

The exoskeleton of the lobster *Homarus americanus* as an example of a smart anisotropic biological material [☆]

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Abstract

Many biological materials are composed of fibrils arranged according to well-ordered three-dimensional patterns. These materials often show a strong anisotropy in their properties. An essential characteristic of biological structures is their hierarchical organization from the nanometer to the millimeter scale. Lobster cuticle is a good example of this and a suitable model for studying these properties. In this study the structure of untreated as well as chemically and physically treated cuticle from the exoskeleton of the American lobster (*Homarus americanus*) was investigated using scanning electron microscopy. Fresh samples have been chemically decalcified and deproteinated and thermally treated to evaluate their resistance to degradation. Results showed that their structure is more complex than the commonly assumed model for arthropod cuticles. Stacked chitin–protein planes create the characteristic twisted plywood pattern found in arthropod cuticles. However, due to a well-developed pore canal system these planes are not simple arrays of parallel chitin–protein fibers. In lobster cuticle, interconnected fibers bend around the continuous lenticellate cavities of the pore canals to form a planar honeycomb-like structure. The chemically and thermally treated samples showed that the organic matrix retains its shape and structure despite the attack of chemical compounds or heat. It was also possible to study the distribution of the biominerals after the removal of the organic matrix. The observed residual structure gives a good impression of how the minerals (mainly calcite) are distributed inside the polymeric network.

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1. Introduction

Many skeletal tissues found in nature are composite materials with associated organic fibrils and mineral particles where the fibrous matrix is first deposited and then orientates the subsequent mineral nucleation and growth. In fact, skeletal tissues are fiber-reinforced composites where the whole is more important than the sum of its parts. Separately, the mineral or the fibrils show much weaker

mechanical properties than the entire composite, as the mineral is made of brittle crystals and the polymer is supple. Nevertheless, as a composite structure they resist strong forces. The reason for this behavior is that crystal fractures stop where they meet fibrils, which in turn do not bend, because the distances between them are fixed in the mineral [1]. Good examples of this are the bones of vertebrates, the shells of molluscs and the cuticles of crustaceans. The cuticles of crustaceans and arthropods in general act as exoskeletons, functional units which supply mechanical support to the body of the animals, enable movement through the formation of joints and attachment sites for muscles, and provide protection against predators. In order to grow, these exoskeletons regularly have to be shed and replaced by a new, larger one. Our model organism, the American lobster *Homarus americanus*, is a

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decapod crustacean whose relatively large size and good availability makes it an excellent model for studying its exoskeleton.

The cuticle of the Crustacea comprises two main layers, the epicuticle and the procuticle. The epicuticle is a thin waxy layer which acts as a diffusion barrier to the environment. The procuticle is further divided into an exocuticle and an endocuticle which are chiefly designed to resist mechanical loads (Fig. 1b). The organic matrix of crustacean cuticles is secreted by a single-layered epithelium and is composed of chitin associated with proteins where eventually the calcite crystals will grow [2–4]. Chitin is a biopolymer whose ideal structure is a linear polysaccharide

of β -(1,4)-2-acetamido-2-deoxy-D-glucopyranose, where all the residues are comprised entirely of *N*-acetyl-glucosamine, i.e. fully acetylated. However, in nature, the biopolymer exists as a co-polymer together with its deacetylated derivative, chitosan. When the number of acetamido groups is more than 50%, the biopolymer is termed chitin [5].

In many crustacean groups the hard parts of the exo- and endocuticle are mineralized, essentially by precipitation of crystalline calcium carbonate and, to a lesser extent, of amorphous calcium carbonate into the twisted lamellar structure of the chitin–protein cholesteric matrix [6–13]. The cuticle of the crustaceans is a complex structure in

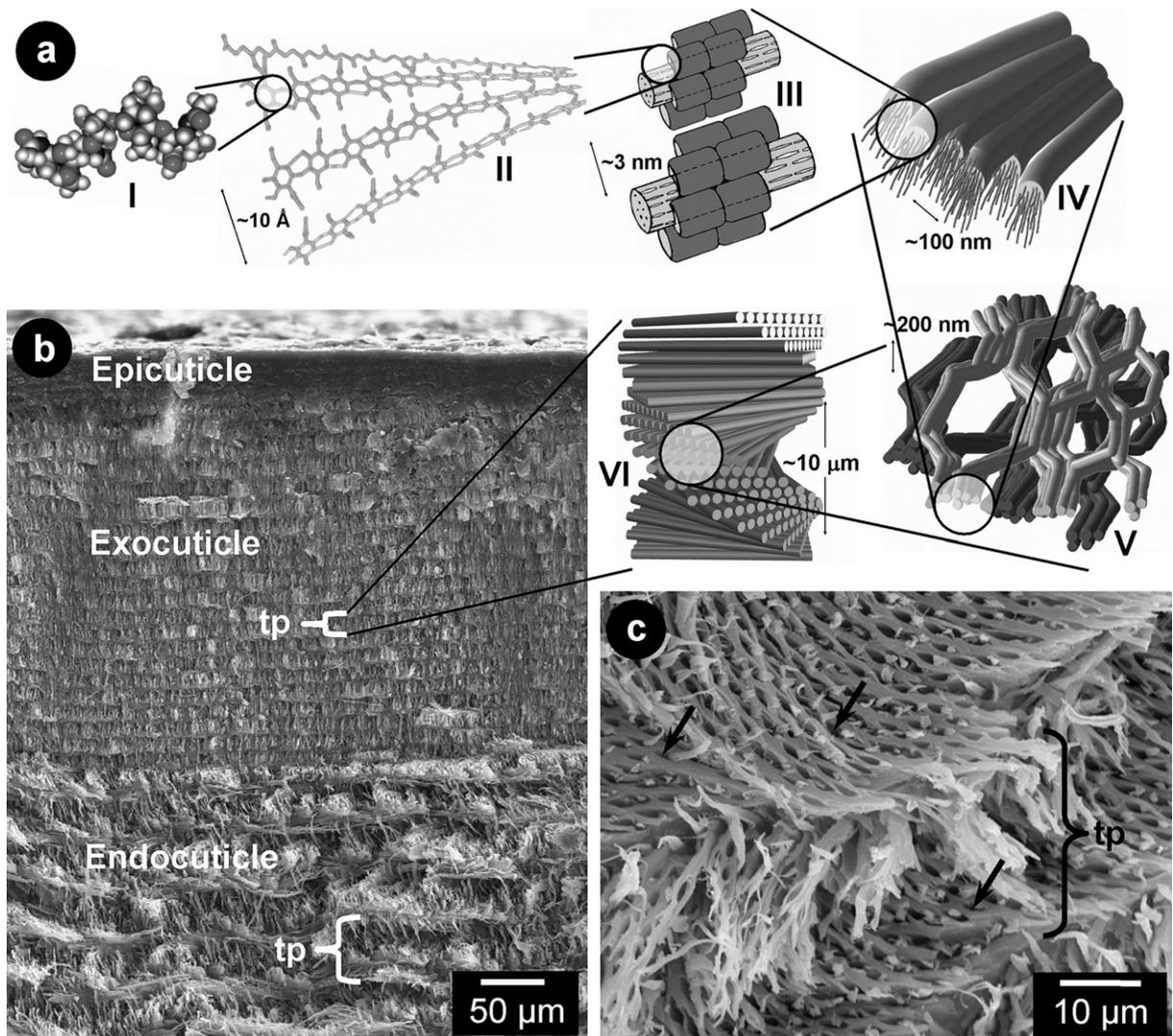


Fig. 1. Microstructure of lobster cuticle. (a) Schematic representation of the different hierarchical levels in the microstructure of lobster cuticle starting with the *N*-acetyl-glucosamine molecules (I) forming anti-parallel α -chitin chains (II). Between 18 and 25 of these molecules wrapped with proteins form nanofibrils (III), which cluster to form chitin protein fibers (IV) that are arranged in horizontal planes in which the long axes of the fibers are all oriented in the same direction. The fibers are arranged around the cavities originating from the extremely well-developed pore canal system which gives the structure a honeycomb-like appearance (V). These chitin protein planes are stacked with the orientation of the fibers in superimposed layers rotating gradually around the normal axis of the cuticle, thus creating a typical twisted plywood structure (VI). (b) SEM micrograph showing a cross-section through the three-layered cuticle. The different stacking density of the twisted plywood layers (tp) in the exo- and endocuticle can be clearly seen. (c) SEM micrograph of obliquely fractured endocuticle displaying two superimposed twisted plywood layers (tp) and showing their typical honeycomb-like structure. The arrows indicate the pore canals.

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