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Comparative trichome morphology in feather-legged assassin bugs (Insecta: Heteroptera: Reduviidae: Holoptilinae)

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Abstract

The trichome in ant-feeding Holoptilinae (Insecta: Heteroptera: Reduviidae) comprises remarkable modifications of abdominal sternites 2 and 3. It has been hypothesized that this structure plays a role in attracting and drugging ants. In the present study the trichome of 14 species of Holoptilini, comprising 11 species of *Ptilocnemus* Westwood and representatives of three additional genera of Holoptilini, is examined using scanning electron and light microscopy. The astoundingly diverse species-level modifications of sternites and vestiture are described and primary homology hypotheses are proposed. The trichome provides species-specific diagnostic characters within *Ptilocnemus* and evidence for species-groups within the genus, but also for the sistergroup relationship of *Ptilocnemus* and *Smiliopus* Bergroth. The comparative morphology establishes a framework for investigations into systematics, functional morphology, and behavioral ecology of these myrmecophagous assassin bugs.

Keywords: Reduviidae; Formicidae; Ant predator; Morphology; Homology; Systematics

1. Introduction

The subfamily Holoptilinae or "feather-legged" assassin bugs (Insecta: Heteroptera: Reduviidae) comprise myrmecophagous species, which exhibit fascinating and specialized ant capture and feeding behaviors (Jacobson 1911, McKeown 1945; Malipatil 1985; Hölldobler and Wilson 1990; Cassis and Gross 1995; Weirauch and Cassis 2006). Jacobson observed the Javanese species, *Ptilocerus venosus* (Walker, 1873), luring and drugging *Dolichoderus* ants; he postulated that an elevation on the second abdominal sternite beset with a "tuft of hairs", the so-called *trichome*, was central to prey capture. McKeown (1945) reported that the Australian species *Ptilocnemus femoralis* Horvath, 1902 also possesses a trichome and lures ants in a similar fashion to *P. ochraceus*. Miller (1956) and Carayon et al. (1958) first proposed that the trichome is associated with glands and may be the source of ant-luring substances.

Much of what is known about this ant–bug interaction, both in terms of the behavioral ecology and functional morphology, is based on the limited natural history observations. In response, Weirauch and Cassis (2006) made detailed observations, including histology,

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of the trichome morphology of an Australian holoptiline species [*Ptilocnemus lemur* (Westwood, 1840)], as part of an ongoing comparative research program on feather-legged bugs. They established the existence of unicellular glands on the trichome of *P. lemur* and found additional glandular areas on the lateral parts of the abdominal sternites. The trichome is relatively complex in this species, involving vast modifications of the anterior abdominal sternites and specialized vestiture (Weirauch and Cassis 2006).

The Holoptilinae are a small subfamily of Reduviidae, with less than 80 described species. They are nested within the Phymatine complex at the base of the Reduviidae (Carayon et al. 1958; Weirauch 2008). Holoptilinae are diagnosed on the basis of the long setae on body and appendages and the reduced wing venation (Schuh and Slater, 1995); potential synapomorphies are the desklerotisation of the corium, the loss of the fore tibial cleaning comb, and the swollen basiflagellomere (Weirauch, unpub). Holoptilinae are widespread in the Eastern Hemisphere, with species in the Ethiopian, Oriental, and Australian zoogeographical regions. The subfamily comprises 15 recent genera in three tribes (Wygodzinsky and Usinger 1963, Maldonado 1990), Aradellini (2 genera), Dasycnemini (5 genera), and Holoptilini (8 genera). Trichomes occur in all 8 genera of the Holoptilini and the tribe was diagnosed on the basis of this character (Wygodzinsky and Usinger 1963). All Aradellini and Dasycnemini lack the trichome. *Ptilocnemus* Westwood has nine species, eight restricted to mainland Australia (Malipatil 1985; Maldonado 1990). Rigorous tests, based on cladistic analyses, of the tribal and genus-level classification are nonexistent and relationships within the group are unknown.

In this contribution, we document trichome morphology of eight described and three undescribed species of *Ptilocnemus* Westwood, 1840, members of three additional Holoptilini genera (*Holoptilus* Lepeletier and Serville, 1825, *Ptilocerus* Gray, 1832, and *Smiliopus* Bergroth, 1901), and the abdominal sternites of a single species of Aradellini (*Aradellus* Westwood, 1874) that lacks the trichome. We propose homology statements of trichome elements and test them in a cladistic framework with the aim of establishing a comparative foundation for future ecological and evolutionary studies.

2. Materials and methods

2.1. Material examined

Eleven species of *Ptilocnemus* were examined, including three undescribed species, herein referred to as *Ptilocnemus* sp. #1, #2 and #3. Malipatil (1985) synonymized *Ptilocnemus vittatus* Miller, 1950 with *Ptilocnemus pallidus* Miller, 1950; in contrast, we found differences in trichome structure between these taxa, and we treat them as distinct in this work.

Specimens were borrowed from the following institutions (acronyms to be used hereafter): AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, Canberra; NTMAG, Northern Territory Museum of Arts and Sciences, Darwin; SAMA, South Australian Museum, Adelaide; UCR, University of California Riverside. The following species were examined: *Ptilocnemus borealis* Malipatil, 1985 [AM]. *Ptilocnemus distinctus* Malipatil, 1985 [SAMA]. *P. femoralis* Horvath, 1902 [AM]. *Ptilocnemus kakaduensis* Malipatil, 1985 [NTMAG]. *P. lemur* (Westwood, 1840) [AM]. *P. pallidus* Miller, 1950 [AM]. *Ptilocnemus sidnicus* Mayr, 1865 [ANIC]. *P. vittatus* Miller, 1950 [AM]. *Ptilocnemus* sp. 1, Victoria [ANIC]. *Ptilocnemus* sp. 2, South Australia [NTMAG]. *Ptilocnemus* sp. 3, Tasmania [ANIC]. **Other Holoptilini**: **Aradellini**: *Aradellus* sp. [AM]: **Holoptilini**: *Holoptilus* sp., South Africa [AM]. *Ptilocerus* sp., Indonesia [AM]. *Smiliopus quadrinotatus* (Reuter, 1881) Australia [AM]. **Phymtinae**: **Phymatini**: *Phymata pacifica* Evans, 1931 [UCR].

2.2. Light microscopy and macrophotography

The abdomen of dried specimens was removed from the thorax, macerated in KOH (approx. 10%), and the abdominal tergites were separated from the sternites. Dissections were examined in glycerin using a Nikon SMZ 1800 dissecting microscope and a Nikon Eclipse 801 compound microscope. The sternum was imaged in ventral perspective using a Microptics-USA photographic system with an Infinity Photo-Optical K-2 lens system and a Canon EOS 1D digital camera. For some individuals, 5–10 images were taken at different focal planes and merged with Helicon Focus 4.16 software.

2.3. SEM

Specimens were cleaned, dried, and sputter coated. For *P. kakaduensis* (paratype) and the three undescribed species, uncoated specimens were examined due to limited availability of specimens. Coated specimens were either observed and documented using a Leo 435VP (Australian Museum), a Hitachi S-4700 (American Museum of Natural History), or a Philips XL30 (Imaging Core Facility, University of California, Riverside). All uncoated specimens were studied using a Hitachi TM-1000 Tabletop Scanning Electron Microscope (Center for Plant Cell Biology, University of California, Riverside). Scale bars are in micrometers unless indicated otherwise.