Naturwissenschaften (2008) 95:257–261
DOI 10.1007/s00114-007-0316-1

SHORT COMMUNICATION

Convergent evolution in the antennae of a cerambycid beetle, *Onychocerus albitarsis*, and the sting of a scorpion

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Received: 12 July 2007 / Revised: 10 October 2007 / Accepted: 14 October 2007 / Published online: 15 November 2007

Abstract Venom-injecting structures have arisen independently in unrelated arthropods including scorpions, spiders, centipedes, larval owlflies and antlions, and Hymenoptera (wasps, ants, and bees). Most arthropods use venom primarily as an offensive weapon to subdue prey, and only secondarily in defense against enemies. Venom is injected by biting with fangs or stinging with a specialized hypodermic structure used exclusively for the delivery of venom (usually modified terminal abdominal segments). A true sting apparatus, previously known only in scorpions and aculeate wasps, is now known in a third group. We here report the first known case of a cerambycid beetle using its antennae to inject a secretion that causes cutaneous and subcutaneous inflammation in humans. Scanning electron microscopy revealed that the terminal antennal segment of *Onychocerus albitarsis* (Pascoe) has two pores opening into channels leading to the tip through which the secretion is delivered. This is a novel case of convergent evolution: The delivery system is almost identical to that found in the stinger of a deadly buthid scorpion.

Keywords Anisocerini · Aculeus · Cerambycidae · Defense chemicals · *Leiurus quinquestriatus* · *O. crassus*

Electronic supplementary material The online version of this article (doi: 10.1007/s00114-007-0316-1) contains supplementary material, which is available to authorized users.

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Introduction

Beetles (Coleoptera) are one of the most diverse orders of arthropods: one in four animal species is a beetle (Grimaldi and Engel 2005). Numerous families including ground beetles (Carabidae), blister beetles (Meloidae), darkling beetles (Tenebrionidae), ladybird beetles (Coccinellidae), fireflies (Lampyridae), and rove beetles (Staphylinidae) produce defensive chemicals that function as vesicants, contact irritants, or bitter-tasting feeding deterrents (Weatherston and Percy 1978; Mebs 2002; Laurent et al. 2005). These chemicals, including acids, quinones, esters, aldehydes, alkaloids, amides, steroids, terpenoids, and iridoids, often occur in complex mixtures. They are sometimes free in the hemolymph and released via reflex bleeding when the insect is disturbed. Pederin, a vesicant that accumulates in the hemolymph of female rove beetles (genus *Paederus*), appears to be of endosymbiotic origin (Laurent et al. 2005). Other defense chemicals are products of exocrine glands, frequently located in the abdomen or thorax (Weatherston and Percy 1978; Laurent et al. 2005). Glandular secretions are usually released through ducts to the body exterior, but bombardier beetles (Carabidae) discharge them in a forceful directional spray (Weatherston and Percy 1978). Poisons produced by these beetles are not considered venoms because the insects lack a venom apparatus and the chemicals are not injected into the victim (Mebs 2002).

A cerambycid beetle in the genus *Onychocerus* (= *Scorpionus*) was first reported to use its antennae to sting unwary handlers by Smith (1884): "Seizing it with my forefinger and thumb, I was about transferring it to the collecting bottle, when, to my surprise, it inflicted on me a pretty sharp sting or prick, which caused me to drop it quickly. In defending itself thus, the insect used its antennae spreading them out and then throwing them backward and upward with a strong jerk...." Cerambycids (longicorns, long-horned wood-boring beetles), with at least 35,000 described species (Lawrence 1982), belong to a monophyletic group of phytophagous beetles including the leaf beetles and weevils. Their long antennae, which usually extend beyond the apex of the body, bear sensilla believed to play critical roles in host plant location or the reception of sex pheromones (Linsley 1959; Allison et al. 2004). Some adult cerambycids bear sharp protuberances that make the beetles painful to handle: lateral tubercles on the pronotum, long spines at the apices of femora or, in the case of *Onychocerus* and other genera in the tribe Anisocerini, spines on their antennal segments. Smith (1884) found no evidence of a secretory gland in *Onychocerus* and concluded that the small puncture made by the sharply pointed antenna was responsible for the stinging sensation. No cerambycid has previously been reported to use any specialized structure to inject chemicals.

An adult specimen of the rarely collected cerambycid beetle *Onychocerus albitarsis* (Pascoe) used its antennae in the manner described by Smith (1884) to sting P. C., who reported an inflammation similar to that of a bee sting (Fig. 1b). The objective of the scanning electron microscopy (SEM) study presented here was to determine if any secretory structures were present in the terminal antennal segments of *O. albitarsis* and its more commonly collected congener *O. crassus* (Voet). If such structures were found, our second objective was to compare them to the sting apparatus found in other arthropods.

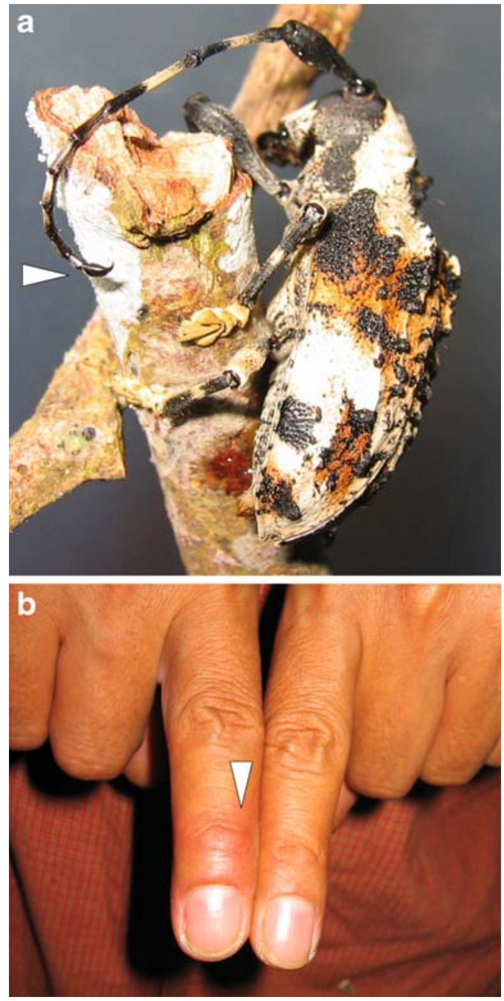

Fig. 1 The stinging antennae of *O. albitarsis*. **a** The *arrow* indicates the scorpion-like terminal antenna segment. **b** The *arrow* indicates the site of the sting; the finger is slightly swollen

Materials and methods

Onychocerus albitarsis was collected at a mercury light trap (28 Nov. 2005) at the Los Amigos Research Center located in lowland moist forest in SE Peru (12°33–34′S, 70°05–06′W; 268 m above sea level; Pitman 2005). We used a Canon Elph S400 to take photographs (Fig. 1) and record its response to harassment with forceps (see S1 for video). The specimen was euthanized and dissected to determine gender; we transported the antennae to the City College of New York. We also processed specimens of *O. crassus* and an immature specimen of the buthid scorpion *Leiurus quinquestriatus* (Hemprich & Ehrenberg) provided by the Division of Invertebrate Zoology, American Museum of Natural History (AMNH). We photographed specimens at 20×, 30×, and 50× magnification using a Spot Insight camera and software (v. 3.5) with a Nikon SMU-1500 microscope. The terminal antennal segments and the scorpion telson were dehydrated in 100% ethanol, critical-point-dried, mounted on carbon-coated specimen stubs, dried overnight at 70°C, and gold-plated. We took digital micrographs with a DSM 940 SEM at 200×, 500×, 1000×, and 2,000× magnification using the program PGT Spirit (v. 1.07).

Results

The specimen of *O. albitarsis* collected in Peru was female (Fig. 1). Figure 2 shows images of the terminal antennal segments from *O. albitarsis* and *O. crassus* (also female), along with the stinging telson from the buthid scorpion *L.*

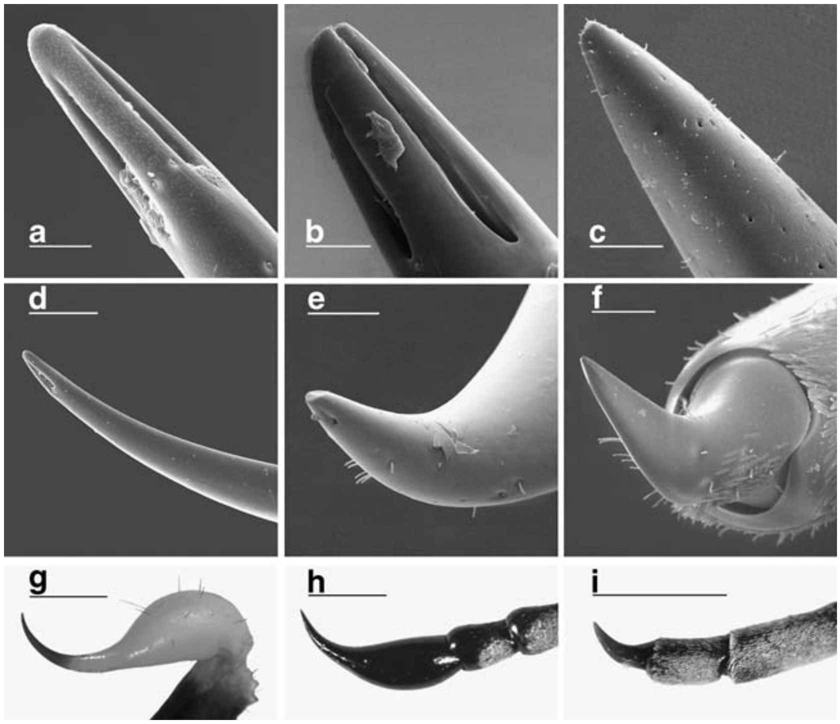

Fig. 2 Convergent evolution in the beetle *O. albitarsis* and a scorpion, *L. quinquestriatus*. **a** The aculeus of *L. quinquestriatus* shows two channels leading to the tip. **b** The terminal antennal segment of *O. albitarsis* shows two channels leading to the tip. **c** The terminal antennal segment of *O. crassus* lacks channels. **d** Lateral view of the *L. quinquestriatus* aculeus shows a pore near the tip. **e** Lateral view of the *O. albitarsis* terminal antennal segment shows a pore near the tip. **f** Lateral view of the *O. crassus* terminal antennal segment lacks a pore near the tip. **g** The telson of *L. quinquestriatus* is expanded to house a venom reservoir. **h** The terminal antennal segment of *O. albitarsis* is expanded and may house a chemical reservoir. **i** The terminal antennal segment of *O. crassus* is sharply pointed but not expanded. *Scale bars*: 20 μm (**a**–**c**), 100 μm (**d**–**f**), 1 mm (**g**–**i**)

quinquestriatus. *O. albitarsis* has a scorpion-like expansion at the base of its terminal antennal segment (Fig. 2h). Under 500× magnification, a pore was visible near the apex (Fig 2e). Under 1,000× magnification, we determined that two pores opened into narrow channels leading to the sharp tip of the antenna (Fig. 2b). Under 2,000× magnification, a chemical residue was visible inside a pore (Fig. 3). *Onychocerus crassus* has pointed terminal antennal segments (Fig. 2i), but they are shorter and not basally expanded into sting bulbs like those of *O. albitarsis*. This species lacks conspicuous pores or channels in the terminal segment (Fig. 2f,c). The expanded telson of the scorpion *L. quinquestriatus* (Fig. 2g) terminates in a pointed tip, or aculeus, narrower than the tip of the *O. albitarsis* antennal segment, but Fig. 2a shows twin channels leading to the apex that are remarkably similar to those seen in the beetle.

Discussion

Arthropod stings are specialized tools that can be maneuvered, are sharp enough to penetrate cutaneous tissue, and strong enough to withstand the stress of making the puncture. As punctures are inflicted, chemicals are injected that induce effects ranging from mild discomfort to acute pain and, occasionally, death (Mebs 2002). In scorpions, the sharply pointed aculeus of the telson inflicts the wound. The expanded bulb houses a pair of venom glands, each with an exit duct leading to an aperture just before the tip of the aculeus (Hjelle 1990). Venom is used primarily to subdue prey, and the aculeus must be withdrawn intact for

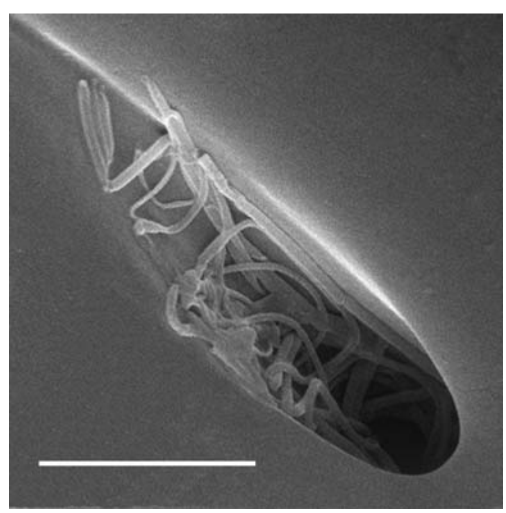

Fig. 3 Residue inside of one of the pores in the terminal antennal segment of *O. albitarsis*. *Scale bar*: 10 μm

future service. In aculeate wasps the sting is usually a modified ovipositor. It includes two piercing lancets that move independently to insert themselves progressively more deeply into the puncture, enabling the sting shaft to deliver venom, through a single aperture, directly into the wound (Hermann 1971). In honeybees, some social wasps, and some ants, enlarged barbs at the apices of the lancets anchor the sting so effectively that it cannot be withdrawn, and the departing insect tears off the end of its abdomen, thereby sacrificing its life. This lethal sting, which leaves the entire venom apparatus pumping venom into the victim, can be used on a single occasion: principally in colony defense.

Cerambycid antennae are highly maneuverable due to their length and segmentation: in addition to their chemosensory role, they are sensitive tactile instruments. The terminal antennal segments of *O. albitarsis* are clearly sharp enough to puncture human skin and, although we think that the expanded segments house secretory tissue and/or a chemical reservoir, the shape and cuticular thickness (about 10 μm) may add strength to the piercing structure. Like mandibles and other cuticular tools used by arthropods (Schofield et al. 2003), the terminal antennal segments may accumulate minerals such as zinc to increase structural integrity. Our SEM study revealed residue of a coagulated filamentous chemical secretion from the terminal antenna segment of *O. albitarsis* (Fig. 3). We interpret the pores opening into channels leading towards the antenna tip as a sophisticated delivery system very similar to that observed in the buthid scorpion *L. quinquestriatus*. Pores set back from the tip of the injecting device would be less susceptible to damage, and channels leading toward the tip direct the secretion to the deepest part of the wound. Even after stinging the collector, *O. albitarsis* continued making attempts (see S1), suggesting that like scorpions, it can administer multiple stings. Like social hymenoptera, the stings are administered in defense. This defense strategy would not be of assistance during the imperiled immature stages, but would probably be directed towards vertebrate predators of adult cerambycids, including birds, lizards, or even monkeys (Linsley 1959; Veiga and Ferrari 2006).

Although *O. albitarsis* presents a remarkable case of convergent evolution with the chemical delivery system of the scorpion stinger, we do not assume chemical convergence. A sting from *L. quinquestriatus* is potentially lethal to humans (Taib and Jarrar 1993; Mebs 2002), while a sting from *O. albitarsis* results in mild inflammation. Scorpion venoms typically consist of mixtures of polypeptides with up to 70 amino acid residues, but are diverse in size, composition, and activity (Mebs 2002). The venomous peptides, which act upon Na^+ or K^+ channels, share a common structural motif with insect defensins, a family of inducible antimicrobial peptides isolated from a variety of unrelated insects (Ehret-Sabatier et al. 1996). Although a defensin has been isolated from larvae of the cerambycid species *Acalolepta luxurosa* Bates (Ueda et al. 2005), proteinaceous substances are not represented among the semiochemicals thus far identified from cerambycids (Allison et al. 2004). Our attempts to acquire samples of the secretion shown in Fig. 3 for chemical analysis have been hindered by the apparent rarity of *O. albitarsis*. It is represented by a single specimen at AMNH, was collected once during a full year of light trapping in SE Peru (Centeno, personal communication), and was collected once during monthly light trapping experiments at a canopy tower near Manaus (Martins et al. 2006).

Conspicuous pores and associated channels are absent from *O. crassus*, which lacks the bulbous expansion of the terminal segment (that we think serves as a chemical reservoir). Other species of *Onychocerus* also lack these bulbous expansions (Júlio and Monné 2001), and we predict that they too will lack pores associated with channels. Hypotheses about the evolution of the unique defensive apparatus of *O. albitarsis* must be tested with phylogenetic analysis, but we can propose a possible scenario. Species of *Onychocerus* lacking the expansion in the terminal segment display conspicuous sexual dimorphism in the antennae. Males bear a fringe of long, dense hairs on the proximal surface of the terminal and subterminal segments, which is absent in females (Júlio and Monné 2001). The function of the fringe hairs is not known, but they may play a role in broadcasting or receiving pheromones. Other cerambycid sex pheromones are associated with cuticular pores (Allison et al. 2004), and if the hairs are associated with secretory cells, the defensive strategy of *O. albitarsis* may be derived from a pheromonal communication system [in keeping with Blum's (1996) hypothesis of semiochemical parsimony]. Alternately, although host plant data are not available for *O. albitarsis*, some of its congeners have been reared from trees with irritating saps or resins, e.g., from trees in the poison ivy family (Anacardiaceae) and *Hura crepitans* (Euphorbiaceae) (Tavakilian et al. 1997; Monné 2001). It is possible that adult beetles emerging from these trees collect irritating exudates on their antennal hairs and incidentally inject them if they happen to prick a predator, thereby co-opting plant toxins.

Acknowledgments This work was supported by grants from The American Philosophical Society, The City University of New York PSC-CUNY Research Award Program, and The National Science Foundation RIG 0542276. Specimens were generously provided by Dr. Lorenzo Prendini and Randy Mercurio (*L. quinquestriatus*) and Dr. Lee Herman (*O. crassus*) at the Division of Invertebrate Zoology, American Museum of Natural History. Special thanks to Cláudia Moreno and João Vasconcelos (UNICAMP, Brazil), who first drew our attention to the stinging cerambycid, the Asociación para la

Conservación de la Cuenca Amazónica and INRENA for facilitating field research in Peru, Dr. Scott Mori (New York Botanical Garden) for manuscript review, Dr. Jorge Morales (CCNY), for guidance with SEM, and Frank Hovore, for unflagging skepticism. This study complies with the laws of Peru and the USA.

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