

# Sensilla Density Corresponds to the Regions of the Horn Most Frequently Used During Combat in the Giant Rhinoceros Beetle *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae: Dynastinae)

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**ABSTRACT** In the Japanese horned beetle, *Trypoxylus dichotomus* (L.), males have a long forked head horn that they use in fights with other males over access to sap sites that attract females. Because of the high risk of injury from these contests, males should assess the fighting potential of their rivals before escalating to direct combat. Indeed, male rhinoceros beetles only escalate to intense fighting when matched with equal-sized rivals. Males often tap their opponents with their head horn before and during fights, so it is likely that beetles assess the size of their competitors via sensory input from their horns. Here, we used scanning electron microscopy to examine the density and distribution of sensory hairs along the length of the males' horn. To assess the potential functional significance of variation in hair density, we combined our microscopy observations with a behavioral analysis of how males use their horns during fights. We found a strong correlation between the density of sensory hairs and the regions of the horns that were used most during combat. The distal tips of the horns had the highest hair density, and were also the region of the horn most frequently in contact with an opponent. Given the shaft and socket morphology of these hairs, which is the characteristic morphology of mechanoreceptors, we expect that they provide mechanosensory input. Thus, although beetle horns are often described as dedicated weapons, our results suggest that the head horns of *T. dichotomus* also play an important sensory role.

**KEY WORDS** horn, sensillum, male–male competition, rhinoceros beetle, *Trypoxylus dichotomus*

The horns of rhinoceros beetles are among the most striking and exaggerated structures found in the animal kingdom (Darwin 1871, Arrow 1951). These rigid extensions of the beetles' exoskeleton have fascinated biologists for centuries because of their incredible variability in form (Mizunuma 1999). Rhinoceros beetle species vary from having one to five horns, which may extend anteriorly, laterally, or dorsally from the head and front, middle, or sides of the pronotum. Moreover, these horns exhibit a variety of fantastic shapes and sizes: from long branched pitchforks [e.g., *Trypoxylus dichotomus* (L.)], to broad spade-like paddles (e.g., *Golofa pizarro* Hope), to robust toothed pinchers [e.g., *Dynastes hercules* (L.)]. Whereas some males develop only short stubby horns, other males wield horns that are longer than the rest of their body (Mizunuma 1999). Darwin himself noted, "If we could imagine a male *Chalcosoma*... with its polished bronzed coat of mail, and vast complex horns, magnified to the size of a horse or even a dog, it would be

one of the most imposing animals in the world" (Darwin 1871).

Despite the diversity in horn morphology among species, all rhinoceros beetles appear to use their horns for exactly the same purpose: they are weapons that aid their bearers in male–male competitions (Beebe 1947; Eberhard 1979, 1980). Specifically, horns are used in fights over access to resource sites that attract females. Males with the longest horns are the most likely to win fights and gain access to these resource sites (Siva–Jothy 1987; Hongo 2003, 2007; Karino et al. 2005), and thereby mate with the most females (Hongo 2007). Therefore, horns are critical to a male's fighting performance and hence his reproductive success.

Male–male combats, however, can also be energetically expensive, injurious, and possibly even fatal. Indeed, male rhinoceros beetles often show signs of damage as a result of intense fights, including puncture wounds on their elytra and pronota and chipped or broken horns (Siva–Jothy 1987, E.L.M., unpublished data). Because of the potentially serious injuries that can be incurred from fights, male rhinoceros beetles should avoid male–male competitions whenever possible by assessing the size, condition, and fighting potential of their rivals before escalating to direct combat (Parker 1974, Maynard Smith and Parker 1976,

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Parker and Rubenstein 1981). Male–male assessment presumably benefits small and large males alike, as the competitively weaker males avoid being injured in fights that they would certainly lose, and competitively superior males avoid wasting time and energy on fights that they would easily win (Maynard Smith and Parker 1976, Parker and Rubenstein 1981, Taylor and Elwood 2003).

Precombat assessments are used by males across diverse taxa (reviewed in Arnott and Elwood 2009), and are expected to be particularly important among males that possess dangerous weapons, given the high risk of injury in these species (Geist 1966, Clutton-Brock and Albon 1979, Clutton-Brock et al. 1979). Rhinoceros beetle horns are, in relation to the size of the beetles themselves, among the largest weapons in the animal kingdom. Despite their extreme weapon size, surprisingly little is known about the ability and tendency for male rhinoceros beetles to assess their rivals before and during combat.

Male rhinoceros beetles only escalate to intense head-on combats with size-matched males (Hongo 2003, 2007), which suggests that they are capable of assessing the size of their competitors. Because most rhinoceros beetle species are nocturnal, it is unlikely that males can accurately assess their opponents by using visual cues (Arrow 1951). However, males often tap their rivals with their horns during male–male interactions (E.L.M., unpublished data), which suggests that they gain sensory input from the horn itself.

Insect exoskeletons are covered with sensory organs, known as sensilla, that allow insects to detect mechanical, thermal, and chemical stimuli (Snodgrass 1935, Dethier 1963, McIver 1985). These hairs, pits, and other cuticular modifications are particularly abundant on the insects' sensory appendages, such as the antennae and mouthparts (Harbach and Larsen 1977, McIver and Siemicki 1984, Zacharuk 1985, Faucheux 1995, de Fernandes et al. 2004, Hu et al. 2010), but are also numerous on the tarsi and ovipositors (Ganesalingam 1972, Faucheux 1991, Dey et al. 1995, Brown and Anderson 1998), where chemical and tactile information is important. Whether the horns of rhinoceros beetles are also well-endowed with sensilla, which would allow males to gain chemosensory and mechanosensory input about their opponents before or during fights, is currently unknown.

Here, we used scanning electron microscopy to examine for the first time the ultrastructure of a rhinoceros beetle horn. Specifically, we investigated the density and distribution of sensory hairs on the long branched head horn of the Japanese horned beetle, *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae: Dynastinae). We combined this microscopy work with a behavioral analysis of how *T. dichotomus* males use their horns during fights to assess the potential functional significance of variation in hair density along the length of the beetles' horns. We hypothesized that the density of sensory hairs (and sensitivity) would correspond with the regions of the horns that are used most in both precombat assessment and actual combat. As a result, we expected hair density to

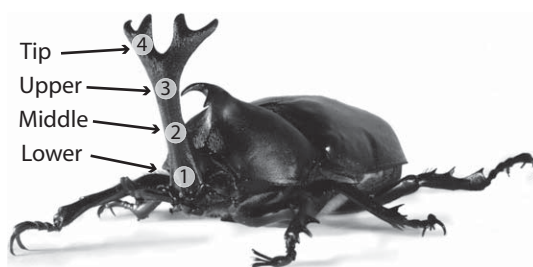


Fig. 1. Large male *Trypoxylus dichotomus* showing the long forked head horn. Numbers are on the anterior face and indicate the four horn regions: 1) lower shaft, 2) middle shaft, 3) upper shaft, and 4) the tips.

increase distally along the length of the horn, and to be more abundant on the anterior, or forward-facing, surface of the horn.

## Materials and Methods

**Behavioral Observations.** Beetles were observed fighting on their natural feeding trees on the National Chi Nan University campus in central Taiwan. The campus grounds contain many (>120) ash, or *Fraxinus*, trees, which is the exclusive host plant of *T. dichotomus* in Taiwan. Beetles were observed in June and July, when adults were most abundant. Male–male fights were filmed on an opportunistic basis from 1900 to 2400 hours, when the beetles were most active. Fights were filmed with a digital camcorder (Sony Handycam DCR-TRV250, Sony, San Diego, CA) by using the night-shot function. We filmed >200 male–male encounters and analyzed each to determine how the horns are used during combat. Specifically, we scored each fight according to the horn region(s) that contacted the opponent, the primary tactic that was used (prying, pushing, or binding, see Results), and the duration and outcome of each encounter.

**Electron Microscopy and Image Analysis.** Beetles were purchased as final-instar larvae from a commercial insect distributor (Yasaka Kabuto Kuwagata World, Hamada City, Japan) and reared to adulthood in the laboratory. Six males across a range of body and horn sizes were chosen for investigation by scanning electron microscopy. The head from each male was placed in a dessicator and dried for 3 d. After drying, the heads were mounted on stubs by using double-sided carbon tape and coated with a thin layer (1.5 nm) of argon-gold in a Technics Hummer V Sputter Coater (Technics, Arlington, VA). The sputter-coated horns were visualized on a Hitachi S-570 Scanning Electron Microscope (Hitachi, Tokyo, Japan) operated at 20 kV.

We sampled four roughly equal-sized horn regions on each male's horn (Fig. 1): the lower, middle, and upper regions of the shaft and the distal tips of the horn. We also examined both horn faces: the anterior face, which was contiguous with the clypeus, and the opposite, posterior face. We collected three nonoverlapping images for each of the eight areas of the horn,

**Table 1.** Horn regions used during combat by male *T. dichotomus*

Horn region	No. observed encounters	Percentage of observed encounters <sup>a</sup>
Tip	191	92%
Upper shaft	105	50%
Middle shaft	44	21%
Lower shaft	0	0%

<sup>a</sup> Based on 208 total encounters.

and then imported the images into imaging software (ImageJ v1.41, National Institutes of Health, Bethesda, MD) for analysis. Because of the complex forked shape at the tip of the horn, we were unable to take consistent images at the distal-most tips. Therefore, we measured hair density in the grooves between each "tine," rather than the distal tips themselves. The number of sensory hairs on each horn area was counted manually and converted to hair density (hair number per square millimeters) for comparison.

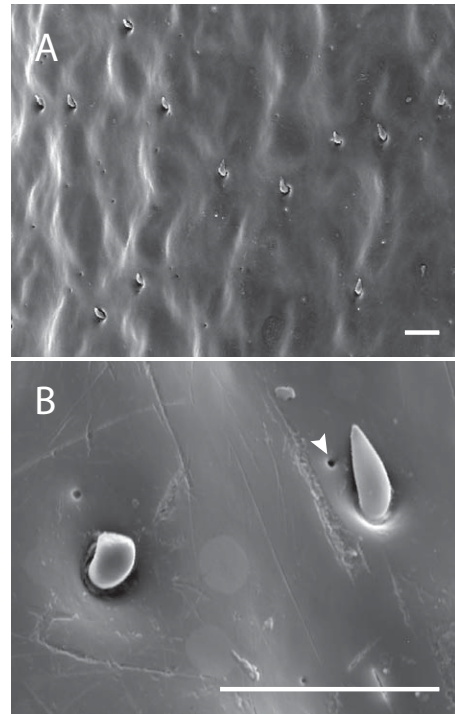
We tested for a difference in hair density between anterior and posterior horn faces by using Student's *t*-test. We compared hair density among the horn zones by using an analysis of variance (ANOVA). A post hoc Tukey's test was performed to separate significantly different means. All statistical analyses were performed in R.

## Results

**Fighting Behavior.** Males use their head horn to remove rivals from sap sites on the trunks and branches of trees. Three main tactics are used during fights: prying, pushing, and binding (Hongo 2003; E.L.M., unpublished data). During a pry, a male inserts the horn tip underneath the body of his rival and uses the horn like a pitchfork to lift the opponent up and off the tree. During a push, a male shoves his rival forward along the trunk or branch with the upper shaft and tips of his horn. During a bind, a male crosses his horn with a rival's horn and pushes him sideways, similar to two dueling fencers who cross their swords and try to push their opponent off the diagonal.

Males had a strong tendency to fight with the tips of their horns (Table 1). Nearly all (92%) of the fights observed involved use of this distal region of the horn. Specifically, males wedged the tip of their horn beneath their opponent and used it like a pitchfork to pry their opponent off the tree and toss him to the ground. Importantly, the tips were used in 99% (87/88) of the fights in which a male successfully dislodged his opponent from the tree, and all of the most intense and sustained fights involved tip contact.

The upper shaft was the second-most contacted region of the horn (Table 1). In 50% of the encounters, males would shove and push away their opponent with the upper shaft of their horn. One male was successful at pushing his opponent off of the tree, but typically this maneuver was only successful in chasing the opponent away from the sap site but not tossing him to the ground.

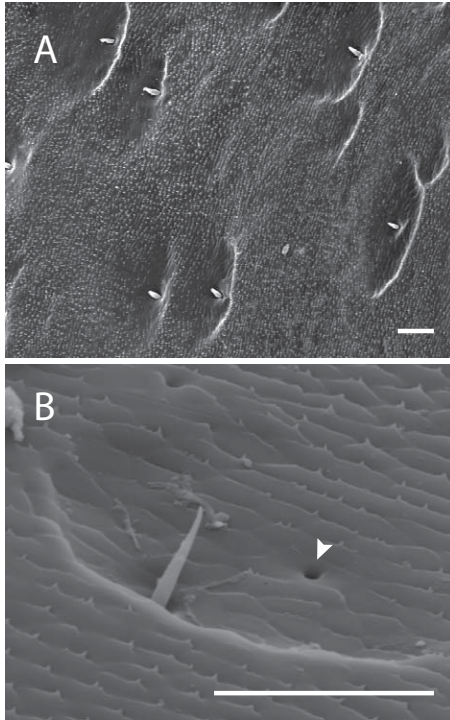


**Fig. 2.** Scanning electron micrographs of the anterior face of the horn. (A) Ultrastructure of the smooth cuticle surface. (B) Enlarged view of the sensory hairs and pit glands (arrowhead). Note the scarring on the cuticle and the broken hair on the left. Scale bar = 50  $\mu$ m.

The middle shaft of the horn was contacted in 21% of the fights observed (Table 1). These fights primarily involved males crossing their horns and pushing laterally to knock their opponent off-balance. No encounters were observed where males used the base of their horns.

**Ultrastructure of Horns.** Both the cuticular morphology and the distribution of sensilla were markedly different between the anterior and posterior faces of the horn. The cuticle on the anterior face of the horn was covered with smooth bumps, like a field of rolling hills and valleys (Fig. 2A). However, the anterior face was also pockmarked in many places with scars and gashes (Fig. 2B), which were conspicuously absent from the posterior face of the horn. The anterior face was densely covered with sensory hairs, which were often found in the valleys between cuticular hills. The hairs had a smooth surface and were set in a socket (Fig. 2B), which suggests that they are mechanosensory sensilla (McIver 1975, Hiraguchi et al. 2003).

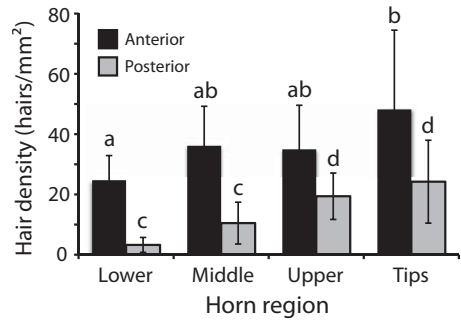
In contrast to the smooth anterior face, the posterior face of the horn was covered in overlapping scales (Fig. 3A and B). Previous studies indicate that these "scales" may represent the outline of individual epidermal cells (Green and Hartenstein 1997). Hairs on the posterior face generally occurred in circular or ovoid depressions (Fig. 3B). Like the hairs on the anterior face, the posterior hairs had a smooth surface,



**Fig. 3.** Scanning electron micrographs of the posterior face of the horn. (A) Ultrastructure of the scaly cuticle surface. (B) Enlarged view of a sensory hair and pit gland (arrowhead). Scale bar = 50  $\mu\text{m}$ .

and were set in deep sockets. Thus, the sensilla on both the anterior and posterior faces exhibited the shaft and socket morphology characteristic of mechanoreceptors (McIver 1975, Harbach and Larsen 1977, McIver and Siemicki 1984, Hiraguchi et al. 2003).

We found no pores at the tip of the hair or along the hair shaft for any of the sensilla on the anterior or posterior faces. This observation suggests that the hairs primarily function as mechanoreceptors, rather than chemoreceptors (Jez and McIver 1980, Fauchaux 1991), although additional transmission electron microscopy investigations are necessary to determine if the hairs are indeed aporous. The cuticle on both the anterior and posterior faces had many deep pits, which



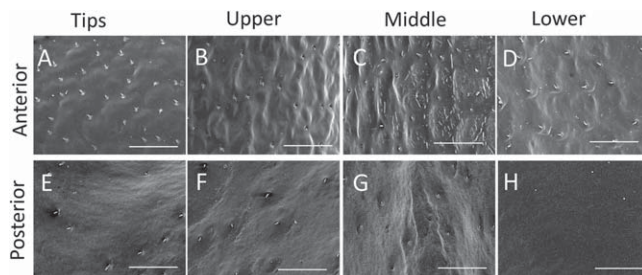
**Fig. 5.** Average hair density (mean  $\pm$  SD) for the four horn regions on the anterior (black bars) and posterior (gray bars) faces of the horn. Different letters denote means that are significantly different from each other ( $P < 0.05$ ; Tukey's test). Hair density increased distally from the lower shaft to the tines for both the anterior and posterior faces.

were often closely associated with the hairs. The pits were  $\approx 2 \mu\text{m}$  in diameter on both the anterior and posterior faces, and are probably the pores of dermal glands (Harbach and Larsen 1977, Quennedey 1998).

There were significantly more hairs on the anterior face than on the posterior face of the horn ( $T = 8.31$ ;  $df = 118$ ;  $P < 0.001$ ). Average hair density (mean  $\pm$  SD) was  $14.3 \pm 11.8$  hairs/ $\text{mm}^2$  on the posterior face and  $36.3 \pm 18.6$  hairs/ $\text{mm}^2$  on the anterior face (Fig. 4). Many of the hairs on the anterior face were broken, although how the hairs were damaged (e.g., during fights or from digging through the soil) is unknown. Hair density increased distally along the length of the horn for both anterior (ANOVA:  $F_{3,67} = 5.8$ ,  $P = 0.001$ ) and posterior (ANOVA:  $F_{3,68} = 20.7$ ,  $P < 0.001$ ) faces (Fig. 5). Specifically, hair density was two times greater at the horn tips than on the lower shaft on the anterior face, and 7.5 times greater at the tips compared with the lower shaft on the posterior face. The density of sensilla was highest at the tips on the anterior face ( $48.2 \pm 26.3$  hairs/ $\text{mm}^2$ ) and lowest at the lower shaft on the posterior surface ( $3.2 \pm 2.5$  hairs/ $\text{mm}^2$ ).

**Discussion**

This study is the first to examine the distribution of sensory sensilla for any insect weapon. We combine



**Fig. 4.** Scanning electron micrographs showing the distribution of sensilla on the four horn regions for the anterior (top row) and posterior (bottom row) faces. (A and E) Tips, (B and F) upper shaft, (C and G) middle shaft, (D and H) lower shaft. Scale bar = 250  $\mu\text{m}$ .



these observations with an analysis of how *T. dichotomus* males use their horns during fights to investigate the potential functional significance of variation in hair density along the length of the beetles' horns.

We found an association between the density of sensory hairs and the regions of the horns that were used most during combat. Specifically, we found that hair density was the highest at the distal tips of the horns, and that this horn region was also the most likely to be in contact with an opponent during male-male fights. The hairs on both the anterior and posterior face had a smooth surface and were set in deep cuticular sockets surrounded by pit glands, which matches the morphology of mechanosensory sensilla in other insects (McIver 1975, Harbach and Larsen 1977, McIver and Siemicki 1984, Quennedey 1998, Hiraguchi et al. 2003, Page and Matheson 2004). Therefore, we expect that the hairs on *T. dichotomus* head horns provide males with tactile information during fights. Mechanosensory input may be beneficial to males by allowing them to detect the relative position of an opponent and continuously adjust the placement of their horn over the course of a contest.

Because the tips are likely to be the first horn region to contact an opponent during a male-male encounter, the hairs at the tips of the horns may also be important before actual combat by allowing males to assess the size and condition of their opponents. Both the anterior and posterior surfaces were covered with the pits of dermal glands, and it is possible that these pit glands secrete chemicals that signal a beetle's size or condition (Faustini and Halstead 1982, Quennedey 1998). However, we did not find any distinct pores on the tip of the hairs or along the hair shaft, which are characteristic of chemosensory sensilla (Jez and McIver 1980, Faucheux 1991). Future studies, including electrophysiological investigations and detailed observations by using transmission electron microscopy of the cross-sections of the sensilla, are therefore necessary to determine if the hairs are capable of detecting chemical stimuli. Moreover, experimental ablations of the hairs on different horn regions and additional behavioral studies will be important to elucidate how important the sensilla are in allowing males to assess their competitors and effectively wield their horns during fights.

We did not detect any differences in the distribution of hairs among males of different body sizes; hairs were always more abundant on the anterior face than on the posterior face, and hairs increased distally from the lower shaft to the horn tips. However, our sample sizes were quite small, and additional studies may find more subtle differences in the patterns of sensilla distribution between large and small males. In many species of horned beetles, small "minor" males use alternative reproductive tactics and avoid competitively superior "major" males (Eberhard 1982, Rasmussen 1994, Emlen 1997). Interestingly, even small *T. dichotomus* males sometimes engage in fights with rival males (Hongo 2007; E.L.M. unpublished data). Therefore, we expect that small and large *T. dichotomus* males alike will benefit from having sensory hairs that are concentrated at the tips of their horns.

Beetle horns are typically described as dedicated weapons (Bonduriansky 2007). That is, they are used exclusively in the context of male-male combats (Eberhard 1979, 1980). Our results, however, indicate that head horns of *T. dichotomus* may also play an important role as a sensory structure. The thoracic horns of many other rhinoceros beetles (e.g., *Dynastes* spp. and *Golofa* spp.) are densely covered with hairs (Mizunuma 1999), so it is highly likely that these horns have a sensory role as well. *T. dichotomus* males also have several very long sensory hairs on the undersides of their thoracic horns (unpublished data), yet more detailed analyses are necessary to determine if the sensilla on the head and thoracic horns are homologous structures. Furthermore, phylogenetic studies may be important to decipher whether head horns evolved first as a weapon with few sensilla that eventually gained greater sensory capabilities, whether horns emerged first as a sensory organ that were then also used as a weapon in male-male combats, or whether the density of sensory hairs and the elongation of horns evolved in concert. Given the low abundance of sensory hairs on the lower shaft of the horn and particularly on the posterior surface, we expect that horns evolved first and foremost as a sexually selected weapon, but that increases in the density of sensory hairs allowed these structures to be used more effectively during combat. Whether the sensilla on the horns also provide sensory input in contexts other than male-male fights (e.g., as proprioceptors during flight) remains to be tested.

**Acknowledgments**

We thank Doug Emlen, Laura Lavine, and Keaton Wilson for valuable comments on earlier versions of this manuscript, and Paul Weingarden for his help with preliminary scanning electron microscopy observations. We are also grateful to Jim Driver at the UM Electron Microscopy facility and the staff at the WSU Franchesi Microscopy Imaging Center for their guidance. Funding for this project was provided by the National Science Foundation (DGE-0809127 and OISE-0912433 to E.L.M.).

### Acknowledgments

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Received 20 December 2012; accepted 4 June 2013.