

Review of the Oriental genus *Hesperomimus* CAMERON, 1937 with descriptions of two new bamboo-inhabiting species feeding on mosquito larvae and reflections on the invasion of the aquatic habitat by rove beetles (Coleoptera: Staphylinidae: Staphylininae)

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Abstract

The genus *Hesperomimus* CAMERON, 1937 (Coleoptera: Staphylinidae: Staphylininae) and its type species, *H. abdominalis* CAMERON, 1937, are redescribed. Two new species, *H. bambusae* sp.n. from West Malaysia and *H. ruficollis* sp.n. from northern Thailand, and their immature stages are described and illustrated (*H. bambusae*: first and third instar, male pupa; *H. ruficollis*: third instar exuvia, female pupa). Both new species are specialized inhabitants of water-filled internode cavities of immature bamboo culms of *Gigantochloa*, *Dendrocalamus*, and *Cephalostachyum*. The specimens were found in internodes up to eight meters high, which they had entered through small holes bored by larvae of *Lasiochila* spp. (Coleoptera: Chrysomelidae). Both *Hesperomimus* species feed on mosquito larvae. *Hesperomimus ruficollis* captures its prey from the water's edge, while *H. bambusae* adults and their larvae also hunt in the water. The biology of *Hesperomimus* and their adaptations to their habitat are outlined and compared with other bamboo-inhabiting Staphylinini hunting mosquito larvae (*Hesperus* FAUVEL, 1895, *Platydracus* THOMSON, 1858, *Acylophorus* NORDMANN, 1837). We assume that the rich source of mosquito larvae as food was the selective force leading to the colonization of bamboo internodes by Staphylininae. The low predatory pressure occurring in bamboo internodes enabled them to penetrate into the water and develop adaptations to the aquatic lifestyle.

Key words: Coleoptera, Staphylinidae, Staphylininae, Staphylinini, Philonthina, *Hesperomimus*, re-description, new species, larva, pupa, taxonomy, systematics, bionomics, bamboo phytotelmata, *Gigantochloa*, *Dendrocalamus*, *Cephalostachyum*, *Lasiochila*, Culicidae.

Introduction

Over the past few decades, the junior author carried out extensive fieldwork in West Malaysia and northern Thailand to study the fauna associated with bamboo. His focus was on insects occurring in water-filled cavities of bamboo internodes ("bamboo phytotelmata"). Insect specimens accumulated during these studies comprised several species of rove beetles belonging to the subfamily Staphylininae: *Hesperus kovaci* SCHILLHAMMER, 2002 (Peninsular Malaysia), *Platydracus gemmatus* (FAUVEL, 1895), *Platydracus* sp. (Peninsular Malaysia), two undescribed species of *Hesperomimus* CAMERON, 1937 (Peninsular Malaysia, northern Thailand) and *Acylophorus* sp. (Peninsular Malaysia, northern Thailand).

Staphylininae and their immature stages live in moist habitats such as leaf litter, rotting fruits, dung, carrion, accumulations of seaweed or other decaying organic matter. Adults and larvae are predatory, usually live in the same habitat and feed on terrestrial insects. Only a few Staphylininae living in phytotelmata are known to capture aquatic organisms such as mosquito larvae. In the Neotropical Region, these are *Odontolinus fasciatus* SHARP, 1885, *Belonuchus cephalotes* (SHARP, 1885), *B. satyrus* ERICHSON, 1840, *B. rufipennis* (FABRICIUS, 1801), *Platydracus orizabae* (BERNHAEUER, 1917), *P. fauveli* (SHARP, 1884), *P. gracilipes* (SHARP, 1884) and *Platydracus* sp., which live obligately or facultatively in water-filled bracts of *Heliconia* (Zingiberales: Heliconiaceae) (SEIFERT & SEIFERT 1976, FRANK & BARRERA 2010, FRANK & MORON 2012). In the

Oriental Region, *Hesperus kovaci* and *Acylophorus* sp., which inhabit water-filled cavities of bamboo internodes, also feed on mosquito larvae (KOVAC & STREIT 1996, SCHILLHAMMER 2002). Phytotelmata-inhabiting Staphylininae hunt aquatic organisms from the water's edge (SCHILLHAMMER 2002), immerse their heads and thorax and snap at passing Diptera larvae ("fishing", FRANK & MORON 2012) or even dive into the water to catch prey (SEIFERT & SEIFERT 1976).

In the present paper, we focus on morphology, biology and ecology of the two newly described *Hesperomimus bambusae* sp.n. and *H. ruficollis* sp.n., which are specialized inhabitants of living immature bamboo culms and feed on mosquito larvae. We describe *Hesperomimus* adults as well as their larvae and pupae where available, discuss adaptations to their aquatic habitat, report on larvae of *Lasiochila* WEISE, 1916 (Coleoptera: Chrysomelidae: Hispinae), which create the entrance holes for *Hesperomimus* and outline the composition of the animal community occurring in their secluded habitat. Furthermore, we present scattered data on other Southeast Asian bamboo-inhabiting Staphylininae feeding on mosquito larvae. Finally, we hypothesize on why phytotelmata-inhabiting Staphylininae are the only rove beetles known so far to capture aquatic organisms.

Material and methods

Specimens of *Hesperomimus bambusae* sp.n. were collected in Peninsular Malaysia in 1993, 1995, 1996 and 1999. The collecting sites were located in Selangor, near Kuala Lumpur, on the western slopes of the Main Range and in Hulu Perak, near the Malaysian-Thai border. The main study site was located at the Ulu Gombak Field Studies Centre (University of Malaya, altitude ca. 250 m). Additional collecting took place in the nearby Genting Highlands (altitude ca. 900 m). Specimens from Hulu Perak were collected during two short expeditions to the Temengor Forest Reserve (1–4 October and 27–31 December 1993) organized by the Malaysian Nature Society (Belum Expedition). All specimens from Malaysia were collected between August and January.

Specimens of *Hesperomimus ruficollis* sp.n. were collected in northern Thailand in the Mae Hong Son Province, Pangmapha District, near Ban Nam Rin (altitude 600–900 m) in 2002, 2003, 2004, 2007, 2008 and 2022. All specimens from northern Thailand were collected between October and April.

The climate in Peninsular Malaysia was considerably different from that of northern Thailand. In Peninsular Malaysia, the rainy season was approximately between August and December, but it rained throughout the year to varying degrees, and humidity and temperature remained high. In northern Thailand, the rainy season was approximately between mid-May and mid-October. During the remaining months, rain was scarce or lacking. Between November and mid-February climate was cool and night temperatures sometimes decreased to about 10 °C (cold season), between mid-February and end of April the climate was hot, fires were frequent and day temperatures often rose up to 40 °C (hot season).

For the collection of *Hesperomimus* specimens, immature bamboo culms of *Dendrocalamus*, *Gigantochloa* and *Cephalostachyum*, already several meters high, were felled. Internodes possessing holes were cut open with a folding saw and a parang (large knife). The length of the bamboo culms, dimensions of internodes, thickness of the bamboo walls and size of holes were measured with a flexible tape and slide callipers, the amount of water collected in the internode cavities with a measuring cylinder. Specimens were collected with soft forceps or an aspirator. Beetles were killed with ethanol acetate. They were either pinned, glued or transferred to 70% ethanol for permanent storage. In the laboratory, specimens were kept individually in cut bamboo inter-

node pieces filled with water and sealed with gauze. Feeding trials were conducted in small glass tubes (20 ml) or in cut internodes. *Hesperomimus* specimens were not fed for one week prior to the feeding trials. Specimens immersed in water were photographed in small glass aquaria.

The distribution of *Hesperomimus* and the composition and succession of the animal community occurring in their habitat were investigated during two long-term studies.

Long-term study I: A battery-operated drill was used to create observation holes in 100 internodes of immature *Gigantochloa scortechinii* culms at the Ulu Gombak Field Studies Centre. The culms were 2–3 m high and the diameter of the holes was 9 mm. Each hole was drilled in the center of accessible lower internodes, which were freshly pierced by larvae of *Lasiochila goryi* (GUÉRIN-MENEVILLE, 1840). The artificial holes were used to observe the internode inhabitants by sliding a Classen rigid endoscope tube (diameter 8 mm) into the internode cavities. Observation holes were sealed with plastic stoppers when not in use. The composition of the fauna occurring in 100 internode cavities was checked daily between 13 August 1993 and 4 January 1994, except during the two short stays in Belum.

Long-term study II: On 4 October 1993, during the first stay in Belum, 100 easily accessible intact internodes of immature *Gigantochloa latifolia* culms lacking *Lasiochila goryi* holes were provided with artificial holes (diameter 9 mm). The culms were more than five meters high. The artificial holes remained open. They served as entrance holes for animals and allowed to lead the endoscope tube into the internode cavities. On 29 December 1993, during the second stay in Belum, the composition of the internode fauna was examined with the endoscope. Subsequently, culms containing *Hesperomimus* were felled and all internode inhabitants collected.

Other rove beetle species were collected in the same way as *Hesperomimus*. For the observation of *Acylophorus* and the collection of its prey items, “experimental internodes” were used, i.e., internodes of felled bamboo culms provided with a lid, which could be opened or closed for inspection (see KOVAC & STREIT 1996). Hundred experimental internodes were examined over a period of several months in three different years.

Terminology: Larval terminology follows STANIEC (2004), pupal terminology STANIEC & PIETRYKOWSKA-ZUDRUJ (2019), and bamboo taxonomy OHRENBERGER (1999).

Acronyms

BMNH	Natural History Museum, London, UK (M. Barclay, M. Brendell)
NMW	Naturhistorisches Museum Wien, Austria
SMF	Senckenberg Naturmuseum Frankfurt, Germany

Hesperomimus CAMERON, 1937

Typus generis: *Hesperomimus abdominalis* CAMERON, 1937.

REDESCRIPTION: Body form elongate, very slender, parallel; head and pronotum glabrous, with a few setiferous punctures; scutellum, elytra and abdominal tergites very densely punctate and pubescent; macrosetae as in most *Hesperus* FAUVEL, 1895.

Head (Figs. 2–4): Variably shaped, rounded quadrangular, egg-shaped or suborbicular, with moderately large, slightly protruding eyes; neck about half as wide as head, impunctate; mandibles slender, sickle-shaped, about as long as (♀) or conspicuously longer (♂) than head, sharply pointed, distal half moderately curved, lateral margin with furrow, bearing fine hairs, medial margin with one small, acute tooth, mandibular prostheca well developed; maxilla and entire labium (including respective palpi) of the *Hesperus*-type (Figs. 2, 5–6); mentum with one setiferous puncture in each antero-lateral corner, gular sutures contiguous for almost two thirds of their length.

Pronotum: Pronotal hypomera hardly deflexed, forming only very obtuse angle with dorsal face; superior line of pronotal hypomeron strongly bent ventrad, meeting inferior line well before anterior angles; prothoracic epimera absent.

Abdomen: Parallel; all tergites with only one basal line; first four visible tergites with basal depression; all tergites densely and uniformly punctate and pubescent, punctuation somewhat coarser in basal depressions; first four visible tergites with transverse row of setiferous punctures, equidistant between anterior and posterior margins, bearing exceedingly long, erect setae; posterior halves of tergites with dense silvery pubescence, forming transverse fasciae; posterior margin of tergite VIII with whitish seam of palisade fringe.

Ventral side: Prosternum triangular, rather flat, with acutely pointed prosternal process, pair of large prosternal setae lacking; mesoventrite triangular, with fine margin laterally, margin becoming obsolete toward apex, intercoxal process narrow, with rounded apex, middle coxae almost contiguous; metaventrite extremely elongate.

Legs: Very long and slender; mesocoxae unusually long; protarsus with first four segments moderately dilated in both sexes, slightly bilobed, bearing modified pale setae; spines on lateral faces of meso- and metatibiae rather fine, more resembling large setae; ventral face of fourth tarsomeres asymmetrically extended apico-laterad; segment five without empodial setae.

DIAGNOSIS AND SYSTEMATIC POSITION: Although habitually different, the genus shares a lot of characters with *Hesperus*, particularly the shape of the mouthparts and macrosetation; the lack of the two large prosternal setae and the abdominal tergites having only one basal line occurs in several species groups of *Hesperus*. It may be easily distinguished by the conspicuously parallel body shape, the pronotal hypomera forming only a very obtuse angle with the dorsal face of the pronotum, the conspicuously elongate metaventrite, the exceedingly dense punctuation of elytra and abdominal tergites and the presence of the dense silvery pubescence in posterior halves of tergites.

The genus is definitely closely related to certain species groups of *Hesperus*, the latter being probably polyphyletic in its current treatment. It was resolved as sister to *Hesperus babai* SHIBATA, 1990, *H. amabilis* KRAATZ, 1859 and *H. beijingensis* LI et al., 2010 by LI & ZHOU (2011), however, *Hesperus* and related genera are in need of a more thorough phylogenetic study with a larger data set, including molecular data.

Key to the species of *Hesperomimus*

- 1 Pronotum red; Thailand *ruficollis* sp.n.
- Pronotum black 2
- 2 Head (above eyes) wider than long; Java *abdominalis*
- Head (above eyes) as long as wide; West Malaysia *bambusae* sp.n.

Hesperomimus abdominalis CAMERON, 1937

Hesperomimus abdominalis CAMERON 1937: 17.

TYPE MATERIAL: **Holotype** ♀ (by monotypy): "Batoerraden G. Slamet. Java F.C. Drescher. 21.X.1928 \ M. Cameron Bequest. B.M. 1955-147 \ *Hesperomimus abdominalis* Cam. TYPE" (BMNH).

REDESCRIPTION: 12.5 mm long (reduced body length was not measured at the time when the holotype was studied). Black, elytra and first two visible tergites reddish-testaceous; mandibles dark reddish-testaceous, mouthparts reddish; first antennal segment yellowish, 2nd and 3rd segments reddish, 4th segment dark reddish-testaceous, remaining segments black, apical

segment slightly paler; legs yellowish; apical halves of middle and hind femora, tops of middle and hind tibiae and tarsi brownish; surface of head and pronotum very shining, due to very faint microsculpture.

Head (Figs. 2–3) suborbicular; slightly transverse (eyes included), 1.13 times as wide as long; tempora regularly arcuately narrowed toward neck; eyes very large, 1.57 times as long as tempora, distinctly prominent; chaetotaxy of head as in Fig. 3; antennal segment 4 very slightly oblong, penultimate segments distinctly transverse; pronotum oblong, 1.24 times as long as wide, widest at anterior angles; distinctly, slightly concavely narrowed toward base; surface impunctate (i.e. no dorsal rows of punctures), almost regularly vaulted; peripheric parts with few large setiferous punctures; both head and pronotum with exceedingly fine scattered punctures; elytra slightly longer than pronotum, exceedingly densely punctate, covered with golden-yellow pubescence; punctation and pubescence of scutellum likewise.

First four visible abdominal tergites with deep transverse basal impression; first five visible tergites with basal half moderately densely and rather coarsely punctate, with dark pubescence; apical half with much denser and finer punctation, with silvery pubescence; tergite VIII more finely punctate at base, more coarsely and sparingly punctate apically.

Male unknown.

DISTRIBUTION: The species is at present known only from the type locality.

Hesperomimus bambusae sp.n.

TYPE MATERIAL: **Holotype** ♂: “W-MALAYSIA: E Gerik, 30.12.1994, Belum-Expedition, leg. D. Kovac \ im Sproß von [in shoots of] *Gigantochloa latifolia* \ Senckenberg Museum Frankfurt/Main” (SMF). – **Paratypes** (7 exs.): 1 ♂: same data as holotype (NMW); 3 exs.: similar data as holotype, but 28.12.1993 (1 ♀ SMF, 1 ♂ NMW, 1 ♀ BMNH); 2 exs.: “Selangor, 13 1/2 ml. Ulu Gombak, 28.10.[19]58 \ N° 0874 From Internode of *Dendrocalamus pendulus* \ Pres. by Com. Inst. Ent. B.M. 1962-2” (1 ♂ BMNH, 1 ♀ NMW); 1 ♂: “25.11.93 Malaysia/Gombak, in the internode of *G. scortechinii*, shoot No 22 Int No 2, leg. D. Kovac” (BMNH).

DESCRIPTION: Habitus (Fig. 1). 11.5–13.5 mm long (6.3–6.8 mm, abdomen excluded). Coloration identical with that of *H. abdominalis* but last segment of antennae distinctly reddish; also very similar in body shape, but differing as follows: head (Fig. 4) as long as wide (eyes included), with setiferous punctures more numerous; tempora longer, eyes 1.00–1.12 times as long as tempora; maxillary and labial palpi more elongate; pronotum more oblong, 1.40–1.45 times as long as wide, distinctly flattened dorsally, with narrow, moderately deep median furrow occupying basal half or 2/3 of pronotal length; basal marginal bead slightly widened medially; disc (in addition to large setiferous punctures) with a group of sublateral punctures in posterior third; head and pronotum with distinct microsculpture, formed by exceedingly fine striae, causing distinct iridescence, especially on pronotum; elytra longer, male with longitudinal lateral carina; punctation on tergites denser.

Male sternite VIII: Fig. 12; male sternite IX: Fig. 14; male tergite X and stylus of tergite IX: Fig. 15; gonocoxites of female genital segment: Fig. 13.

Aedeagus (Figs. 7–9): Median lobe rather slender, apical portion very narrow in ventral view, in lateral view distinctly bent dorsad, bearing conspicuous dent-like extension dorsally; paramere transparent, very large, covering basal two thirds of median lobe; peg setae lacking; internal sac (Fig. 9) with pair of conspicuous sclerites usually protruding laterad.

Egg: Eggs white, relatively large and striped.

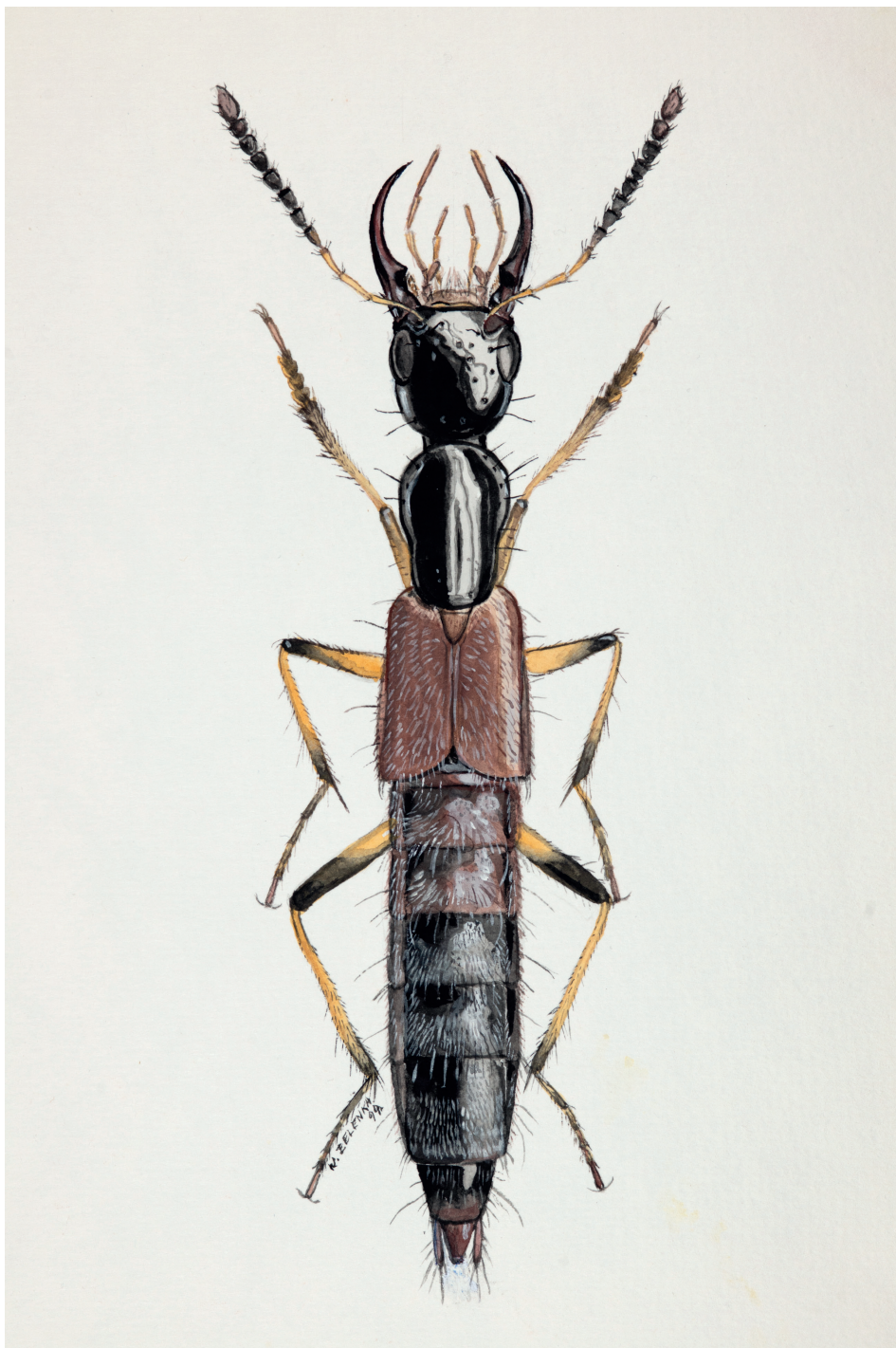
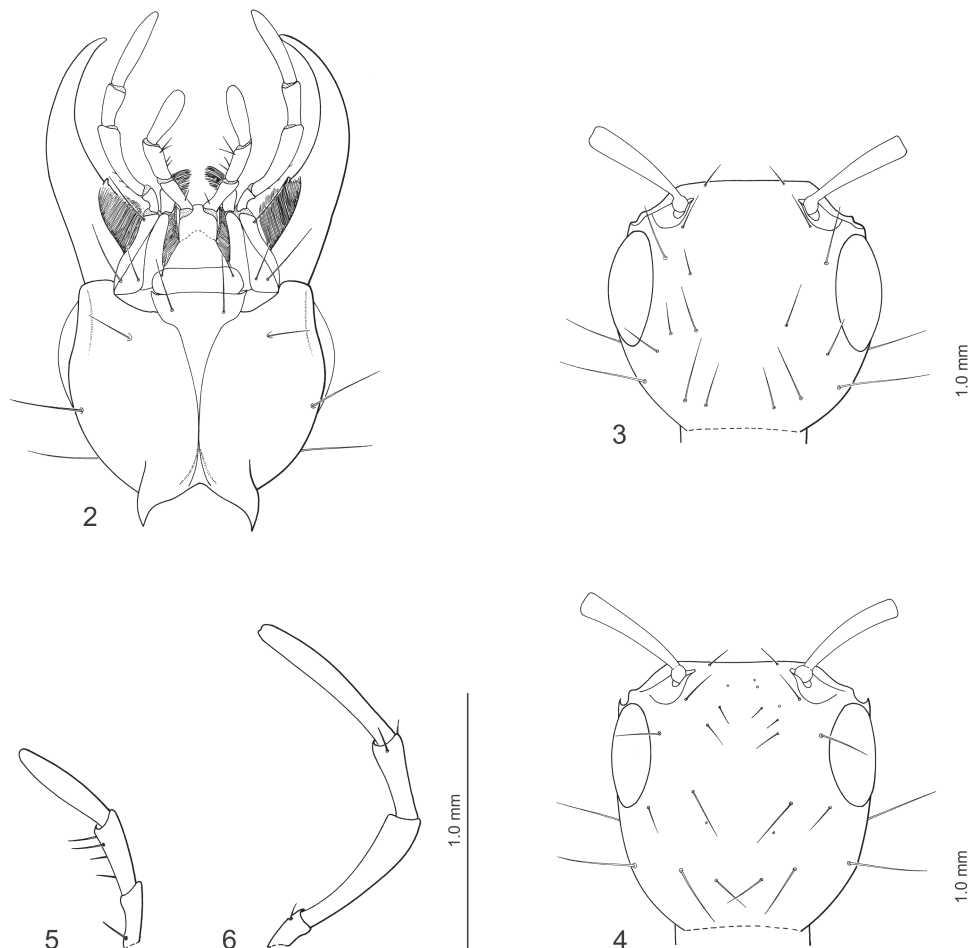


Fig. 1: *Hesperomimus bambusae*, habitus.



Figs. 2–6: *Hesperomimus abdominalis* (2–3) and *H. bambusae* (4–6): 2) head, ventral view; 3) same, dorsal view; 4) head, dorsal view; 5) labial palpus; 6) maxillary palpus.

Third instar larva (L3):

MATERIAL EXAMINED: 1 third instar larva, West Malaysia, Hulu Perak, Temengor Forest Reserve, collected from internode of immature *Gigantochloa latifolia* culm, 29 December 1993, D. Kovac (SMF); 1 third instar exuvia, idem, retrieved from pupal cell found in internode of immature *G. latifolia* culm, 28 December 1993, D. Kovac (SMF); 1 third instar exuvia, idem, retrieved from pupal cell found in internode of immature *G. latifolia* bamboo culm, 29 December 1993, D. Kovac (SMF); 1 third instar exuvia, idem, retrieved from pupal cell found in internode of immature *G. latifolia* bamboo culm, 30 December 1993, D. Kovac (SMF).

DESCRIPTION: Length: 12.5 mm, greatest width (forehead): 1.7 mm, pronotum width: 1.4 mm. Color: Yellowish-brown. Body long and narrow, pronotum twice as long as meso- or metanotum, first abdominal segment narrower than metanotum, following abdominal segments slightly widened toward segment V (width: 1.5 mm) and then gradually narrowing toward terminal part of the body. Macro- and microsetae usually simple, macrosetae on abdomen frayed with two or more points apically.

Head: Prognathous, triangular, tapering posteriorly, head width 1.6 mm, about 1.2 times as long as broad, four stemmata on each side of the head, ventral side of head with two slightly curved tentorial pits (Fig. 17). Antenna with four segments, length ratio of segments I–IV 1:1.9:1.5:0.9, segment I with one pore, segment II with at least one pore, segment III with three macrosetae, one club-shaped sensory appendage and two indistinct structures (solenidia? pores?), segment IV with three setae and four solenidia apically. Nasale on anterior margin of head with nine teeth, median tooth triangular, paramedian teeth almost twice as long as median tooth, neighbouring pair of teeth slightly smaller than paramedian teeth, third and fourth neighbouring teeth much smaller than preceding ones. Seven pairs of mid-sized setae and four pairs of small setae on dorsal portion of head. In addition, eight setae placed between teeth of nasale (Fig. 16), setae mostly small but between second and third teeth 2–3 times as long as remaining ones. Two sense organs and two pores in apical portion of dorsal head. Six large setae on ventral portion of head, one pair in area below mandibles, one pair in central part of head and one pair in basal part, additional small seta laterally at the base of mandible. Mandible falciform, slender with two setae laterally and two pores dorsally.

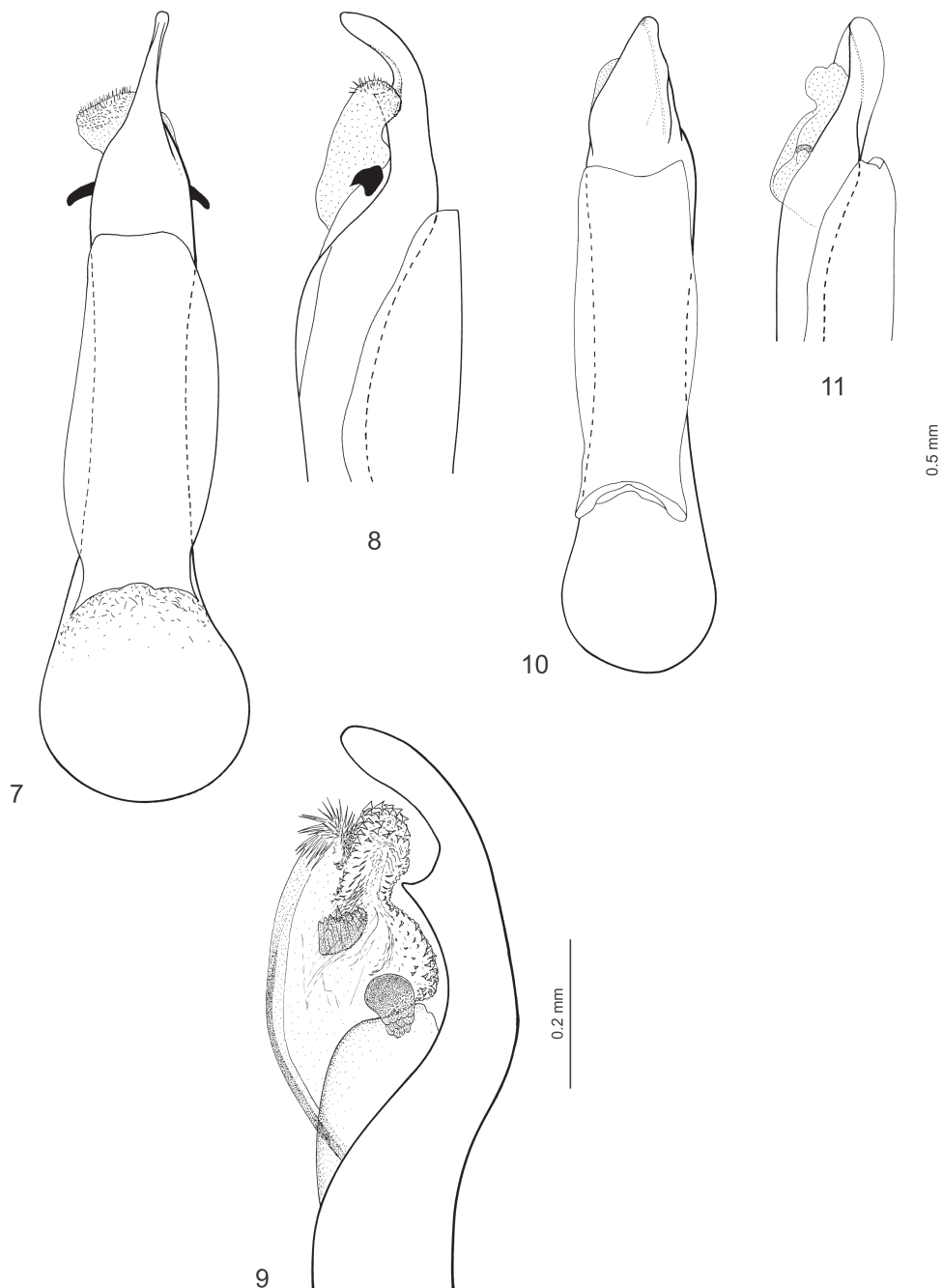
Maxilla (Fig. 17): Length ratio of cardo and stipes 1:1.2; cardo rectangular, 1.8 times as long as wide, bearing one seta on outer ventral margin, stipes with nine setae and two pores, mala conical, tapering towards apex, 2.4 times as long as wide at the base, two microsetae dorso-apically, maxillary palp four-segmented, length ratio of segments I–IV: 2.2:3.7:2.5:1; segment I with two pores; segment II with one seta on inner margin, one seta on outer margin and two pores ventro-apically; segment III with one sensory appendage basally on outer margin and one pore apically; segment IV with one pore.

Labium (Fig. 17): Ventral side of prementum sclerotized, apically with two setae and two microsetae, sclerites extending around margins to dorsal side of prementum; dorsal side membranous and pubescent. Ligula conical, about as wide as segment I of labial palps, with two microsetae. Apotome with six setae and four pores, distinctly extending behind tentorial pits. Labial palps three-segmented; length ratio of segments I–III: 5:2.3:1; segment I with one pore on inner margin; segment III with one pore on outer margin and a few micro-sensory appendages apically.

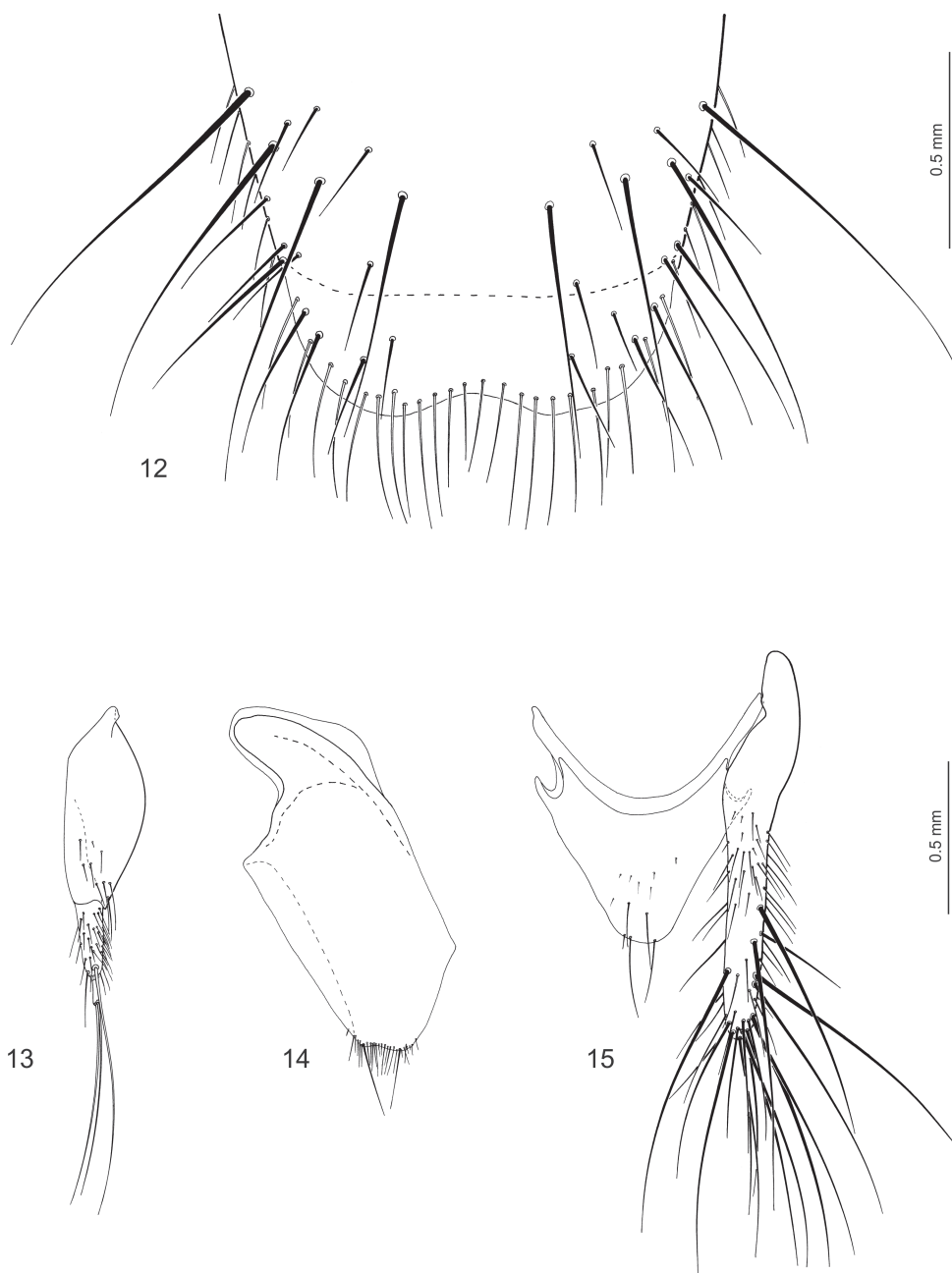
Thorax: Pro-, meso- and metanotum sclerotized and smooth, with two transverse brown lines near the anterior and posterior edges and mid-longitudinal ecdysial lines, dorsal pronotum with 10 macrosetae, on each side of the body two setae near anterior edge of pronotum, two setae near the posterior edge of pronotum and one seta laterally, closer to the posterior seta, only two microsetae medially near the anterior edge and additional microsetae laterally and ventrally, a pair of sensilla laterally in anterior half of pronotum; dorsal mesonotum and metanotum with 10 macrosetae and two microsetae each, same distribution as on pronotum.

Cervicosternum not clearly visible. Coxa with about 15 micro- and macrosetae and several pores, trochanter with six setae and several pores or sensilla. Femur with about 30 micro- and macrosetae, all macrosetae (about 12) on ventral face, several pores present. Protibia with about 40 micro- and macrosetae (macrosetae mostly ventral, partly spine-shaped), and one pore. Length ratio of femur and protibia: 1.3:1. Tarsungulus with three pairs of spine-shaped setae dorso-laterally (Fig. 25).

Thorax with a pair of large oval spiracles located laterally between pro- and mesothorax, greatest width of spiracular openings 0.12 mm.



Figs. 7–11: Aedeagus: *Hesperomimus bambusae*: 7) ventral view; 8) lateral view; 9) internal sac, lateral view; *H. ruficollis*: 10) ventral view; 11) lateral view.



Figs. 12–15: *Hesperomimus bambusae*: 12) male sternite VIII; 13) gonocoxites of female genital segment; 14) male sternite IX; 15) male tergite X and stylus of tergite IX.

Abdomen: First abdominal tergite chitinous and smooth with mid-longitudinal ecdysial line and a medial transverse brown line, four large setae along anterior edge, abdominal tergites and sternites II–VIII with uneven surface, divided by membranous area mid-longitudinally, each tergite with two macrosetae postero-laterally, remaining setae small and irregularly distributed, lacking along anterior margin, longer and more densely distributed in the posterior half of tergite. Pleural membranes of abdominal segments II–VIII each with a long and narrow chitinous dorsal paratergite and ventral parasternite, paratergites with two setae at each end, parasternites with one seta at posterior end, setae becoming longer towards the posterior end of abdomen. Tergites I–IX with segmental campaniform sensillum on sides. Tergite IX with four large setae along posterior margin and a pair of two-segmented, slender urogomphi; segment I with 18 setae and several pores; segment II with two setae, one at proximal third and one apically, length ratio of segments I, II and apical seta 2:1:0.6. Pygopod, abdominal segment X, about 2.2 times as long as segment IX, distinctly shorter than urogomphi (excluding apical seta); dorsal side with ca. 20 micro- and macrosetae, few bifurcate setae on dorsal side and a few pores.

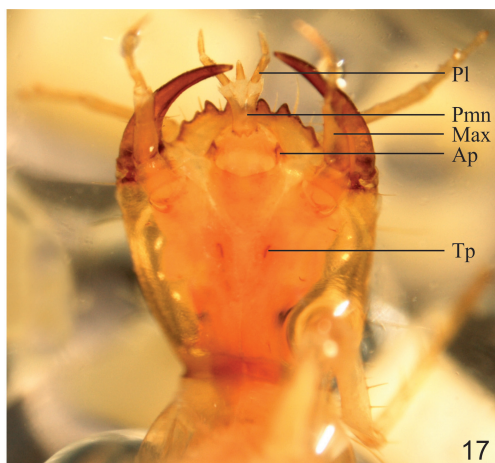
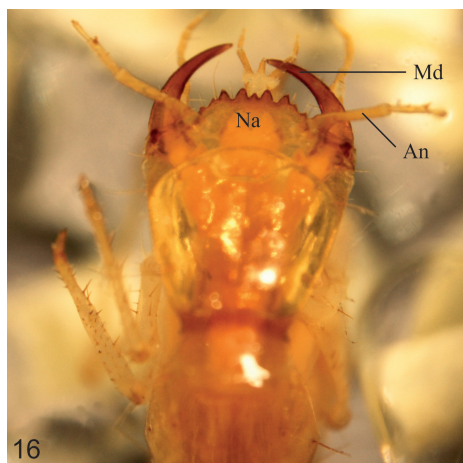
Abdominal segments I–VIII each with a pair of spiracles, first abdominal spiracles located between tergites and paratergites, annular and smaller than metathoracic spiracle (diameter 0.08 mm), opening pointing to the side, abdominal spiracles II–VIII shifted dorsad, with tube-like bulbous wall extensions with the openings pointing upwards or slightly tilted backwards, walls enlarged laterally, inner margin of enlarged area with triangular projections pointing towards the center of the spiracle, spiracle openings closed by projections, projections and inner walls densely covered with hydrofuge microstructures, second abdominal spiracles almost as wide as thoracic spiracles (diameter 0.11 mm), remaining abdominal spiracles gradually getting smaller towards the abdominal segment VIII (Figs. 18, 23–24).

First instar larva (L1, Fig. 19):

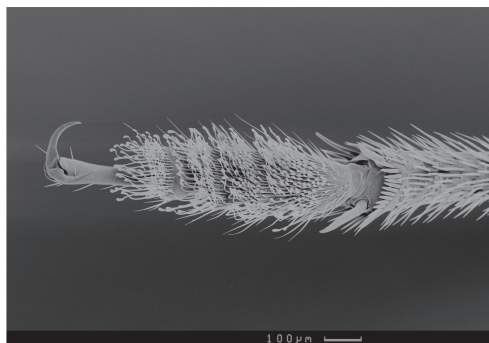
MATERIAL EXAMINED: 1 larva, West Malaysia, Hulu Perak, Temengor Forest Reserve, in internode of immature *Gigantochloa latifolia* culm, 30 December 1993, D. Kovac (SMF).

DESCRIPTION: Body length 5.5 mm, head width 1.2 mm, pronotum width 0.65 mm, body yellowish brown, some body parts darker, probably due to temporary desiccation in ethanol. Larva similar to third instar larva, but tarsungulus with two small spines and abdominal spiracles oriented sideways. Length ratio of urogomphi segments I, II and apical setae 1.8:1:1.

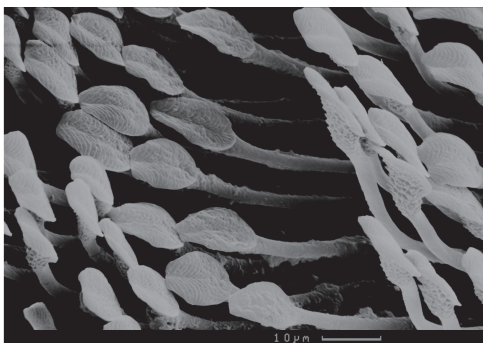
TAXONOMIC REMARKS: Larvae of *Hesperomimus bambusae* are categorized as Staphylininae, because they possess four stemmata and their labrum is fused to the head capsule to form a nasale (FOOTE & STEHR 1991). Identification of *H. bambusae* larvae using Staphylininae keys provided by KASULE (1970), TOPP (1978) and NEWTON (1990) leads to *Philonthus* or other *Philonthina* genera. The generic larval characters of *Philonthus* and *Hesperus* (see BOLLER 1983, STANIEC & PIETRYKOWSKA-TUDRUJ 2010), which are more or less identical (see STANIEC 2004), match up with characters found in *Hesperomimus*. However, some morphological characters of the third instar larvae of *Hesperomimus* differ from other *Philonthina*. Namely, the head of *H. bambusae* is triangular rather than parallel-sided and the abdominal spiracles II–VIII are relatively large, with tube-like extensions and laterally enlarged walls and oriented dorsad instead of laterad. Furthermore, the tarsungulus has six setae, whereas third and second instar larvae of Staphylininae as well as Xantholininae usually have three setae (TOPP 1978). We classify the small *H. bambusae* larva as a first instar because its tarsungulus possesses two setae, the same as first instar larvae of other Staphylininae or Xantholininae (TOPP 1978). A comparison of the ratio of the larval head and body measurements with *Hesperus rufipennis* GRAVENHORST, 1802 (STANIEC 2004) also supports this view.



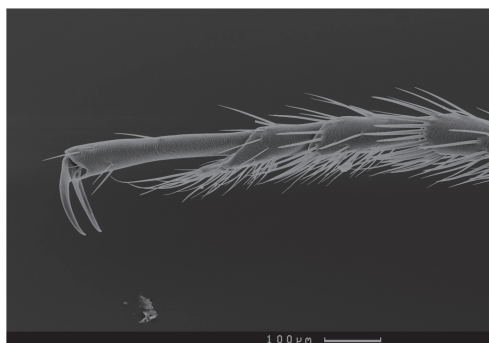
Figs. 16–19: *Hesperomimus bambusae*: 16) head of third instar larva, exuvia dorsal; 17) head of third instar exuvia, ventral; 18) abdominal segments 2–4 of third instar larva, dorsal, arrows point to spiracles; 19) first instar larva, ventral. An (antenna), Ap (acute projections), Max (maxilla), Md (mandible), Na (nasale), Pl (labial palp), Pmn (prementum), Tp (tentorial pit).



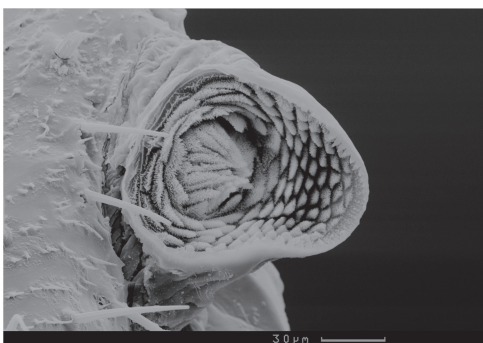
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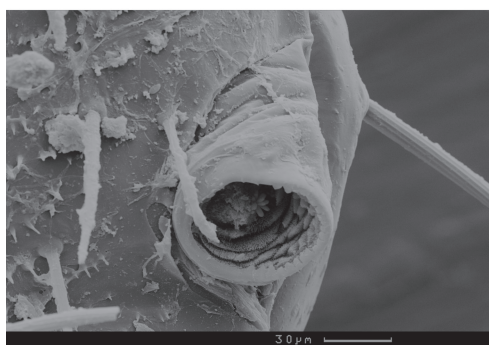
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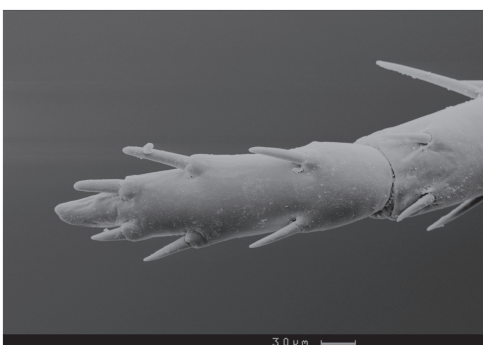
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Figs. 20–25: *Hesperomimus ruficollis* (20–22) and *H. bambusae* (23–25), SEM photographs: 20) protarsomeres, ventral; 21) detail of protarsomere showing spatulate hairs; 22) metatarsomeres, lateral; 23) spiracle of third instar larva, second abdominal segment, dorsal; 24) spiracle of third instar larva, seventh abdominal segment, dorsal; 25) tarsungulus of third instar larva, dorsal.

Pupa:

MATERIAL EXAMINED: 1 male pupa, West Malaysia, Hulu Perak, Temengor Forest Reserve, in internode of immature *Gigantochloa latifolia* culm, 28 December 1993, D. Kovac (SMF); 1 male pupa, idem, in internode of immature *G. latifolia* culm, 29 December 1993, D. Kovac (SMF); 1 male pupa, idem, in internode of immature *G. latifolia* culm, 30 December 1993, D. Kovac (SMF).

DESCRIPTION: Pupa obtect, with elongated slender body (Figs. 26–28). Length (without terminal prolongations): 8.7/ 8.8/ 8.7 mm, greatest width 3.4/ 3.2/ 3.3 mm, head between eyes 1.8/ 1.7/ 1.7 mm, greatest width of pronotum 1.6/ 1.5/ 1.6 mm. Body surface smooth, yellowish-brown, head, pronotum, knees and terminal segment darker. Head directed ventrally towards thorax, 1.3–1.4 × as long as wide, labrum V-shaped, 1.1 × as wide as long. Antennae curved, bending around anterior and middle knees, reaching proximal third of middle tibia in lateral view. Mandibles pointed and crossed in apical portion, maxillary palps touching each other at apex, not protruding beyond apices of middle legs. Pronotum 1.3 × as long as broad, anterior margin with approximately 10 setiform projections located on protuberances, numbers of projections on sides of the same larva may differ between specimens (5/5, 5/5, 4/5). Side margins of pronotum in basal third approximately parallel to concave. Wings extending to ventral side, reaching middle of abdominal segment III. Hind knees protruding far beyond tergites (lateral view), hind tarsi adhering to abdomen, reaching basal third of abdominal segment VI. Mid and hind legs with small indistinct roundish protuberances distally, lined up close together, one pointed protuberance at distal end of middle tibia. Abdomen with nine segments, first and second segment widest, following segments narrower, of about the same width, distal portion of segment VI and following segments tapering caudally (Fig. 27). Abdominal tergite I 1.5 times as long as abdominal tergite II. Abdominal segments VII and VIII with long curved setiform projections covered with tiny processes especially at apex. Setiform projections of abdominal segment VII broken off in all specimens, setiform projection of abdominal segment VIII slightly longer than corresponding segment. Terminal prolongations of last sternite broken off at apex in all specimens. Abdominal tergites I–IV with tuberculate functional spiracles, first pair located more lateral than remaining ones, moderately protruding.

TAXONOMIC REMARKS: Pupae of *H. bambusae* are sexually dimorphic, like those of other Philonthina (see STANIEC & PIETRYKOWSKA-ZUDRUJ 2019). An examination of the terminal abdominal (ninth) segment of *H. bambusae* showed that all collected *H. bambusae* pupae are males. Pupae of *H. bambusae* are categorized as Staphylinini, because they possess a hard and pigmented surface (obtect type) and setiform projections on pronotum and abdomen (see STANIEC & PIETRYKOWSKA-TUDRUJ 2019). Identification of *H. bambusae* pupae using the Staphylinini key provided by STANIEC & PIETRYKOWSKA-TUDRUJ (2019) leads to Philonthina, because of the presence of long setiform projections located on protuberances of the anterior pronotum. The diagnostic characters of Philonthina pupae (see PIETRYKOWSKA-TUDRUJ & STANIEC 2011) are consistent with characters found in *H. bambusae*, however, in *H. bambusae* tubercles are inconspicuous and lacking, especially on the forelegs. Furthermore, abdominal tergite I is not twice as long as abdominal tergite II. Among Philonthina, the pupa of *H. bambusae* is similar to *Hesperus* due to its crossed mandibles and the elongate labrum. *Hesperomimus bambusae* pupae differ from other Philonthina in their narrow body shape (exception: *Neobisnius* GANGLBAUER, 1895), maxillary palps touching each other at apex, pronotum longer than wide and parallel at base, and hind knees protruding far beyond the tergites in lateral view.

DISTRIBUTION: The species is at present known from Selangor and Perak in Peninsular Malaysia.

ETYMOLOGY: The epithet, a noun in the genitive case, refers to the peculiar habitat requirements of the species.



Figs. 26–28: *Hesperomimus bambusae*, male pupa: 26) ventral; 27) dorsal; 28) lateral.

***Hesperomimus ruficollis* sp.n.**

TYPE MATERIAL: **Holotype** ♂: “N-THAILAND: NE Mae Hong Son nr. Pangmapa 20.10.2000 leg. D. Kovac (B82/00)” (SMF). – **Paratypes** (5 exs.): 1 ♀: “N-THAILAND: NE Mae Hong Son nr. Pangmapa 26.10.2000 leg. D. Kovac (B102/00)” (NMW); 1 ♂: “N-THAILAND: NE Mae Hong Son nr. Pangmapa 27.10.2000 leg. D. Kovac (B121/00)” (NMW); 3 exs.: “N-THAILAND: NE Mae Hong Son near Soppong 20.4.2001 im aufrechten Bambus [in standing bamboo] leg. D. Kovac” (1 ♂, 1 ♀ SMF, 1 ♂ NMW).

DESCRIPTION: 10.5–13.2 mm long (5.5–6.1 mm, abdomen excluded). Coloration similar to that of the preceding two species, but pronotum rather bright reddish-testaceous; basal four segments and last segment of antennae reddish, bases of segments 5 and 6 frequently reddish, rarely basal three segments and basal half of segment 4 reddish; entire femora black, tibiae pale yellow with apices of middle and hind tibiae narrowly blackish, apices of protibiae narrowly obscurely brownish.

Head broadly ovoid to slightly trapezoid, weakly transverse (ratio 1.02–1.06), eyes slightly protruding, large, 1.24–1.50 as long as tempora, tempora strongly convergent, usually in almost regular arc, rarely inconspicuously angulate; frons and clypeus without or with only a few scattered punctures in addition to macrosetae; proportions of antennal segments as in *H. bambusae*; pronotum 1.27–1.36 as long as wide, widest in anterior third (at level of large lateral seta), narrowed toward base in distinct concave arc; disc impunctate except for a sublateral row composed of three punctures; disc flattened and shallowly sulcate in posterior half, posterior margin not widened medially; without group of sublateral punctures in posterior third; elytra finely and very densely punctate, pubescence silvery around scutellum, along suture and pos-

terior margin, greyish on disc; abdominal tergites uniformly but more finely and less densely punctate as in remaining species, bands of silvery pubescence thus slightly less conspicuous.

Aedeagus (Figs. 10–11): Apical portion of median lobe asymmetrical, short, with obtusely pointed apex; in lateral view less distinctly bent dorsad; paramere of similar shape as in *H. bambusae*.

Egg: Not known.

Exuvia of third instar larva (L3):

MATERIAL EXAMINED: 1 third instar exuvia, northern Thailand, Mae Hong Son, Pangmapha, between Soppong and Ban Nam Rin, retrieved from pupal cell found in felled bamboo culm of *Cephalostachyum pergracile* (HB18/22), relatively well preserved, 11 March 2022, D. Kovac (SMF); 1 third instar exuvia, idem, retrieved from pupal cell found in felled bamboo culm of *C. pergracile* (HB49/22), largely destroyed, head capsule preserved but most appendages missing, 17 March 2022, D. Kovac (SMF).

DESCRIPTION: Length: ca. 8.2 mm, greatest width (forehead): 1.4 mm. Color: yellowish-brown. Exuvia long and narrow, pronotum twice as long as meso- or metanotum. Macro- and microsetae usually simple, macrosetae on abdomen frayed with two or more points apically.

Head: Prognathous, triangular, tapering posteriorly, head width 1.4 mm, about 1.3 times as long as broad, with imprints of four stemmata on each side of the head, ventral side of head with two slightly curved tentorial pits. Antenna with four segments, length ratio of segments I–IV 1:2.1:1.75:0.87, segment III with three macrosetae, one club-shaped sensory appendage, segment IV with three setae and four solenidia apically. Nasale on anterior margin of head with nine teeth. Macrosetae on head distributed as in *H. bambusae*, mandible falciform. Maxillae missing. Labium: Ventral side of prementum sclerotized, apically with two setae and two microsetae, sclerites extending around margins to dorsal side of prementum; dorsal side membranous and pubescent. Ligula conical, about as wide as segment I of labial palps, with two microsetae. Apotome with six setae, distinctly extending behind tentorial pits. Labial palps three-segmented; length ratio of segments I–III: 4.8:2.2:1.

Thorax: Pro-, meso- and metanotum sclerotized and smooth, macrosetae distributed as in *H. bambusae*. Legs with micro- and macrosetae, profemur with about 10 macrosetae on ventral face, protibia with about 15 macrosetae ventrally and dorsally. Length ratio of femur and protibia: 1.2:1. Tarsungulus with three pairs of spine-shaped setae dorso-laterally. Pair of large oval spiracles located lateral between pro- and mesothorax, greatest width of spiracular openings 0.09 mm.

Details of abdominal segments hard to see due to folding of the exuvial skin, but a closer examination indicates that the setae on abdominal segments and on the two-segmented urogomphi are distributed as in *A. bambusae*. First abdominal spiracle smaller than metathoracic spiracle and pointing laterad. Abdominal spiracle II located lateral on dorsum and the opening points upwards like in *H. bambusae*, other spiracles not recognizable.

TAXONOMIC REMARKS: The description of the third instar larva of *H. ruficollis* is incomplete, because we only possess two badly preserved exuviae. Recognizable characters of the third instar exuviae of *H. ruficollis* were identical with characters found in *H. bambusae* third instar larvae, including the triangular head, shape and dorsal location of abdominal spiracles (at least abdominal spiracle II) and presence of six setae located on the tarsungulus. At present, third instar larvae of *H. ruficollis* can be distinguished from those of *H. bambusae* only by their smaller size.

Pupa:

MATERIAL EXAMINED: 1 female pupa, Thailand, Mae Hong Son, Pangmapha, between Soppong and Ban Nam Rin, internode cavity of *Cephalostachyum pergracile* (HB18/22), 11 March 2022, D. Kovac (SMF); 1 female pupa, idem, internode cavity of *C. pergracile* (HB49/22), 17 March 2022, D. Kovac (SMF).

DESCRIPTION: Pupa obtect with elongate, slender body (Fig. 38). Length (without terminal prolongations): 7.7 and 7.9 mm, greatest width 2.8 and 2.9 mm, head width between eyes in both specimens 1.6 mm, greatest width of pronotum 1.6 and 1.7 mm. Body surface smooth, yellowish-brown, tips of mandibles, knees, terminal appendages and spiracles darker. Head directed ventrally towards thorax, 1.3 and 1.4 × as long as wide, labrum V-shaped, 1.1 × as wide as long. Antennae curved, bending around anterior and middle knees, reaching proximal third of middle tibia in lateral view. Tips of mandibles crossed, maxillary palps tapering but not touching each other at apex (Fig. 38), not protruding beyond apices of middle legs. Pronotum in both specimens 1.2 as long as broad, rather parallel-sided, base of pronotum as wide as head between eyes, anterior margin in both specimens with 11 setiform projections located on protuberances, five setiform projections on one side and six projections on the other side of the body. Wings extend to ventral side, reaching the proximal third of sternite IV. Hind knees protruding far beyond the tergites in lateral view, hind tarsi adhering to abdomen, apex of hind tarsi almost reaching middle of sternite VI. Small, faintly visible roundish single protuberances at distal ends of mid and hind tibiae. Nine abdominal segments, fifth segment widest. Abdominal tergite I 1.4 times as long as abdominal tergite II. Setiform projections of abdominal segments VII and VIII and accessories of terminal prolongations broken off in both specimens. Abdominal tergites I–IV with tuberculate, moderately protruding functional spiracles, first pair largest and located more lateral than the remaining ones. Terminal sternite with a pair of prominent acute prolongations, about as long as terminal prolongations, but narrower.

TAXONOMIC REMARKS: *Hesperomimus ruficollis* pupae can be distinguished from *H. bambusae* by their smaller size and the width of their abdominal segments: in *H. bambusae* the first abdominal segment is the widest, while in *H. ruficollis* the fourth or fifth segments are widest. Since all *H. ruficollis* pupae collected were females and all *H. bambusae* collected were males, we are unable to compare specimens of the same sex.

DISTRIBUTION: The species is at present known only from two adjacent localities in northern Thailand (northeast of Mae Hong Son).

ETYMOLOGY: The epithet, a Latin adjective, refers to the red pronotum.

Bionomics

Hesperomimus bambusae: Adults and larvae of *H. bambusae* were collected in Peninsular Malaysia between October and January. They inhabited internode cavities of bamboo culms of *Gigantochloa scortechinii* (Fig. 29), *G. latifolia* and *Dendrocalamus pendulus*. Culms containing *Hesperomimus* were three to four months old and between seven and 15 m tall. *Gigantochloa scortechinii* internodes inhabited by *H. bambusae* were 19–50 cm long ($n = 8$), had a diameter of 8.4–10.0 cm ($n = 8$), and bamboo wall thickness was 1.1–2.0 cm ($n = 9$). Basal internodes were shorter than apical ones and their diameter and thickness were larger. The height of the internodes inhabited by *H. bambusae*, measured between their bases and the ground, was 0.13–7.98 m ($n = 10$). All internodes inhabited by *H. bambusae* possessed holes created by *Lasiochila goryi*. *H. bambusae* did not colonize internodes pierced by Lepidoptera (Crambidae) larvae or *Tetraponera* ants (Hymenoptera: Formicidae) (see below, under *H. ruficollis*).



Fig. 29: Bamboo stand of *Gigantochloa scortechinii* in Ulu Gombak, West Malaysia. The immature bamboo culms enclosed by the colorful internode sheaths are the habitat of *Hesperomimus bambusae*.

Most *Lasiochila* internodes contained just one *H. bambusae* specimen ($n = 22$). In two internodes there were two specimens and in one internode four specimens. Eleven immature culms felled at the Genting Highlands location contained 44 internodes pierced by *Lasiochila*, 11 of which were occupied by *H. bambusae*. Six out of eleven felled culms contained *H. bambusae*, three out of six culms contained a single internode per culm inhabited by *H. bambusae*, one culm contained two internodes inhabited by *H. bambusae* and two culms contained three inhabited internodes. At the end of “long-term study II” conducted in Hulu Perak, i.e., three months after artificial holes were bored, seven out of 100 internodes contained *Hesperomimus* adults, larvae or pupae, and one pupal cell was already deserted.

In nature, *H. bambusae* occurred exclusively in bamboo internodes pierced by larvae of *Lasiochila goryi*. However, *H. bambusae* also colonized internodes provided with artificial holes (long-term experiment II). Internodes inhabited by *Lasiochila* contained 100–500 ml liquid. In freshly pierced internodes, bamboo sap oozed out from the bamboo wall and collected in the internode cavity, but after 3–4 days, the only source of liquid was rainwater, which ran down along the bamboo stem and penetrated into the internodes through the holes. Even in the dry season when rain was less frequent, internode cavities contained some water.

Lasiochila goryi created two types of holes: smaller entrance and larger exit holes. The entrance holes were bored from mid-August onwards, after the immature culms had reached a height of ca. 2 m. Each *L. goryi* larva pierced an entrance hole in the middle of elongated lower internodes, usually in the triangle area formed by the overlapping sheaths (see Fig. 36). There were up to five entrance holes per internode. The entrance holes were about 1.0×0.8 mm. They probably became slightly longer during the elongation process of the internode. The larger exit holes were bored in the basal third of the internodes, already a few days after colonization of the internode.



Figs. 30–33: *Hesperomimus bambusae*: 30) beetle feeding on a mosquito larva (arrow pointing to breathing tube of mosquito larva); 31) submerged beetle enveloped by an air layer; 32) pupal cell made of bitten off pieces of bamboo wall; 33) beetle larva feeding on a mosquito larva while hanging down from the water surface.

Later, they became larger, either through further widening by *Lasiochila* or due to the elongation process of the internode. There was only one exit hole per internode even if it contained several larvae and the holes were ca. 6 mm long. The internode sheaths tightly enclosed the *Lasiochila* exit holes (see Fig. 36).



Fig. 34: Bamboo stand of *Cephalostachyum pergracile*, habitat of *H. ruficollis*.

The first *H. bambusae* specimen detected during “long-term study I” arrived on 19 November, i.e., about three months after *Lasiochila* had colonized the internodes. *Hesperomimus bambusae* mated in the internodes and the females laid a single egg per internode on the bamboo walls above the water surface ($n = 4$). Mature larvae created pupal cells in the upper part of the internode cavity ($n = 12$). The pupal cells were made of pieces of tissue bitten off from the bamboo wall. The cells were pear-shaped, about two cm long with the narrow end pointed upwards (Fig. 32). The pupal heads were oriented towards the narrow end of the pupal cell. The pupae laid flat on the ground and adhered only weakly to the bamboo wall.

In the laboratory, a *H. bambusae* specimen walked deliberately into the water during a feeding trial and hunted mosquito larvae at the bottom of the internode. The beetle emerged from the water after capturing a mosquito larva and devoured its prey above the water surface (Fig. 30). In the field, two *H. bambusae* stayed right beside a dead, bitten aquatic syrphid larva, which they had apparently dragged from the water. Upon disturbance, *H. bambusae* adults fled into the water and remained motionless at the bottom of the internode. A silvery shiny air layer surrounded their bodies (Fig. 31).

One *H. bambusae* larva kept in the laboratory walked into the water during a feeding trial and remained motionless at the bottom of the small aquarium. When mosquito larvae passed by, the beetle larva snatched at them with its mandibles. Finally, the beetle larva managed to capture a mosquito larva and started to devour it on the spot. During feeding, pumping movements of the intestine were visible. After 19 minutes, the positively buoyant larva floated upwards and continued to feed while hanging down from the water surface (Fig. 33). In that position, the tips

of the cerci and the pygopod with extruded anal vesicles were resting on the underside of the water surface. The cerci and the pygopod did not pierce the water film. After six more minutes, the beetle larva released the empty body shell of the mosquito larva and remained below the water surface for a few more minutes. After ca. 30 minutes the observation was terminated.

Animals sharing their habitat with *H. bambusae* in *Gigantochloa scortechinii* internodes were mosquito larvae (Diptera: Culicidae), aquatic ceratopogonid and syrphid larvae (Diptera), semi-aquatic Diptera (Tephritidae: *Felderimyia* HENDEL, 1914) and Heteroptera (Veliidae: *Lathriovelis rickmersi* KOVAC & YANG, 2000) – see KOVAC & KROCKE (2013), terrestrial Coleoptera (Chrysomelidae: *Lasiochila goryi*), and occasionally small staphylinids and the bug *Carvalho-fulvius gigantochloae* (STONEDAHL & KOVAC 1995) (Heteroptera: Miridae). Predatory larvae of *Toxorhynchites* THEOBALD, 1901 (Diptera: Culicidae) never occurred in internodes examined during both long-term studies.

***Hesperomimus ruficollis*:** Specimens were collected in northern Thailand between October and April in internode cavities of immature bamboo culms of *Cephalostachyum pergracile* (Fig. 34). Most culms were felled between the end of February and April, when they had reached their final length of about 10–12 m. The culm walls were already relatively hard, but the side branches were still lacking. Internodes inhabited by *H. ruficollis* were between 30–70 cm long ($M = 45$ cm; $n = 16$), the diameter was 4.7–8.9 cm ($M = 5.5$ cm; $n = 18$) and the wall thickness was 3.6–23.0 mm ($M = 6.7$ mm; $n = 16$). The height of *H. ruficollis* internodes, measured from the internode base to the ground, was 0.24–5.58 m ($M = 3$ m; $n = 18$).

Hesperomimus ruficollis usually entered the internode cavities through holes created by *Lasiochila gestroi* (BALY, 1888). The smaller entrance holes were located in the triangle formed by the internode sheaths (Fig. 36) or further up. The exit holes were located in the lower third of the internodes (Fig. 35), sometimes also above the upper edge of the sheaths. There were up to three entrance holes per internode and usually one or sometimes two exit holes. The length of the oval entrance holes was 1.2–4.6 mm ($M = 1.9$ mm; $n = 14$) and the width 0.8–2.4 mm ($M = 0.97$ mm; $n = 14$). The length of the exit holes was 1.52–7.80 mm ($M = 5.0$ mm; $n = 17$) and the width 1.00–3.50 mm ($M = 2.5$ mm; $n = 17$).

Besides *Lasiochila* other insects also drilled holes in immature bamboo culms of *Cephalostachyum pergracile*. Crambidae holes were common in the upper part of the bamboo culms, usually above the *Lasiochila* internodes. Their entrance holes were circular, about 1 mm in diameter and located in the upper third of the internode. The exit holes were oval, 1.13–2.90 mm long ($M = 2$ mm; $n = 26$) and 0.80–2.50 mm wide ($M = 1.52$; $n = 26$). Holes created by *Tetraponera* ants were round to slightly oval and 1.6–1.8 mm in diameter ($n = 5$). A single *H. ruficollis* specimen occupied an internode pierced by a crambid moth larva (hole size 2.00×1.54 mm), but they never inhabited *Tetraponera* internodes.

Most internodes inhabited by *Hesperomimus* contained just one *Hesperomimus ruficollis* specimen each ($n = 31$). In three cases, there were two specimens per internode, in two cases three and in one case four specimens. Nine *Cephalostachyum pergracile* culms felled in March 2008 yielded 96 internodes pierced by *Lasiochila gestroi*. Seven of these internodes contained eleven *H. ruficollis* specimens. All internodes occupied by *Hesperomimus* contained water and mosquito larvae. Even in the dry season, when the temperature was high and fires were frequent, 15 out of 16 *H. ruficollis*-internodes opened between mid-February and end of March still contained 50–480 ml water.

Two out of six pupal cells collected between 11 and 17 March 2022 contained pupae, the other four were already deserted. The pupal cells were located in the upper third of the internode cavity and consisted of small bamboo particles. The upper part of the pupa formed a narrow exit

tube (Fig. 37). The length of the oval pupal cells was 13.9–15.8 mm ($M = 14.9$ mm; $n = 6$) and the width 7.6–10.0 mm ($M = 8.45$ mm; $n = 6$).



Figs. 35–36: Immature culms of *Cephalostachyum pergracile*, showing holes (see arrows) bored by the leaf beetle *Lasiochila gestroi*: 35) Internode sheath partly removed in order to show the large exit hole (length about 6 mm, lower arrow); upper arrows pointing to *L. gestroi* entrance holes; 36) internode with a small entrance hole (arrow); basal portion of internode tightly enveloped by internode sheath; 37–38: *Hesperomimus ruficollis*: 37) pupal cell; 38) female pupa, ventral.

Some *H. ruficollis* beetles kept in the laboratory tried to escape and fly away, but others usually stayed motionless close to the water surface during many consecutive days. Their head was pointing upwards, while the tip of the abdomen was very close to the water surface. The reflections of the water surface indicated that bristles located on the tip of the abdomen touched the water surface or penetrated it. From time to time, beetles walked back and forth along the water's edge near their resting place (walking distance ca. 3–4 cm) with their heads kept close above the water surface. On two such occasions, the beetles suddenly grabbed mosquito larvae near the base of their respiratory horn, pulled them out of the water and devoured them. Predation of mosquito larvae was also evident from the fact that skins of sucked out mosquito larvae were frequently adhering on the walls of bamboo internodes inhabited by *H. ruficollis*. The beetles could survive more than two months without food ($n = 3$).

Hesperomimus also attacked other Diptera larvae occurring in their habitat, at least when both predator and prey were placed in small 20 ml glass tubes. In that situation, *Hesperomimus* devoured *Felderimyia* tephritid larvae, attacked large syrphid (*Evaza* WALKER, 1856) and tipulid larvae and fed on pieces of a cut earthworm. In bamboo internodes, which offered more space to avoid *Hesperomimus*, already mature *Felderimyia*, *Evaza* or tipulid larvae were still alive after several days. Tipulid larvae soon built a partly submerged tunnel made of small bamboo particles in which they quickly retreated when being threatened.

Hesperomimus ruficollis did not hunt in the water, but in case of a threat beetles fled to the bottom of the bamboo container (up to 4 cm below water surface). During submergence, an air bubble covered their thorax and abdomen, with the exception of the caudal fifth of their abdomen. After prolonged submergence, the thoracic air bubble disappeared and the abdominal bubble became smaller. During their stay in the water, *H. ruficollis* repeatedly walked upwards every 5–7 minutes and touched the water surface from below for about 2–3 seconds with the entire lateral side of their abdomen. Sometimes, ventilation movements occurred while the body side was touching the water surface. Subsequently, the beetles walked down again, however, not as deep as during their first descent. Altogether, the beetles stayed in the water for 41 and 70 minutes ($n = 2$). After that, they emerged from water, groomed intensively and repeatedly dabbed the underside of their bodies on the bamboo wall.

Animals sharing their habitat with *H. ruficollis* adults in immature culms felled in March were filter-feeding mosquito larvae (Culicidae), predatory *Toxorhynchites* mosquito larvae, and Diptera larvae belonging to Ceratopogonidae (*Dasyhelea* KIEFFER, 1911) Syrphidae (*Evaza*), Tephritidae (*Felderimyia*) and Tipulidae. Terrestrial inhabitants comprised larvae or pupae of the hispine beetle *Lasiochila gestroi*, occasional web-spiders, small staphylinids, true bugs (*Carvalhofulvius* STONEDAHN & KOVAC, 1995 and Pentatomidae), the semiaquatic bug *Lathriovelis rickmersi*, ants, and centipedes (in the lower internodes). Filter-feeding mosquito larvae were the dominant inhabitants in internodes of immature bamboo culms, while terrestrial inhabitants were rather scarce.

Other bamboo-inhabiting Staphylininae feeding on mosquito larvae

Hesperus kovaci and *H. birmanus* CAMERON, 1932 from West Malaysia occurred in stumps of bamboo culms or in water-filled cut culms laid on the ground. The beetles entered damaged culms through large openings created by humans, large animals or fallen trees. Decaying bamboo culms contained numerous large mosquito larvae, which were available for a relatively short time, because cut culms and bamboo stumps decomposed fast, and after about 10 days, the water leaked out of the internode cavities (KOVAC & STREIT 1996).

Field-observed specimens of both species were lying in wait at the water's edge in order to capture mosquito larvae. *Hesperus kovaci* waited motionless close above the water surface with open mandibles until mosquito larvae approached in order to breathe at the water surface. Then the rove beetles grabbed them with their mandibles, pulled them on land and devoured them on the spot. *Hesperus kovaci* also hunted in the water (SCHILLHAMMER 2002) and fled into the water when being disturbed. Staphylininae larvae perhaps belonging to *Hesperus* or *Platydacus* sp. dug protective tunnels in the soft tissue of immature bamboo culms above the water surface.

Tab. 1: Overview of Staphylinidae that hunt mosquito larvae. Specimens that immersed head and thorax for hunting are denoted by an asterisk (*).

Species	Subtribe	Habitat	Adults hunt from land	Adults hunt in water	Adults take refuge in water	Larvae hunt from land	Larvae hunt in water	Larvae take refuge in water	References
<i>Hesperomimus bambusae</i>	Philonthina	living immature bamboo culms	yes	yes	yes	yes	yes	–	present study
<i>Hesperomimus ruficollis</i>	Philonthina	living immature bamboo culms	yes	no	yes (M = 55.5 min.)	–	–	–	present study
<i>Hesperus kovaci</i>	Philonthina	dead immature bamboo culms	yes	yes	yes	–	–	–	SCHILLHAMMER (2002)
<i>Hesperus birmanus</i>	Philonthina	dead immature bamboo culms	yes	–	–	–	–	–	present study
<i>Odontolinus fasciatus</i>	Philonthina	<i>Heliconia</i> bracts	–	yes	–	–	–	–	SEIFERT & SEIFERT (1976)
<i>Belonuchus cephalotes</i>	Philonthina	<i>Heliconia</i> bracts	–	yes	–	–	–	–	FRANK & BARRERA (2010)
<i>Belonuchus satyrus</i>	Philonthina	<i>Heliconia</i> bracts, cacao husks	yes	no	–	yes?	–	–	FRANK & BARRERA (2010)
<i>Belonuchus rufipennis</i>	Philonthina	<i>Heliconia</i> bracts, decaying plant material	yes	no	–	–	–	–	FRANK & BARRERA (2010)
<i>Platydacus gemmatus</i>	Staphylinina	dead immature bamboo culms	yes	yes	yes	–	–	–	present study
<i>Platydacus</i> sp.	Staphylinina	dead immature bamboo culms	yes	–	yes	–	–	–	present study
<i>Platydacus orizabae</i>	Staphylinina	<i>Heliconia</i> bracts	yes*	–	–	–	–	–	FRANK & MORON (2012)
<i>Platydacus fauveli</i>	Staphylinina	<i>Heliconia</i> bracts	yes	–	yes	–	–	–	FRANK & MORON (2012)
<i>Platydacus gracilipes</i>	Staphylinina	<i>Heliconia</i> bracts	yes	–	–	–	–	–	FRANK & MORON (2012)
<i>Platydacus</i> sp.	Staphylinina	<i>Heliconia</i> bracts	yes	yes	–	–	–	–	FRANK & MORON (2012)
<i>Acylophorus</i> sp.	Acylophorina	dead mature bamboo culms	yes	no	yes (M = 16 min.)	yes*	no	yes (3 sec.)	KOVAC & STREIT (1996); present study

Platydracus gemmatus FAUVEL, 1895 and *Platydracus* sp. from West Malaysia occurred in damaged immature bamboo culms. *Platydracus* sp. seized mosquito larvae from the water's edge, while *P. gemmatus* also captured a mosquito larva in the water and devoured it above the water surface.

The small-sized and slender *Acylophorus* sp. were common in old fallen bamboo culms in West Malaysia and northern Thailand. A few specimens also temporarily occupied internodes of living mature bamboo stems. *Acylophorus* sp. colonized internodes through holes created by various insects or woodpeckers, or through long narrow slits, which arose from splitting of the bamboo culms during dry weather. Fallen bamboo culms were a relatively long-lived and species-rich habitat (see KOVAC & STREIT 1996).

Acylophorus were lying in wait at the water's edge or on the water surface. They did not hunt in the water. They devoured their prey on the spot, either on the water surface or on land. About 60% out of 51 prey items retrieved from *Acylophorus* sp. in the field were mosquitoes (mostly larvae, but also pupae and one adult). Other prey items included larvae or pupae of aquatic or semiaquatic Diptera (Ceratopogonidae, Psychodidae, Tephritidae), nymphs of the semiaquatic bug *Lathriovelina rickmersi* (see KOVAC & KROCKE 2013), one collembolan and one small earthworm. *Acylophorus* adults fled into the water when being molested. In the water, an air layer enveloped their entire body and legs. Beetles remained motionless 1–2 cm below the water surface for 4–67 minutes ($M = 16$ min., $n = 24$) and then climbed on land.

Acylophorus sp. larvae developed in the same habitat as the adults. They hunted aquatic insects as well as insects occurring in the wet area above the water surface (wet strip ca. 2 cm wide). Younger larvae were active and walked along the water's edge most of the time, while older ones were rather sluggish and laid in wait for prey just above the water surface. Eight prey items collected in the field included one mosquito larva, one tiny *Toxorhynchites* larva, two ceratopogonid pupae, three nymphs of *Lathriovelina* ANDERSEN, 1989 and one small earthworm. Larvae did not hunt on the water surface or in the water, but one larva immersed its head in the water in order to capture a ceratopogonid pupa. *Acylophorus* larvae escaped into the water when being molested, but they stayed submerged for just about three seconds. Prior to pupation, mature larvae attached themselves with the tip of their abdomen to the bamboo wall above the water surface. Pupal cells were lacking, but sometimes a flat wall made of debris surrounded the pupae (see KOVAC & KLAUSNITZER 2020).

Discussion

Hesperomimus species are special among the bamboo-inhabiting Staphylininae feeding on mosquito larvae, because they are specialized on living immature bamboo culms with small holes, have a very slim body shape, possess specific morphological leg modifications for climbing on smooth bamboo surfaces (see below), and *H. ruficollis* replenishes air at the water surface and has a remarkable hunting strategy. Larvae possess six setae on the tarsungulus, and large, dorsally oriented abdominal spiracles (II–VIII); they hunt and devour mosquito larvae in the water (*H. bambusae*) and construct pupal cells.

The slim and elongate body allows *Hesperomimus* to squeeze into internode cavities through small holes (smallest used hole about 2×1.5 mm). All specimens, except one, inhabited internodes pierced by *Lasiochila* larvae. There was only one observation of the smaller *H. ruficollis* in an internode bored by a Crambidae moth larva, because most Crambidae holes were too small. Internodes pierced by *Tetraponera* were not suitable as habitat, because the ants guarded their entrance holes and kept the internodes dry by spitting out water (KLEIN et al. 1993). *Hesperomimus* readily used artificial holes to colonize internodes, i.e., the beetles were not specialized on

Lasiochila holes. In nature, however, exit holes bored by *Lasiochila* were virtually the only holes suitable for *Hesperomimus* to enter the internode cavities.

It is remarkable, that *H. bambusae* colonized *Lasiochila goryi* internodes only about three months after the leaf beetles had bored their entrance and exit holes ("long-term study I"). In contrast to that, *H. bambusae* immediately colonized internodes with artificial holes ("long-term study II"). This was because artificial holes were open throughout, whereas *Lasiochila* exit holes were blocked by internode sheaths. *Hesperomimus* could enter the internode cavities only after internode sheaths had started to loosen, thus allowing beetles to squeeze beneath them and reach the internode opening.

The relatively long legs of *Hesperomimus* possess adhesive pads with spatulate hairs on the protarsomeres like other Philonthina (Figs. 20–21), but also closely spaced hairs on the middle and hind tarsomeres (Fig. 22). These features possibly help to achieve a strong adhesion to the substrate and allow *Hesperomimus* to climb on smooth external surfaces of the bamboo culms (see BULLOCK & FEDERLE 2011). The relatively long legs (hind tarsomeres elongated) are perhaps also beneficial for climbing, especially on larger bamboo culms. Males of the spider *Argiope keyserlingi* KARSCH, 1878 (Arachnida: Araneae: Arachnidae), also with relatively long legs for their body size, perform better on wider diameter substrate than specimens with shorter legs (PRENTER et al. 2010).

Hesperomimus ruficollis are special among Staphylininae inhabiting internodes, because they assume a peculiar posture with abdominal bristles touching or penetrating the water surface. It is possible that through this behavior they perceive vibrations of the water surface caused by mosquito larvae and then start to walk along the water's edge in order to capture them. Also unique is the ability to replenish their air store when being submerged, by touching the underside of the water surface with their abdominal spiracles. This behavior increases the length of their stay in water to more than an hour.

Hesperomimus larvae are special among Staphylininae for their tarsungulus possessing six setae (Fig. 25), whereas other Staphylininae have only three (TOPP 1978). The numerous and relatively large and stout setae on the tarsungulus possibly improves the ability of the larvae to adhere to the vertical bamboo walls inside the internode cavities (tarsungulus angled downwards during walking). Abdominal spiracles II–VIII of third instar larvae are also remarkable because they are oriented dorsad instead of laterad as in other Staphylininae. The dorsal orientation of the spiracles and their tube-like walls possibly allow respiration at the water surface when walking in the thin layer of water in the wet area of the internode. Furthermore, it seems that the abdominal segments II–VIII are better protected against wetting than the spiracles of the entirely terrestrial *Hesperus rufipennis*, because in the latter the spiracles are not closed like in *Hesperomimus ruficollis* (see STANIEC 2004, fig. 37).

Hesperomimus bambusae larvae superficially resemble certain species of aquatic Dytiscidae. They have a similar body shape, including the triangular head with slender falcate mandibles, they possess a nasale, are positively buoyant and maintain a similar posture stabilized by their urogomphi when resting suspended from the water surface. The falcate mandibles and toothed nasale in Staphylininae and Dytiscidae are probably adaptations to their predatory lifestyle and occur in several adephagan and polyphagan groups using extra-oral digestion (CROWSON 1981), while the positive buoyancy is an adaptation to their aquatic habits.

In aquatic insects dependent on atmospheric air, positive buoyancy prevents drowning and helps them reach the water surface in order to respire. *Hesperomimus bambusae* larvae easily float towards the water surface, but they cannot connect to atmospheric air when resting suspended from the water surface, because the tip of their abdomen (pseudopod, 10th abdominal segment) does not break through the water surface film and the last abdominal spiracles on 8th abdominal

segment are too far away from the water surface. Despite this, the larva can stay in the water for more than 30 minutes, possibly because of large tracheal air stores, diffusion of oxygen through the cuticle and the spiracles, or because of low metabolic rates.

Predatory aquatic larvae employing extra-oral digestion have evolved different mechanisms in order to prevent dilution of digestive juices in the water. Some dytiscid larvae possess channeled or grooved mandibles for injecting enzymes into the prey's body to suck out the digested products, while hydrophilid larvae lift their prey out of water during feeding (CROWSON 1981). An examination of *Hesperomimus* larvae did not reveal any such conspicuous morphological or behavioral modifications. It rather seems that the *Hesperomimus* larva firmly presses the mosquito larva against the narrow mouth with its mandibles and pierces its cuticle with the two acute projections located laterally besides the mouth opening. Thus, the prey's cuticle remains almost intact and prevents dilution of body juices into the surrounding water.

Staphylininae possess obtect pupae with a hard and pigmented surface and rarely build pupal cells (CROWSON 1981, STANIEC & PIETRYKOWSKA-ZUDRUJ 2019). In contrast, *Hesperomimus* always create pupal cells. The explanation for this behavior could be that the pupa is lying flat on the ground being only weakly attached to the bamboo wall. Therefore, pupal cells are perhaps needed as a safeguard against falling into the water in case of strong mechanical vibrations of the bamboo culm. *Acylophorus* larvae, which strongly attach themselves to the bamboo wall with the tip of their abdomen, just hang down freely from the bamboo wall and pupal cells are usually lacking (KOVAC & KLAUSNITZER 2020). This is also the case for pupae of *Exochomoscirtes* scirtid beetles, which share their secluded habitat with *Acylophorus*. The soft-bodied (exarate) pupae of *Exochomoscirtes* protected themselves with the bristles of their shed larval skins and with vigorous up and down movements of their bodies (KOVAC & KLAUSNITZER 2020).

Hesperomimus develop during the rainy season, when immature bamboo culms are available and mosquito larvae abundant. *Hesperomimus bambusae* females lay a single egg per internode, thereby preventing competition and cannibalism among larvae. The total development time of *H. bambusae* is probably considerably less than three months, because three months after artificial holes were bored ("long-term study II"), a specimen had already abandoned its pupal cell. Other Staphylininae examined so far have a rather short development time. For example, the European *Hesperus rufipennis*, which inhabits rotting holes of deciduous trees, develops in less than 1.5 months from egg laying to adult emergence (STANIEC 2004). Since *Hesperomimus bambusae* inhabits different bamboo species growing at different times of the rainy season, immature bamboo culms are available for about six months per year. Therefore, it is possible that *H. bambusae* is multivoltine.

So far, 15 species of Staphylinidae, mostly belonging to Philonthina, are known to capture mosquito larvae in their aquatic habitat (Tab. 1): eight South American species occurring in water-filled *Heliconia* bracts and seven Southeast Asian species inhabiting water-filled bamboo internodes. Although mosquito larvae are the staple food of these rove beetles, their diet and the proportion of mosquito larvae in the total diet varies, depending on their habitat. *Hesperomimus* species inhabiting living immature bamboo culms mainly feed on mosquito larvae, because they are by far the most abundant food source occurring in their habitat. *Acylophorus* species capture a larger array of different prey species, because the animal community of decaying mature stems is more species-rich than living immature bamboo culms (see KOVAC & STREIT 1996). Almost half of the prey items retrieved from *Acylophorus* sp. are semiaquatic or aquatic insects other than mosquito larvae. *Acylophorus* larvae feed on the same organisms as the adults, but the early stages capture smaller prey and the proportion of mosquito larvae as food is lower than in the adults. Thus, prey availability in the habitat is the most likely determinant of diet for the Staphylininae investigated, as was already proposed for the New World *Odontolinus* SHARP,

1885 and *Belonuchus* NORDMANN, 1837 by FRANK & BARRERA (2010). Other important factors are the predator size and hunting strategies.

The hunting methods of phytotelmata-inhabiting Staphylininae are manifold (Tab. 1). Most bamboo-inhabiting species lurk for mosquito larvae at the water's edge with their open mandibles kept close above the water surface. *Platydracus orizabae* immerses its head and thorax, with open mandibles, to snap at Diptera larvae (FRANK & MORON 2012), while several of the larger species capture mosquito larvae in the water. The small and lightweight *Acylophorus* sp. is the only species hunting on the water surface (Tab. 1).

Most, if not all mosquito-feeding Staphylininae, including those hunting solely from the water's edge, flee into the water when being molested (Tab. 1). They never move around while being submerged. Usually, they emerge from the water after several minutes (Tab. 1). *Hesperomimus ruficollis* stays in the water for a longer time, probably because the beetle can replenish air at the water surface. All submerged beetles possess a silvery air layer held by hydrofuge hairs. The air layer probably plays a role as a physical gill and increases the buoyancy of the beetles, thus preventing drowning.

Many Staphylinidae species live in wet habitats along streams, lakes or seashores. They possess hydrofuge hairs as protection against wetting and one would expect that some of them temporarily enter water in order to hunt for aquatic organisms. However, the only rove beetles observed so far to seize prey in the water are the phytotelmata-inhabiting species listed in Tab. 1. Although some rove beetles living along seashores are able to stay submerged in direct contact with seawater for many days, they move only occasionally or become quiescent, and neither adults nor larvae have been observed to hunt in the water for aquatic organisms (TOPP & RING 1988a, b, FRANK & AHN 2011).

We suspect that the main reason why most rove beetles living at the edge of large waters avoid entering the water is the high predatory pressure occurring in these habitats. Large insects, crabs, amphibians, fishes or birds endanger rove beetles and prevent them from adapting to the aquatic lifestyle. In contrast, most types of bamboo and *Heliconia* phytotelmata have a low predatory pressure, because the largest aquatic predators occurring in these habitats are usually *Toxorhynchites* mosquito larvae. Although *Toxorhynchites* larvae are voracious predators (mature larvae are about 1 cm long), they can hardly overwhelm large rove beetles. On the contrary, *Belonuchus satyrus* and *Platydracus orizabae* are able to drag large *Toxorhynchites* larvae or pupae from the water and to devour them (FRANK & BARRERA 2010, FRANK & MORON 2012). Thus, large rove beetles are apparently top predators in some types of phytotelmata and therefore can safely seek water for hunting. On the other hand, *Acylophorus* sp. is probably more vulnerable to predation due to its small size. *Acylophorus* usually remains in the dry portion of the internode and only enters the water when being threatened. Submerged *Acylophorus* sp. always remain motionless, thus reducing the possibility of detection by *Toxorhynchites*.

Larvae of Staphylininae, especially younger larval stages, are soft and more vulnerable to predation than the adults are. That was evident by the fact that *Toxorhynchites* captured a second instar *Acylophorus* larva in the field (observation by the second author). Therefore, one would expect that Staphylininae larvae remain in the dry part of the internode at all times. This was apparently the case, because they were never observed in the water, with the exception of *H. bambusae* (Tab. 1).

We presume that *H. bambusae* larvae are able to stay in the water safely, because *Toxorhynchites* or other large aquatic predators were never found in their habitat. *Toxorhynchites* colonize internodes by shooting their eggs through internode holes while hovering in front of them (observation by the second author). Since internode sheaths block the larger *Lasiochila* exit holes and their entrance holes are too small, colonization by *Toxorhynchites* seems not possible.

Lasiochila holes are accessible for *Toxorhynchites* only after the internode sheaths loosen and lean strongly to the sides or fall off, or when the internodes grow, thus shifting the entrance hole in the bamboo wall beyond the edge of the sheath. At the time when *Toxorhynchites* larvae succeed to colonize a *Lasiochila* internode, they do not pose a danger to *H. bambusae* larvae, because they have already completed their development. This may be different in *H. ruficollis*, because *Lasiochila gestroi* exit holes sometimes occur above the internode sheaths.

Bamboo is unique among phytotelmata, because it offers a wide array of subhabitats with different animal communities, depending on the developmental stage of the bamboo and the size of the entrance hole (KOVAC & STREIT 1996). The large diversity of bamboo habitats may explain why there are so many Staphylininae species occurring there. Some species, like *Hesperomimus bambusae*, *H. ruficollis* and *Acylophorus* spp., are clearly specialized on bamboo because they apparently occur in the internodes during the whole year and develop there. Other species are probably facultative inhabitants of bamboo phytotelmata.

Mosquito-feeding Staphylininae are common in internode habitats with a rich mosquito fauna, such as internodes of immature bamboo culms, but they are rare in upright mature bamboo stems containing very few mosquito larvae. Therefore, we assume that the rich presence of mosquito larvae in bamboo internodes was the selective force leading to the colonization of this habitat by Staphylininae. The low predatory pressure in bamboo phytotelmata allowed *Hesperomimus* to penetrate into the water and develop adaptations to the aquatic environment. The trend to hunt mosquito larvae as staple food or capture prey in the water is also apparent in other terrestrial inhabitants of bamboo phytotelmata. For example, the jumping spider *Paracyrba wanlessi* ŽABKA & KOVAC, 1996 (Arachnida: Araneae: Salticidae) captures mosquito larvae, including *Toxorhynchites*, from the water's edge in decaying bamboo culms (ŽABKA & KOVAC 1996), and the nitidulid beetle *Amphicrossus japonicus* REITTER, 1873 seizes mosquito larvae with its forelegs while being submerged in water-filled bamboo stumps (KOVAC et al. 2007). We expect that there are many more Staphylininae species hunting aquatic organisms in phytotelmata or other aquatic habitats with low predatory pressure.

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