticle, or elsewhere, cannot be taken as proof of the presence of chitin (HACKMAN, 1982).

The procuticle of T. urticae consists of an outer unlamellated exocuticle which is of unknown structure (CROWE, 1975), and an inner lamellated endocuticle. HENNEBERRY et al. (1965) reported the presence of seven endocuticular lamellae, but MOTHESWAGNER (1982) found that the number of lamellae varies with different body regions, and with sex (four to six for the female opisthosoma, and sixteen for the male opisthosoma). The exocuticle takes part in the formation of the cuticular ridges and lobes which are characteristic surface differentiations of tetranychids. Function of these ridges is suggested to be in a stabilization of the cuticle. GIBBS and MORRISON (1965) reported
a capability of stretching following food ingestion which is due to the ridges. In this context, ALBERTI et al. (1981) showed that the cuticle of ticks is polymorphous compared to that of spider mites. The capacity for stretching is based upon special structures of the basal layers. A thickened procuticle and an increased number of wax channels which are characteristic for stretchable soft-cuticles (ALBERTI et al., 1981) were not observed in T. urticae. Additionally, electron microscopical differences in appearance and height of the ridges are not obvious between fed and unfed animals. According to MAYR (1971), procuticular lamellation is due to a helicoidal arrangement of chitin fibrils embedded in a proteinaceous matrix, as reported for insects (ANDERSEN, 1977, 1979; LOCKE et al., 1975, 1980; NEVILLE, 1963a, b, 1965). However, conclusions on components forming endocuticular lamellation based only on electron microscopical pictures should not be made without simultaneous histochemical tests. Investigations on the insect egg shell (MAZUR et al., 1982) showed that a helicoidal arrangement of fibrils can be formed only by proteins. Consequently, one should consider the possibility that the fine-structurally demonstrable fibrils in the epi- and endocuticle of T. urticae may be due to chitin or protein. Although the present results do not answer the question of chitin content and distribution in the cuticular layers of the spider mite, histopathological effects of the chitin synthesis inhibitor complex, Nikkomycin, are conspicuous (MOTHES, 1981; MOTHES and SEITZ, 1982; MOTHES-WAGNER, 1982). At the moment, such effects could only be interpreted with the suggestion that the cuticle of T. urticae contains chitin (MOTHES and SEITZ, 1982). Fine structural investigations on the moulting processes in T. urticae which are presented in a later paper (MOTHES-WAGNER and SEITZ, 1984) do not contribute to a solution of this question. To what extent proteins and chitin (if present) are linked, and which additional components (inactive chitin synthetase, polyphenols, lipids, etc.) occur in the cuticle of tetranychids, should be cleared in subsequent investigations. Studies performed in animals can be used as model systems, although the size of tetranychids (0.1-0.4 mm) may create technical difficulties.

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