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Review article

Damage, repair and regeneration in insect cuticle: The story so far, and possibilities for the future

Eoin Parle [a,*], Jan-Henning Dirks [b], David Taylor [a]

[a] Trinity Centre for Bioengineering, Trinity College the University of Dublin, Dublin, Ireland
[b] Department for Biomimetics, City University of Applied Sciences Bremen, Neustadtswall 30, 28199 Bremen, Germany

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ABSTRACT

The exoskeleton of an insect can contain countless specializations across an individual, across developmental stages, and across the class Insecta. Hence, the exoskeleton's building material cuticle must perform a vast variety of functions. Cuticle displays a wide range of material properties which are determined by several known factors: the amount and orientation of the chitin fibres, the constituents and degree of cross-linking and hydration of the protein matrix, the relative amounts of exo- and endocuticle, and the shape of the structures themselves. In comparison to other natural materials such as wood and mammal bone, relatively few investigations into the mechanical properties of insect cuticle have been carried out. Of these, very few have focussed on the need for repair and its effectiveness at restoring mechanical stability to the cuticle. Insect body parts are often subject to prolonged repeated cyclic loads when running and flying, as well as more extreme "emergency" behaviours necessary for survival such as jumping, wedging (squeezing through small holes) and righting (when overturned). What effects have these actions on the cuticle itself? How close to the limits of failure does an insect push its body parts? Can an insect recover from minor or major damage to its exoskeleton "bones"? No current research has answered these questions conclusively.

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1. Introduction

The mechanical properties of natural materials such as wood and bone have been extensively researched. Despite being the second-most abundant natural material on the planet (second only to cellulose found in plants), very little research has been carried out to classify the material properties of insect cuticle. Previous investigations by a wide variety of researchers over the last century have established properties such as strength and elasticity (Jensen and Weis-Fogh, 1962; Vincent and Wegst, 2004; Dirks and Taylor, 2012a), and hardness and stiffness of various body parts of a wide variety of insects and arthropods (Hillerton et al., 1982; Muller et al., 2008; Sun et al., 2008; Klocke and Schmitz, 2011). More recently, fracture toughness properties have been published by our research group (Dirks and Taylor, 2012a, 2012b). Different techniques employed include nano-indentation, tensile testing of whole tibia or of excised sections, and three-point and cantilever bending tests. The more recently published values for material properties together with the body part tested and the researcher are summarized in Table 1.

Owing to their complex nature, many natural materials can display a wide range of material properties. Wood, for example can have a stiffness (Young's Modulus, E) ranging from approx. 500 MPa–15 GPa when measured perpendicular or parallel to the grain respectively (Vincent and Wegst, 2004). Cuticle displays a far wider range that can vary over several orders of magnitude depending on the type of cuticle tested. For example, the intersegmental membrane is highly flexible, having a stiffness of roughly 1 kPa, while the tanned, hardened elytra (forewing) can have a stiffness in excess of 20 GPa (Vincent and Wegst, 2004). Different types of cuticle must perform different functions – soft extensible cuticle facilitates movement by changes in body form for many larval insects, while harder stiffer cuticle is required for support and protection. This wide range of stiffness is achieved with little variation in material density.

* Corresponding author. Present address: Biomedical Engineering Department, College of Engineering and Informatics, National University of Ireland, Galway (NUIG), Ireland.
E-mail address: parlee@tcd.ie (E. Parle).

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Table 1
Recently published values for stiffness (E), strength (bending and tensile), fracture toughness (K_{ic}), work of fracture (or strain energy release rate) Gc, hardness (tested by nano-indentation normal and transverse to the fibre orientation), and the fatigue limit. All data relate to fresh cuticle from mature adult desert locusts, specifically the tibia (unless otherwise stated).

Property	Result	Researcher
E	3.05 GPa	Dirks and Taylor (2012a)
$\sigma_{bending}$	72.05 MPa	Dirks and Taylor (2012a)
$\sigma_{tensile}$	78–257 MPa (femur)	Hepburn and Joffe (1974)
K_{ic}	4.12 MPa$\sqrt{m}$	Dirks and Taylor (2012a)
G_c	5.56 kJ/m^2	Dirks and Taylor (2012a)
Hardness	0.05–0.15 GPa (sternum)	Klocke and Schmitz (2011)
Fatigue limit (10^5 cycles)	61.7 MPa (tibia) 14.3 MPa (wings)	Dirks et al. (2013)

Countless specialisations can be observed across insect species. The inherent material properties of the cuticle hinge on the interaction of a number of variables including the amounts of chitin fibres and the degree of sclerotization within the protein matrix. Different proteins (e.g. resilin) and the texture and orientation of the microfibrils can also give the cuticle different properties, independent of the degree of hardening or cross-linking (Andersen et al., 1996). Metals and minerals can also be used to increase hardness (e.g. zinc reinforcement of the mandibles of the caterpillar (Fontaine et al., 1991)).

There are also some transient factors that can affect the mechanical properties of a single body part. For instance, the degree of hydration of the protein matrix has been experimentally shown to affect the materials stiffness, hardness, toughness and strength (Schoberl and Jager, 2006; Muller et al., 2008; Dirks and Durr, 2011; Klocke and Schmitz, 2011; Dirks and Taylor, 2012a). Are there other factors that could influence cuticle's mechanical properties? The shape of the cuticle itself can contribute to rigidity. Insects vary greatly in terms of size, shape and different *in vivo* activities. Locusts use their back legs for jumping, and their front two pairs for balancing/walking/grasping. Nature strives to optimize the skeleton or bone size of each animal species. Can biomechanical forces experienced *in vivo* influence the size and shape of an insect leg?

2. Biomechanical forces

Natural materials must be built for purpose. Wood must withstand damaging effects in the growth environment (e.g. loads due to wind, snow and self-weight, Smith et al., 2003). Similarly bone must withstand varied loading regimes (compression, tension, bending and torsion) during normal daily locomotion. The ability of these materials to withstand both static and dynamic stresses is owed to several factors: the constituent material micro- and macro-structures, its overall geometry, and the material's ability to self-repair.

Similarly, insect exoskeletons are subject to complex loading regimes. When walking and running, six-legged insects commonly use an alternating tripod gait. Similar to mammalian running bipeds or trotting quadrupeds (Cavagna et al., 1964, 1977), there is interplay of potential energy due to gravity and horizontal kinetic energy as the insect's centre of mass undergoes repeated accelerations and decelerations with each step, even when travelling at a constant average velocity. Previous work has examined the ground reaction forces experienced by various insect species due to walking and running (Full and Tu, 1990, 1991; Reinhardt et al., 2009; Full et al., 1995), the locust jump (Bennet-Clark, 1975), and other so-called "emergency behaviour" which is more seldom performed behaviour such as "righting" (when overturned, (Full et al., 1995)) and "wedging" (squeezing through a tight space, Full and Ahn (1995)). Like wood or bone, the ability of the insect to withstand such loads is dependent on the material structure and its ability to repair from micro and macro level damage.

3. Fatigue properties

Some natural materials tend to have favourable fatigue properties due to their composite nature. Cracks, once initiated, can be trapped and redirected by the fibres in these materials. This requires more loading energy to propagate the crack through the material to cause a failure than with a uniformly isotropic material. The ability of the insect to withstand repeated cyclic loads was investigated by Dirks et al. (2013). It was found that cuticle could be induced to fail by fatigue. The two body parts examined (hind tibia and hind wing) behaved quite differently, with legs out-performing wings by almost double. It was found that a leg could withstand 10^5 cycles at 76% of its material strength, while wings could only withstand 46% of their ultimate strength for similar cycle ranges. This was explained by the composite nature of the two structures. The fibres in the legs are mostly are aligned parallel to the longitudinal axis of the leg (Neville, 1965) similar to the cellulose fibres in a tree trunk, lending it resistance to the bending forces applied *in vivo* (and during the tests). The membrane of the hind-wing of the locust is probably not reinforced with chitin fibres (Smith et al., 2000) and thus is not exceptionally resistant to crack growth, but the thin cross-veins present act as crack-stoppers, increasing its toughness by 50% (Dirks and Taylor, 2012b), which presumably also increases its fatigue life, just not to the same extent as the fibrous structure of the leg.

Another study (Parle et al., 2016a) showed that cuticle of various body parts is customized to suit a particular function. In engineering terms, a safety factor is defined as the ratio of a material or component's failure strength to its in-service stress. This study compared the safety factors calculated by comparing the aforementioned biomechanical (*in vivo*) ground reaction forces to the failure strength of four types of insect tibiae. The tibiae examined included the hind-leg of the desert locust (*Schistocerca gregaria*), which encounters large forces during jumping, the mid-leg of the same insect, used primarily for walking or running, and the hind-legs of two types of cockroach (*Periplaneta americana* and the much larger *Blaberus discoidalis*) which normally encounter smaller forces when used for running or walking, but can also encounter relatively large forces when used for emergency activities defined as righting or wedging. The results showed that for normal locomotion (running and walking), there was little probability of failure (safety factors ranged from 6 to 7), but for emergency behaviour, safety factors ranged from 1.7 to 4. The tibia of an insect must be durable enough to withstand countless cyclic forces during running and walking without succumbing to a fatigue failure, and must also possess sufficient static strength to withstand forces experienced during emergency behaviour. This study observed that tibia geometry and stiffness can differ significantly between species (and from one leg to another on a single insect). The low safety factors observed suggests that each leg seems built to operate close to its individual structural limit when emergency behaviour is encountered. This establishes that the tibiae of insects, similar to bones or trees, have the necessary structure both in terms of geometry and stiffness to withstand applied loads encountered on a daily basis within a certain factor of safety, but what about the ability to repair or maintain the strength of these structures? And would self-repair be necessary at all if the safety factors of the legs deem them adequate to resist the applied loads?

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