

RESEARCH PAPER

## Taxonomic review for the Asian taxa of plant bug tribe Hallodapini, with emphasis on stridulatory mechanism (Hemiptera: Heteroptera: Miridae)

Tomohide YASUNAGA<sup>1)</sup>, Yui TAMADA<sup>3)</sup>, Haruka HINAMI<sup>3)</sup>, Ayana MIYAZAKI<sup>3)</sup>, Ram Keshari DUWAL<sup>2)</sup> & Tetsuya NAGASHIMA<sup>3)</sup>

<sup>1)</sup>Research Associate, Division of Invertebrate Zoology, American Museum of Natural History, New York, NY 10024, USA; e-mail: tyasunaga@amnh.org

<sup>2)</sup>Visiting Researcher, Agriculture & Agri-Food Canada Environmental Health, K.W. Neatby: Bldg#20, 960 Carling Avenue, Central Experimental Farm, Ottawa Ontario, Canada K1A 0C6; e-mail: ramkeshariduwal@gmail.com

<sup>3)</sup>Nagasaki West High School, Biology Club, Takenokubo 12-9, Nagasaki 852-8014, Japan; e-mail: ssh@news.ed.jp

Accepted:  
18<sup>th</sup> February 2019

Published online:  
26<sup>th</sup> February 2019

**Abstract.** Asian genera and species of the plant bug tribe Hallodapini are reviewed. The present classification system is based particularly on detailed morphology and function of the stridulatory device and concealed habitat preference. Our recent efforts successfully demonstrated that the stridulatory devices of the forewing edge and dorsal metafemur are doubtlessly used for intraspecific communication (at least for courtship behavior). Based on the stridulatory structures and additional characters, *Cleotomiris* Schuh, 1995, *Cleotomiroides* Schuh, 1984, *Hallodapus* Fieber, 1858 and *Wygomiris* Schuh, 1984, are re-diagnosed and discussed; *Alloeomimella* Yasunaga & Duwal gen. nov. is proposed to accommodate *Alloeomimus muiri* Schuh, 1984 and a new combination, *Alloeomimella muiri* (Schuh) comb. nov., is accordingly established. Six new species are further described: *Cleotomiroides ishikawachui* Yasunaga & Duwal sp. nov. (Indonesia: Java); *Hallodapus jingfui* Yasunaga & Duwal sp. nov. (Taiwan); *H. spinosus* Yasunaga & Duwal sp. nov. (Thailand); *H. susurratus* Yasunaga & Duwal sp. nov. (Thailand); *Wygomiris paveli* sp. nov. (Taiwan); and *W. phormictes* sp. nov. (Taiwan). The male of *Wygomiris nanae* Yasunaga, 2012 is reported for the first time. A teratological form found on the antennae in two *Wygomiris* species is also documented.

**Key words.** Hemiptera, Heteroptera, Miridae, Phylinae, Hallodapini, new genus, new species, biology, morphology, stridulation, Asia

**Zoobank:** <http://zoobank.org/urn:lsid:zoobank.org:pub:027CE86F-9E75-44C3-A35E-E0C20BA4B693>

© 2019 The Authors. This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Licence.

### Introduction

Based mainly on morphological classification, the Asian fauna of the plant bug tribe Hallodapini (Miridae: Phylinae) has been the subject of recent taxonomic works (cf. YASUNAGA 2012; YASUNAGA et al. 2013a, b; YASUNAGA & DUWAL 2015, 2016; DUWAL et al. 2017) as well as a comprehensive revision on the tribes in the Indo-Pacific Phylinae (SCHUH 1984). Because of their concealed habitat, however, almost nothing is currently known about the natural history of hallodapine bugs. Except for some members inhabiting the aerial parts of plants (e.g., species of *Acrorrhinium*

Noualhier, 1895, *Cleotomiris* Schuh, 1995, *Cleotomiroides* Schuh, 1984, *Systellonotus* Fieber, 1858 and *Wygomiris* Schuh, 1984) (cf. WAGNER 1976, YASUNAGA 2001, DUWAL et al. 2017, YASUNAGA et al. 2018), quite a few hallodapines prefer to inhabit the ground densely covered with deep shrubs of mostly graminoid grass (YASUNAGA 2001, DUWAL et al. 2017, IKEDA et al. 2019). Therefore, sweep-netting and beating methods usually cannot yield sufficient samples of these epigeic mirids.

Although SCHUH (1974, 1984) presumed the minutely serrated or notched edge of forewing (exocorium or



embolium) and minute bumps or plectra on the dorsal surface of metafemur found in some members of *Hallodapini* as a stridulatory device, the practical function – do they really produce a sound? – is yet to be verified. The present work was initiated to prove the stridulation as well as to clarify the cryptic ecology for Japanese species of *Hallodapus* Fieber, 1858. During the course of our research on the natural history (including stridulation) of Japanese *Hallodapus* species carried out between March and December in 2018, an engine-vacuum-netting method has successfully provided more than 200 specimens of four *Hallodapus* spp., including quite a few immature forms and brachypterous female adults that cannot take flight. We also have succeeded in rearing all developmental stages in the laboratory, in exploring synthetic diet and in demonstrating that the device (the forewing edge – metafemur) undoubtedly performs stridulatory function [herein proven for *Hallodapus centrimalaculatus* (Poppius, 1909) and *H. ravenar* (Kirkaldy, 1902)]. Further, detailed observations on the surface structures for 33 species in nine Asian hallodapine genera by a tabletop scanning electron microscope and a compound microscope have confirmed that 18 species in four genera, *Alloeomimella* gen. nov., *Cleotomiris*, *Hallodapus* and *Wygomiris*, are also equipped with the similar stridulatory mechanism that also exhibits interspecific variations.

This paper represents the first part of recent attempt to document the novel taxonomic, morphological and ecological findings for the taxa of Asian *Hallodapini*, subsequent to IKEDA et al. (2019). The present part focuses on the taxonomic and morphological progress, including descriptions of a new genus and six new species that have been found during close examination of relevant Asian hallodapine materials. The male of *W. nanae* Yasunaga, 2012 that was described on a single female specimen is reported for the first time. Based on the stridulatory structures and some additional characters, five Asian genera are rediagnosed and discussed. The ecological topic including stridulatory mechanism is only briefly mentioned herein but will be argued in detail in a subsequent paper scheduled (TAMADA et al. in prep). A teratological form found on the antennal segments in two *Wygomiris* species is also documented.

## Material and methods

Thirty-three species in nine hallodapine genera were examined. The species treated in this work are summarized in the checklist below and Table 1. The depositories of type specimens are abbreviated in the text as follows:

DOAT Insect Collection, Entomology & Zoology Group, Plant Protection Research & Development Office, Department of Agriculture, Bangkok, Thailand;  
 NMNS National Museum of Natural Science, Taichung, Taiwan;  
 NMPC National Museum, Prague, Czech Republic;  
 NSMT National Science Museum, Tsukuba, Ibaraki, Japan;  
 TUAK Tokyo University of Agriculture, Atsugi, Kanagawa, Japan;  
 TYCN Tomohide Yasunaga collection, Nagasaki, Japan.

Matrix code labels are attached to the holotype and selected paratype specimens, which uniquely identify each specimen, and are referred to as ‘unique specimen identi-

fiers’ (USIs). The USI codes [e.g., AMNH\_PBI 0012345] comprise an institution and project code (AMNH\_PBI) and a unique number (0012345). These data were digitized on the Arthropod Easy Capture (formerly the Planetary Biodiversity Inventory) database maintained by the American Museum of Natural History, New York, USA (<http://research.amnh.org/pbi/>) and are also searchable on the ‘Heteroptera Species Pages’ (<http://research.amnh.org/pbi/heteropteraspeciespage/>). Scanning electron micrographs were taken with the Hitachi Tabletop Microscope® TM3030; genitalic structures and stridulatory device were also observed and photographed by the Nikon Eclipse-Ci upright microscope with a phase-contrast unit.

Four Japanese species of the genus *Hallodapus* were collected using a 2-cycle engine vacuum insect collector powered by a ‘Ryobi EBVK-2650 Handheld Blower/Vacuum’ (Figs 3–4); this effective, unique method for sampling various ground-inhabiting heteropterans is also introduced by KORN et al. (2015) and IKEDA et al. (2019) who captured a number of epigeic heteropterans. Our new methodology and artificial diet ingredient (derived from a fermented milk beverage) for rearing all developmental stages of *Hallodapus* species will be documented in TAMADA et al. (in prep). For recording and detecting the subtle sounds produced by two *Hallodapus* species (*H. centrimalaculatus* and *H. ravenar*), an Insect Microphone INS-M with a Highly Sensitive Multi-Amplifier MA-T (Narika Corporation, Tokyo, Japan) and a Wave-Pad Audio Editor (NCH Software, Colorado, USA) were applied. All measurements are given in millimeters in the text; for most of the SEM images, scale bars are shown in micrometer (µm).

Suprageneric classification of the Phylinae is based on SCHUH & MENARD (2013). The synonymic lists for known taxa are omitted, as comprehensive catalogs are now available (AUKEMA et al. 2013, KERZHNER & JOSIFOV 1999, SCHUH 1995, SCHUH 2013 online catalog). Terminology of the genitalia mainly follows DAVIS (1955), SCHUH (1984), WYNIGER (2006), YASUNAGA (2012), YASUNAGA & DUWAL (2016) and SCHWARTZ et al. (2018). For the stridulatory devices, some terms are employed from SCHUH (1984) and GOULA (2008); the following abbreviations are used throughout the text and figure legends:

FWS forewing (hemelytral or embolial) stridulitrum;  
 MFP metafemoral plectrum.

## Checklist of species examined in this study

### *Hallodapini* Van Duzee, 1916

= Auricillocorini Schuh, 1984

### *Acrorrhinium* Noualhier, 1895

*Acrorrhinium inexpectatum* Josifov, 1984 – Japan (Honshu).

*Acrorrhinium kranion* Yasunaga, Yamada & Artchawakom, 2013 – Thailand (Nakhon Ratchasima).

*Acrorrhinium lancialium* Yasunaga, Yamada & Artchawakom, 2013 – Thailand (Nakhon Nayok, Nakhon Ratchasima).

*Acrorrhinium tritonion* Yasunaga, Yamada & Artchawakom, 2013 – Thailand (Nakhon Nayok, Rayong).

***Alloeomimella* Yasunaga & Duwal gen. nov.**

*Alloeomimella muiri* (Schuh, 1984) **comb. nov.** – Thailand (Chaiyaphum, Nakhon Nayok), Indonesia (Lombok).

***Clapmarius* Distant, 1904**

*Clapmarius thailandana* Schuh, 1984 – Thailand (Nakhon Nayok).

***Cleotomiris* Schuh, 1995**

*Cleotomiris miyamotoi* Yasunaga, 2012 – Japan (Ryukyus).

*Cleotomiris sakaeratensis* Yasunaga & Duwal, 2015 – Thailand (Nakhon Ratchasima).

*Cleotomiris yamadakazi* Yasunaga, 2012 – Thailand (Nakhon Nayok, Nakhon Ratchasima).

*Cleotomiris* sp. – China (Yunnan).

***Cleotomiroides* Schuh, 1984**

*Cleotomiroides ishikawachui* Yasunaga & Duwal, **sp. nov.** – Indonesia (Java).

*Cleotomiroides tobii* Yasunaga, 2012 – Thailand (Nakhon Nayok, Nakhon Ratchasima).

***Hallodapus* Fieber, 1858**

*Hallodapus albofasciatus* (Motschulsky, 1863) – Thailand (Nakhon Nayok, Suphan Buri).

*Hallodapus brunneus* (Poppus, 1915) – Japan (Ryukyus).

*Hallodapus centrimaculatus* (Poppus, 1909) – Japan (Kyushu: Nagasaki), Thailand (Nakhon Ratchasima).

*Hallodapus fasciatus* (Poppus, 1909) – Thailand (Nakhon Nayok).

*Hallodapus jingfui* Yasunaga & Duwal **sp. nov.** – Taiwan (Pingtung).

*Hallodapus kyushuensis* (Miyamoto, 1965) – Japan (Nagasaki).

*Hallodapus linnavuorii* (Miyamoto, 1965) – Japan (Nagasaki, Ryukyus).

*Hallodapus ravenar* (Kirkaldy, 1902) – Japan (Nagasaki, Ryukyus).

*Hallodapus sibiricus* Poppus, 1912 – Russia (Primorsky).

*Hallodapus spinosus* Yasunaga & Duwal **sp. nov.** – Thailand (Nakhon Nayok).

*Hallodapus susurratus* Yasunaga & Duwal **sp. nov.** – Thailand (Chiang Mai).

*Hallodapus* sp. [near *H. maculatus* (Distant, 1904)] – China (Tianjin).

***Peniculimiris* Yasunaga & Duwal, 2016**

*Peniculimiris meniscus* Yasunaga & Duwal, 2016 – Thailand (Nakhon Ratchasima).

***Systellonotus* Fieber, 1858**

*Systellonotus malaisei* Lindberg 1934 – Japan (Hokkaido).

***Wygomiris* Schuh, 1984**

*Wygomiris indochinensis* Schuh, 1984 – Thailand (Nakhon Ratchasima).

*Wygomiris kaliyahae* Yasunaga, 2012 – Thailand (Chaiyaphum, Nakhon Ratchasima).

*Wygomiris nanae* Yasunaga, 2012 – Thailand (Nakhon Nayok), Vietnam (Son La).

*Wygomiris paveli* Yasunaga & Duwal **sp. nov.** – Taiwan (Pingtung).

*Wygomiris ramae* Yasunaga, 2012 – Nepal (Kathmandu).

*Wygomiris phormictes* Yasunaga & Duwal **sp. nov.** – Thailand (Nakhon Ratchasima).

**Taxonomy****Tribe Hallodapini Van Duzee, 1916**

**Diagnosis.** Distinguished from any other tribes in the subfamily Phylinae by the following combination of characters: Body elongate to elongate oval, sometimes more slender (e.g., *Podullahas* Schuh, 1984, *Sohenus* Distant, 1910) variable in size (2.2–7.0 mm), more or less antlike (Figs 9–24), with simple vestiture, lacking scalelike setae; brachypterous form often present mostly in female (coleoptery or staphylinoidy sensu SCHUH & SLATER 1995); basic coloration brownish or reddish, without green tinge; eyes small; antenna uniformly long, almost linear and often thickened, as long as or longer than body; pronotum usually constricted anteriorly, with distinct, flat collar; margin of exocorium (FWS) minutely notched or serrate and dorsal surface of metafemur furnished with minute bumps (plectrum, MFP) forming a stridulatory device in six genera; legs generally long; left paramere with developed sensory lobe tightly holding phallosome; right paramere usually reduced, tiny; endosoma elongate in most members, often sigmoid or coiled, with more or less elaborated apical part and thick-rimmed secondary gonopore; sclerotized ring ovoid to elongate oval, clearly rimmed.

**Distribution.** Nearly cosmopolitan but majority of species known from the Old World tropics, subtropics and warm temperate zones; no reliable record existing from Pacific islands or atolls; only 13 species in three genera, *Cyrtopeltocoris* Reuter, 1876, *Lapazphylus* Carvalho & Costa, 1992 and *Phoradendrepulus* Polhemus & Polhemus, 1985 known in New World and *Acrorrhinium spicatum* (Distant, 1904) in Australian Region (SCHUH 2013). However, some New World genera treated by SCHUH & MENARD (2013) as incertae sedis in the Phylini could be true hallodapine members (K. L. Menard, pers. comm.).

**Discussion.** SCHUH (1984) proposed Auricillocorini composed of five Oriental genera, *Auricillocoris* Schuh, 1984, *Cleotomiris*, *Cleotomiroides*, *Wygomiris* and *Zaratus* Distant, 1909. Although this classification was followed by YASUNAGA (2012), the Auricillocorini is now regarded as a junior synonym of Hallodapini, involving 14 valid genera in Asia (cf. SCHUH 2013, SCHUH & MENARD 2013). Possession of the stridulatory device is currently confirmed in members of six Old World genera. In addition to Asian *Alloeomimella* new genus, *Cleotomiris*, *Hallodapus*, and *Wygomiris* (Table 1), two Ethiopian genera, *Laemocoris* Reuter, 1879 and *Trichophthalmocapsus* Poppus, 1914, were reported to have the lateral hemelytral margins (FWS) and dorsobasal surface of metafemora (MFP) modified to

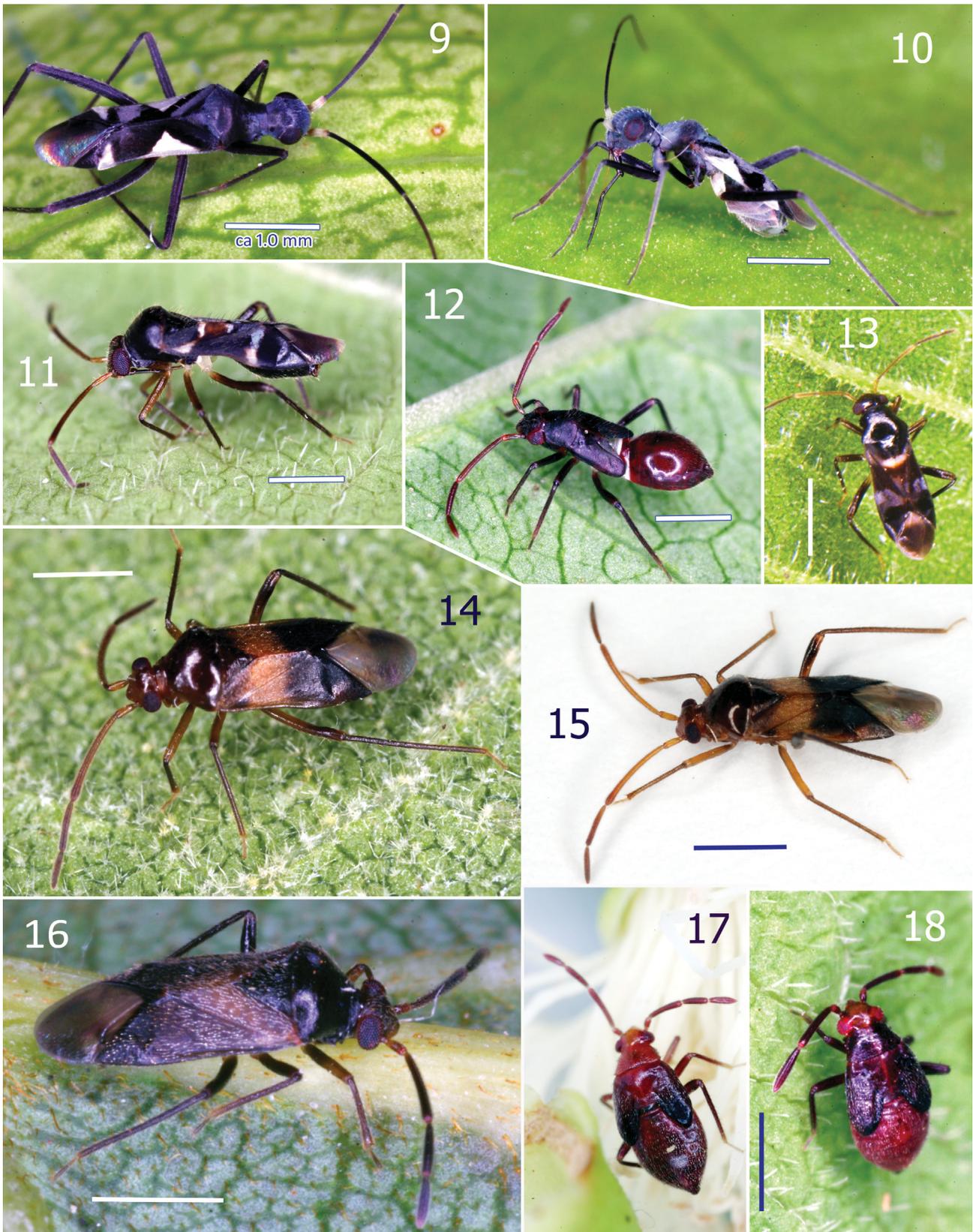
form a stridulatory mechanism (SCHUH 1974).

We have successfully confirmed that *Hallopapus centrimaculatus* (approx. 2,100 Hz) and *H. ravenar* (800 Hz) produced sounds, using the stridulatory device (FWS+M-FP) during courtship behavior (Fig. 32). Nonetheless,

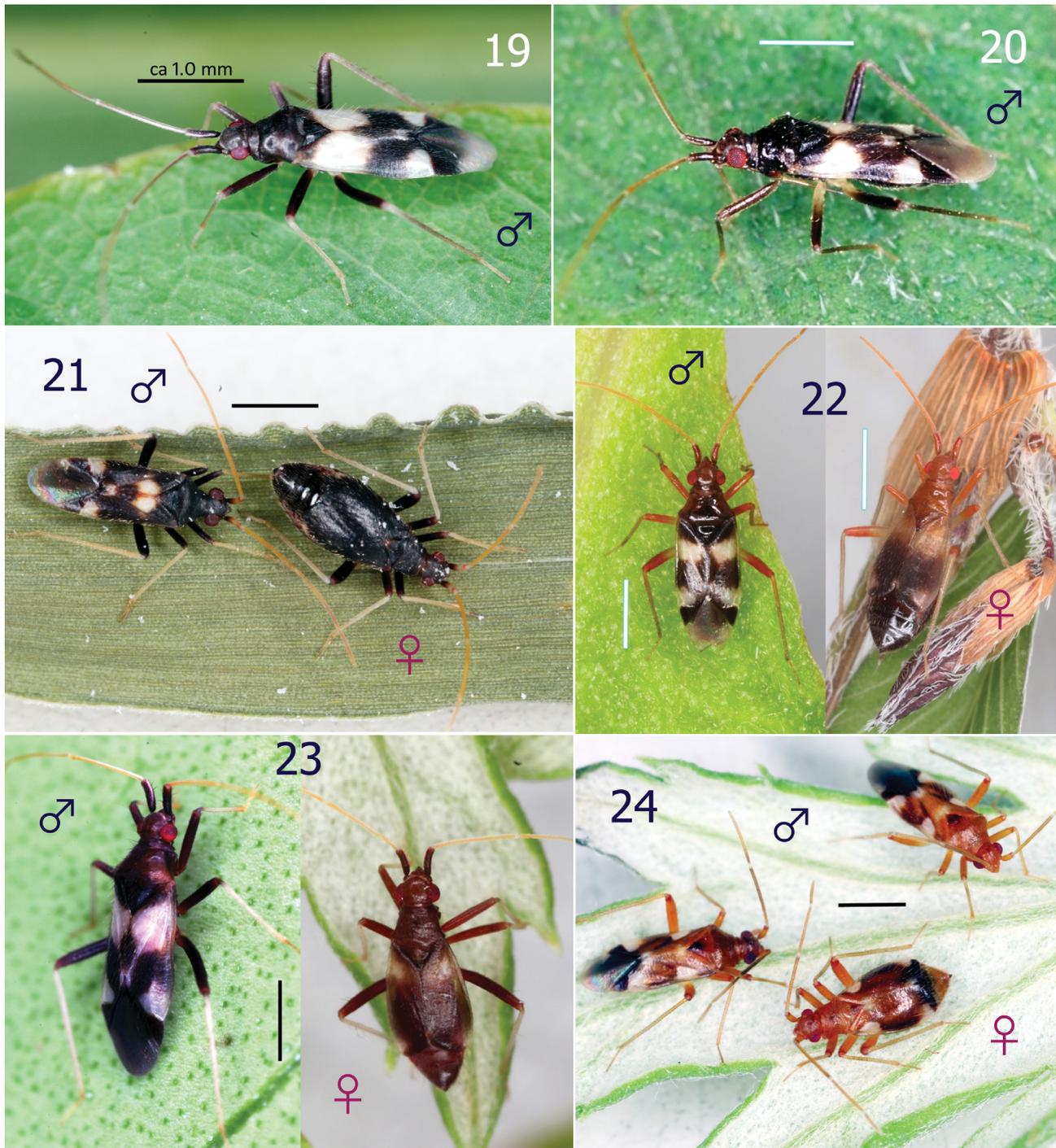
our recent observations suggest that the presence of the stridulatory device may be homoplasious in some species of a certain genus. This character status is evidenced by closely related species of *Wygomiris*; in *W. indochinensis* (Fig. 145) vs. *W. paveli* (Figs 141–142) and *W. kaliyahae*



Figs 1–8. Habitats of epigeic hallopadine plant bugs (1–2), sampling method (3–5), and oviposition (6) and eggs of Japanese *Hallopapus* species (laboratory observation) (7–8). 1 – typical habitat of *Hallopapus centrimaculatus* (Poppius, 1909), *H. kyushuensis* Miyamoto, 1965 and *H. linnavuorii* Miyamoto, 1965 in Nagasaki, Japan; 2 – habitat of *Alloeomimella muiri* (Schuh, 1984), *Hallopapus albofasciatus* (Motschulsky, 1863), *H. ravenar* (Kirkaldy, 1902) and *H. spinosus* sp. nov. in Nakhon Nayok, Thailand; 3–5 – engine vacuum netting method for sampling ground-inhabiting heteropterans; 6 – brachypterous female of *H. centrimaculatus* ovipositing into weed (*Artemisia* sp.) stem near root; 7 – eggs (opercula) of *H. centrimaculatus*; 8 – egg of *H. ravenar* (same egg as in Figs 108–109).



Figs 9–18. Habitus images of Asian species of Hallopadini. 9–10 – *Alloemimella muiri* (Schuh, 1984) (Nakhon Nayok, Thailand): 9 – ♂; 10 – ♀. 11–12 – *Cleotomiroides tobii* Yasunaga, 2012 (Nakhon Ratchasima, Thailand): 11 – ♂; 12 – 5th instar nymph. 13 – *Cleotomiris miyamotoi* Yasunaga, 2012 (Okinawa, Japan), ♂. 14–15 – *Wygomiris paveli* sp. nov., ♂ (Pingtung, Taiwan). 16–18 – *W. kaliyahae* Yasunaga, 2012 (Thailand): 16 – holotype, ♂ (Nakhon Ratchasima, AMNH\_PBI 00379521); 17 – 5th instar nymph found from broadleaf inflorescence (Chaiyaphum); 18 – 5th instar nymph with teratological antenna, collected by sweep-netting Lauraceae tree leaves (Nakhon Ratchasima).



Figs 19–24. Habitus images of Asian *Hallodapus* species. 19 – *H. spinosus* sp. nov., ♂ (Nakhon Ratchasima, Thailand); 20 – *H. brunneus* (Poppus, 1915), ♂ (Ishigaki Island, Japan). 21–24 – *Hallodapus* species collected by engine vacuum netting method in Nagasaki, Japan: 21 – *H. centrimalatus* (Poppus, 1909); 22 – *H. linnavorii* Miyamoto, 1965; 23 – *H. kyushuensis* Miyamoto, 1965; 24 – *H. ravenar* (Kirkaldy, 1902).

(Fig. 58) vs. *W. phormictes* (Figs 150, 153) – the former species lacks the device, whereas the latter possesses it (see Table 1).

Little has been known about the biology of species grouped into Hallodapini as most available specimens were collected using UV light traps. The immature forms of a few Asian members were found to inhabit and/or propagate on inflorescence and leaves (e.g., *Wygomiris kaliyahae*, as in Figs 17–18), leaves (*Cleotomiroides tobii*, Fig. 12), tree bark or branches (*Acrorrhinium* spp.; see

YASUNAGA et al. 2013a, DUWAL et al. 2017) of broadleaf trees (YASUNAGA et al. 2013a, DUWAL et al. 2017). Thus far as known, most Asian species of *Alloeomimella* and *Hallodapus* were confirmed to be epigeic and have the distinct stridulatory device (Table 1). The females of these hallodapines are predominantly brachypterous (forewing coleoptery with rudimentary hindwings, cf. Figs 104, 216–217); the females of *Systellonotus* species are exceptionally staphylinoidy (YASUNAGA 2001; WYNGER 2006). Due to sexual dimorphism of the wings (brachyp-

Table 1. Significant taxonomic characters and known habitats for 33 Asian species of Hallodapini. Abbreviations: SD – stridulatory device; PS – male pygophoral spine; OS – female ovipositor spine. Hab (habit or habitat): inhabiting ground (G) or aerial parts of plants (P); collected at UV light (L).

Species examined	SD	PS	OS	Hab
<i>Acrorrhinium inexpectatum</i>			+	L, P
<i>Acrorrhinium kranion</i>			+	L
<i>Acrorrhinium lancialium</i>			+	L, P
<i>Acrorrhinium tritonion</i>			+	L, P
<i>Alloeomimella muiri</i>	+			G, L
<i>Clapmarius thailandana</i>		+	+	L
<i>Cleotomiris miyamotoi</i>	+			L
<i>Cleotomiris sakaeratensis</i>		+		L
<i>Cleotomiris yamadakazi</i>		+		L
<i>Cleotomiris</i> sp.	+	?		?
<i>Cleotomiroides ishikawachui</i>		+		L
<i>Cleotomiroides tobii</i>		+		L, P
<i>Hallodapus albofasciatus</i>	+			G, L
<i>Hallodapus brunneus</i>	+			G, L
<i>Hallodapus centrimaculatus</i>	+			G, L
<i>Hallodapus fasciatus</i>	+			L
<i>Hallodapus jingfui</i>	+			L
<i>Hallodapus kyushuensis</i>	+			G, L
<i>Hallodapus linnavuorii</i>	+			G, L
<i>Hallodapus</i> [near] <i>maculatus</i>	+			?
<i>Hallodapus ravenar</i>	+			G, L
<i>Hallodapus sibiricus</i>	+			G, L
<i>Hallodapus spinosus</i>	+	+	?	L
<i>Hallodapus susurratus</i>	+	+	?	?
<i>Hallodapus</i> sp.	+			?
<i>Peniculimiris meniscus</i>		+	+	L
<i>Systellonotus malaisei</i>				P
<i>Wygomiris indochinensis</i>		+		L
<i>Wygomiris kaliyahae</i>		+		L, P
<i>Wygomiris nanae</i>		+		L
<i>Wygomiris paveli</i>	+	+		L
<i>Wygomiris phormictes</i>	+	?		L
<i>Wygomiris ramae</i>		+		L

terous females that cannot take flight), the majority of individuals attracted to UV light are male as a matter of course. The brachypterous males are known in European hallodapines (e.g., *Hallodapus montandoni* Reuter, 1895 and *Omphalonotus quadriguttatus* (Kirschbaum, 1856), see WYNIGER 2006). KMENT & BAŇAŘ (2012) also reported that *Hallodapus montandoni* is an epigeic species inhabiting xerothermic habitats, mostly on limestone, rarely on sandy ground and possibly associated with ants, especially *Myrmica* spp.

YASUNAGA & DUWAL (2016) discussed a spine on the genital segment (cf. Figs 30, 124, 130, 136) that is recognized in some members of Hallodapini; however, the spine is usually possessed only by males (Table 1). Within Asian hallodapines, presence of the spine in each sex (both P- and O-spines) was confirmed in *Clapmarius thailandana* and *Peniculimiris meniscus*. Although the P- and O-spines of these taxa were assumed to stabilize the mating position, the actual functions of these spines are yet to be demonstrated (YASUNAGA & DUWAL 2016).

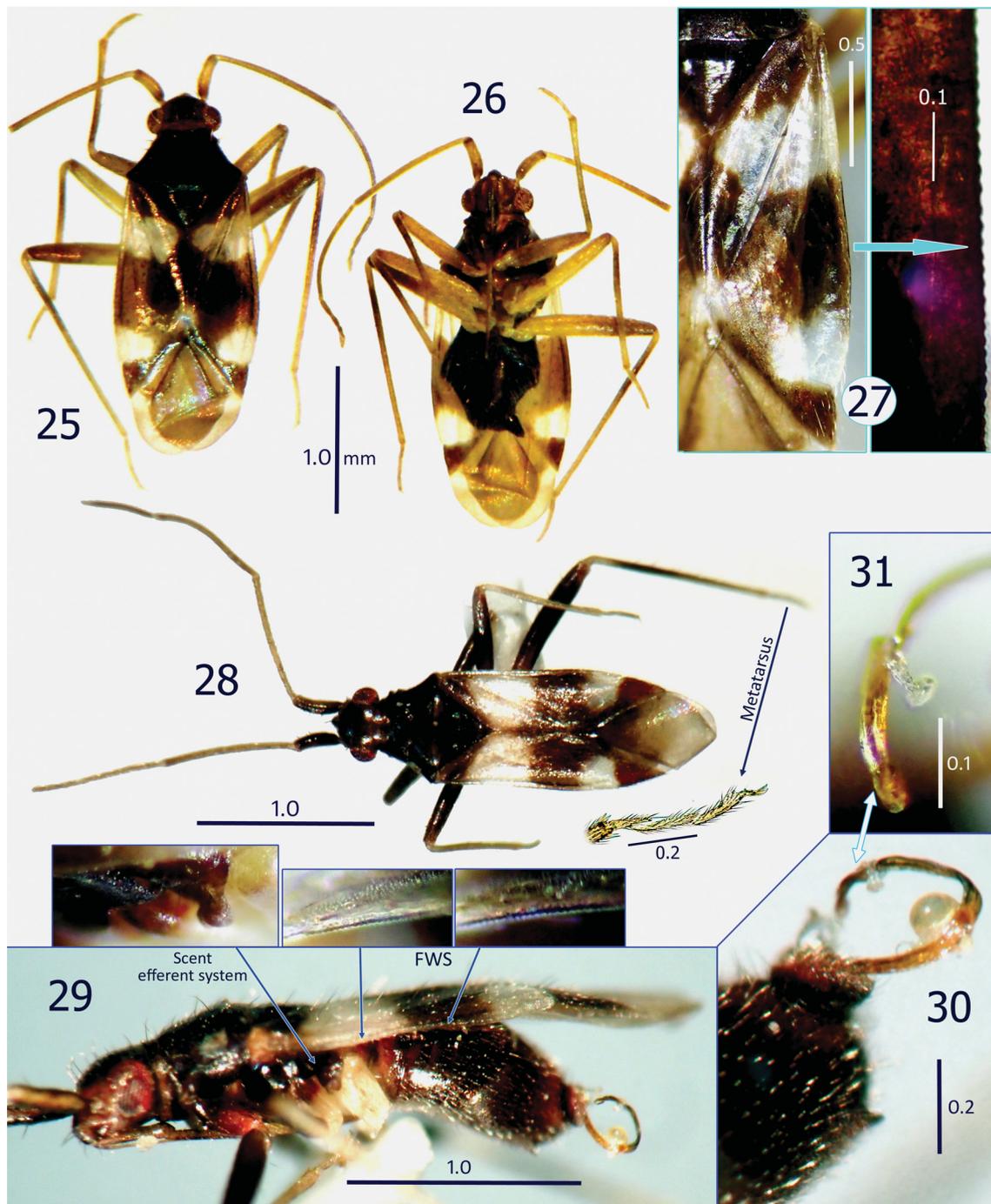
On the other hand, the stridulatory device (FWS+MFP) is currently assumed to be synapomorphy for the four Asian genera (*Alloeomimella*+*Hallodapus*+*Cleotomiris*+*Wygomiris*) plus two Afrotropical *Laemocoris*+*Trichophthalmocapsus*. The well-developed device has hitherto been found only in ground-inhabiting hallodapines. The devices in *Cleotomiris miyamotoi* (Figs 66–67) and *Wygomiris paveli* (Figs 55, 141–142) are obviously reduced and seems to lose its original function. Incidentally, the scent efferent system is noticeably small in two epigeic genera, *Alloeomimella* and *Hallodapus*, whereas it is enlarged in *Cleotomiris* and *Wygomiris*. The current evidence suggests that the ground-inhabiting hallodapines (in *Alloeomimella* and *Hallodapus*) may utilize sound for intraspecific communication rather than pheromones (from the scent gland). In addition, the parempodia of all the epigeic *Alloeomimella* and *Hallodapus* species we examined are setiform; such species frequently slip and walk clumsily on smooth surface (e.g., acrylic or glass Petri dish) but the simplified pretarsal structure possibly enables agile and comfortable movement on the chaotic, messy ground of deep meadows. Nonetheless, much broader morphological and ecological survey treating all hallodapine taxa is required to elucidate the evolution and phylogeny of Hallodapini.

#### *Alloeomimella* Yasunaga & Duwal gen. nov.

**Type species.** *Alloeomimus muiri* Schuh, 1984, present designation.

**Diagnosis.** Distinguished from the most closely related genus, *Alloeomimus* Reuter, 1910, by the following combination of characters: Body generally slender, constricted at middle of hemelytron, myrmecomorphic (Figs 9–10); female sometimes brachypterous (Fig. 59); dorsum dark gray, generally matte; head bulbous, rounded, with eye removed from pronotal collar (Figs 9, 62); pronotum trapezoidal, weakly constricted anteriorly (Fig. 62); scutellum weakly swollen, without any projection; metathoracic scent efferent system reduced, small (Figs 59–60); hemelytron with a large, white triangular macula on middle corium across embolium and a wedge-shaped macula at apex of corium across embolium along anterior margin of cuneus (Fig. 9); forewing margin and metafemur equipped with a distinct stridulatory device (Figs 54, 63–64); endosoma slender, C-shaped, similar in overall appearance to that of *Hallodapus* (cf. SCHUH 1984, YASUNAGA et al. 2013a); bursa copulatrix and ovipositors rather toughened (Fig. 210–211), with sclerotized rings small, ovoid (Fig. 210).

**Description. Male.** Macropterous; body small, slender, myrmecomorphic (Figs 9–10); dorsum dark gray, matte, with uniformly distributed, short, reclining setae and sparsely distributed, stiff, erect setae (Fig. 62); head bulbous, rounded, less prognathous (Fig. 56); eye removed from pronotal collar but diameter of neck shorter than length of an eye in dorsal view (Figs 9, 62). Antenna generally slender, slightly longer than body; segment I short, about as long as height of an eye; segment II longer than III; segment IV about 3 times as long as I. Labium long, exceeding apex of metacoxa, reaching abdominal sternum IV. Pronotum



Figs 25–31. Two new species of *Halodapus*. 25–27 – *H. jingfui* sp. nov., holotype ♂ (Taiwan): 25 – dorsal habitus; 26 – ventral habitus; 27 – hemelytron (FWS, right). 28–31 – *H. spinosus* sp. nov., holotype ♂ (Thailand): 28 – dorsal habitus, with metatarsus; 29 – left lateral habitus; 30 – pygophore with pygophoral spine and exposed endosoma (see also Fig. 124); 31 – apical structure of endosoma.

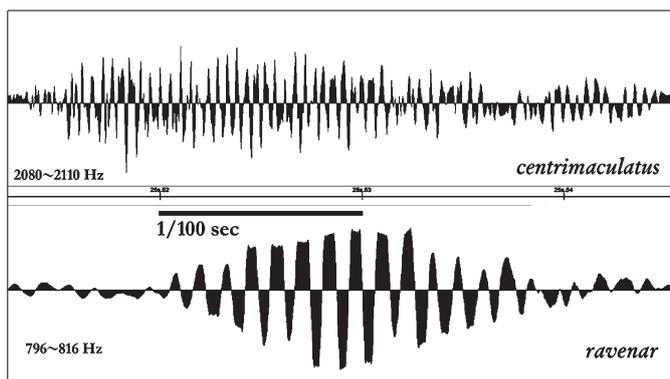


Fig. 32. Sound patterns emitted by two Japanese *Halodapus* species (detected with courtship behavior).

matte, trapeziform, weakly constricted anteriorly (Fig. 62); metathoracic scent efferent system reduced, narrower than each coxa (Fig. 56); hemelytron with a large, white triangular macula on middle corium across embolium and a wedge-shaped macula at apex of corium across embolium along anterior margin of cuneus (Fig. 9); embolium with distinct FWS (Fig. 60). Legs long; metafemur equipped with distinct MFP; total length of metafemur+metatibia longer than body; parempodia setiform (Fig. 58). Male genitalia (Fig. 61): Pygophore smooth, narrow, with the apically tapered phallosome; left paramere with stout sensory lobe; endosoma slender, C-shaped (cf. YASUNAGA et al. 2013a).

**Macropterous female.** Almost similar to male (Fig. 10). Stridulatory device as in male. Female genitalia (Figs 210–211): Bursa copulatrix relatively narrow, widely spinulate, with small, ovoid sclerotized rings (Fig. 210); ovipositors (gonapophyses) rather short; gonapophysis II sword-like, not expanded subapically (Fig. 211).

**Brachypterous female.** As in Fig. 59. Apex of forewing reaching anterior margin of abdominal tergum VI. Stridulatory device present (Figs 63–64).

**Etymology.** From the halledapine generic name *Alloeo-mimus* combined with a diminutive suffix (-ella); gender feminine.

**Distribution.** Oriental Region: Indonesia (Java, Lombok), Laos and Thailand (SCHUH 1984, YASUNAGA 2013a); new record from Lombok Island, or Wallacea, based on two female specimens collected at Dasambaru, Lombok on 5 Mar 2005 by Ishikawa (deposited in TUAK).

**Discussion.** SCHUH (1984) described *Alloeo-mimus muiri*, based on Indochinese and Indonesian specimens. *Alloeo-mimus* is an Old World genus, currently composed of six species (including *A. muiri*) but five congeners (incl. type species of the genus) are restricted to the western Palearctic and Ethiopian Regions (Mediterranean, Middle East and Africa, cf. SCHUH 2013). Our present examination suggested that the Schuh's species (*muiri*) can be evidently separated from the members of *Alloeo-mimus* in having some different characters mentioned above as well as disjunct distribution in the Oriental Region. We therefore propose a new genus *Alloeo-mimella* for it, and a new combination is accordingly established: *Alloeo-mimella muiri* (Schuh, 1984) comb. nov. (see SCHUH 1984 and YASUNAGA et al. 2013a for detailed diagnostic characters of this species).

*Alloeo-mimella muiri* was confirmed to be epigeic; several individuals including brachypterous females were found from the ground at tropical grasslands (cf. Fig. 2). On the other hand, *Alloeo-mimus unifasciatus* (Reuter, 1879) was reported to be associated with *Ononis natrix* L. (Fabaceae) (SCHUH 2013). In addition, a congener from the Middle East, *A. kurdus* Hoberlandt, 1953, was reported to occasionally inhabit galls of aphids (WAGNER 1974), which implies that *Alloeo-mimus* members may be associated with aerial parts of plants and may not prefer an epigeic habitat. Color habitus images of the five *Alloeo-mimus* species are available on a website (<https://www.discoverlife.org/mp/20q?search=Alloeo-mimus>).

Based on the developed stridulatory device (Figs

63–64), reduced scent efferent system (Figs 59–60), setiform parempodia, similar male and female genital structures and habitat preference, *Alloeo-mimella* is assumed to be most closely allied to *Halledapus* rather than *Alloeo-mimus*.

### *Cleotomiris* Schuh, 1995

**Diagnosis.** General shape rather ant-like (Fig. 13); small to moderate size (total length 3.0–4.5 mm); brown to fuscous basic coloration; more or less terete antennal segments II–IV; weakly swollen, trapezoidal pronotum that is not much constricted anteriorly (Fig. 65); ear-like ostiolar peritreme (Figs 71, 131); presence of white fascia on clavus just posterior to scutellum (Fig. 13); possession of stridulatory device (currently confirmed in two species, see Table 1 and Figs 66–67, 132–133); weakly fleshy, apically convergent parempodia (Fig. 68); and short endosoma with an apical spine of various length and a developed secondary gonopore. Further diagnostic characters and detailed description were provided by SCHUH (1984).

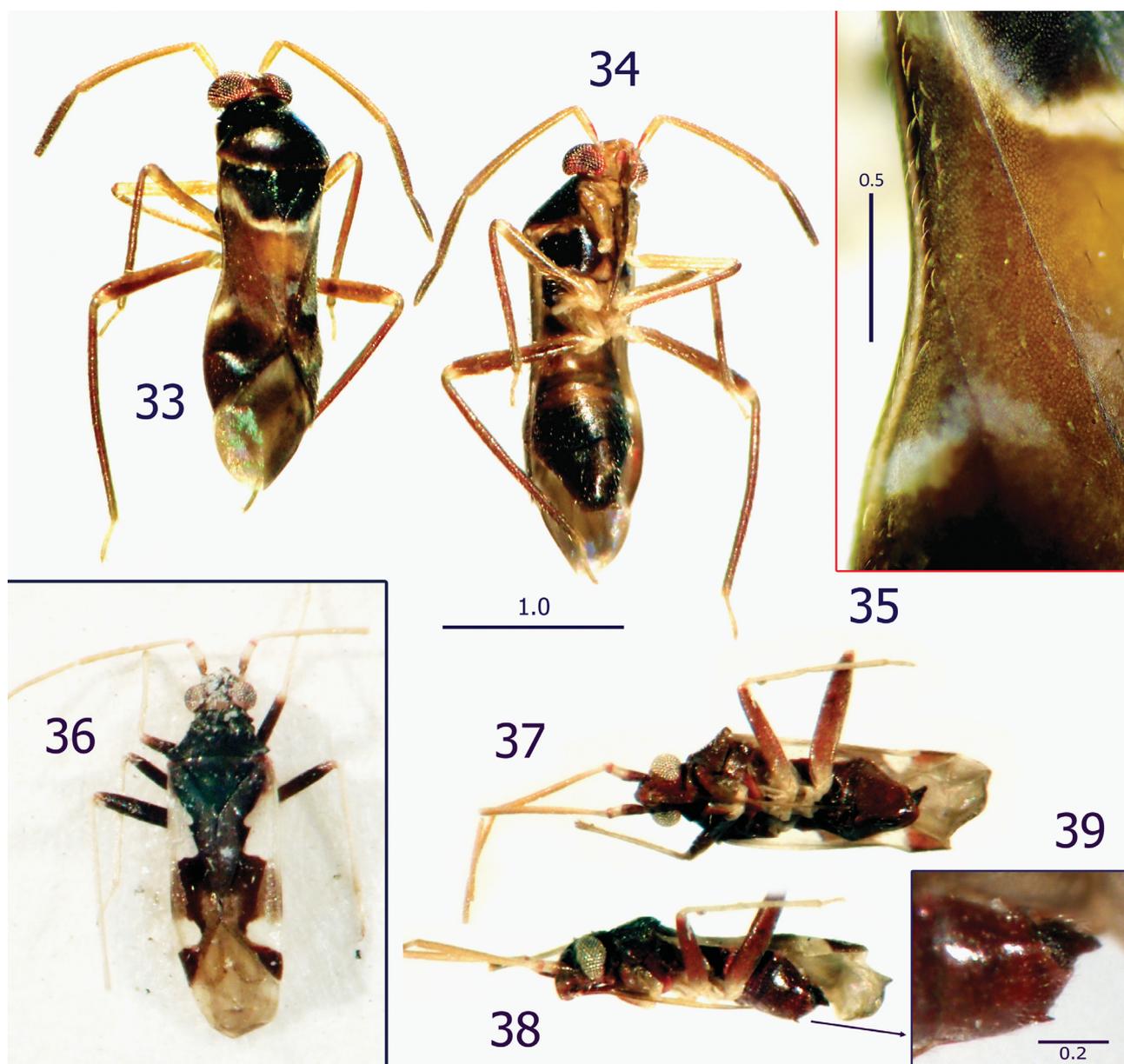
**Distribution.** Known widely from the Sundaland west of the Wallacea, Indochina, southern China, Philippines and Japanese Okinawa Island (YASUNAGA 2001, 2012).

**Discussion.** Although this genus is superficially similar to *Cleotomiroides*, the male and female genital structures of these genera are significantly different from each other (see YASUNAGA 2012, DUWAL et al. 2017). YASUNAGA (2012) suggested that the similarity between *Cleotomiris* and *Cleotomiroides* was only superficial. Present observation also confirmed that some species of *Cleotomiroides* and *Wygomiris* are associated with broadleaf trees (on which immature forms were found, cf. Figs 12, 17) and lack the stridulatory mechanism. General shape of the female genitalia of *Cleotomiris* rather resembles that of *Wygomiris*. Almost all of the available specimens of these three genera were collected using UV light traps at well preserved subtropical or tropical forests. Therefore, members of these genera are currently considered to be arboreal.

Our examination by a SEM could find out the stridulatory devices in two *Cleotomiris* species, *C. miyamotoi* Yasunaga (Figs 66–67) from Okinawa Island, Japan and an (presumably) undescribed species currently represented by a single female from Yunnan Province, China (NMPC). This unique Chinese species has rather developed FWS+MFP (Figs 132–133) which appear to retain the original function (stridulation) although it is superficially most similar to *C. miyamotoi* or *C. schneirlai* Schuh, 1984 (Philippines). From southern China (Yunnan, Sichuan) to northern Indochina, more than a few undetermined specimens representing at least three closely related species of *Cleotomiris* or *Cleotomiroides* are present. Therefore, definitive determination of these taxa is beyond a scope of the present study.

### *Cleotomiroides* Schuh, 1984

**Diagnosis.** Externally very similar to *Cleotomiris*, from which this genus can be distinguished by slender and almost linear antennal segments II–IV (Figs 11–12), strongly



Figs 33–39. Two new species of Asian halloedapines. 33–35 – *Cleotomiroides ishikawachui* sp. nov., holotype ♂ (Java): 33 – dorsal habitus, 34 – ventral habitus, 35 – hemelytron; 36–39 – *H. susurratus* sp. nov., (Thailand): 36 – dorsal habitus, holotype ♂; 37 – ventral habitus, paratype ♂; 38 – ditto, left lateral view; 39 – pygophore, with pygophoral spine.

protruding evaporative area of scent efferent system (Figs 74–75), remarkably broadened endosoma that is more or less elaborated apically with some appendages (Fig. 195), and small but thick-rimmed sclerotized ring (see YASUNAGA 2012). Detailed diagnosis and description were provided by SCHUH (1984).

**Discussion.** See discussion under *Cleotomiris*.

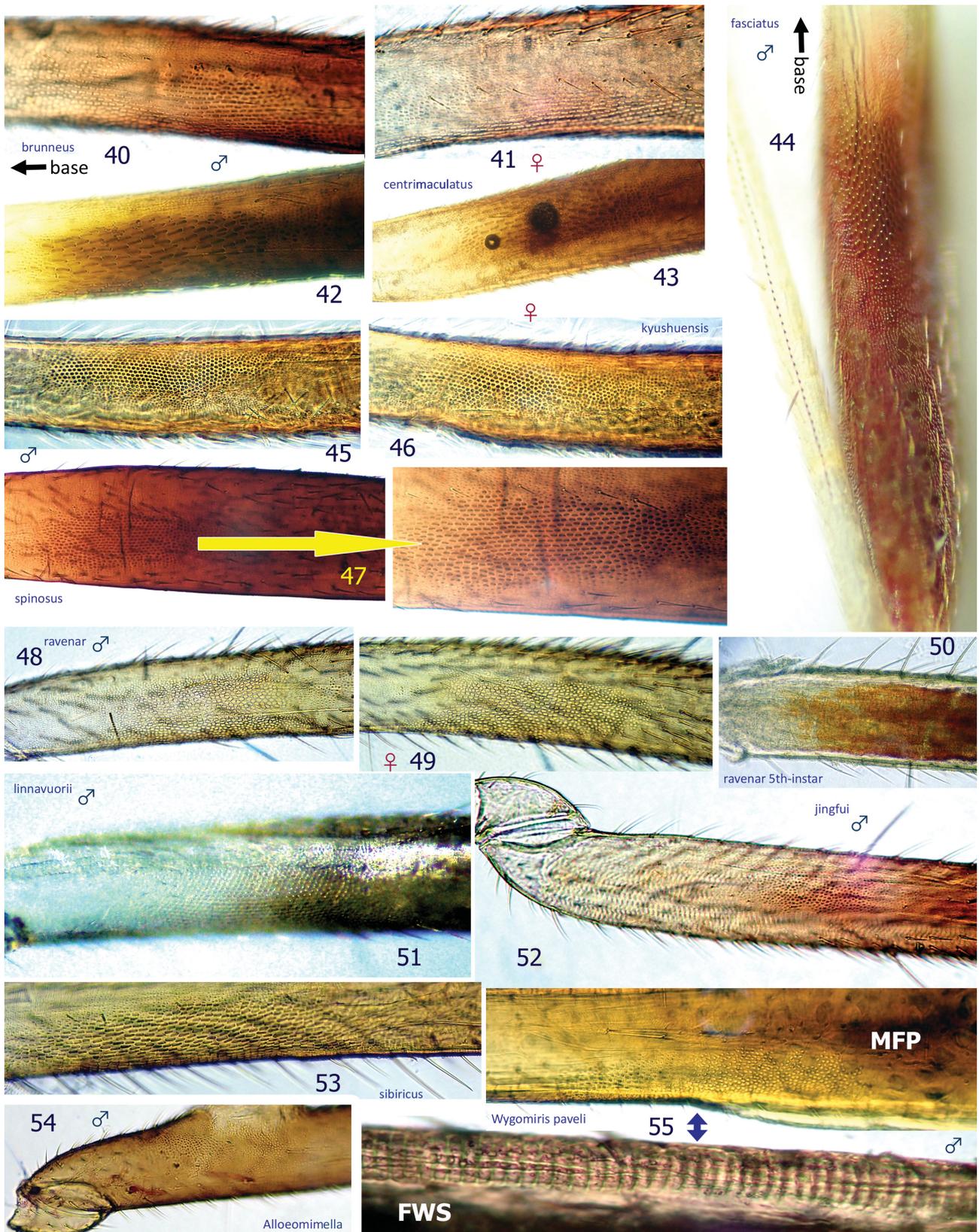
***Cleotomiroides ishikawachui* Yasunaga & Duwal,  
sp. nov.**

(Figs 33–35, 74–76, 192–195)

**Type material.** HOLOTYPE: ♂, INDONESIA: JAVA: Malang, Buring, S07°59'40.0"–42.0" E112°39'38.0"–39.1", 513–518 m alt., 24 Aug 2005 (afternoon), T. Ishikawa (TUAK) (AMNH\_PBI 00380631).

**Differential diagnosis.** Recognized by its relatively large size; fuscous basic coloration contrasting with rusty apical half of the clavus (Fig. 33); conspicuous white fascia and maculae on hemelytron (Figs 33, 35); and form of male genitalia (Figs 192–195). This new species can be distinguished from two known congeners by the fuscous general coloration, broad hypophysis of the left paramere (Fig. 193), and elongate apical appendage and spinulate flap-like process of the endosoma (Fig. 195).

**Description. Male.** Body generally blackish brown, relatively small, myrmecomorphic; dorsal surface weakly shining, widely shagreened or roughened, with sparsely distributed, woolly semierect setae and with more sparsely distributed, longer, upright setae (Fig. 35). Head dull brown, oblique; eyes large; vertex narrowly carinate basa-



Figs 40–55. Stridulatory device (MFP, except for FWS on 55) of Asian halodapines observed by a compound microscope. 40–41 – *Halodapus brunneus* (Poppius, 1915); 42–43 – *H. centrimaculatus* (Poppius, 1909); 44 – *H. fasciatus* (Poppius, 1909) (Nakhon Nayok, Thailand); 45–46 – *H. kyushuensis* Miyamoto, 1965; 47 – *H. spinosus* sp. nov.; 48–50 – *H. ravenar* (Kirkaldy, 1902); 51 – *H. linnavuorii* Miyamoto, 1965; 52 – *H. jingfui* sp. nov.; 53 – *H. sibiricus* Poppius, 1912 (S. Primorsky, Russia); 54 – *Alloeomimella muii* (Schuh, 1984); 55 – *Wygomiris paveli* sp. nov.

lly. Antenna dull yellowish brown, almost linear; segment II slightly incrassate toward apex; segments III and IV brown, weakly terete. Labium shiny dark brown, reaching subapical part of mesocoxa. Pronotum with a narrow collar, narrower than all antennal segments; pleura shiny fuscous, minutely rugose; ostiolar peritreme strongly protruding medially, with ivory white posterior margin of evaporative area. Hemelytron with a white, continuous fascia posterior to scutellum across clavus, corium and exocorium (Fig. 33); apical 1/4 of corium rusty; membrane smoky brown, except for pale, translucent base. Coxae and legs brown or darker; meso- and metacoxae widely pale brown; pretarsus with rather fleshy, apically convergent parempodia (Fig. 76). Abdomen wholly dark brown, somewhat shagreened (Fig. 34). Male genitalia (Figs 192–195): Genital segment with a ventral spine (Fig. 192). Left paramere with rather stout hypophysis (Fig. 193). Phallosome almost straight, tapered, with a spine near apex (Fig. 194). Endosoma J-shaped, stout, with an elongate apical appendage and a weakly sclerotized, rounded flap-like process beside thick-rimmed secondary gonopore (Fig. 196).

**Measurements.** Male (holotype): Total length of body 3.33; head width including eyes 0.72; vertex width 0.21; lengths of antennal segments I–IV 0.30, 1.07, 0.60, 0.44; total labial length 1.28; basal width of pronotum 1.02; maximum width across hemelytron 1.05; and lengths of metafemur, tibia and tarsus 1.14, 1.70, 0.30.

**Female.** Unknown.

**Etymology.** Named after a Japanese heteropterist, Dr. Tadashi (nickname Chu) Ishikawa who collected the holotype specimen of this new species; a noun in genitive case.

**Biology.** Unknown; Dr. Ishikawa collected the holotype female by sweep-netting an unidentified broadleaf tree.

**Distribution.** Indonesia: Java (this paper).

### *Hallodapus* Fieber, 1858

**Diagnosis.** Body rather small, elongate, slender but female predominantly brachypterous (Figs 19–24); dorsum weakly shining, impunctate, with sparsely distributed, pale, simple, upright setae; general coloration basically brown, with pale or white maculae on corium and/or clavus, lacking greenish tinge; more or less prognathous head; eye small, contiguous to flattened pronotum collar; stridulatory device involving dorsobasal surface of metafemur and embolial edge present both in macropterous and brachypterous forms; scent efferent system small; parempodia setiform (Figs 91, 129); pygophore usually smooth, rarely with a pygophoral spine (in *H. spinosus* sp. nov. and *H. susurratus* sp. nov.); left paramere developed (Figs 85, 130); endosoma slender, elongate or sometimes very long, with well-marked secondary gonopore (Figs 94, 107, 178–180); ovipositors short, with developed apices; posterior wall simple; sclerotized ring small but clearly rimmed (Figs 201–209).

**Distribution.** Known widely from the Old World (Palearctic Region to southern Africa, northeast to Japan, Korea and Russian Far East, and Oriental Region southeast across Wallacea to New Guinea and northern Australia); most speciose in the Ethiopian and Oriental Regions (SCHUH 2013).

**Discussion.** This is the most speciose genus in the tribe *Hallodapini*, including about 50 valid species from the Old World. Majority of them are thermophilic, known predominantly from tropical and subtropical climate zones. All *Hallodapus* species we have examined (Table 1) are equipped with the distinct stridulatory device (e.g., Figs 41–53, 77–78, 81–84). Our recent attempt successfully detected stridulation in two Japanese species, *H. centrimaculatus* (approx. 2,100 Hz) and *H. ravenar* (800 Hz), in laboratory observation (Fig. 32). As exhibiting significant interspecific variation, extent and shape of MFP can be regarded as the effective key character for species identification (as in Figs 40–53). The stridulatory mechanism is equally possessed by both male and female adults (cf. Figs 40–46, 48–49) but absent in immature forms (Fig. 50).

In addition to stridulation, we observed and videoed remarkable intraspecific conflict occasionally occurring between males of each *Hallodapus centrimaculatus* and *H. ravenar* in laboratory condition. Thus far as we recognized, no previous work has ever reported such fighting behavior for the Miridae. We have not yet clarified when and why they fight, and further continuing investigation is required to elucidate the meaning of their conflict. Some of our sample movies are available from the the websites mentioned in Online supplementary data (p. 98).

All *Hallodapus* congeners are presumed to be epigeic, inhabiting ground densely covered with weeds and/or shrubs (cf. Figs 1–2). YASUNAGA (2001) considered that (at least Japanese) species of *Hallodapus* are predaceous. During our laboratory observation, four Japanese species, *H. centrimaculatus*, *H. kyushuensis*, *H. linnavuori*, and *H. ravenar*, did not attack or prey on live tiny arthropods but prefer to feed on the cadavers of various insects and spiders (sometimes much larger than these hallodapines) as well as birds' droppings. This evidence could imply that *Hallodapus* species are scavengers instead of predators. The eggs and oviposition were for the first time confirmed for *H. centrimaculatus* and *H. ravenar* (Figs 7–8, 108–109); the female adults of both species were found to oviposit near the roots of weeds (Fig. 6).

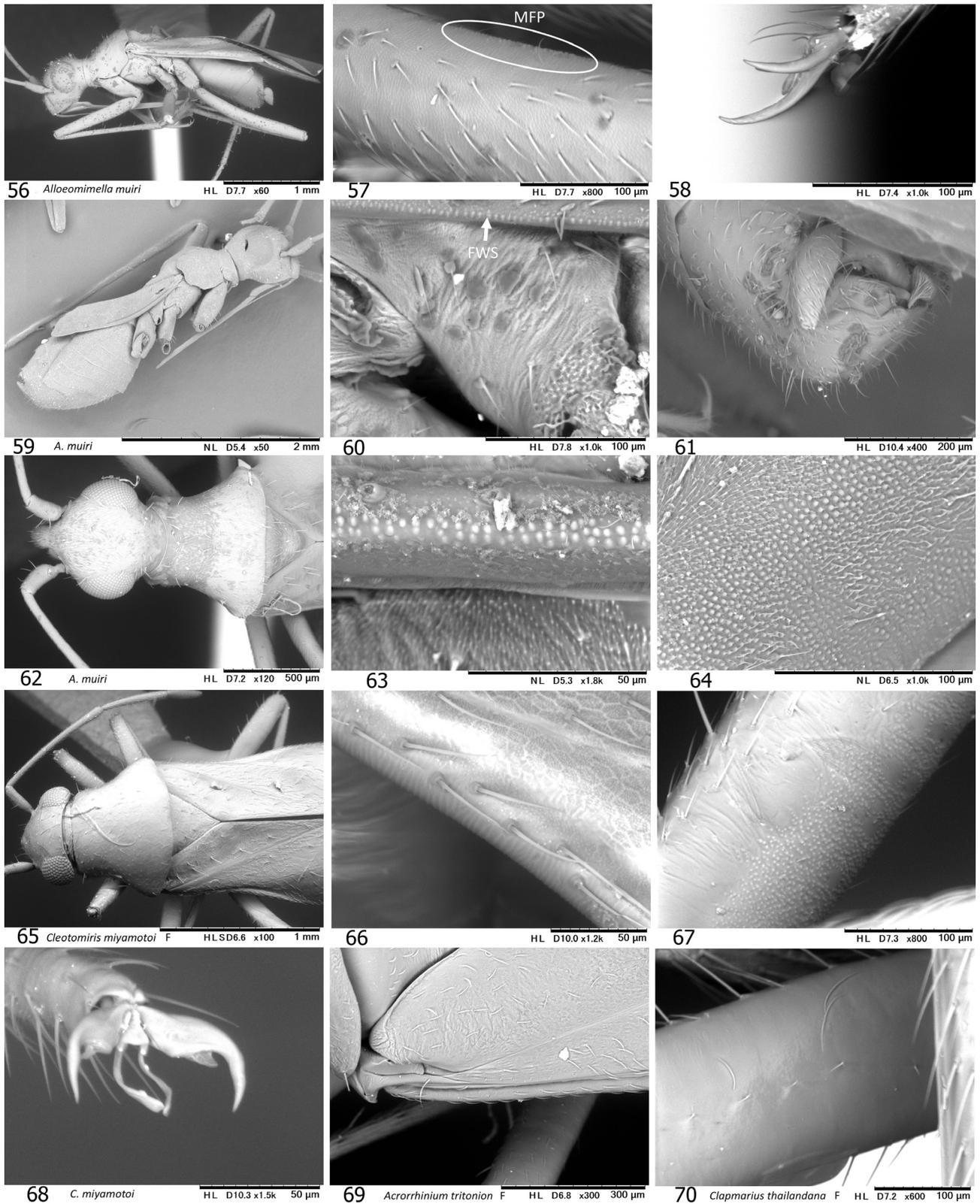
### *Hallodapus jingfui* Yasunaga & Duwal sp. nov.

(Figs 25–27, 52, 116–118, 174–176)

**Type material.** HOLOTYPE: ♂, TAIWAN: PINGDONG (= PINGTUNG): Shending, 21°57'24.7"N, 120°49'40"E, UV lighting, 22 Sep 2012, J.F. Tsai & Y.C. Lan (NMNS) (AMNH\_PBI 00380632).

**Differential diagnosis.** Recognized by its tiny size; relatively ovoid body; yellowish brown antenna with reddish extreme base of segment I; narrowly distributed MFP (Fig. 52); triangular pygophore (Fig. 174); roundly inflated sensory lobe of left paramere (Fig. 175); and C-shaped endosoma, with an apically bulbous process near apex (Fig. 176). Combination of these characters enables this new species to be distinguished from other Asian congeners.

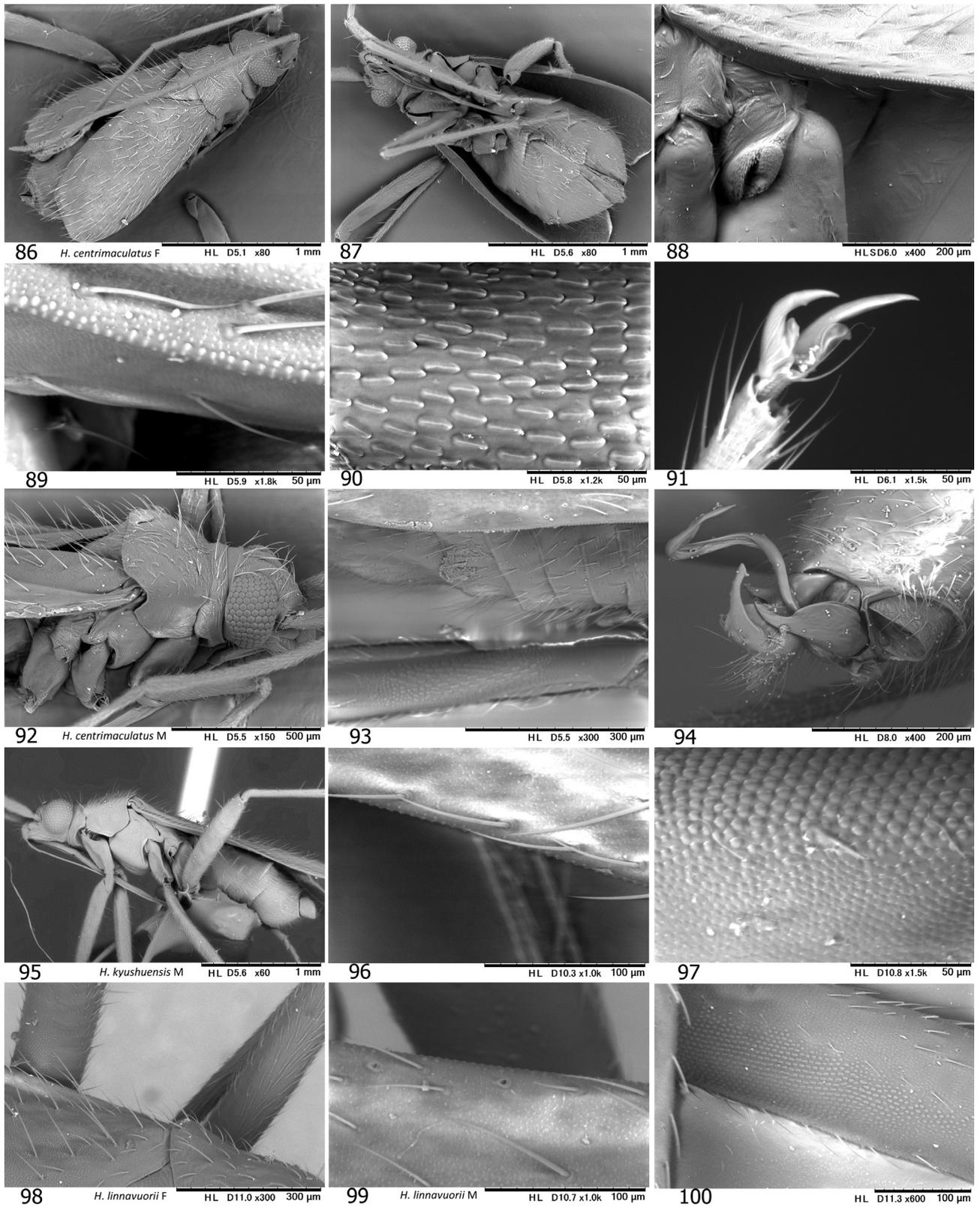
**Description.** **Male** (holotype). Body generally coffee brown, small, rather ovoid (Figs 25–26); dorsal surface weakly shining, with sparsely distributed, pale, simple, semierect setae. Head short, with reddish basal margin; eyes small, less than half as wide as vertex in dorsal view.



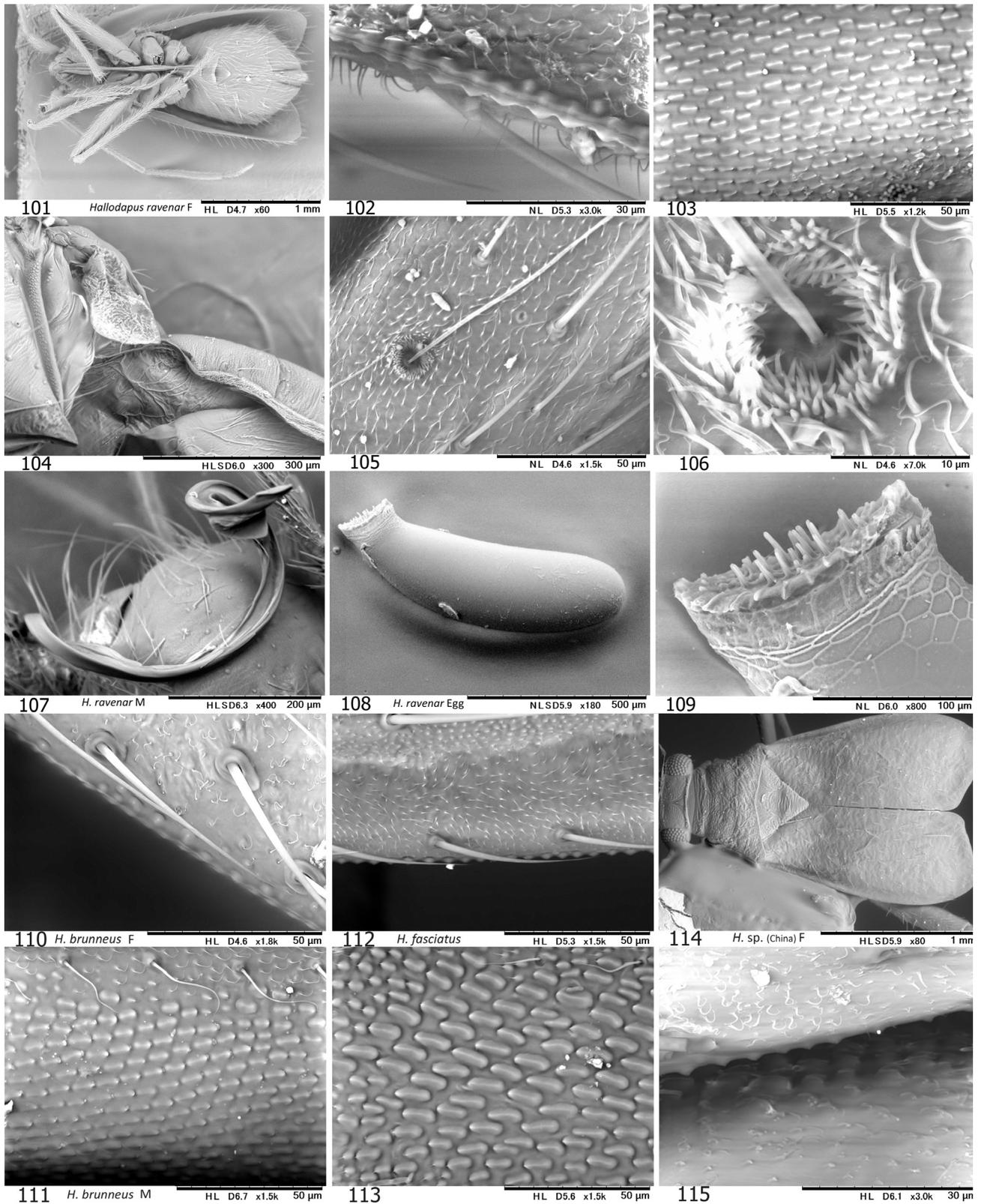
Figs 56–70. Scanning electron micrographs for Asian halodapines. 56–64 – *Alloeomimella muiri* (Schuh, 1984): 56 – ♂ from Thailand, left lateral view; 57 – ♂ MFP; 58 – ♂ pretarsus (hind leg); 59 – ♀ from Lombok, Indonesia, right lateral view; 60 – ♂ thoracic pleura; 61 – apical part of pygophore, caudal view; 62 – ♂ head and thorax, dorsal view; 63 – ♂ FWS, 64 – ♀ MFP. 65–68. *Cleotomiris miyamotoi* Yasunaga, 2012, paratype ♀ (Okinawa, Japan): 65 – head and thorax, dorsal view; 66 – FWS, 67 – MFP, 68 – pretarsus (hind leg). 69 – *Acrorrhinium tritonion* Yasunaga, Yamada & Antchawakom, 2013, paratype ♀ (Thailand), anterior forewing and basal part of metafemur. 70 – *Clapmarius thailandana* Schuh, 1984, smooth dorsal surface of ♀ metafemur.



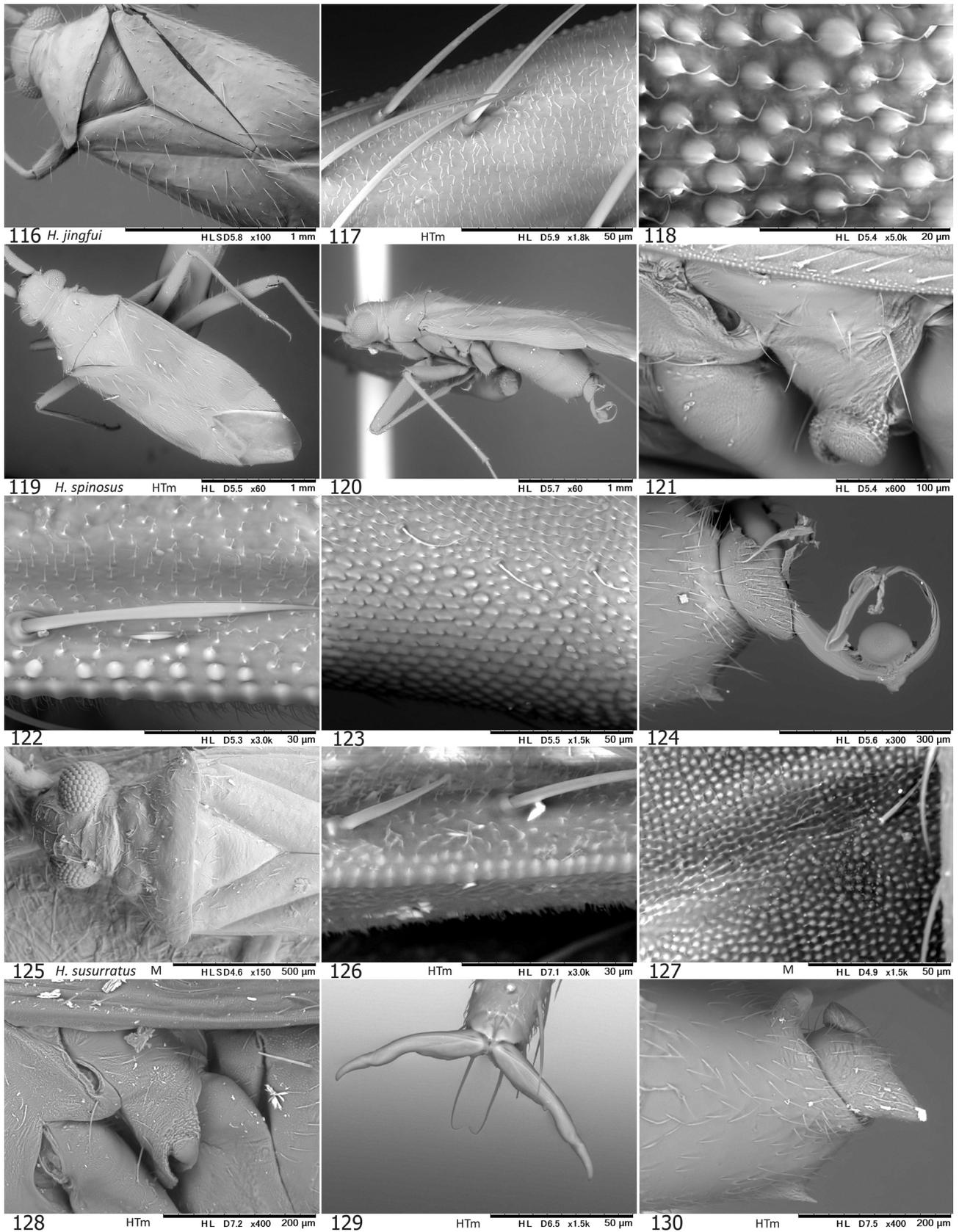
Figs 71–85. Scanning electron micrographs for Asian halloedapines. 71–72 – *Cleotomiris yamadakazi* Yasunaga, 2012, paratype ♂ (Thailand): 71 – thorax, left lateral view; 72 – smooth dorsal surface of metafemur. 73 – *Cleotomiroides tobii* Yasunaga, 2012, paratype ♂ (Thailand), head and thorax, left lateral view. 74–76 – *C. ishikawachui* sp. nov., holotype ♂: 74 – head and thorax, left lateral view; 75 – basal part of metafemur; 76 – pretarsus (hind leg). 77–82 – *Halloedapus albofasciatus* (Motschulsky, 1863) (Thailand): 77 – ♂ FWS; 78 – ♂ MFP; 79 – metatarsus; 80 – brachypterous ♀, habitus; 81 – ♀ FWS; 82 – ♀ MFP. 83–85 – *H. sibiricus* Poppius, 1912, ♂ (Russian Primorsky): 83 – FWS; 84 – MFP; 85 – metatarsus; 86 – apical part of pygophore, caudal view.



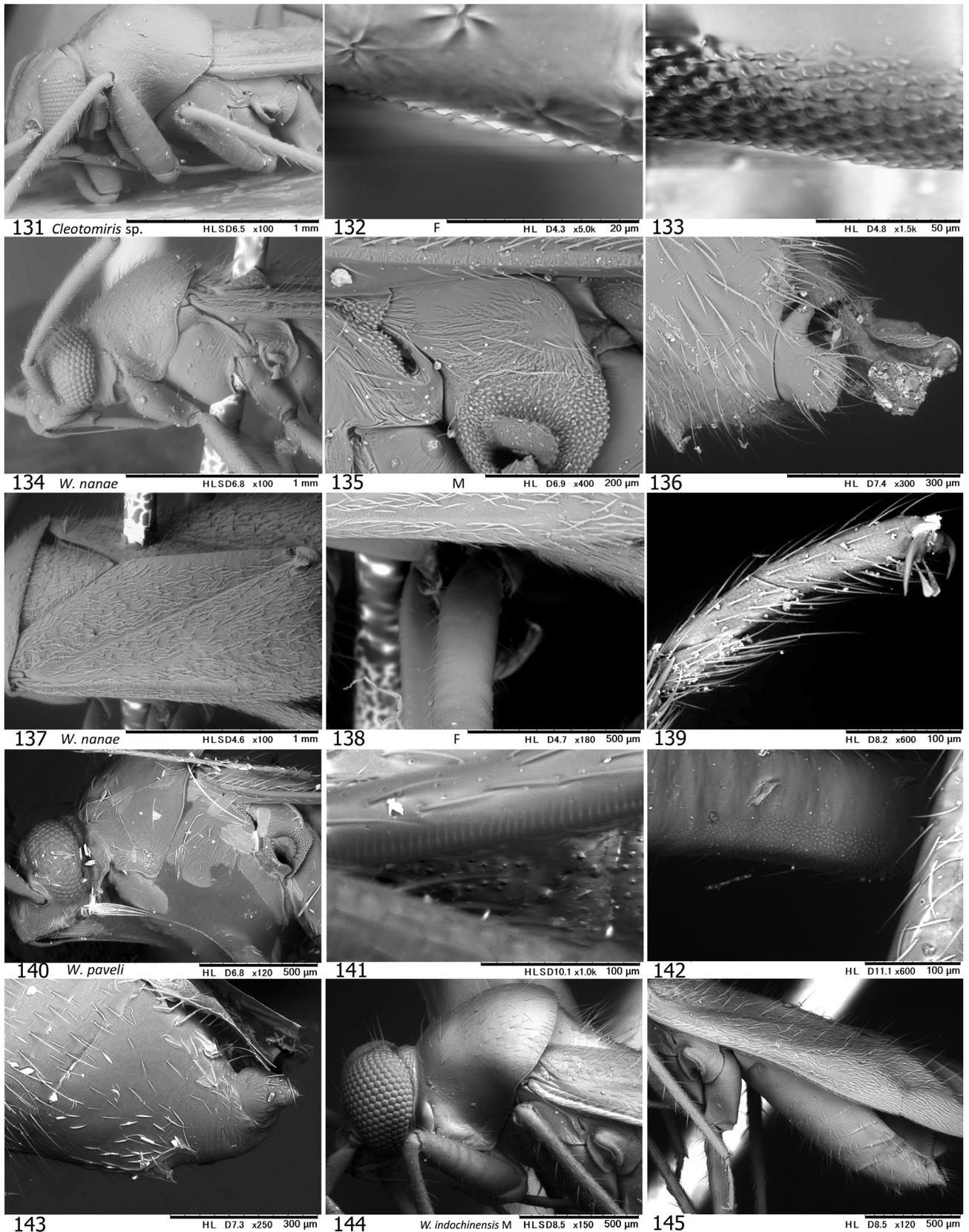
Figs 86–100. Scanning electron micrographs for Japanese *Hallocladus* species (Nagasaki). 86–94 – *Hallocladus centrimaculatus* (Poppius, 1909): 86 – brachypterous ♀, dorsal habitus; 87 – ditto, ventral habitus; 88 – thorax, left lateral view; 89 – ♀ FWS; 90 – ♀ MFP; 91 – ♂ pretarsus (hind leg); 92 – ♂ head and thorax, right lateral view; 93 – ♂ stridulatory device (right); 94 – pygophore, right lateral view. 95–97 – *H. kyushuensis* Miyamoto, 1965, ♂: 95 – left lateral habitus; 96 – FWS; 97 – MFP. 98–100 – *H. linnavuorii* (Miyamoto, 1965), brachypterous ♀: 98 – stridulatory device (left); 99 – FWS; 100 – MFP.



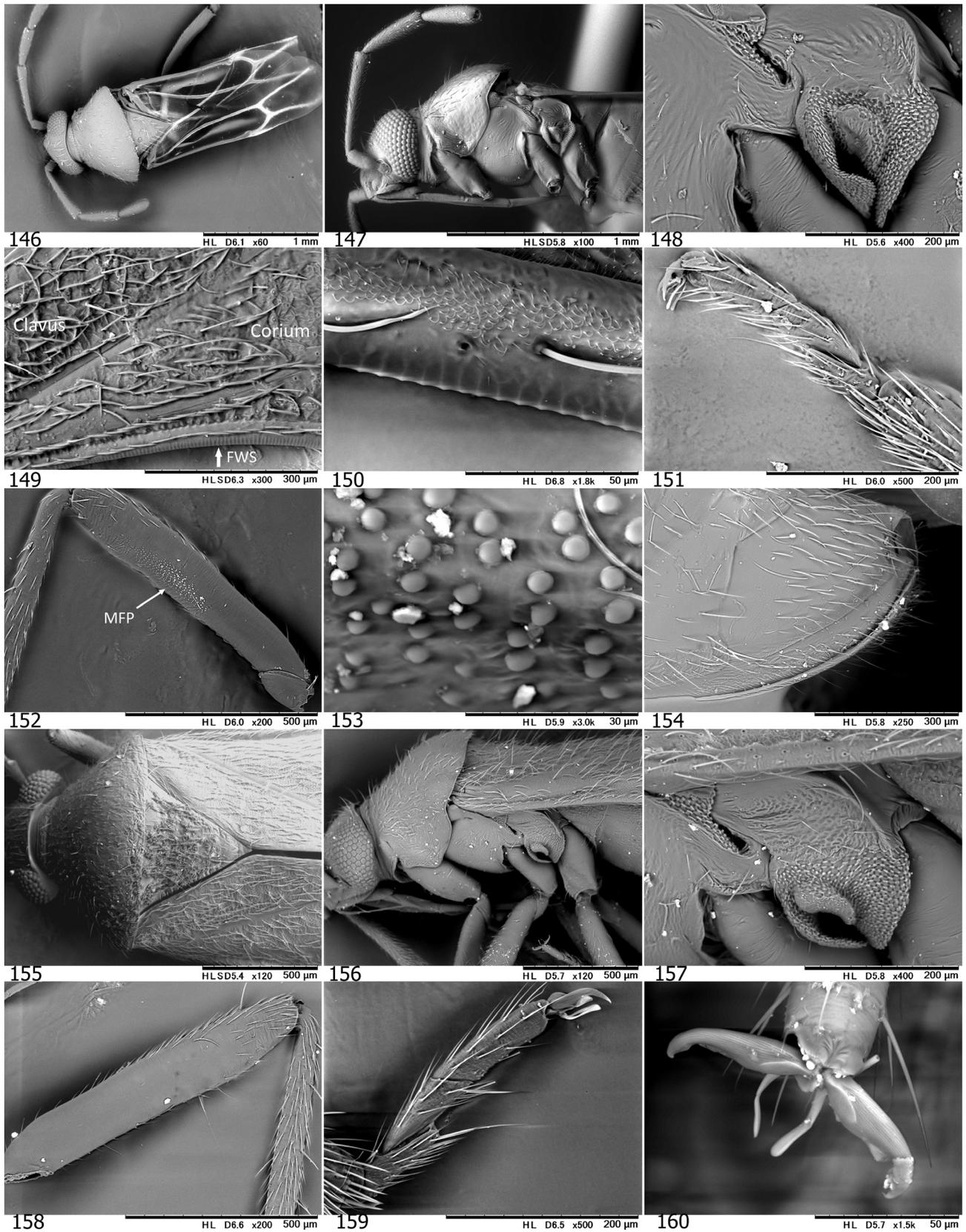
Figs 101–115. Scanning electron micrographs for *Hallodapus* species. 101–109 – *H. ravenar* (Kirkaldy, 1902) (Nagasaki, Japan): 101 – brachypterous ♀, ventral habitus; 102 – ♀ FWS; 103 – ♀ MFP; 104 – rudimental hindwing of brachypterous ♀; 105 – mesofemoral trichobothria; 106 – metafemoral trichobothrium; 107 – ♂ apex of pygophore with exposed endosoma, ventral view; 108 – egg; 109 – operculum. 110–111 – *H. brunneus* (Poppius, 1915): 110 – ♀ FWS; 111 – ♂ MFP. 112–113 – *H. fasciatus* (Poppius, 1909), ♂: 112 – FWS; 113 – MFP. 114–115 – *H. sp.* (China) ♀ (Tianjin, China): 114 – dorsal habitus; 115 – stridulatory device (left).



Figs 116–130. Scanning electron micrographs for new *Hallodapus* species. 116–118 – *H. jingfui* sp. nov., ♂ (Taiwan): 116 – dorsal habitus; 117 – FWS; 118 – MFP. 119–124 – *H. spinosus* sp. nov., ♂ (Thailand): 119 – dorsal habitus; 120 – left lateral habitus; 121 – scent efferent system; 122 – FWS; 123 – MFP; 124 – pygophore with exposed endosoma. 125–130 – *H. susurratus* sp. nov., ♂ (Thailand): 125 – dorsal habitus of anterior body; 126 – FWS; 127 – MFP; 128 – thoracic pleura; 129 – pretarsus (hind leg); 130 – pygophore.



Figs 131–145. Scanning electron micrographs for Asian hallopadines. 131–133 – *Cleotomiris* sp., ♀ (Yunnan, China): 131 – left lateral habitus of anterior body; 132 – FWS; 133 – MFP. 134–139 – *Wygomiris nanae* Yasunaga, 2012: 134 – ♂, left lateral habitus; 135 – ♂, thoracic pleura; 136 – pygophore; 137 – ♀, hemelytral vestiture pattern; 138 – ♀, exocorium and metafemur without stridulatory device; 139 – ♀, metatarsus. 140–143 – *W. paveli* sp. nov., ♂ (Pingtung, Taiwan): 140 – head and thorax, left lateral view; 141 – FWS; 142 – MFP; 143 – pygophore, left lateral view. 144–145 – *W. indochinensis* (Schuh, 1984), ♂ (Thailand): 144 – head and thorax, left lateral view; 145 – thorax and abdomen, left lateral view.



Figs 146–160. Scanning electron micrographs for *Wygomiris* species. 146–154 – *W. phormictes* sp. nov., holotype ♀ (Thailand): 146 – dorsal habitus (forewing removed); 147 – anterior body, left lateral view; 148 – scent efferent system; 149 – hemelytron; 150 – FWS; 151 – metatarsus; 152 – metafe-mur; 153 – MFP; 154 – abdominal sterna. 155–160 – *W. kaliyahae* Yasunaga, 2012, ♀ (Thailand): 155 – dorsal habitus of anterior body; 156 – left lateral habitus; 157 – scent efferent system; 158 – metafemur (without MFP); 159 – metatarsus; 160 – pretarsus (hind leg).

Antenna almost uniformly yellowish brown; extreme base of segment I reddish brown; segment II slightly longer than III. Labium reddish brown, exceeding apex of metacoxa, reaching abdominal sternum VIII. Pronotum weakly shining, trapezoidal, not strongly constricted anteriorly; pleura shiny dark brown; scent efferent system somber pale brown, small. Hemelytron with two pairs of white maculae as in Fig. 25 (anterior macula across clavus, corium and embolium rectangular and posterior macula across apices of corium and embolium triangular); FWS roundly notched (Figs 27, 117); cuneus brown, narrowed; membrane pale smoky brown. Coxae and legs pale brown; apical half of metafemur and basal 1/3 of each tibia obscure; MFP distributed narrowly on median part of metafemur, with each plectrum tiny, circular (Figs 52, 118). Abdomen wholly fuscous, short. Male genitalia (Figs 174–176): Pygophore triangular (Fig. 174); left paramere with roundly expanded sensory lobe (Fig. 175); endosoma C-shaped, with an apically bulbous process near apex (Fig. 176).

**Measurements.** Male (holotype, mm): Total length of body 2.65; head width including eyes 0.51; vertex width 0.29; lengths of antennal segments I–IV 0.30, 0.97, 0.90, 0.48; total labial length 1.28; basal width of pronotum 0.78; maximum width across hemelytron 0.93; and lengths of metafemur, tibia and tarsus 1.02, 1.47, 0.41.

**Female.** Unknown.

**Etymology.** Named after a Taiwanese heteropterist, Dr. Jing-Fu Tsai who collected a valuable specimen herein designated as the holotype.

**Biology.** Unknown; the holotype specimen was collected by a UV light trap at rather sparse subtropical forest in Sheding National Park, southernmost part of Taiwan.

**Distribution.** Taiwan (this paper).

#### *Hallodapus spinosus* Yasunaga & Duwal sp. nov.

(Figs 19, 28–31, 47, 119–124)

*Hallodapus brunneus* Poppius, 1915 (misidentification): YASUNAGA et al. (2013a): 442 (checklist).

**Type material.** HOLOTYPE: ♂, THAILAND: NAKHON NAYOK: Sarika (at garden lawn), 14°18'07"N 101°18'09"E, at FL light, 20 Dec 2010, T. Yasunaga (AMNH\_PBI 00380633) (DOAT). **Additional specimen examined.** THAILAND: NAKHON RATCHASIMA: Wang Nam Khiew, Sakaerat Environmental Research Station, 14°30'27"N, 101°55'39"E, 410 m alt., UV light trap, 20 Aug 2008, T. Yasunaga, 1 ♂ (TYCN).

**Differential diagnosis.** Superficially most similar to *H. brunneus* (Poppius) (Fig. 20), from which the present new species (Fig. 19) can be distinguished by the larger anterior pair of white maculae contiguous to each other (Fig. 28), totally fuscous femora, narrowly distributed MFP with each plectrum somewhat ovoid (Figs 47, 123), presence of pygophoral spine (Figs 30, 124), and C-shaped endosoma (Fig. 30) with an apically bulbous process near the apex (Fig. 31). In *H. brunneus*, the maculae of the anterior pair are smaller and separated each other, bases of meso- and metafemora are creamy white, FWS is rather sparsely distributed (Fig. 110), MFP is more widely distributed and each plectrum squared (Figs 40, 111), pygophore lacks any spine, and endosomal subapical process is short and thickened (Fig. 178).

**Description.** **Male** (holotype). Macropterous; body generally dark brown, almost medium-sized, elongate, parallel-sided (Figs 19, 28); dorsal surface weakly shining, with uniformly distributed, woolly, reclining setae and sparsely distributed, dark, simple, semierect setae. Head tinged with red, pointed in front; eyes small, less than half as wide as vertex in dorsal view. Antenna pale brown; segment I dark brown, with yellow fascia inward; segment II slightly darkened, inwardly with a weak stripe that is nearly invisible in dry-preserved specimen, subequal in length to III; segment IV about twice as long as I. Labium reddish brown, reaching but not exceeding apex of metacoxa; segment III and base of IV pale brown. Pronotum weakly shining, weakly constricted laterally at calli; pleura shiny dark reddish brown; scent efferent system with knob-like ostiolar peritreme (Fig. 121). Hemelytron with two pairs of white maculae as in Fig. 28 (anterior pair of maculae larger, contiguous to each other and posterior macula squared); FWS as in Figs 29, 122; membrane pale smoky brown. Coxae and femora dark brown, except for meso- and metacoxae yellowish brown; MFP rather narrowly distributed, with each plectrum rectangular (Figs 47, 123). Abdomen wholly reddish dark brown, relatively long. Male genitalia (Figs 30–31, 124): Pygophore with a distinct pygophoral spine (Fig. 30); endosoma C-shaped (Figs 30, 124), with an apically bulbous process near the apex (Fig. 31).

**Measurements.** Male (holotype, mm): Total length of body 2.94; head width including eyes 0.55; vertex width 0.32; lengths of antennal segments I–IV 0.35, 1.05, 1.01, 0.69; total labial length 1.25; basal width of pronotum 0.81; maximum width across hemelytron 0.92; and lengths of metafemur, tibia and tarsus 1.05, 1.52, 0.39.

**Female.** Unknown.

**Etymology.** From Latin, *spinosus* [= spiny, thorny], referring to a characteristic ventral spine on the pygophore of this new species; an adjective.

**Biology.** Unknown; habitat environment as in Fig. 2.

**Comment.** YASUNAGA et al. (2013b) reported *H. brunneus* from Thailand, but the present examination revealed the Thai specimen represents an undescribed species herein documented as *H. spinosus* sp. nov. which is unique by having a noticeable pygophoral spine (see Table 1).

#### *Hallodapus susurratus* Yasunaga & Duwal sp. nov.

(Figs 36–39, 125–130, 181–185)

**Type material.** HOLOTYPE: ♂, THAILAND: CHIANG MAI: Chom Thong, 18°25'N, 98°40'E, 24–27 Apr 1991, J. Horák (NMPC) (AMNH\_PBI 00380644). **PARATYPES:** THAILAND: CHIANG MAI: Same locality as for holotype, 23–27 Apr 1991, S. Bílý (NMPC).

**Differential diagnosis.** Recognized by its small size (<2.5 mm) comparable with *H. centrimaculatus*; widely darkened dorsum; notched inner margin of anterior white macula on corium (Fig. 36); rather granulate, rounded MFP (Fig. 127); enlarged, stout left paramere (Fig. 183); presence of distinct spine and dorsal knob on pygophore (Figs 130, 181); slender phallosome (Fig. 184); and rather sigmoid endosoma (Fig. 185). This new species is most similar to or conspecific with a New Guinean species identified by

SCHUH (1984) as *H.* 'near' *pseudosimilis* (Schuh, 1974) originally described from South Africa (SCHUH 1974, Fig. 28); however, *H. pseudosimilis* is obviously larger in size (total length 3.2 mm and maximum width across hemelytra 1.04 mm), and the color pattern (e.g. broadly pale corium and pale basal 1/3 of metafemur) significantly differs from that exhibited by *H. susurratus* (cf. SCHUH 1974).

**Description. Male** (holotype). Macropterous; body generally coffee brown, small-sized (< 2.5 mm), nearly parallel-sided (Fig. 36); dorsal surface matte, with sparsely distributed, woolly, reclining setae and dark, simple, erect setae. Head weakly shining. Antenna creamy white, partly tinged with red; segment I with pale brown basal half and reddish extreme apex. Labium reddish brown, long, exceeding apex of metacoxa, reaching apical margin of abdominal sternum VII; segment III and base of IV pale brown. Pronotum weakly shining, almost trapezoidal (Fig. 125); pleura shiny dark reddish brown; scent efferent system yellowish brown, with ostiolar peritreme not produced (Fig. 128). Hemelytron with two pairs of white maculae as in Fig. 36 (anterior pair of maculae larger, separated from each other and notched inward); FWS as in Fig. 126; membrane pale smoky brown, with slightly darkened veins. All coxae and trochanters yellowish brown, except for basal part of each coxa more or less obscure; all femora reddish or chocolate brown, with pale extreme apices; MFP rather granulate, with each plectrum rounded (Fig. 127); tibiae creamy white; parempodia setiform, long (Fig. 129). Abdomen wholly reddish dark brown, shining. Male genitalia (Figs 180–185): Pygophore with a distinct pygophoral spine and a dorsal knob-like protuberance (Figs 130, 181); left paramere enlarged, stout (Fig. 183); right paramere tiny (Fig. 182); phallosome slender (Fig. 184); endosoma slender, sigmoid, tapered apically, without noticeable process or branch (Fig. 185).

**Measurements.** Male (holotype, mm): Total length of body 2.32–2.45; head width including eyes 0.45–0.47; vertex width 0.18–0.19; lengths of antennal segments I–IV 0.24–0.25, 0.75–0.76, 0.54–0.57, ?; total labial length 1.05–1.17; basal width of pronotum 0.69–0.74; maximum width across hemelytron 0.72–0.75; and lengths of metafemur, tibia and tarsus 0.90, 1.36–1.37, ?.

**Female.** Unknown.

**Etymology.** From Latin, *susurratus* [= muttering, whispering], referring to the small size and rather granulate meta-femoral plectrum of this new species; adjective.

**Biology.** Unknown; two available specimens were collected at montane zone of northern Thailand.

**Distribution.** Thailand (this paper).

### *Wygomiris* Schuh, 1984

**Diagnosis.** Always macropterous in both sexes; body elongate oval, nearly parallel-sided, small to moderate in size (total length 3–5 mm), not very ant-like (rather conventional habitus in the Miridae); basic coloration brown to fuscous; dorsum weakly shining or matte, usually with pale, simple, upright setae and silvery or golden, reclining setae; head short, rather vertical; antenna uniformly thick; pronotum more or less shining; metathoracic scent efferent system large, usually produced at middle; stridulatory

device (FWS+MFP) missing (currently possessed only by *W. paveli* and *W. phormictes* described below); pygophoral spine (PS) present; endosoma J- or L-shaped, usually with simple apical spine and small secondary gonopore; and bursa copulatrix with enlarged, ovoid sclerotized ring. Further diagnostic characters were provided by SCHUH (1984) and YASUNAGA (2012).

**Distribution.** Oriental Region: SE China (including Hong Kong), Laos, Nepal, Philippines, Taiwan, Thailand, Vietnam (DUWAL et al. 2017). Several undescribed species of *Wygomiris* appear to occur in India, the Philippines and New Guinea (SCHUH 1984).

**Discussion.** *Wygomiris* is now represented by nine species (including two new species below) from the Oriental Region. Members of this genus appear to be associated with aerial parts of plants (possibly broadleaf trees as mentioned in above tribal discussion). Currently, the stridulatory device is confirmed only in *W. paveli* sp. nov. and *W. phormictes* sp. nov.; however, FWS and MFP of them are both reduced (Figs 141–142, 150, 152–153), similar in overall appearance to those possessed by *Cleotomiris miyamotoi* (Figs 66–67). Judging from the condition of the stridulatory device, we presume that (1) modern members of *Alloeomimella*, *Cleotomiris*, *Hallodapus* and *Wygomiris* had been derived from the epigeic common ancestor migrating from aerial parts of plants, (2) the derived element of *Cleotomiris* + *Wygomiris* subsequently returned to the original habitat (aerial parts of plants), and (3) the stridulatory device may be obsoleted or reduced in modern *Cleotomiris* and *Wygomiris*, as seen in the species of *Acrorrhinium*, *Cleotomiroides* and *Systellonotus malaisei* Lindberg, 1934 which inhabit the aerial parts of plants and lack the stridulatory device.

During examining specimens or photographic images, teratological antennal segments (possibly fused segments III+IV) were confirmed in the fifth instar nymph of *Wygomiris kaliyahae* collected in Nakhon Ratchasima, Thailand (Fig. 18, left antenna) and adult male of *W. paveli* sp. nov. from Pingtung, Taiwan (AMNH\_PBI 00380635) (Figs 14–15, 166–167, right). Although teratological specimens occur less frequently in Cimicomorpha than in the Pentatomomorpha (WHEELER 2001), a similar antennal aberration in *Apolygus nigrovirens* (Kerzhner, 1988) (Mirinae: Mirini) was recently documented by YASUNAGA (2018).

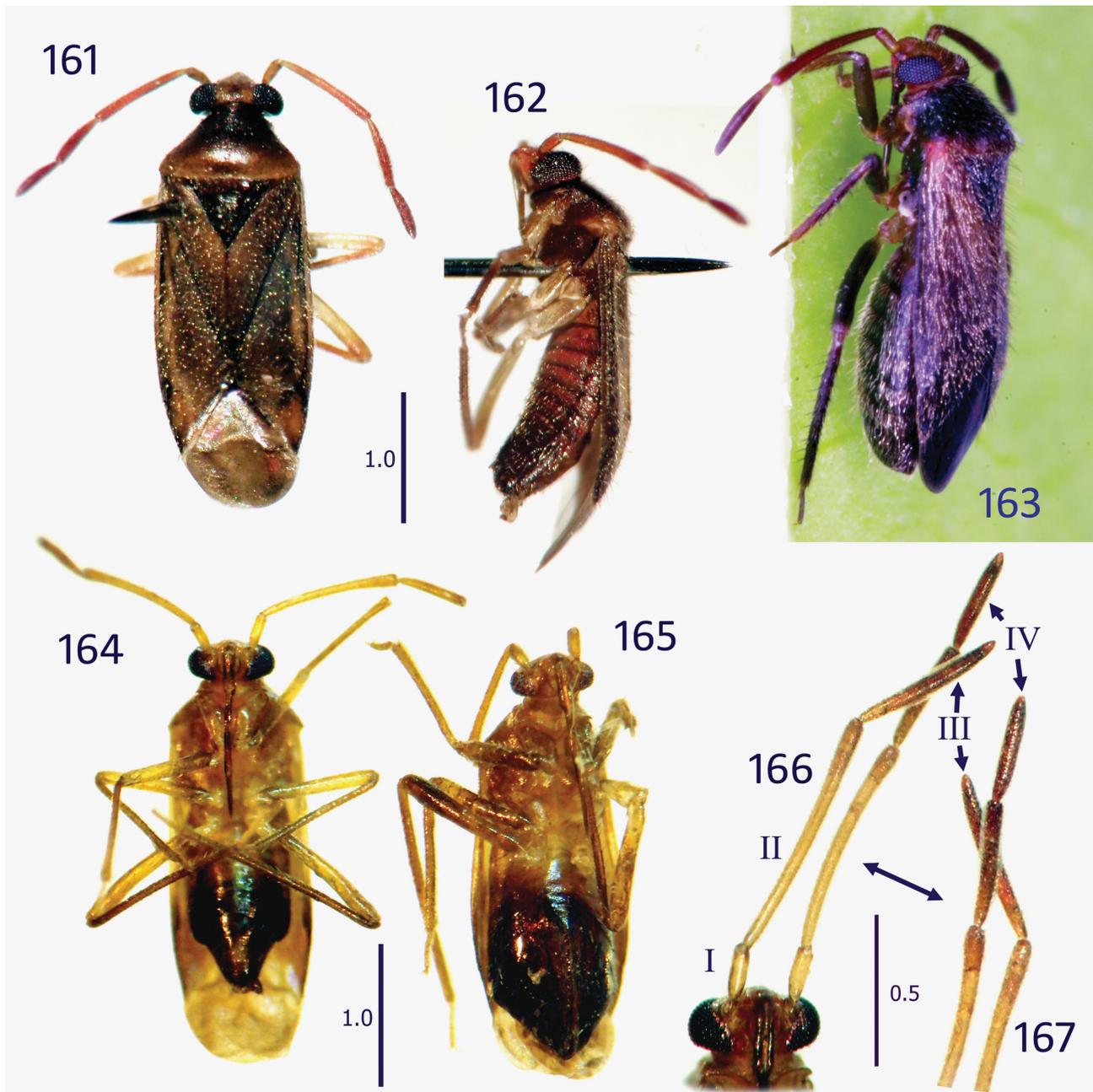
### *Wygomiris nanae* Yasunaga, 2012

(Figs 14–15, 140–143, 164–167)

*Wygomiris nanae* Yasunaga, 2012: 20 (original description).

**Type material examined.** HOLOTYPE: ♀, THAILAND: NAKHON NAYOK: Sarika (lodge garden), 14°18'39"N 101°18'00"E, at light, 13 Mar 2009, T. Yasunaga (AMNH\_PBI 00379518) (DOAT). **Additional material examined.** VIETNAM: SON LA PROVINCE: Moc Chau, 940 m alt., 20°49'N 104°42'E, light trap, 19 Jun 1997, M. Tomokuni, 2 ♂♂ (NSMT); Dao Cao Pha, 420 m E of Ban Song, 21°09'39"N 103°35'46"E, 23 Jun 1997, M. Tomokuni, 1 ♀ (NSMT).

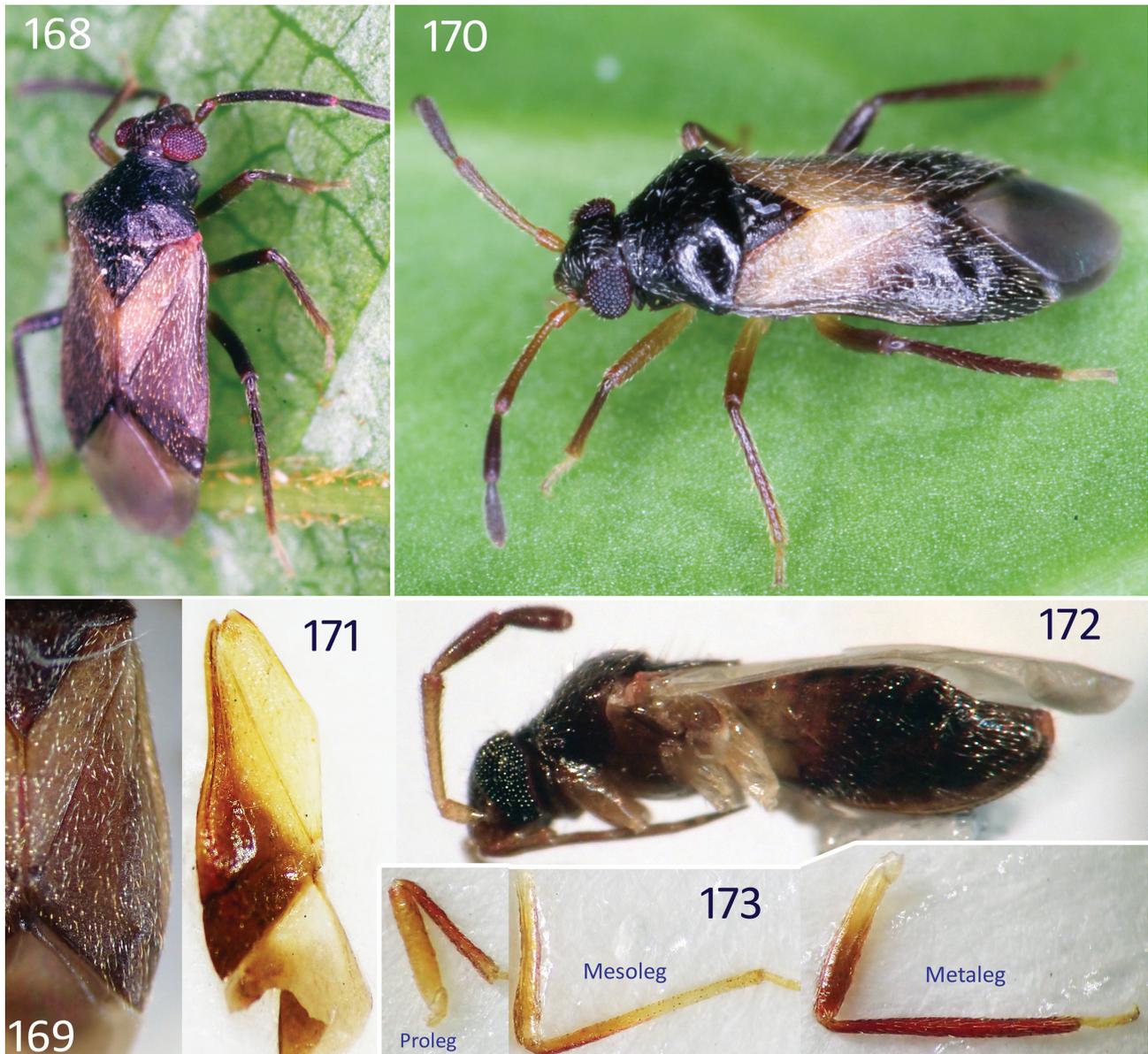
**Differential diagnosis.** Most closely related to *P. minigorum* Schuh, 1984; distinguished by its uniformly dark brown body; smaller eyes; wider vertex; weakly shining, matte pronotum; densely distributed, silvery, reclining setae on hemelytron (Figs 161–163); tapered apical part



Figs 161–167. Habitus images for Asian *Wygomiris* species. 161–163 – *W. nanae* Yasunaga, 2012: 161 – ♂, dorsal habitus (Vietnam); 162 – ditto, left lateral habitus; 163 – holotype ♀ (Thailand, AMNH\_PBI 00379518). 164–167 – *W. paveli* sp. nov. (Taiwan): 164 – ventral habitus, ♂; 165 – ditto, ♀; 166 – asymmetrical (teratological) antennal segments, ventral view; 167 – ditto, dorsal view.

of left paramere hypophysis (Fig. 188) and longer apical branches on endosoma (Fig. 190), in addition to developed female genital chamber (Fig. 191). Although YASUNAGA (2012) supposed *W. nanae* as the closest relative of *W. indochinensis* Schuh, 1984, *W. mingorum* is now considered to be sister to *W. nanae*, judging from the similar shape of endosoma bearing three apical branches. In external appearance, *W. nanae* can be readily distinguished from *W. indochinensis* and *W. mingorum* by the uniformly dark brown coloration and dense dorsal vestiture (Figs 161, 163); the latter two species have contrasting two-tone pattern (SCHUH 1984, YASUNAGA 2012) as seen in *W. phormictes* sp. nov. (Fig. 170).

**Redescription. Male.** General coloration and shape similar to those of female. Macropterous; body almost uniformly chestnut or dark brown, elongate oval, comparatively large in size; dorsal surface rather matte, with simple, semierect setae, long, erect setae and wooly, reclining setae. Head tinged with red, weakly shining. Antenna reddish brown. Labium reddish brown, reaching apex of mesocoxa. Pronotum somewhat roughened, with uniformly distributed, simple, semierect setae; collar pruinose, narrower than base of antennal segment II; scent efferent system widely ivory white, with a median knob. Hemelytra somewhat lighter than pronotum and scutellum, with uniformly distributed, silvery, reclining setae and sparsely distributed, simple,



Figs 168–173. Habitus images for Thai *Wygomiris* species. 168–169 – *W. kaliyahae* Yasunaga, 2012: 168 – paratype ♀, dorsal habitus (AMNH\_PBI 00379524); 169 – ♀, forewing. 170–173 – *W. phormictes* sp. nov., holotype ♀ (AMNH\_PBI 00379645): 170 – dorsal habitus; 171 – forewing; 172 – left lateral habitus; 173 – each leg.

long, erect setae; membrane smoky brown. All coxae and legs brown, partly tinged with red; meso- and metacoxae lighter. Abdomen shiny chestnut brown, partly reddish except for posterior margin of each sternum (Fig. 161). Male genitalia (Figs 186–190): Pygophore with distinct PS (Fig. 186). Left paramere with apically tapered hypophysis (Fig. 188); endosoma three-branched, with a wide membranous area along secondary gonopore (Fig. 190).

**Measurements** (♂♂/♀♀, mm) [holotype from Thailand]. Total length of body 3.43–3.78 / 3.43 [3.60]; head width including eyes 0.72–0.75 / 0.71 [0.71]; vertex width 0.30 / 0.33 [0.33]; lengths of antennal segments I–IV 0.25–0.26, 0.93, 0.60, 0.48 / 0.24 [0.19], 0.87 [0.90], 0.57 [0.57], 0.51 [?]; labial length 1.20–1.22 / 1.08 [1.20]; basal width of pronotum 1.09–1.16 / 1.19 [1.08]; maximum width across hemelytron 1.32–1.35 / 1.49 [1.39]; and lengths of

metafemur, tibia and tarsus 1.09–1.14, 1.65, 0.30 / 1.10 [1.13], 1.59 [1.50], 0.29 [0.30].

**Biology.** Unknown; all available specimens were collected by UV lightings around arable lands or secondary forests.

**Distribution.** Thailand (Nakhon Nayok) (YASUNAGA 2012), Vietnam (Son La) (this paper).

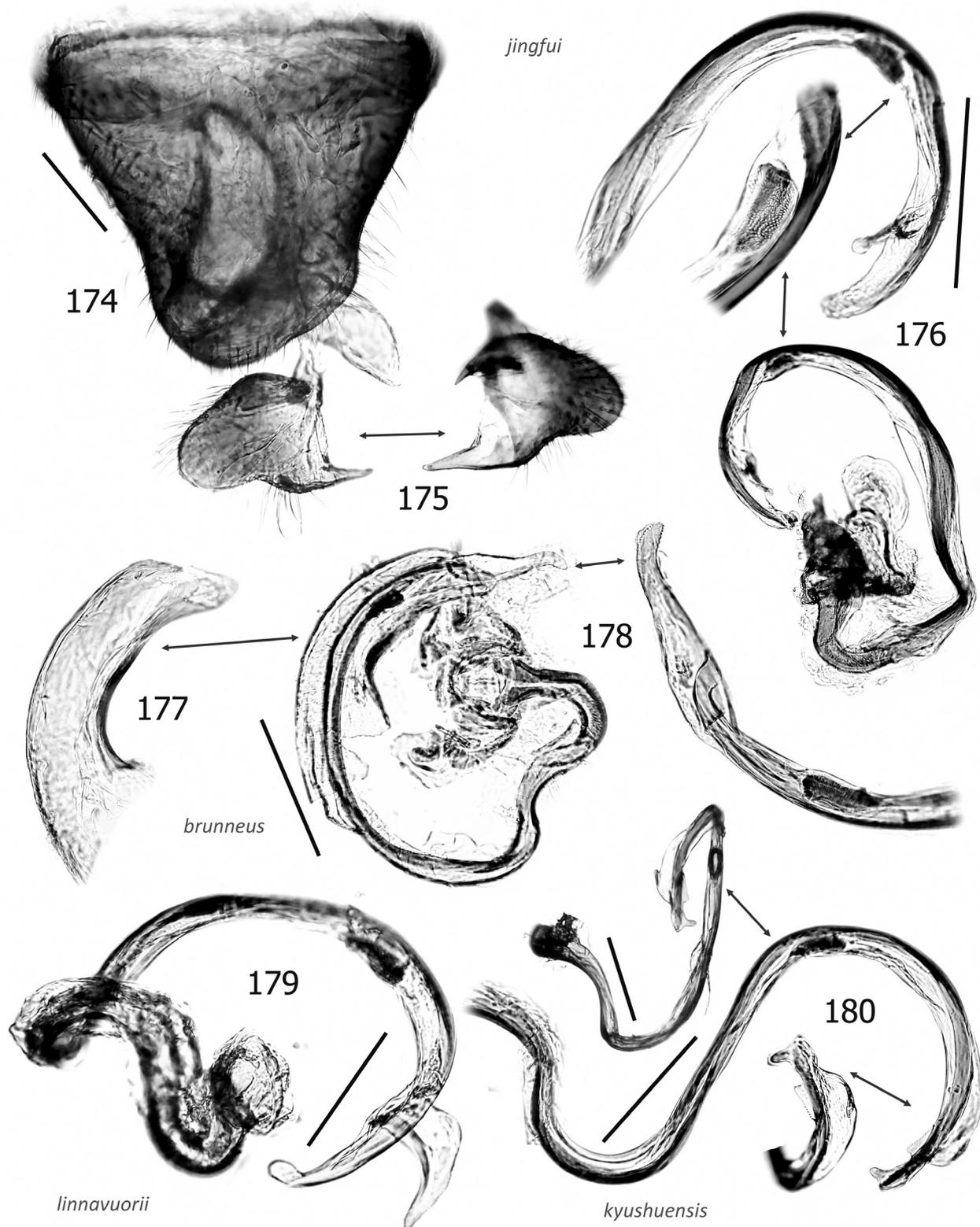
***Wygomiris paveli* Yasunaga & Duwal sp. nov.**

(Figs 14–15, 36–39, 140–143, 196–200)

**Type material.** HOLOTYPE: ♂, TAIWAN: PINGDONG (= PINGTUNG): Siangjiao Bay, 21°55'42.7"N, 120°49'40"E, UV lighting, 16 Feb 2011, C.T. Chiu & Y.C. Lan (AMNH\_PBI 00380634) (NMNS). PARATYPES: TAIWAN: PINGDONG: Same locality as for holotype, 14 Mar 2012, Y.C. Lan & J.Z. Wang, 1 ♂ (NMNS); Nanrenshan, UV lighting, 26 Apr 2011, Y.C. Lan & Y.H. Peng, 1 ♂ (NMNS); Mutan, Cacevakan, 22°06'34.9"N, 120°48'06.1"E, UV lighting, 16 Mar 2017, T. Yasunaga, 1 ♂ (00380635) (TYCN). HUALIEN: Yuri, Chohsishan, Malaise trap, 24 Apr 2009 – 12

Dec 2012, W.T. Yang & K.W. Huang, 5 ♂♂, 2 ♀♀ (NMNS); Hsiulin, Wenlan, Malaise trap, 24 Jun–25 Aug 2009, K.W. Huang & W.T. Yang, 1 ♂ (00380636) (NMNS); same data except for date 13 Sep–24 Nov 2010, 1 ♂ (NMNS). CHIAVI: Chungpu, Yunshui Station, Mercury lighting, 7–8 Nov 2006, Lin, Chan, Liang & Lan, 1 ♂ (00380637) (NMNS).

**Differential diagnosis.** Recognized readily by its moderate size; generally castaneous basic coloration (Figs 14–15); rather small eyes; rather slender antenna; weakly shining pronotum; yellowish brown fascia on hemelytron; possession of stridulatory device (FWS+MFP, Figs 55, 141–142);

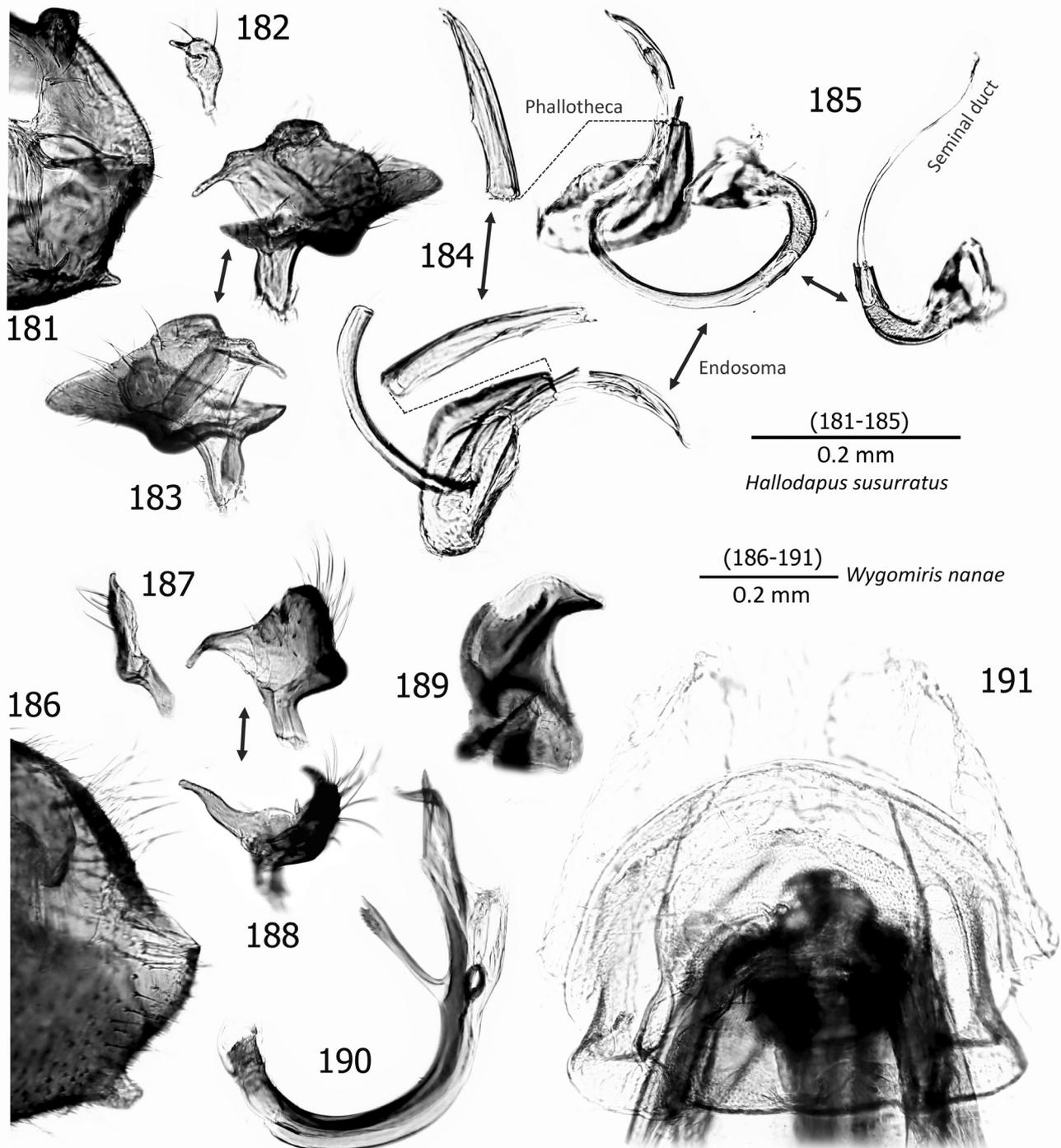


Figs 174–180. Male genitalia of *Hallopadus* species. 174–176 – *H. jingfui* sp. nov., holotype: 174 – pygophore with phallosome, ventral view; 175 – left paramere; 176 – endosoma. 177–178 – *H. brunneus* (Poppius, 1915) (Ishigaki Island, Japan): 177 – phallosome; 178 – endosoma. 179 – *H. linnavuorii* (Miyamoto, 1965) (Nagasaki, Japan), endosoma; 180 – *H. kyushuensis* (Miyamoto, 1965) (Okinawa, Japan), endosoma. Scale bars 0.2 mm.

and contrastingly darkened abdomen (Figs 164–165). Based on the similar genitalic structure (endosomal shape in particular), this new species is apparently sister to *W. indochinensis* which however has larger eye (Fig. 144) and rather terete antennal segments, and lacks the stridulatory device (Fig. 145) (see YASUNAGA 2012 and DUWAL et al. 2017, for detailed diagnosis and color habitus images of *W. indochinensis*).

**Description. Male.** Macropterous; body generally castaneous, elongate oval, parallel-sided, moderate in size; dorsal

surface weakly shining, with sparsely distributed, simple upright setae and woolly (not scalelike) reclining setae. Head somewhat produced anteriorly, with pale, short, erect setae. Antenna pale reddish brown, rather slender, not significantly terete; apex of segment II slightly inflated, about as long as basal width of pronotum; two distal segments reddish brown. Labium shiny pale reddish brown, slightly exceeding apex of mesocoxa, slightly longer than antennal segment II or metafemur; segment IV dark reddish brown. Pronotum weakly shining, not polished; pleura including



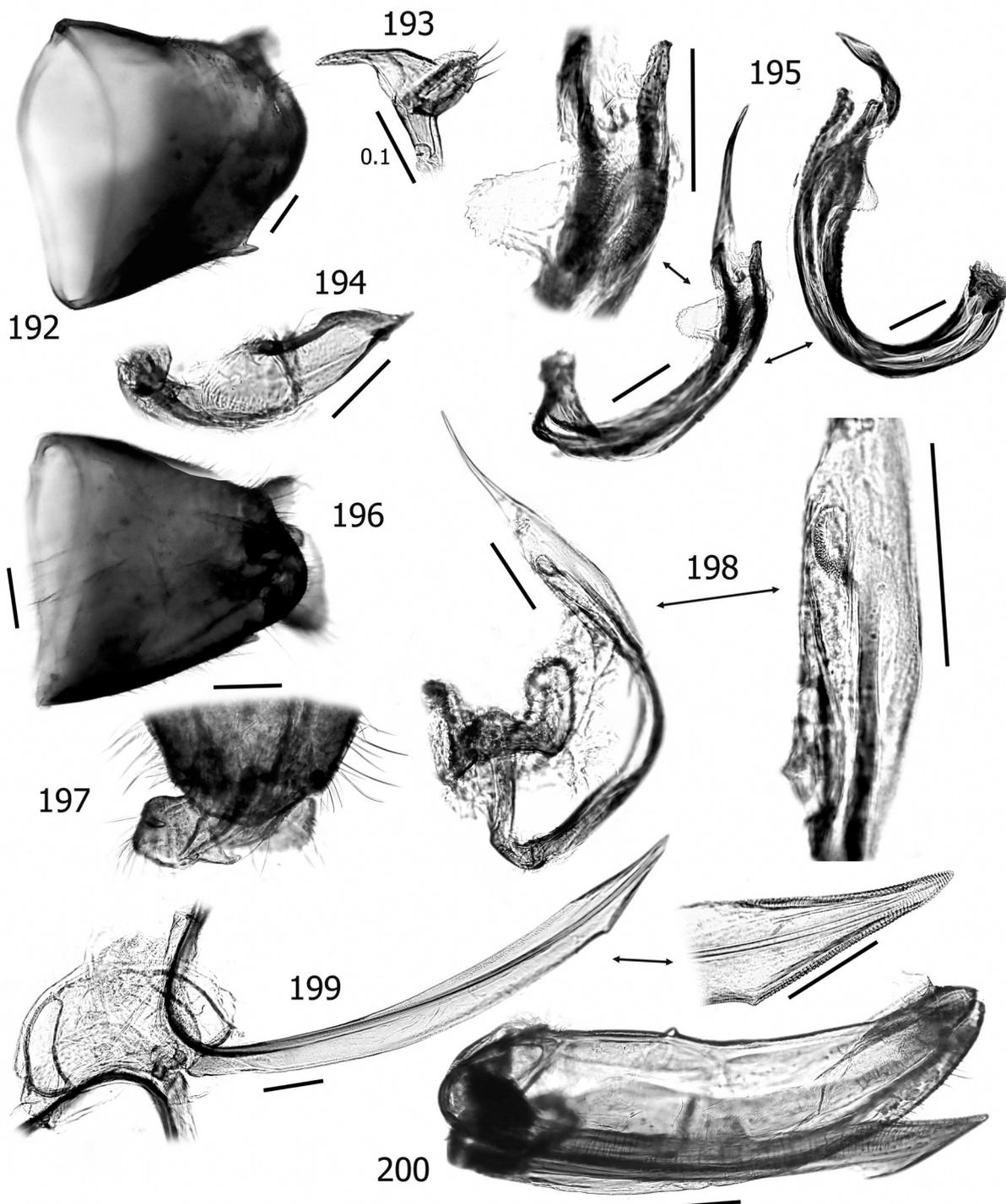
Figs 181–191. Male (181–190) and female (191) genitalia of Asian hallopadines. 181–185 – *Hallodapus susurratus* sp. nov. (Thailand): 181 – pygophore, left lateral view; 182 – right paramere; 183 – left paramere; 184 – phallotheca; 185 – endosoma. 186–191 – *Wygomiris nanae* Yasunaga, 2012 (Vietnam): 186 – pygophore, left lateral view; 187 – right paramere; 188 – left paramere; 189 – phallotheca; 190 – endosoma.; 191 – bursa copulatrix.

scent efferent system yellowish brown. Hemelytron chestnut brown, with a yellowish transverse fascia posterior to scutellum; FWS weak, minutely sutured (Figs 55, 141); membrane smoky brown, with pale, translucent basal half. Coxae and legs pale brown; each femur and tibia partly obscure; MFP minutely scattered (Figs 55, 142). Abdomen widely shiny dark brown. Male genitalia (Figs 196–198): Pygophore with a small pygophoral spine (Figs 143, 196). Left paramere with tumid, bulbous sensory lobe (Fig. 197).

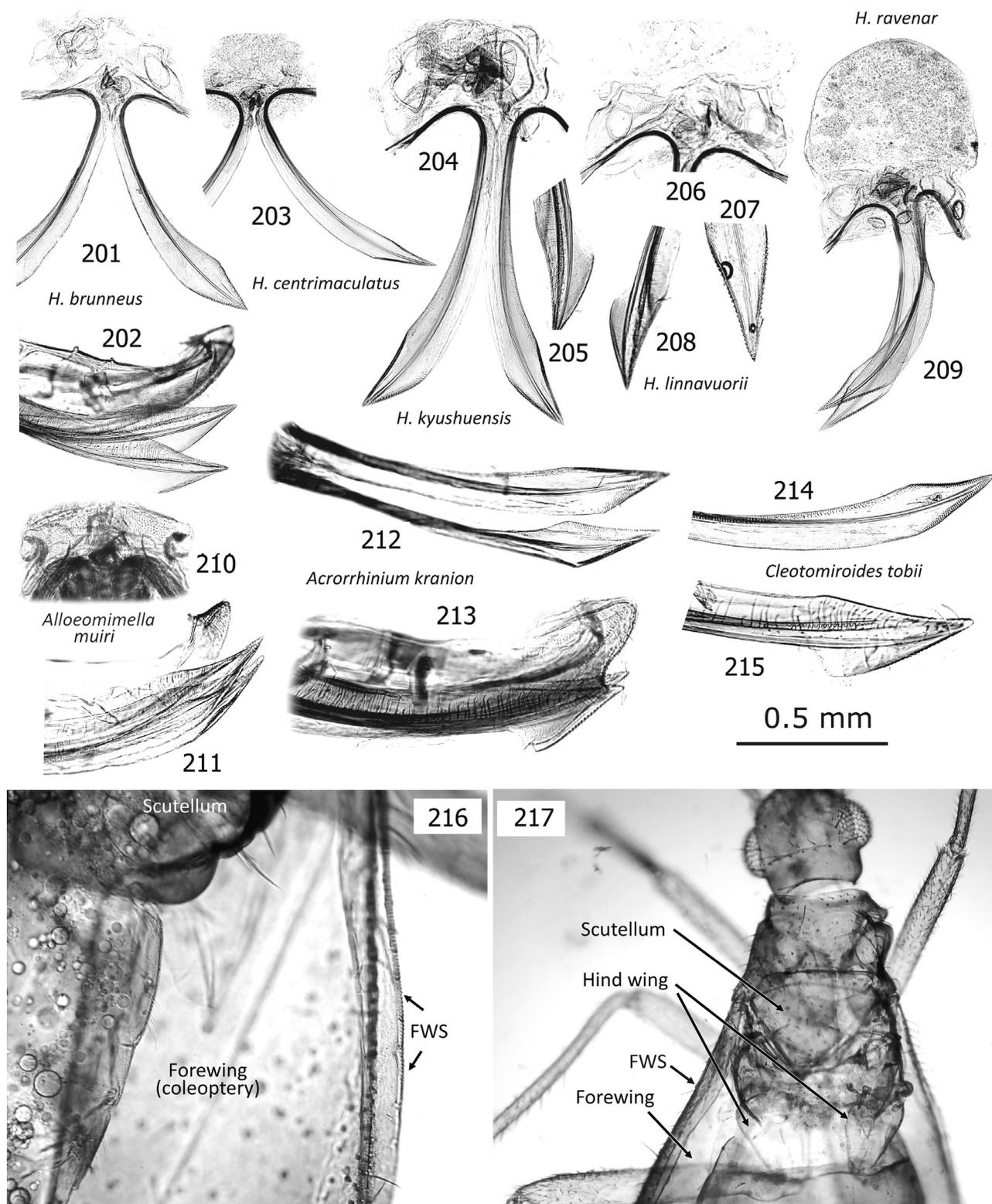
Endosoma L-shaped, with a long, tapered apical process (Fig. 198).

**Female.** Similar in overall appearance to male; body somewhat rounded laterally. Female genitalia (Figs 199–200): Bursa copulatrix rather narrow, not strongly sclerotized; sclerotized ring thickened posteriorly (Fig. 199); ovipositors (gonapophyses I and II) rather elongate.

**Measurements** (♂♂/♀♀, mm). Total length of body 3.18–3.26 / 3.18–3.43; head width including eyes 0.67–



Figs 192–200. Male (192–198) and female (199–200) genitalia of Asian hallozapines. 192–195 – *Cleotomiroides ishikawachui* sp. nov. (Java): 192 – pygophore, left lateral view; 193 – left paramere; 194 – phallosome; 195 – endosoma. 196–200 – *Wygomiris paveli* sp. nov. (Taiwan): 196 – pygophore, left lateral view; 197 – apex of pygophore, ventral view; 198 – endosoma; 199 – bursa copulatrix and gonapophysis I; 200 – posterior wall and gonapophysis II. Scale bars 0.1 mm.



Figs 201–217. Female genitalia and wing structures (216–218) of Asian hallodapines. 201–202 – *Hallodapus brunneus* (Poppius, 1915) (Yonakuni Island, Japan): 201 – bursa copulatrix with gonapophysis I, ventral view; 202 – gonapophysis II. 203 – *H. centrimaculatus* (Poppius, 1909) (Nagasaki), bursa copulatrix with gonapophysis I. 204–205 – *H. kyushuensis* (Miyamoto, 1965) (Okinawa Island): 204 – bursa copulatrix with gonapophysis I; 205 – gonapophysis II. 206–208 – *H. linnavuorii* (Miyamoto, 1965) (Nagasaki): 206 – bursa copulatrix; 207 – apex of gonapophysis I; 208 – gonapophysis II. 209 – *H. ravenar* (Kirkaldy, 1902) (Nagasaki), bursa copulatrix with gonapophysis I. 210–211 – *Alloeomimella muii* (Schuh, 1984) (Nakhon Nayok, Thailand): 210 – bursa copulatrix; 211 – gonapophysis II. 212–213 – *Acrorrhinium kranion* Yasunaga, Yamada & Artchawakom, 2013 (Nakhon Ratchasima, Thailand): 212 – gonapophysis I; 213 – gonapophysis II. 214–215 – *Cleotomiroides tobii* Yasunaga, 2012 (Nakhon Ratchasima): 214 – gonapophysis I; 215 – gonapophysis II. 216 – forewing of *Hallodapus kyushuensis* (Nagasaki). 217 – dorsal habitus of *H. linnavuorii* (Nagasaki).

0.70/ 0.64–0.70; vertex width 0.28–0.30 / 0.33–0.38; lengths of antennal segments I–IV 0.25–0.27, 1.03–1.05, 0.57–0.60, 0.45–0.47 / 0.24–0.30, 0.91–1.00, 0.54, ? [in aberrant ♂ specimen (Figs 14–15, 142–143): 0.29, 1.19, 0.60, 0.51 (right) and 0.29, 1.35, 0.86 (left)]; labial length 1.21–1.23/ 1.36–1.37; basal width of pronotum 1.03–1.05 / 1.00–1.08; maximum width across hemelytron 1.06–1.16 / 1.21–1.32; and lengths of metafemur, tibia and tarsus 1.03–1.05, 1.66–1.68, 0.30–0.32/ 1.22, 1.53, 0.32.

**Etymology.** Named in honor of the eminent Czech heteropterist, Dr. Pavel Štys (former head of Department of Zoology of the Charles University, Praha), who regrettably passed away in 2018.

**Biology.** Adults were occasionally attracted to UV light at night. Collection records suggest that this mirid has two or three generations per year.

**Distribution.** Taiwan: Hualien, Pingtung (this paper).

### *Wygomiris phormictes* Yasunaga & Duwal sp. nov.

(Figs 146–154, 170–173)

**Type material.** HOLOTYPE: ♀, THAILAND: NAKHON RATCHASIMA: Wang Nam Khieo, Sakaerat Environmental Research Station, 14°30'27"N, 101°55'39"E, 410 m alt., UV light trap, 22 Mar 2014, T. Yasunaga (DOAT) (AMNH\_PBI 00380645).

**Differential diagnosis.** Most similar in general appearance and similarly small size (body length < 3.0 mm) to *W. kaliyahae* Yasunaga, 2012, from which this new species is readily distinguished by the following characters: pale brown antennal segments I and II (Fig. 170); short antennal segment II that is shorter than head width across eyes; relatively shiny pronotum; golden brown anterior part of hemelytron (Fig. 171); constricted middle margin of embolium (Figs 149, 171); possession of noticeable stridulatory device (FWS+MFP, Figs 149–150, 152–153); pale coxae (Fig. 172); short metafemur almost equal in length to mesofemur (Fig. 173); mesotibia longer than mesofemur; and metatarsomere II as long as III (Fig. 151).

**Description.** *Female* (holotype). Macropterous; body small (2.7 mm); dorsal surface relatively shining, with sparsely distributed, simple upright setae and woolly reclining setae. Head dark brown, weakly shining. Antenna pale brown, partly tinged with red, generally short; segments III and IV dark brown. Labium shiny reddish brown, slightly exceeding apex of mesocoxa. Pronotum and propleuron shining, dark brown; epimeron and episternum shiny reddish brown; scent efferent system pale somber brown; scutellum dark brown, somewhat shagreened, flat. Hemelytron dark brown, with anterior part contrastingly golden brown as in Figs 170–171, constricted at middle; embolium with rather developed FWS (Figs 149–150); membrane smoky brown, with pale, translucent basal 1/3. Coxae and legs pale brown; protibia, base of mesotibia, apical half of metafemur and whole metatibia reddish brown (Fig. 173); mesofemur as long as metafemur; mesotibia slightly longer than metatibia; metatibia somewhat inflated; MFP distributed on median metafemur (Fig. 152), with each plectrum hemispherical (Fig. 153). Abdomen widely shiny dark brown; abdominal sterna II–IV paler. Female genitalia: Not examined.

**Measurements** (mm). Female (holotype): Total length of body 2.70; head width including eyes 0.60; vertex width 0.29; lengths of antennal segments I–IV 0.15, 0.53, 0.35, 0.35; labial length 0.98; basal width of pronotum 0.92; maximum width across hemelytron 1.08; lengths of mesofemur and tibia 0.78 and 1.05; and lengths of metafemur, tibia and tarsus 0.78, 1.10, 0.27.

**Male.** Unknown.

**Etymology.** From Greek, *phormictes* (or *phormiktes* = harper), referring to presence of the stridulatory device of this new species; noun in apposition.

**Biology.** A female adult (Fig. 170) was attracted to UV light trap at tropical dry-evergreen forest zone (cf. <https://www.tist.or.th/sakaerat/sakaeratE/Environment/environment.htm>).

**Distribution.** Thailand: Nakhon Ratchasima (this paper).

### Acknowledgements

We are much indebted to the following individuals or institutions for offering or loaning materials, supporting fieldworks and/or sharing valuable information: Dr. R. T. Schuh (AMNH); Dr. A. G. Wheeler (Clemson University, SC, USA); Dr. M. D. Schwartz (Agriculture & Agri-Food Canada, Canadian National Collection of Insects, Ottawa, Ontario); Drs. T. Artchawakom and C. Phuvasa (Sakaerat Environmental Research Station, Thailand Ministry of Science and Technology, Nakhon Ratchasima); Ms. N. B. Rungrueang (Bangkok, Thailand); Prof. S. H. Lee and Mr. M. S. Oh (Seoul National University, Korea); Mr. M. Takai and Mr. T. Befu (Kochi, Japan); Prof. Emer. M. Hayashi (Saitama University, Japan); Dr. K. Takahashi (Tsukuba, Ibaraki, Japan); Dr. P. Kment (NMPC); Dr. T. Ishikawa (TUAK); Dr. J. F. Tsai (NMNS); Mr. K. Tanaka and Mr. G. Fukagawa (Nagasaki, Japan); Dr. Y. Nakatani (NIAES); Mr. T. Tago (Chiba, Japan); Dr. K. Yamada (Tokushima Prefectural Museum, Japan); Mr. T. Nozaki (Fukuoka, Japan); staffs of Plant Protection Division (PPD), Myanmar Ministry of Agriculture & Irrigation (Insein, Yangon) and Natural History Museum, Tribhuvan University (Swayambhu, Kathmandu, Nepal); and members of Nagasaki West High School Biology Club. We also thank Mr. D. Terada and Mr. A. Hama (CSR Division, Hitachi High-Technologies Corporation, Tokyo) for generously allowing to use a tabletop scanning electron microscope and Mr. S. Serrano Leon (Nagasaki West High School) for reviewing the early version of manuscript. Thanks are extended to Dr. K. L. Menard (Sam Noble Museum, University of Oklahoma, USA), Dr. F. Chérot (Département de l'Etude du Milieu Naturel et Agricole, Service Public de Wallonie, Gembloux, Belgium) and Dr. P. Kment for reviewing the manuscript and providing useful comments and suggestions.

### Online supplementary data

**Video 1.** Fighting between males of *H. centrimaculatus* (Poppius). [https://youtu.be/QjM1Q\\_24m9I](https://youtu.be/QjM1Q_24m9I)

**Video 2.** Behavior between females of *H. centrimaculatus*. <https://youtu.be/CWyyv8pIHHtW>

**Video 3.** Conflict between males of *H. ravenar* (Kirkaldy). <https://youtu.be/RW0nHYj9Bw8>

## References

- AUKEMA B., RIEGER C. & RABITSCH W. 2013: *Catalogue of the Heteroptera of the Palearctic Region, Vol. 6, supplement*. The Netherlands Entomological Society, Amsterdam, xxiv + 629 pp.
- DAVIS N. T. 1955: Morphology of the female organs of reproduction in the Miridae (Hemiptera). *Annals of the Entomological Society of America* **48**: 132–150.
- DUWAL R. K., YASUNAGA T., TOMOKUNI M., NAKATANI Y. & HIROWATARI T. 2017: Further records on the plant bug tribe Hallodapini (Hemiptera: Heteroptera: Miridae: Phylinae) in Asia, with proposition of two new species and a new synonymy. *Zootaxa* **4258**(5): 401–424.
- GOULA M. 2008: Acoustical communication in Heteroptera (Hemiptera: Heteroptera). In: CAPINERA J. L. (ed.): *Encyclopedia of Entomology*. Springer, Dordrecht. DOI: <https://doi.org/10.1007/978-1-4020-6359-6>.
- IKEDA N., ASANABE H., TAMADA Y., HINAMI H., MIYAZAKI A., YASUNAGA T., NAGASHIMA T. & TANAKA K. 2019: New distributional records for ten heteropteran species recently found in Nagasaki Prefecture, southwestern Japan. *Rostria* **63**: 45–51.
- KERZHNER I. M. & JOSIFOV M. 1999: Miridae Hahn, 1833. Pp. 1–576. In: AUKEMA B. & RIEGER C. (eds.): *Catalogue of the Heteroptera of the Palearctic Region, vol. 3, Cimicomorpha II*. The Netherlands Entomological Society, Amsterdam, xiv + 577 pp.
- KMENT P. & BAŇAŘ P. 2012: True bugs (Hemiptera: Heteroptera) of the Bílé Karpaty Protected Landscape Area and Biosphere Reserve (Czech Republic). *Acta Musei Moraviae, Scientiae Biologicae* **96**: 323–628.
- KORN R., FRIESS T. & WIESMAIR B. 2015: Wanzen (Insecta: Heteroptera) in Halbtrockenrasen und deren frühen Renaturierungsstadien in der Südoststeiermark. *Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark* **144**: 133–156.
- MIYAMOTO S. 1966: Five new species of Miridae from Japan (Hemiptera, Heteroptera). *Sieboldia* (Fukuoka) **3**: 427–438.
- POPPIUS B. 1915: H. Sauter's Formosa-Ausbeute: Nabidae, Anthocoridae, Termatophylidae, Miridae, Isometopidae und Ceratocombidae (Hemiptera). *Archiv für Naturgeschichte* **80A**(8) [1914]: 1–80. [Published March 1915].
- SCHUH R. T. 1974: The Orthotylinae and Phylinae (Hemiptera: Miridae) of South Africa with a phylogenetic analysis of the ant-mimetic tribes of the two subfamilies for the world. *Entomologica Americana* **47**: 1–332.
- SCHUH R. T. 1984: Revision of the Phylinae (Hemiptera, Miridae) of the Indo-Pacific. *Bulletin of the American Museum of Natural History* **177**: 1–476.
- SCHUH R. T. 1995: *Plant bugs of the world (Insecta: Heteroptera: Miridae)*. Systematic catalog, distributions, host list and bibliography. The New York Entomological Society, New York, xii + 1329 pp.
- SCHUH R. T. 2013: *On-line Systematic Catalog of Plant Bugs (Insecta: Heteroptera: Miridae)*. <http://research.amnh.org/pbi/catalog/> (Last accessed: Feb 20, 2019.)
- SCHUH R. T. & MENARD K. L. 2013: A revised classification of the Phylinae (Insecta: Heteroptera: Miridae): Arguments for the placement of genera. *American Museum Novitates* **3785**: 1–72.
- SCHUH R. T. & SLATER J. A. 1995: *True Bugs of the World (Hemiptera: Heteroptera) – Classification and Natural History*. Cornell University Press, Ithaca, N.Y., xii + 337 pp.
- SCHWARTZ M. D., WEIRAUCH C. & SCHUH R. T. 2018: New genera and species of myrtaceae-feeding Phylinae from Australia, and the description of a new species of Restiophylus (Insecta: Heteroptera: Miridae). *Bulletin of the American Museum of Natural History* **424**: 1–157.
- WAGNER E. 1974: Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makaronesischen Inseln (Hemiptera, Heteroptera). Teil 2. *Entomologische Abhandlungen* **39**(Suppl.): i–ii + 1–421.
- WHEELER A. G. JR. 2001: *Biology of the Plant Bugs (Hemiptera: Miridae), Pests, Predators, Opportunists*. Cornell University Press, Ithaca and London, xv + 507 pp.
- WYNGER D. 2006: The Central European Hallodapini: Studies of the female genitalia (Hemiptera, Phylinae, Miridae). *Denisia* **19**: 711–720.
- YASUNAGA T. 2001: Family Miridae Hahn, plant bugs. In: YASUNAGA T., TAKAI M. & KAWASAWA T. (eds.): *A field guide to Japanese bugs II*. Zenkoku Noson Kyoiku Kyokai Publ. Co. Ltd., Tokyo, pp. 2–96, 111–351 pp. (in Japanese).
- YASUNAGA T. 2012: Review of the phylinae plant bug tribe Auricillocorini from Asia, with descriptions of a new genus and nine new species from Japan, Nepal and Thailand (Hemiptera: Heteroptera: Miridae: Phylinae). *Zootaxa* **3530**: 1–24.
- YASUNAGA T. 2018: Teratological forms found in two Japanese heteropterans (Heteroptera: Gerridae and Miridae). *Rostria* **62**: 55–57.
- YASUNAGA T. & DUWAL R. K. 2015: Further records and descriptions of the plant bug subfamily Phylinae (Hemiptera: Heteroptera: Miridae) from Thailand. *Zootaxa* **3981**(2): 193–219.
- YASUNAGA T. & DUWAL R. K. 2016: A unique new genus and species of the phylinae plant bug tribe Hallodapini from the Philippines and Thailand (Hemiptera: Heteroptera: Miridae: Phylinae: Hallodapini). *Zootaxa* **4173**(3): 251–258.
- YASUNAGA T., MAEHARA S., ISHIKAWA T. & TAKAI M. 2018: *Guidebook to the heteropteran world – Basic ecology, morphology, classification and research methodology*. Zenkoku Noson Kyoiku Kyokai, Publishing Co., Ltd., Tokyo, 212 pp. (in Japanese).
- YASUNAGA T. & SCHUH R. T. 2013: Morphologically novel members of the ant-mimetic plant bug genus Pilophorus Hahn found in Thailand, with descriptions of three new species (Heteroptera: Miridae: Phylinae: Pilophorini). *American Museum Novitates* **3768**: 1–18.
- YASUNAGA T., SCHUH R. T., POORANI J. & CASSIS G. 2015: A remarkable new genus and new species of the plant bug (Heteroptera, Miridae, Phylinae), inhabiting psyllid leaf margin roll gall on Indian banyan, *Ficus benghalensis*. *American Museum Novitates* **3839**: 1–15.
- YASUNAGA T., YAMADA K. & ARTCHAWAKOM T. 2013a: New or little known taxa of the plant bug tribe Hallodapini (Hemiptera: Heteroptera: Miridae: Phylinae) from Thailand, with descriptions of three new species of Acrorrhinium Noualhier. *Zootaxa* **3647**(3): 429–442.
- YASUNAGA T., YAMADA K. & ARTCHAWAKOM T. 2013b: Additional records of the plant bug genus Hallodapus Fieber from Thailand, with proposal of a new synonymy (Hemiptera: Heteroptera: Miridae: Phylinae). *Zootaxa* **3701**(5): 596–599.

