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Short communication

Giant stick insects reveal unique ontogenetic changes in biological attachment devices

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ABSTRACT

A strong modification of tarsal and pretarsal attachment pads during the postembryonic development is described for the first time. In the exceptionally large thorny devil stick insect *Eurycantha calcarata* a functional arolium is only present in the immature instars, enabling them to climb on smooth surfaces, especially leaves. Nymphs are also characterized by greyish and hairy euplantulae on tarsomeres 1–4. The gradual modifications of the arolium and the euplantula of tarsomere 5 in the nymphal development are probably mainly related to increased weight. The distinct switch in the life style between the leaf-dwelling nymphal stages and the ground-dwelling adults results in the final abrupt change of the adhesive devices, resulting in a far-reaching reduction of the arolium, the presence of a fully-developed, elongated euplantula on tarsomere 5, and white and smooth euplantulae on tarsomeres 1–4. The developmental remodelling of attachment pads also reflects a phylogenetic pattern. The attachment devices of the earlier instars are similar to those found in the basalmost lineage of extant stick insects, *Timema*, which is characterized by a very large pan-shaped arolium and a hairy surface of the tarsal and pretarsal attachment pads.

1. Introduction

Locomotory attachment devices played an important role in the evolution of the extremely successful Insecta (Gorb, 2001; Beutel and Gorb, 2001). Especially in predominantly or exclusively herbivorous insect groups a remarkable spectrum of attachment structures has evolved (Beutel and Gorb, 2001, 2006). The function is not just adhesion but they enable insects to walk efficiently on plants through systems providing fast and reversible attachment/detachment (Gorb et al., 2002). Modifications of plant surfaces to impede attacks by phytophagous insects and corresponding variation of insect attachment devices are two counterparts of an evolutionary arms race between the two groups of organisms (Beutel and Gorb, 2001).

Tarsal attachment pads specifically designed to adhere on diverse substrates occur in two main structural types in insects. Hairy systems where the pad is covered with deformable adhesive setae are found in earwigs (Haas and Gorb, 2004), beetles (Stork, 1980), and flies (Friedemann et al., 2014a). Smooth systems without prominent microornamentation of the pad surface are characteristic of cockroaches (Clemente and Federle, 2008), katydids and grasshoppers (Beutel and Gorb, 2001), ants and bees (Federle et al., 2001), and bugs (Friedemann et al., 2014b). An intermediate type of pad structure covered with cone-shaped hairs (i.e. acanthae, unicellular epidermal outgrowths) has evolved in stick insects (Beutel and Gorb, 2008; Bußhardt et al., 2012; Labonte et al., 2014), in some stoneflies (Nelson, 2009), and in sawflies (Schulmeister, 2003).

Biomechanical features of the different designs of insect attachment pads have been analysed in several studies (e.g. Gorb et al., 2002; Gorb, 2007; Bullock et al., 2008), while ontogenetic aspects have been only reported in the leaf-footed bug *Coreus marginatus* (Gorb and Gorb, 2004). However, distinct developmental modifications of attachment pads related to environmental adaptation were not described yet. Here, we report both gradual and 'switch-like' developmental changes in the design of these structures in *Eurycantha calcarata*, a giant stick insect from the rain forests of New Guinea featuring different habitat preferences during its lifetime. Our results show the unprecedented adaptive developmental plasticity of attachment devices of insect cuticle.

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2. Material and methods

The giant stick insect *E. calcarata* Lucas, 1869 belongs to the order Phasmatodea, suborder Euphasmatodea, subfamily Lonchodinae (Bradler et al., 2014). A culture-stock of *E. calcarata* originating from New Britain island (Papua New Guinea) provided the specimens used in this study. The insects were laboratory-reared in a large cage (60 cm high, 50 cm wide, and 80 cm long)

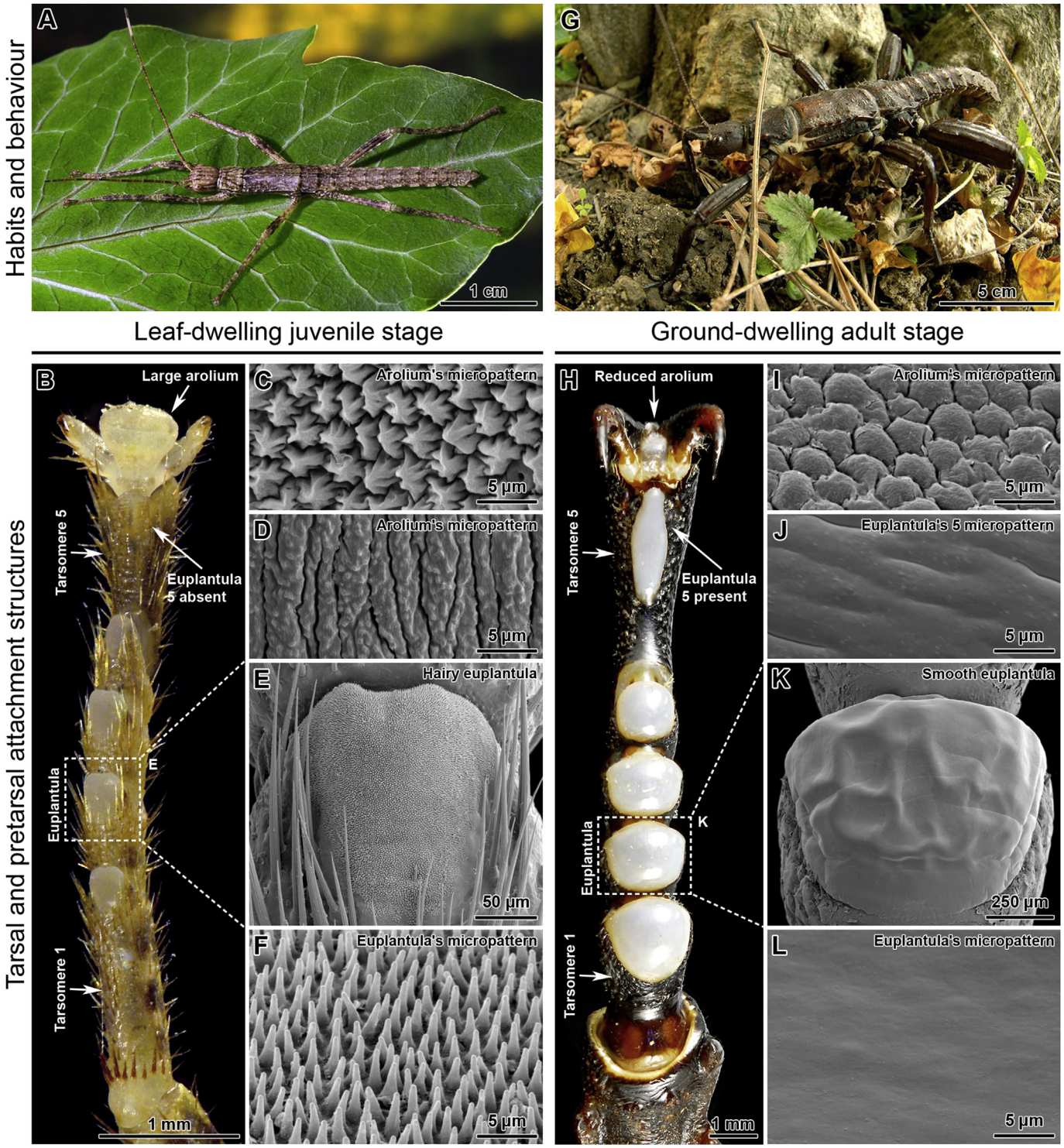

Fig. 1. Dramatic remodelling of attachment devices is concomitant with life-style change in *E. calcarata*. Attachment structures of the leaf-dwelling first instar nymph (A–F) compared to those of the ground-dwelling adult (G–L). (A) Typical resting position of immature instars. (B) Structure of the tarsus, ventral aspect. (C–D) Adhesive microstructures of the arolium. (E) Euplantula with the hairy micropattern, ventral aspect. (F) Detailed view of the dense coverage of acanthae on the surface of the euplantula. (G) Adult male. (H) Structure of the tarsus, ventral aspect. (I) Cuticular outgrowths are found in the reduced arolium. (J) Smooth micropattern of the euplantula of tarsomere 5. (K) Euplantula with the smooth micropattern, ventral aspect. (L) Cuticular microornaments are absent in the smooth euplantula.