



Review of the Pacific leafhopper genus *Hecaloidella* (Hemiptera: Cicadellidae: Deltocephalinae: Selenocephalini) with description of sixteen new species

DELIANG XU^{1,4}, MICHAEL D. WEBB^{2,5}, SUQIN SHANG^{3,6} & YALIN ZHANG^{1,7,8}

¹Key Laboratory of Plant Protection Resources and Pest Management, Ministry of Education, Entomological Museum, College of Plant Protection, Northwest A&F University, Yangling, Shaanxi 712100, China

²Department of Life Sciences, Natural History Museum, Cromwell Road, London, ME15 6QX, UK

³Biological Engineering Laboratory of Crop Diseases and Pests of Gansu Province, College of Plant Protection, Gansu Agricultural University, Lanzhou, Gansu 730070, China

⁴✉ 18710305867@163.com; <https://orcid.org/0000-0003-0106-5570>

⁵✉ mdwebb04@gmail.com; <https://orcid.org/0000-0002-1312-6142>

⁶✉ shangsq@gsau.edu.cn; <https://orcid.org/0000-0001-9376-0735>

⁷✉ yalinzhang@nwsuaf.edu.cn; <https://orcid.org/0000-0002-1204-9181>

⁸Corresponding author

Abstract

Eighteen species of the Pacific leafhopper genus *Hecaloidella* Osborn, 1934 are described and illustrated and a key provided for their separation. The previously described species, *H. nitida* Osborn (type species) and *H. brunnifacialis* Shang & Zhang, and the following sixteen new species are treated: *H. brunifasciata* Zhang & Webb, *H. bimaculata* Zhang & Webb, *H. borneoensis* Zhang & Webb, *H. brevis* Zhang & Webb, *H. brevipenis* Zhang & Webb, *H. brevispina* Zhang & Webb, *H. caudospina* Zhang & Webb, *H. knighti* Zhang & Webb, *H. longipenis* Zhang & Webb, *H. nudapenis* Zhang & Webb, *H. pacifica* Zhang & Webb, *H. quadripecta* Zhang & Webb, *H. quadrispina* Zhang & Webb, *H. sandakanensis* Zhang & Webb, *H. singaporensis* Zhang & Webb and *H. spinosa* Zhang & Webb **spp. nov.**

Key words: Auchenorrhyncha, Selenocephalina, taxonomy, morphology

Introduction

The Pacific leafhopper genus *Hecaloidella* Osborn, 1934 (Cicadellidae: Deltocephalinae: Selenocephalini) was previously known only from its type species, *H. nitida* Osborn, 1934 from Samoa (see Zhang & Webb, 1996: 8) and *H. brunnifacialis* Shang & Zhang, 2012 from Malaysia (Sarawak). In the current work sixteen new species are described from throughout the western Pacific along with a checklist and a key to species. *Hecaloidella* is one of only a few described Pacific Selenocephalini leafhoppers, an Old World tribe defined on a combination of features (Zhaniser & Dietrich, 2013) but principally on the transverse carinae and or striations on the fore margin of the head. This feature is also found in another Old World tribe, Drabescini, but this tribe differs in having longer antennae either just in the nymph (Drabescina) or also in the adult (Paraboloponina) and the antennae placed higher on the face. The main distinguishing feature of *Hecaloidella* is the convex face in profile (Fig. 2B); other features such as the marginal rim of the head (Fig. 2B, D), striations dorsally on the face (Fig. 2C) and sometimes also on the vertex and pronotum (Fig. 2A) and absence of macrosetae on the subgenital plates are also found in the tribe Drabescini (Paraboloponina). Two other unusual features found in most *Hecaloidella* species are the disassociation of the aedeagus from the connective together with the apex of connective extended caudally. These features are also found in a few Drabescini (Paraboloponina) genera, i.e., *Parabolopona* Matsumura, 1912 (see Webb, 1981), *Tenompoella* Zhang & Webb, 1996, *Omanellinus* Zhang, 1999 (in Zhang *et al.*, 1999) and *Forficus* Qu, Webb & Dai, 2015, but found in only one other Selenocephalini genus, i.e., the African *Adama* Dlabola, 1980 (see Linnavuori and Al-Ne'amy, 1983), and rarely in other Deltocephalinae, i.e., *Scaphoideus* Uhler, 1889 and *Scaphytopius* Ball, 1931 (see Zahniser & Dietrich, 2013). Thus, the relationship between *Hecaloidella* and other genera remains unclear while the observed

species diversity in *Hecaloidella* (see species groups below) indicates its included species may represent more than one genus. In addition, the large number of new species described here, from a relatively small sample, indicates that more new species of the genus will probably be found in the future.

Included in the material examined for this study are specimens collected on the Royal Entomological Society of London's, Project Wallace expedition (1985). This, probably the last truly international insect expedition, was organised by William J. Knight, well known for his Pacific leafhopper work and mentor of the second author at the Natural History Museum, London (1967–1992); it is with great pleasure that the second author names one of the Sulawesi species after Dr. Knight. Other colleagues of the second author whose names appear on the labels of *Hecaloidella* specimens described here (all new species Zhang & Webb except *H. brunnifacialis* Shang & Zhang) from this and other expeditions in the Pacific include: Peter Hammond and Jane Marshall (*H. quadrispina*), Mick Day (*H. spinosa*), Jeremy Holloway and Vic Eastop (*H. brunifasciata*), Jon Martin (*H. bimaculata*, *H. caudospina* and *H. nudapenis*), Mick Bacchus and Mike Wilson (*H. pacifica*) and Martin Brendell (*H. brevis*, *H. knighti* and *H. nudapenis*), see Material examined under respective species for further details. The involvement of so many people from the BMNH and other institutions, in the 1980's, reflects the interest in insect studies from South East Asia at that time.

The current work has had a long and chequered history. During a visit by the fourth author (Zhang) to the Natural History Museum, London (BMNH) in 1995, a revision of the Asian and Pacific Selenocephalinae (Zhang & Webb, 1996), now Deltocephalinae (Selenocephalini and Drabescini), was completed. During the course of that work many undescribed species were found, including many new species of *Hecaloidella*, noted under the genus remarks in Zhang & Webb, 1996: 8. These specimens were sorted to new species and subsequently borrowed by Zhang who supervised their study by his student and third author (Shang) resulting in a draft manuscript and formal description of a new species, *H. brunnifacialis* Shang & Zhang, 2012. More recently, the same material was re-worked by Webb, aided by Xu (second and first author respectively), and together with some newly borrowed material, the current manuscript was produced.

Little is known on the biology of *Hecaloidella* species except two species occur on cloves, *Syzygium aromaticum* (L.) Merr. & L.M. Perry (Myrtaceae), i.e., *H. nitida* Osborn and *H. pacifica* Zhang & Webb, with the latter, the only species widely distributed in the Pacific. Most of the specimens studied here from the above mentioned Project Wallace expedition were collected at light. Fogging of tall trees using insecticide, on the expedition, yielded no *Hecaloidella* specimens but was very effective in collecting other leafhoppers. This suggests either the plant hosts of the species were not fogged or they feed on lower growing plants, like the two species feeding on cloves.

Materials and methods

Terminology follows Zhang & Webb (1996). Examination of the genitalia was carried out using the standard procedure, i.e., the abdomen was removed and soaked in 10% NaOH until the soft tissues dissolved and internal parts of the genital capsule became visible. The abdomen was then washed in water and examined in glycerine. Photos of external morphology and male genitalia were taken using an advanced stereomicroscope system (Zeiss, AxioCam ICc5; Carl Zeiss, Discovery. V20; Canon 5D Mark 4; Q-IMAGING RETIGA 2000R) and Auto-Montage software (ZEN 2 pro; SYN.). Photographs were modified with Adobe Photoshop CS.

Material examined is deposited in the following institutions abbreviated in the text as follows:

AMNH	American Museum of Natural History, New York, USA
BMNH	The Natural History Museum, London, UK
BPBM	Bernice Pauahi Bishop Museum, Honolulu, Hawaii, USA
INHS	Illinois Natural History Survey, Champaign, USA
NMW	National Museum of Wales, Cardiff, Wales, UK
NMNH	The National Museum of Natural History, Washington D.C., USA

Under Material examined, reference to RESL-Project Wallace, relates to the 1985 Royal Entomological Society of London's, Project Wallace expedition.

Taxonomy

Subfamily Deltocephalinae Dallas, 1870

Tribe Selenocephalini Fieber, 1872

Subtribe Selenocephalina Fieber, 1872

Genus *Hecaloidella* Osborn, 1934

Hecaloidella Osborn, 1934: 173

Type species: *H. nitida* Osborn, 1934, by original designation.

Diagnosis. Head anteriorly foliaceous, anterior margin rim-like with a pair of marginal carina; vertex longer medially than next to eyes, slightly transversely sulcate between anterior corners of eyes, smooth or finely obliquely striate to sulcus or to anterior margin, transversely striate each side of margin; ocelli on marginal rim close to corresponding eye; face convex in profile, dorsally concave with fine transverse striations extending laterally onto ocellular area and then ventrally to antennal ledge, remaining ventral part of face shagreen; antennae short, arising approximately lower than mid-height of eyes in facial view; anterior tentorial branches Y-shaped with asymmetric arms. Pronotum with sides short, disc finely transversely striate or smooth. Forewing with medial and outer subapical cells closed, inner subapical cell open.

Male subgenital plates without macrosetae, with fine dorsolateral setae, sometimes with digitate apex crenulate. Connective with apices of arms close or touching, sometimes fused but rarely widely spaced (*H. bimaculata*); stem short to long and usually extended caudally into a long distal process, the latter usually bifurcate basally or apically, rarely stem without long extension (*H. spinosa* and *H. brevis*). Aedeagus situated either dorsad of connective and connected to it by membrane or articulated with connective; with basal apodeme short to long, sometimes with a lobe on each side.

Female genitalia with first valvulae with strigate sculpture dorsally; second valvulae with serrate teeth.

Description. Small to medium sized leafhoppers. Sordid or brownish yellow to stramineous. Vertex with or without brown marking. Pronotum and mesonotum laterally sometimes with one or two lateral brown spots, respectively. Forewings brownish hyaline usually with brown spot at apex of claval veins and clavus and usually more heavily marked with brown on veins of fifth apical cells and wing apex, rarely forewing darker brown with outer half of clavus yellow (*H. pacifica*).

Head very slightly wider than pronotum, anteriorly foliaceous with anterior margin rim-like with a pair of marginal carina; vertex approximately one and a half times as long medially than next to eyes (distinctly longer in *H. bimaculata*) and slightly transversely sulcate between anterior corners of eyes, smooth or finely obliquely striate to sulcus or to anterior margin, transversely striate each side of margin; ocelli on marginal rim close to corresponding eye; face convex in profile (except *H. brunifasciata*), dorsally concave with fine transverse striations extending laterally onto ocellular area and then ventrally to antennal ledge, remaining ventral part of face shagreen; antennae short, less than half body length, arising approximately at mid-height of eyes in facial view (higher in *H. brunifasciata*); anterior tentorial branches Y-shaped with asymmetric arms. Pronotum sides relatively short, carinate; disc finely transversely striate or smooth. Forewing with three subapical cells, inner open. Fore femur with AM1 present, IC row with relatively thick setae, AV setae absent. Fore tibia with dorsal setal formula 1+4. Hind femur with apical setal formula 2+2+1. Abdominal basal apodemes without lobes.

Male pygofer tapered to conically rounded apex with several macrosetae distally, without processes. Segment X simple, rarely extended ventrally (*H. brunifasciata*). Subgenital plates wide basally, thereafter lateral margin weak to strongly incurved and then distally evenly tapered to apex or apex digitate, sometimes digitate apex crenulate (Fig. 6H); without macrosetae, with fine dorsolateral setae. Style with apical process hook-like, preapical lobe variable in length. Connective with apices of arms close or touching, sometimes fused but rarely widely spaced (*H. bimaculata*); stem short to long and usually extended caudally into a long distal process, the latter usually bifurcate basally or apically, rarely stem without long extension (*H. spinosa* and *H. brevis*). Aedeagus situated either dorsad of connective and connected to it by membrane or articulated with connective; with or without processes, gonopore apical or apical on ventral surface; with basal apodeme short to long, sometimes with a lobe on each side.

Female first valvulae with strigate sculpture dorsally; second valvulae with serrate teeth.

Distribution. Oriental and Australian Region.

Remarks. *Hecaloidella* can be distinguished by its convex face in profile (Fig. 2B) and sculpture on the head and pronotum (see Diagnosis) and in the male genitalia by lacking macrosetae on the subgenital plate, the connective with a posterior extension (except *H. spinosa* and *H. brevis*) and the connective frequently separated from the aedeagus; all but the first of these characters are shared with some or all Drabescini (Paraboloponina) (see Introduction). Within the genus most species fall into three groups (see below for details). One species (*H. brunifasciata*) is only tentatively included in the genus (*incertae sedis*) (see species Remarks for details). Only one species, *H. pacifica* is widespread in the Pacific (on cloves) and nearly all other species are restricted to Borneo or Sulawesi (see checklist).

Checklist of *Hecaloidella* species

H. nitida species group

H. bimaculata Zhang & Webb **sp. nov.**

Distribution: Brunei, Malaysia (Sarawak).

H. caudospina Zhang & Webb **sp. nov.**

Distribution: Indonesia (Sulawesi).

H. nitida Osborn, 1934: 174, fig. 8; Zhang & Webb, 1966: 8, figs. 2, 6, 10, 24, 99–104, 474; Shang & Zhang, 2012: 2–3, fig. 1.

Distribution: Indonesia (Maluku, Moluccas), Papua New Guinea (Sudest Island), Samoa.

H. nudapenis Zhang & Webb **sp. nov.**

Distribution: Indonesia (Sulawesi).

H. pacifica Zhang & Webb **sp. nov.**

Distribution: Brunei, Indonesia (Java, Sulawesi, Sumatra), Malaysia (Sabah, Sarawak, Selangor), Philippines, Singapore.

H. borneoensis species group

H. borneoensis Zhang & Webb **sp. nov.**

Distribution: Brunei, Malaysia (Sarawak).

H. brevipenis Zhang & Webb **sp. nov.**

Distribution: Malaysia (Sarawak).

H. brevispina Zhang & Webb **sp. nov.**

Distribution: Malay Peninsula.

H. longipenis Zhang & Webb **sp. nov.**

Distribution: Malaysia (Sarawak).

H. quadrispina Zhang & Webb **sp. nov.**

Distribution: Malaysia (Sarawak).

H. spinosa Zhang & Webb **sp. nov.**

Distribution: Brunei.

***H. quadripicta* species group**

H. brevis Zhang & Webb **sp. nov.**

Distribution: Indonesia (Sulawesi).

H. brunnifacialis Shang & Zhang, 2012: 3–4, fig. 2.

Distribution: Malaysia (Sarawak, Sandakan).

H. knighti Zhang & Webb **sp. nov.**

Distribution: Indonesia (Sulawesi).

H. quadripicta Zhang & Webb **sp. nov.**

Distribution: Malaysia (Sarawak).

H. sandakanensis Zhang & Webb **sp. nov.**

Distribution: Malaysia (Sandakan).

H. singaporensis Zhang & Webb **sp. nov.**

Distribution: Singapore.

Incertae sedis

H. brunifasciata Zhang & Webb **sp. nov.**

Distribution: Brunei.

Key to species and species groups of *Hecaloidella* (excluding *H. brunifasciata*)

- 1 Vertex with distinct longitudinal or oblique striations at least to anterior transverse sulcus; pronotum with distinct transverse striations; forewing with outer subapical cell tapered basally (Figs. 2B, 3D); aedeagus disassociated from connective (***H. nitida* species group**) 2
- Vertex and pronotum smooth or with indistinct striations; forewing with outer subapical cell tapered posteriorly (Fig. 1I); aedeagus associated or disassociated from connective 6
- 2 Vertex without brown anterior spots *H. nitida*
- Vertex with pair of brown anterior spots 3
- 3 Vertex spots large (Fig. 1A); rest of vertex uniformly yellow (Fig. 2A) *H. bimaculata*
- Vertex spots small (Fig. 1B) to moderately large (Fig. 1E); rest of vertex orange anteriorly 4
- 4 Vertex spots extending to fore margin; forewing dark with inner margin of clavus variably yellowish (Figs. 1E–F); aedeagus with a basal ventral spine-like process (Fig. 4L) *H. pacifica*
- Vertex spots not extending to fore margin; forewing not as above; aedeagus with basal ventral process not spine-like 5
- 5 Connective caudal extension with a long basal ventral process (Fig. 4C) *H. caudospina*
- Connective caudal extension without a basal ventral process (Fig. 4H) *H. nudapenis*
- 6 Pronotum, mesoscutum and scutellum laterally with one small brown spot (Figs. 1N–S); aedeagus disassociated from connective (***H. quadripicta* species group**) 12
- Pronotum and mesonotum not marked as above; aedeagus associated with connective (***H. borneoensis* species group**) 7
- 7 Vertex with a brownish spot each side of midline nearly coalescing basally (Fig. 1M); connective stem not extended caudally, with a pair of apical spines (Fig. 6Q); aedeagus with a long ventral process from preatrium (Fig. 6S) *H. spinosa*
- Vertex uniformly brown or with a brick shaped brownish band each side of midline and a smaller brown mark next to each eye (Figs 1H–L); connective stem extended caudally, aedeagus without a ventral process from preatrium 8
- 8 Aedeagus with either a single very small subapical process dorsally or two pair of apical processes 9
- Aedeagus without processes 10
- 9 Aedeagus with a single small subapical process (Fig. 6F) *H. brevispina*
- Aedeagus with two pair of apical processes (Fig. 6M) *H. quadrispina*
- 10 Aedeagal shaft less than twice as long as height of atrium (Fig. 6D) *H. brevipenis*
- Aedeagal shaft more than twice as long as height of atrium (Figs 6B, I) 11
- 11 Aedeagus with gonopore arising near mid-length of shaft (Fig. 6I) *H. longipenis*
- Aedeagus with gonopore arising two thirds distance to apex of shaft (Fig. 6B) *H. borneoensis*
- 12 Connective with posterior extension (Fig. 7N) 13
- Connective without posterior extension (Fig. 7D) *H. brevis*
- 13 Aedeagus with processes 14

-	Aedeagus without processes (Fig. 7M, P)	<i>H. knighti</i>
14	Aedeagus with a single pair of apical processes	15
-	Aedeagus with two pairs of apical processes (Fig. 8F)	<i>H. sandakanensis</i>
15	Aedeagus with apical processes bifurcate (Fig. 8J); dorsal processes near mid-length of shaft in lateral view (Fig. 8I)	<i>H. singaporensis</i>
-	Aedeagus with apical processes not bifurcate, sometime with a small subapical spine (Fig. 7H); dorsal process sub-basally on shaft in lateral view (Fig. 7H)	16
16	Style with poorly developed lateral lobe (Fig. 7J); female pregenital sternite truncate with median conical projection (Fig. 7L)	<i>H. brunnifacialis</i>
-	Style with well-developed lateral lobe (Fig. 8C); female pregenital sternite with posterior margin broadly rounded (Fig. 8D)	<i>H. quadripicta</i>

H. nitida species group

This group comprises five species (*H. bimaculata*, *H. caudospina*, *H. nitida*, *H. nudapenis* and *H. pacifica*) with the following combination of characters: vertex usually orange at least anteriorly with a pair of anterior spots; vertex with distinct longitudinal or oblique striations at least to anterior transverse sulcus; pronotum with distinct transverse striations; forewings with outer subapical cell tapered basally (Figs 2B, 3D); aedeagus disassociated from connective, very small or relatively large (*H. bimaculata*), shaft short and robust, laterally compressed, with or without processes.

H. bimaculata Zhang & Webb sp. nov.

Figs. 1A, 2A–K

Description. Body length (including tegmina), male: 4.8–5.3mm; female: 5.3mm.

Stramineous to sordid yellow. Vertex with a large brown spot anteriorly each side of midline. Face with a medial dark brown inverted Y-shaped mark; antennal pedicel dark brown. Forewings brownish hyaline; veins yellowish with brown marking restricted to a small spot at apex of claval veins.

Vertex relatively long, nearly twice as long medially than next to eyes.

Male genitalia with subgenital plate very broadly curved basally with very short digitate apex, with a few short fine setae dorsolaterally. Style apical process rostrate. Connective Y-shaped with short stem and relatively short sharply upturned caudal extension. Aedeagus relatively large, disassociated from connective, with stout ventral process; shaft moderately long, laterally compressed and tapered to acute apex without processes, gonopore apical.

Female pregenital sternite with posterior margin almost straight.

Material examined. Holotype: ♂, Brunei, Temburong District, ridge NE of Kuala Belalong, approx. 300m alt., x.1992, J.H. Martin, m.v. light trap, NHMUK 010591776 (BMNH). Paratypes: 1♂, Malaysia, Sarawak, Gunung Mulu National Park, 30–50m, elevation, 4°02'32.9"N, 114°48'46.7"E, 16–22.x.2006, J.R. Cryan & J.M. Urban (INHS); 1♀, Malaysia, Sarawak, Gunung Mulu National Park, Site 10, February, Camp 1 Mulu, 160m, mixed dipterocarp forest, Ac.-understorey, J.D. Holloway, Royal Geographical Society Mulu Expedition (BMNH).

Etymology. This species is named after the pair of large brown spots on the vertex.

Remarks. This species differs from other species of *H. nitida* group by its large head spots, longer vertex and in the male genitalia by its larger aedeagus and shorter caudal extension of the connective strongly upturned.

H. caudospina Zhang & Webb sp. nov.

Figs. 1B, 4A–E

Description. Body length (including tegmina), male: 4.8–5.8mm.

Stramineous to sordid yellow. Vertex anteriorly orange with a small brown spot each side of midline. Face with variable brown marking dorsally. Forewing veins yellowish.

Male genitalia similar to *H. nudapenis* but caudal extension of connective with a long ventral process and ventral process of aedeagus shorter.

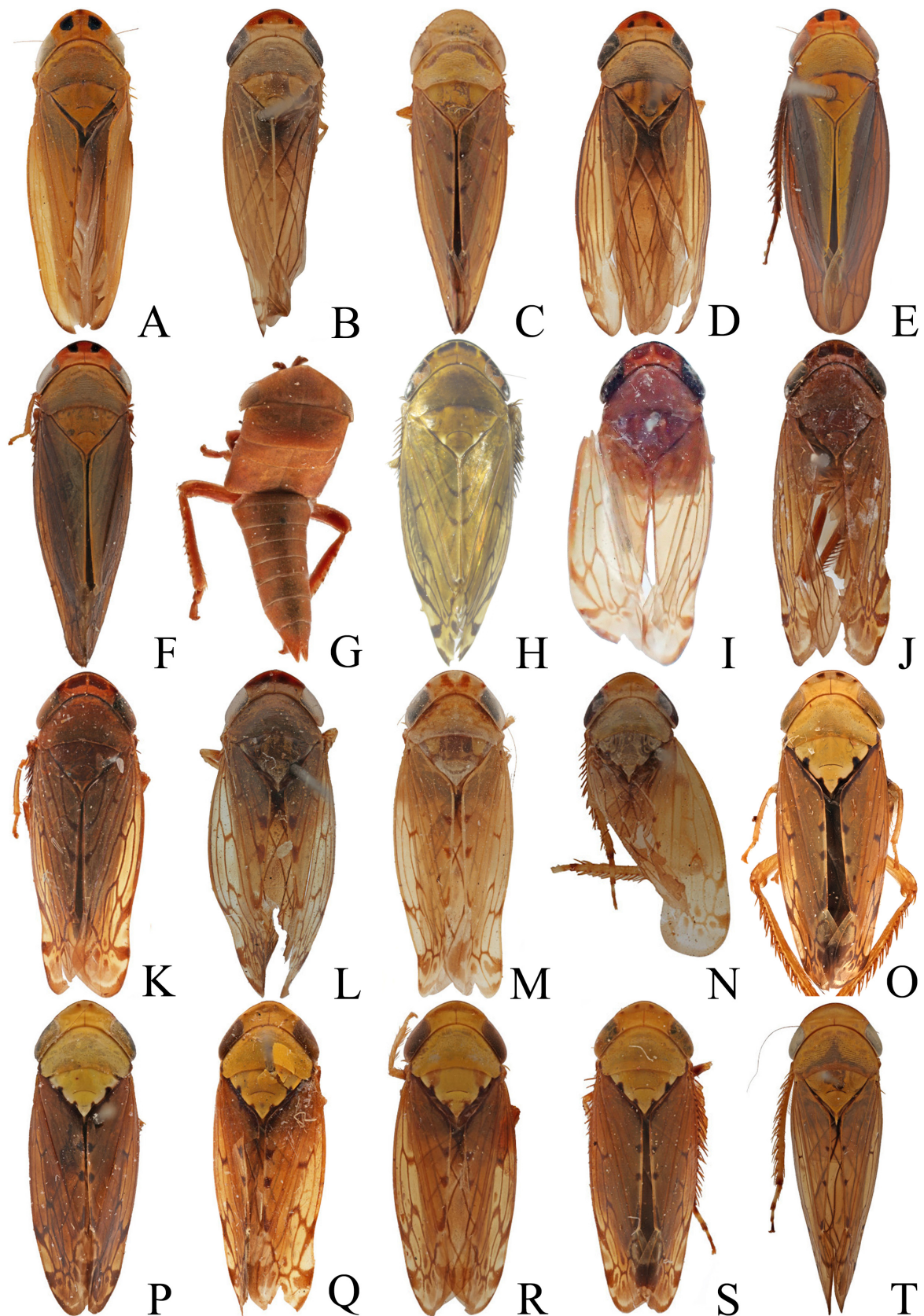


FIGURE 1. Habitus images of *Hecaloidella* species; A, *H. bimaculata* (holotype); B, *H. caudospina* (holotype); C, *H. nitida* (holotype); D, *H. nudapenis* (holotype); E–G, *H. pacifica* (paratypes and immature); H, *H. borneoensis* (holotype); I, *H. brevipenis* (holotype); J, *H. brevispina* (holotype); K, *H. longipenis* (holotype); L, *H. quadrispina* (holotype); M, *H. spinosa* (holotype); N, *H. brevis* (holotype); O, *H. brunnifacialis* (topotype); P, *H. knighti* (holotype); Q, *H. quadripicta* (paratype); R, *H. sandakanensis* (holotype); S, *H. singaporensis* (paratype); T, *H. brunifasciata* (holotype).

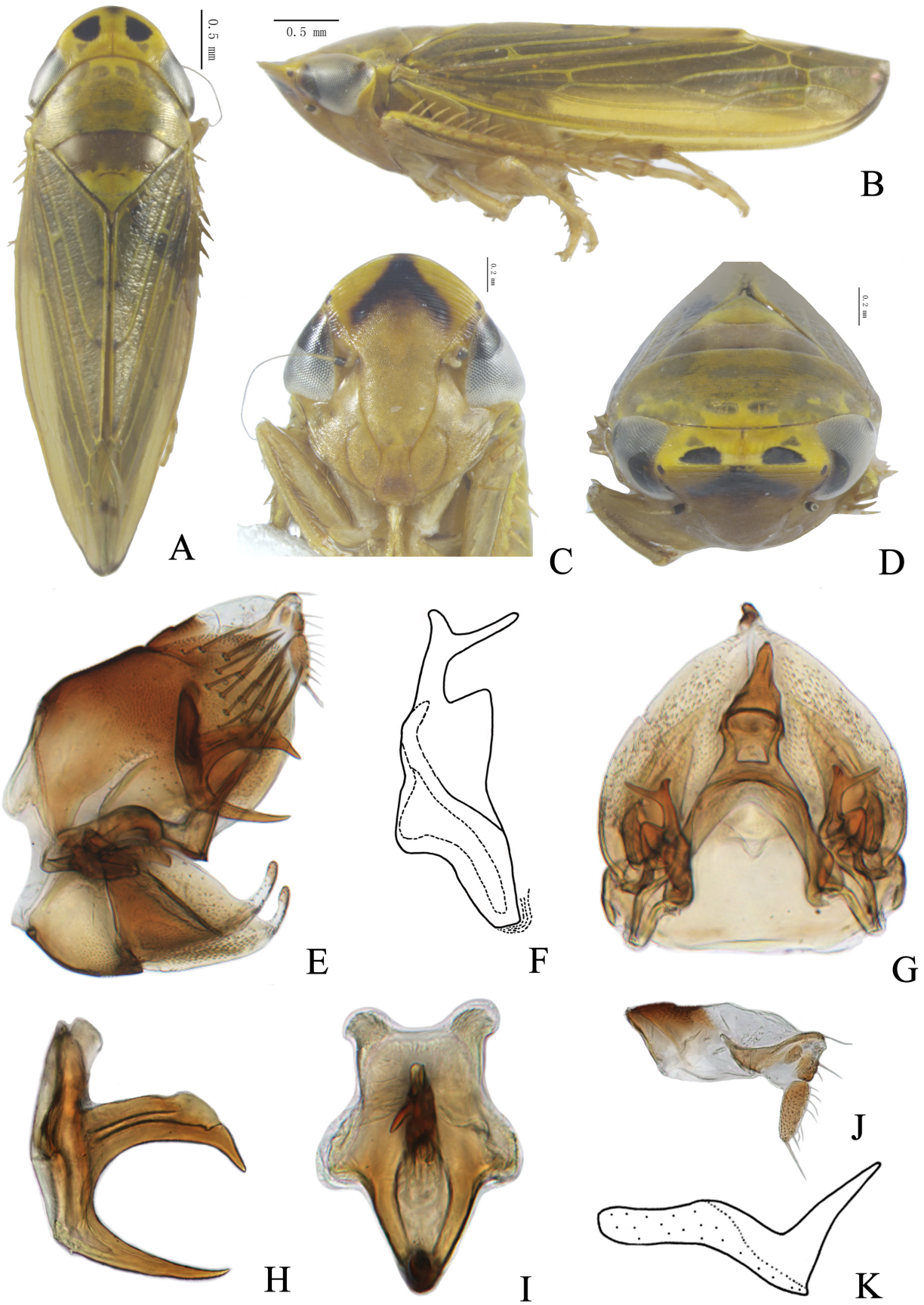


FIGURE 2. *H. bimaculata*; A–B, habitus, dorsal and lateral view; C, face, D, head and thorax, anterior view; E, male genital capsule, lateral view; F, style; G, valve, subgenital plates, styles and connective, dorsal view; H, aedeagus, lateral view; I aedeagus, caudal view; J, anal tube, lateral view; K, connective, lateral view.

Material examined. Holotype: ♂, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, Clark's Camp, at light, 1140m, J.H. Martin, iv.1985, RESL-Project Wallace, NHMUK 010591767 (BMNH).

Other material. 1♀, same data as holotype except v.1985; 1♀1? (abdomen missing), Indonesia, Sulawesi Utara, Dumoga-Bone National Park, ii.1985, RESL-Project Wallace (BMNH).

Etymology. Named after the ventral spine on the caudal extension of the connective.

Remarks. See Remarks under *H. nudapenis*.

H. nitida Osborn

Figs. 1C, 3A–M

H. nitida Osborn, 1934: 174, fig 8; Zhang & Webb, 1966: 8, figs 2, 6, 10, 24, 99–104, 474; Shang & Zhang, 2012: 2–3, fig 1.

Redescription. Body length (including tegmina), male: 4.5–4.8mm; female: 5.2–6.2mm.

Head and thorax dorsally pale sordid yellow. Thorax and abdomen ventrally brown. Forewings brownish hyaline.

Male genitalia with subgenital plate elongate triangular basally with short digitate apex, with a few short fine setae laterobasally. Connective with arms separated distally or joined loop-shaped, stem extended caudally into a long dorsally curved process, distally with a dorsal medial keel. Aedeagus very small, disassociated from connective; shaft very short and stout, terminating in a pair of short recurved hook-like processes, with a short to long spine-like process basally; gonopore apical on ventral surface.

Material examined. Holotype: ♀, Samoa, Upolu, Malololelei, 2000ft, 23.xi.1924, P.A. Buxton and G.H. Hopkins, NHMUK 010591769 (BMNH). Paratypes: 1♂, same data as holotype (BMNH); 10♂12♀, Indonesia (Maluku), Utara and Tengah, C.J. Lomer, iv.1990, on clove (BMNH, NMW); 3♂, Papua New Guinea (Sudest Island), Mt Riu, viii-ix.1956, L.J. Brass, 5th Archbold Expedition to New Guinea (AMNH).

Remarks. This species together with the three following species (*H. caudospina*, *H. nudapenis* and *H. pacifica*) is distinguished by its very small aedeagus disassociated from the connective. It is most similar to *H. pacifica* in having the connective strongly curved dorsally but differs in its paler colour and having the aedeagus with the basal spine narrower and the distal processes apical rather than subapical. The species occurs in two forms in the male genitalia, one from Samoa (single specimen, paratype) with a short basal spine on the aedeagus (Fig. 3I) and another from other islands (see Material examined) with a longer spine (Fig. 3J).

H. nudapenis Zhang & Webb sp. nov.

Figs. 1D, 4F–J

Description. Body length (including tegmina), male: 4.5–5.5mm.

Vertex sordid yellow, anteriorly orange with a small brown spot each side of midline and a faint spot at apex. Face nearly entirely dark brown. Thorax dorsally stramineous to sordid yellow. Thorax and abdomen ventrally brown. Forewing veins dark brown.

Male genitalia as in *H. pacifica* but connective caudal extension straighter and aedeagal shaft without processes.

Material examined. Holotype: ♂, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, Clark's Camp, at light, 1140m., J.H. Martin, iv.1985, RESL-Project Wallace, NHMUK 010591768 (BMNH). Paratype: 1♂, same data as holotype except v.1985, at light (BMNH).

Other material. 1♀, same data as holotype; 1♀, same data as holotype except v. 1985; 1? (abdomen missing), Indonesia, Sulawesi Tengah, nr Morowali, Ranu River area, 27.i.-20.iv.1980, M.J.D. Brendell (all BMNH).

Etymology. Named *H. nudapenis* (Latin *nuda*, without or lacking) referring to the absence of distal processes on the aedeagal shaft.

Remarks. This species is similar to *H. caudospina* collected from the same locality in Sulawesi but lacks a ventral process on the connective caudal extension and the ventral process of the aedeagus is longer. Although the facial marking is almost completely brown in the two males examined compared to only brown dorsally in males of *H. caudospina* this difference needs to be confirmed by examination of further males as the similarly coloured

topotypical females (tentatively identified under the two species) show a little variability in the extremes of facial marking.

***H. pacifica* Zhang & Webb sp. nov.**

Figs. 1E–G, 4K–O

Description. Body length (including tegmina), male: 4.8mm; female: 5.1–5.2mm.

Vertex orange at least distally with a pair of dark brown spots extending from anterior margin to transverse sulcus; face dark brown variably marked with stramineous on clypeus. Thorax dorsally sordid yellow to stramineous. Thorax and abdomen ventrally brown. Forewings brownish hyaline variably marked with yellow on inner area of clavus (see Figs 1E–F).

Male genitalia with subgenital plate elongate triangular basally with short digitate apex, with a few short fine setae laterobasally. Connective with arms distally touching loop-shaped, stem extended caudally into a long strongly dorsally curved process, with a dorsal medial keel. Aedeagus very small, disassociated from connective; shaft very short, digitate, terminating in a pair of short recurved hook-like processes, with a long stout spine-like process basally; gonopore apical.

Nymph as in Fig. 1G.

Material examined. Holotype: ♂, Indonesia, Sulawesi Utara, Manado, Tomohon, M.R. Wilson, v.-vii.1985, on cloves (BMNH). Paratypes: 5♀, same data as holotype including 1♀, NHMUK 010591773 (Fig. 1E) (BMNH); 1♀, Malaysia, Sabah, Tawai Plat., 1300ft, south of Telupid, M.E. Bacchus, 8.ix.1977, NHMUK 010591774 (Fig. 1F) (BMNH).

Other material. Numerous other specimens examined from throughout its range (see checklist) (AMNH, BMNH, NMNH and NMW).

Etymology. This species takes its name from the widespread distribution in the Pacific.

Remarks. This widespread species on clove, is distinguished by its dark colouration with yellow to orange marking (see Figs 1E–F). In the male genitalia it is similar to *H. nitida* but differs in features of the connective and aedeagus (see description).

***H. borneensis* species group**

This group comprises six species (*borneensis*, *brevipenis*, *brevispina*, *longipenis*, *quadrispina* and *spinosa*) with the following combination of characters: head, thorax and abdomen yellowish brown, sometimes darker brown on face; vertex usually with a transverse submarginal brick-shaped mark each side of midline and another mark adjacent anterior corner of eye, dark brown; forewing veins brown, more heavily marked with brown on some veins including a spot on apex of claval veins, on veins of fifth apical cell and on apical cells and on wing apex; vertex smooth or with indistinct longitudinal or oblique striations; pronotum smooth or with indistinct transverse striations; aedeagus joined to connective by short to long preatrium, shaft curved dorsally, elongate, cylindrical with or without processes.

***H. borneensis* Zhang & Webb sp. nov.**

Figs. 1H, 5A–K, 6A–B

Description. Body length (including tegmina), male: 6.2–6.4mm; female: 6.4mm.

Head, thorax and abdomen yellowish brown, sometimes darker brown on face; vertex with a subapical brick-shaped mark each side of midline and another mark in same line touching anterior corner of eye, dark brown; forewing veins brown, more heavily marked with brown on some veins including a spot on apex of claval veins, on veins of fifth apical cell and on apical cells and on wing apex. Male genitalia with subgenital plate strongly incurved sub-basally with long digitate transversely crenulate apex, moderately long fine setae dorsolaterally. Connective with arms short and loop-shaped, stem long and extended into pair of long caudal processes. Aedeagus articulated

with connective by short preatrium; shaft curved dorsally, elongate, cylindrical, with apex sinuate and strongly upturned, without processes, gonopore arising two thirds distance from base to apex of ventral margin.

Female pregenital sternite conical with posterior margin with a broad V-shaped incision medially.

Material examined. Holotype: ♂, Malaysia, Sarawak, Gunung Mulu National Park, 30-50m, elevation, 4°02'32.9"N, 114°48'46.7"E, 16-22.x.2006, J.R. Cryan & J.M. Urban (INHS). Paratypes, 1♂1♀, Brunei, Ulu Temburong, 300m, ii-iii.1982. M.C. Day (BMNH).

Etymology. This species is named after the island of its collection, Borneo.

Remarks. This species can be distinguished by the long aedeagal shaft with sinuate apex. The paratype male is paler with processes of the connective narrower.

H. brevipenis Zhang & Webb sp. nov.

Figs. 1I, 6C–D

Description. Body length (including tegmina), male: 6.0–6.3mm.

Colour as in *H. borneoensis* but head marking sometimes indistinct.

Male genitalia similar to *H. borneoensis* but shaft shorter and more evenly curved dorsally to apex and preatrium slightly longer.

Material examined. Holotype: ♂, Malaysia, Sarawak, Foot of Mt Dulit, junction of rivers Tinjar and Lejok, at light, 29.viii.1932, B.M. Hobby & A.W. Moore, Oxford University Expedition, NHMUK 010591766 (BMNH). Paratypes: 2♂, same data as holotype; 1♂, same data as holotype except 3.ix.1932; 2♂, same data as holotype except 1.ix.1932 and 2.ix.1932 (without old secondary forest label) (BMNH).

Etymology. This species is named for its relatively short aedeagal shaft.

Remarks. This species is similar to *H. longipenis* and from the same locality. It can be distinguished from this and other similar species by its relatively short aedeagal shaft. A series of females with the same data (various dates) similar to this and *H. longipenis* have been seen (BMNH), which could be either species; all have the pregenital sternite triangularly produced medially.

H. brevispina Zhang & Webb sp. nov.

Figs. 1J, 6E–F

Description. Body length (including tegmina), male: 5.4–5.7mm.

Colour as in *H. borneoensis*.

Male genitalia similar to *H. borneoensis* but aedeagal shaft moderately long with a short dorsal spine-like process subapically and preatrium long.

Material examined. Holotype: ♂, Malay Peninsula, S.E. Pahang, Rompin Mining Company railway track, 3.iii.1961, T.C. Maa (BPBM). Paratype: 1♂, Malaya Peninsula, Sungei Emas/Johor, 2°24'N, 103°24'E, D.H. Murphy (BMNH).

Etymology. This species is named for the single subapical spine on the aedeagus.

Remarks. This species can be distinguished by the single small dorsal subapical spine on the aedeagus.

H. longipenis Zhang & Webb sp. nov.

Figs. 1K, 6G–J

Description. Body length (including tegmina), male: 6.2–6.3mm.

Colour as in *H. borneoensis*.

Male genitalia similar to *H. borneoensis* but aedeagal shaft lacking a sinuate apex and the gonopore arising slightly basad of mid-length on ventral surface.

Material examined. Holotype: ♂, Malaysia, Sarawak, Foot of Mt Dulit, junction of rivers Tinjar and Lejok, at light, 25.ix.1932, B.M. Hobby & A.W. Moore, Oxford University Expedition, NHMUK 010591763 (BMNH). Paratype: 1♂, same data as holotype except River Kapah, tributary of River Tinjar (BMNH).

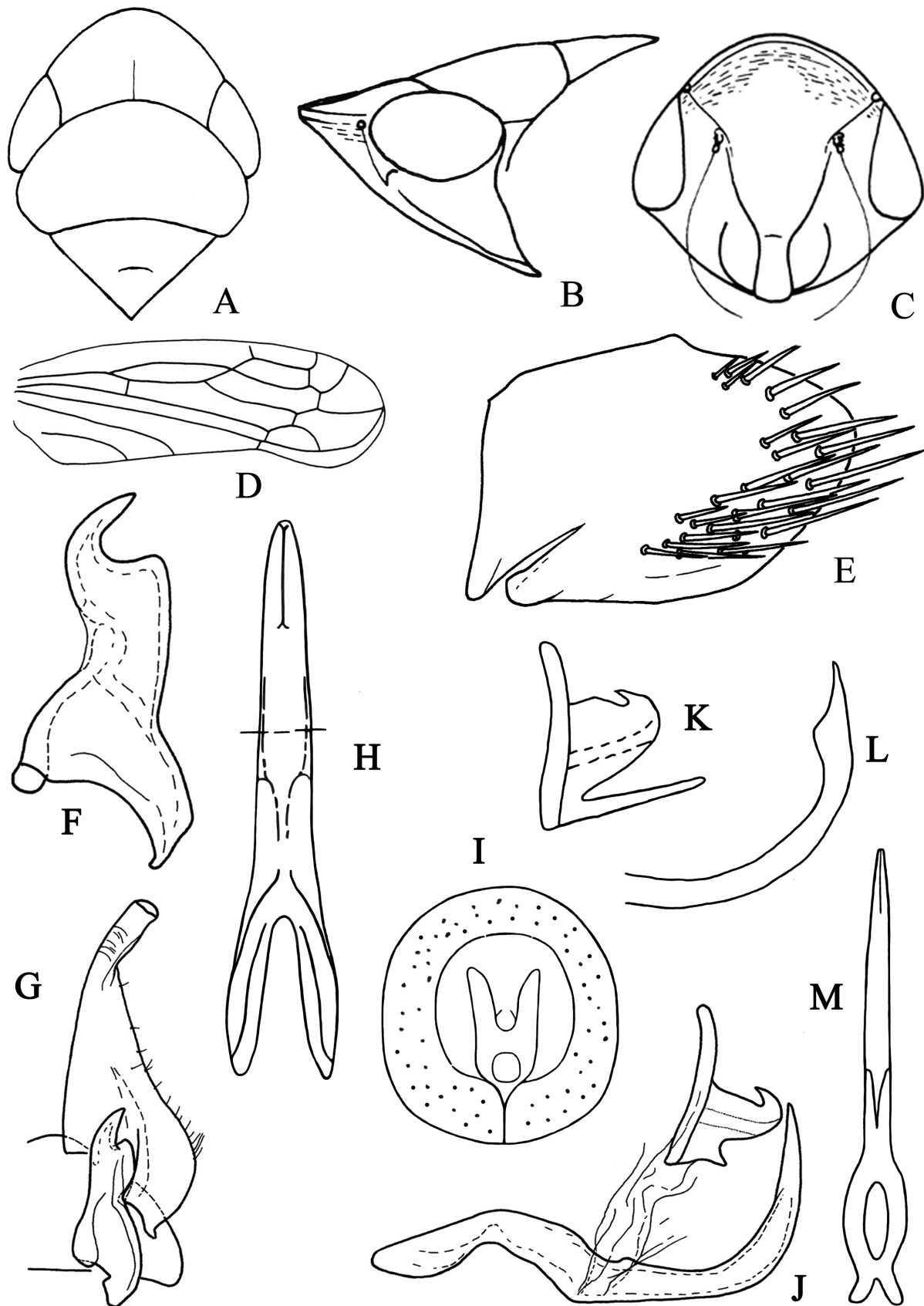


FIGURE 3. *H. nitida*, A–D, holotype, E–I, paratype (Samoa); J–M, Maluku; A–B, head and thorax, dorsal and lateral view; C, face; D, forewing; E, male pygofer; F, style; G, subgenital plate, valve and style, dorsal view; H, connective, dorsal view; I, aedeagus, caudal view; J, aedeagus and connective, lateral view; K, aedeagus, lateral view; L, apex of connective, lateral view; M, connective, dorsal view.

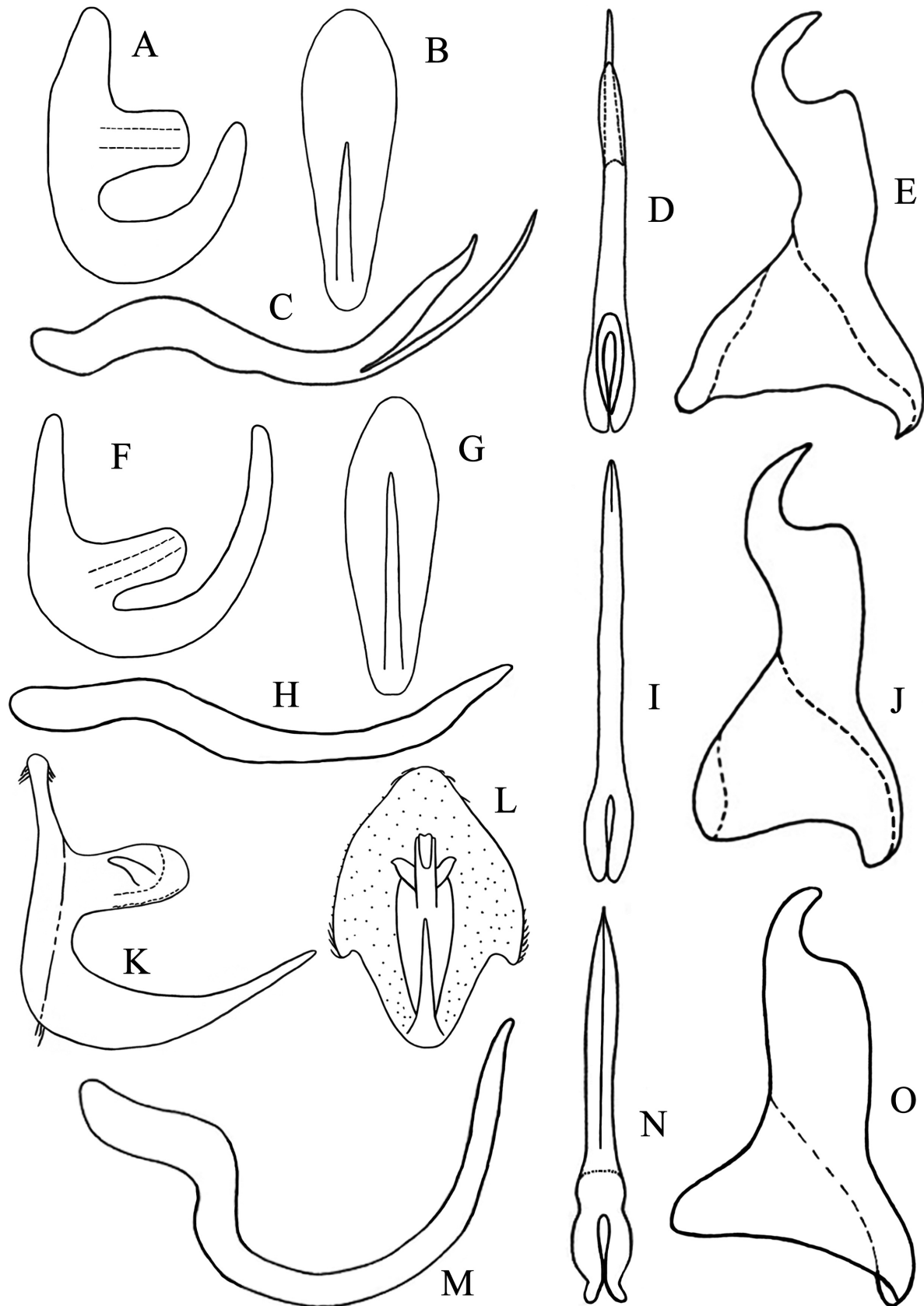


FIGURE 4. Male genitalia of *H. nitida* species group; A–E, *H. caudospina*; A–B, aedeagus, lateral and caudal view; C–D, connective, lateral and dorsal view; E, style; F–J, *H. nudapenis*; F–G, aedeagus, lateral and caudal view; H–I, connective, lateral and dorsal view; J, style; K–O, *H. pacifica*; K–L, aedeagus, lateral and caudal view; M–N, connective, lateral and dorsal view; O, style.

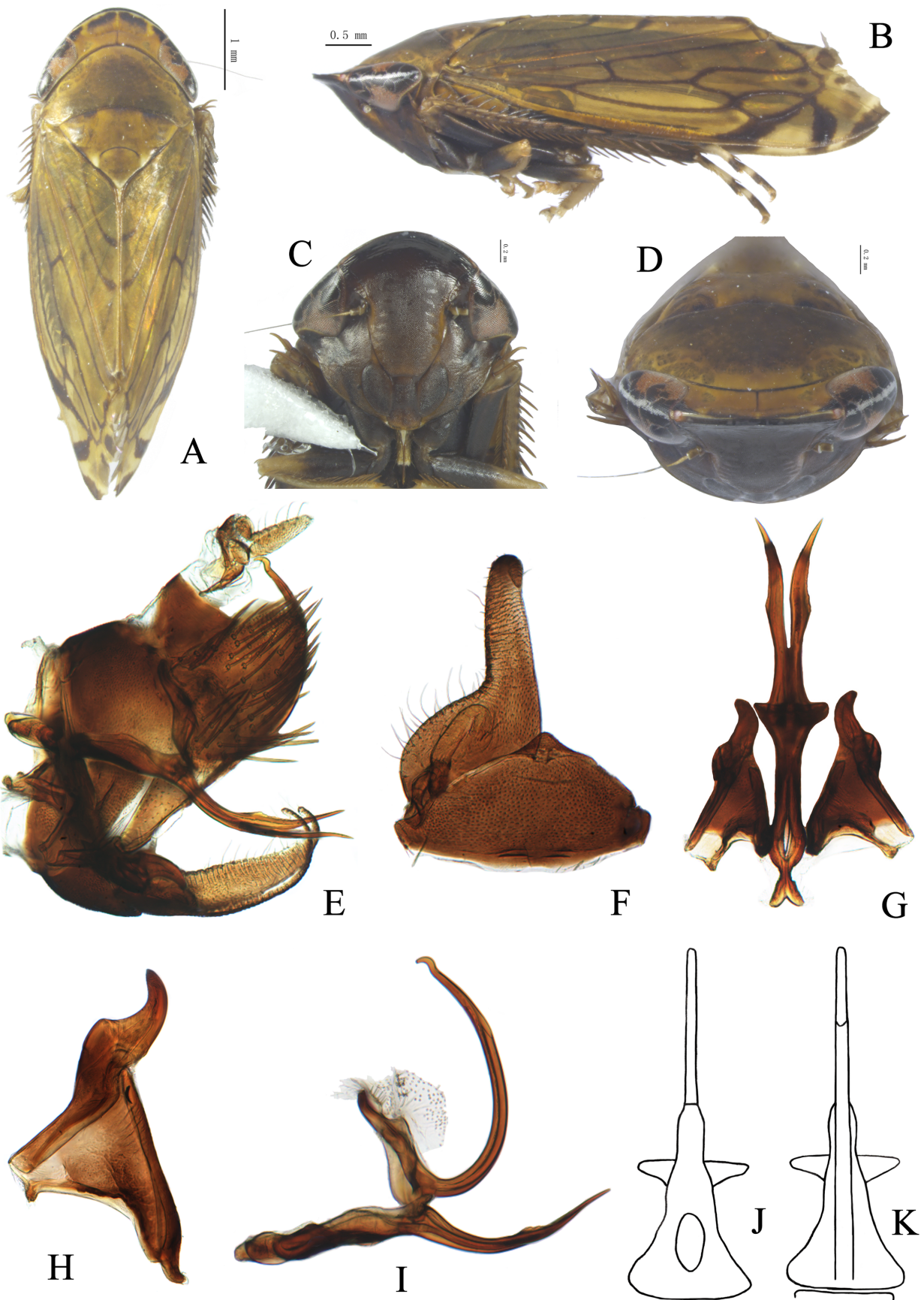


FIGURE 5. *H. borneoensis*; A–B, habitus, dorsal and lateral view; C, face; D, head and thorax, anterior view; E, male genital capsule, lateral view; F, valve and subgenital plate, dorsal view; G, style and connective, dorsal view; H, style; I, aedeagus and connective, lateral view; J–K, aedeagus, anterior and caudal view.

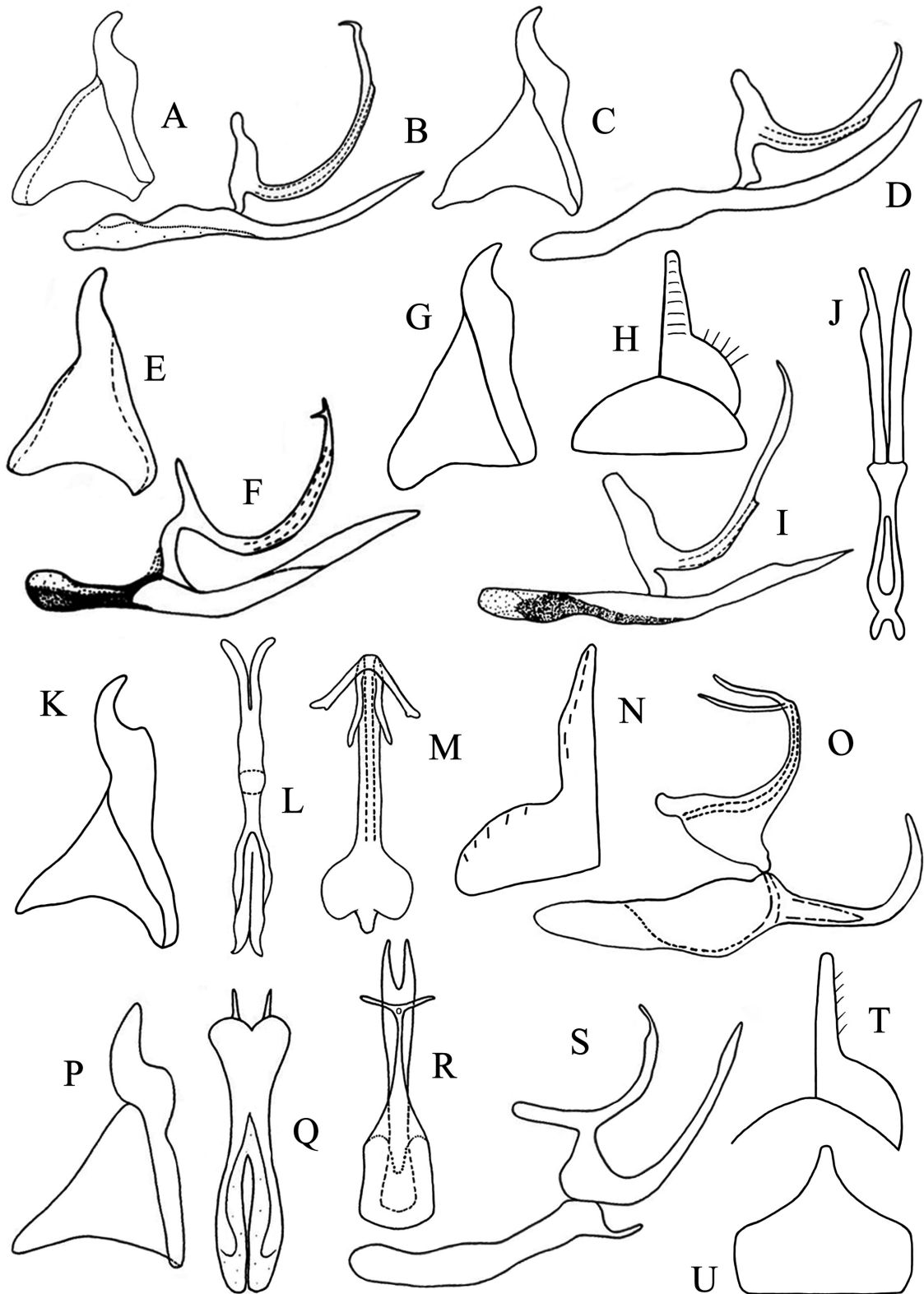


FIGURE 6. Male genitalia and female pregenital sternite of *H. borneoensis* species group; A–B, *H. borneoensis*, A, style; B, connective and aedeagus, lateral view; C–D, *H. brevipennis*; C, style; D, aedeagus and connective, lateral view; E–F, *H. brevispina*; E, style; F, aedeagus and connective, lateral view; G–J, *H. longipennis*; G, style; H, subgenital pate and valve, ventral view; I, aedeagus and connective, lateral view; J, connective, dorsal view; K–O, *H. quadrispina*; K, style; L, connective, dorsal view; M, aedeagus, dorsal view; N, subgenital plate, dorsal view; O, aedeagus and connective, lateral view; P–U, *H. spinosa*; P, style; Q, connective, dorsal view; R, aedeagus, dorsal view; S, aedeagus and connective, lateral view; T, subgenital pate and valve, ventral view; U, female pregenital sternite.

Etymology. This species is named for its relatively long aedeagal shaft.

Remarks. This species is similar to *H. borneoensis* and from the same locality. It can be distinguished from this and other species by its relatively long aedeagal shaft with gonopore arising at approximately mid-length of shaft on ventral surface. See also Remarks under *H. borneoensis*.

H. quadrispina Zhang & Webb sp. nov.

Figs. 1L, 6K–O

Description. Body length (including tegmina), male: 6.2mm.

Colour as in *H. borneoensis*.

Male genitalia with subgenital plate strongly constricted sub-basally with long digitate apex; with short fine dorsolateral setae. Connective with arms long, appressed; stem shorter than arms, broad in lateral view, produced distally into a long caudal process, curved dorsally, bifurcate apically. Aedeagus with basal area broad in lateral and dorsal view, shaft with two pairs of elongate dorsally directed processes the more apical pair bifurcate apically, gonopore arising near apex on ventral surface.

Material examined. Holotype: ♂, Malaysia, Sarawak, Gunung Mulu National Park, P.M. Hammond & J.E. Marshall, v-viii.1978, NHMUK 010591759 (BMNH).

Etymology. This species is named for the four apical processes on the aedeagus.

Remarks. This species can be distinguished from all other *Hecaloidella* species by the shape of the connective in lateral view and aedeagus (see description).

H. spinosa Zhang & Webb sp. nov.

Figs. 1M, 6P–U

Description. Body length (including tegmina), male: 5.2mm; female: 5.2mm.

Vertex pale yellow with a pair of short reddish brown longitudinal bars joined basally. Face brownish yellow. Pronotum brownish yellow, paratype with darker brown irroration. Forewing veins brown, more heavily marked with brown on some veins including a spot on apex of claval veins, on veins of fifth apical cell and on apical cells and on wing apex.

Male genitalia with subgenital plate strongly constricted sub-basally with a long digitate apex with moderately long fine setae. Connective with arms long and appressed; stem short with a pair of apical spines. Aedeagus firmly attached to connective; preatrium with a long ventral process, distally bifurcate; shaft elongate with a pair of widely divergent apical processes, gonopore apical.

Female with pregenital sternite strongly produced medially (Fig. 6U).

Material examined. Holotype: ♂, Brunei, Ulu Temburong Ridge, ii-iii, 1982, M.C. Day, NHMUK 010591778 (BMNH). Paratype: 1♀, Brunei, Ulu Temburong, 300m., ii-iii, 1982, M.C. Day (BMNH).

Etymology. This species is named after the pair of spines on the apex of connective stem.

Remarks. This species can be distinguished from all other *Hecaloidella* species by the unique shape of the connective and aedeagus (see description) and in the female by the greatly prolonged pregenital sternite postero-medially.

H. quadripicta species group

This group comprises six species (*H. brevis*, *H. brunnifacialis*, *H. knighti*, *H. quadripicta*, *H. sandakanensis* and *H. singaporensis*) with the following combination of characters: vertex and thorax dorsally yellow; pronotum, mesonotum and scutellum with one small brown spot laterally; forewing veins brown, more heavily marked with brown on some veins including a spot on apex of claval veins, on veins of fifth apical cell and on apical cells and on wing apex; vertex smooth or with indistinct longitudinal or oblique striations; pronotum smooth or with indistinct transverse striations; aedeagus separated from connective, without preatrium and with long basal apodeme with

side lobes, shaft elongate, cylindrical, with or without processes. One species tentatively included in the group (*H. brevis*) has similar markings to other species but its connective is distinctly different.

***H. brevis* Zhang & Webb sp. nov.**

Figs. 1N, 7A–G

Description. Body length (including tegmina), male: 5.4mm.

Colour as in *H. brunnifacialis*.

Male genitalia with connective very small; arms short, strongly curved and convergent; stem very short. Aedeagus separated from connective; without preatrium; basal apodeme long, laterally compressed, with a lobe on each side; shaft very long and narrow, tapered to acute apex, without processes, gonopore arising subapically on ventral surface.

Material examined. Holotype: ♂, Indonesia, Sulawesi Tengah, nr Morowali, Ranu River area, 27.i.-20.iv.1980, M.J.D. Brendell, NHMUK 010591772 (BMNH).

Etymology. This species is named for its short (*brevis*) connective.

Remarks. This species can be distinguished from all other *Hecaloidella* species by the unique shape of its connective (Fig. 7D–E).

***H. brunnifacialis* Shang & Zhang**

Figs. 1O, 7H–L

H. brunnifacialis Shang & Zhang, 2012: 3–4, fig 2.

Redescription. Body length (including tegmina), male: 5.2–5.3mm; female: 5.5–5.6mm.

Head and thorax dorsally yellow; face yellowish brown, darker brown dorsally; pronotum, mesonotum and scutellum with one small brown spot laterally; thorax and abdomen ventrally yellowish brown; forewing veins brown, more heavily marked with brown on some veins including a spot on apex of claval veins, on veins of fifth apical cell and on apical cells and on wing apex. Male genitalia with subgenital plate strongly incurved sub-basally with long digitate apex and moderately long fine setae dorsolaterally. Connective with arms short and loop-shaped, stem long and extended into a long caudal process, bifurcate apically. Aedeagus separated from connective, without preatrium, with long basal apodeme with side lobes; shaft curved dorsally, elongate, cylindrical with a pair of apical and sub-basal dorsal processes, gonopore apical.

Female pregenital sternite with posterior margin produced medially (Fig. 7L).

Material examined. Holotype: ♂, Malaysia, Sarawak, Gunung Mulu National Park, W. Melinau Gorge, 150m, iii-iv.1978, Kerrangas, J.D. Holloway, Royal Geographical Society Mulu Expedition (BMNH). Non-types: 3♂1♀, same data as holotype, NHMUK 010591761 (BMNH); 1♀, same data as holotype except V.F. Eastop (BMNH).

Remarks. This species can be distinguished by the number and arrangement of processes on the aedeagus. It is similar to *H. quadripicta* and *H. singaporensis* but in addition to the aedeagal differences it has the style lateral lobe less produced and the female pregenital sternite with the posterior margin produced medially rather than conically rounded.

***H. knighti* Zhang & Webb sp. nov.**

Figs. 1P, 7M–Q

Description. Body length (including tegmina), male: 5.3mm; female: 6.0mm.

Colour as in *H. brunnifacialis*.

Male genitalia similar to *H. brunnifacialis*. but aedeagus with shaft tapered to acute upturned apex with processes absent and gonopore arising two thirds distance from base to apex of shaft.

Female pregenital sternite with posterior margin acutely produced medially.

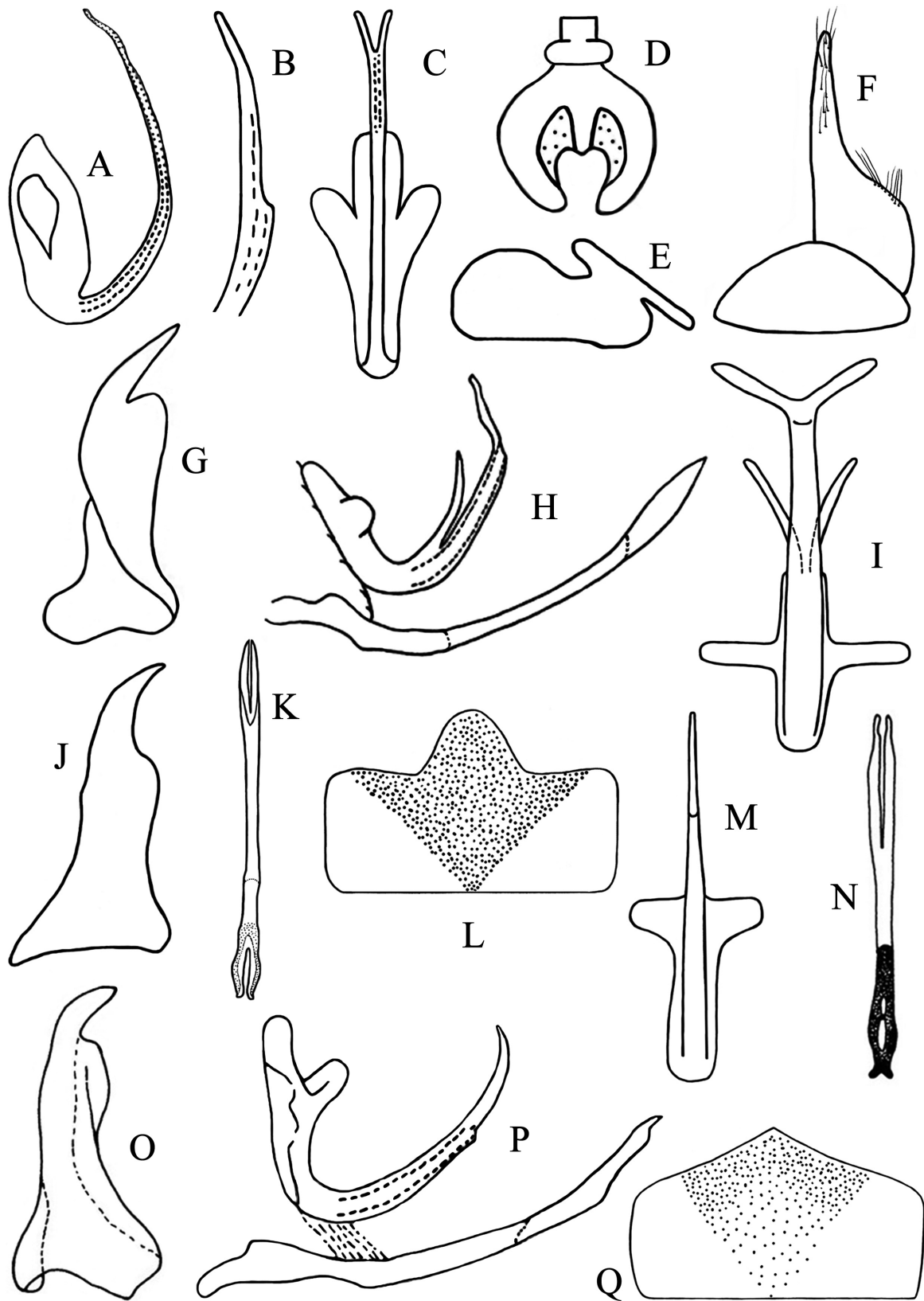


FIGURE 7. Male genitalia and female pregenital sternite of *H. quadripicta* species group; A–G, *H. brevis*; A, aedeagus, lateral view; B, apex of aedeagus, lateral view; C, aedeagus, ventral view; D–E, connective, dorsal and lateral view; F, valve and subgenital plate, dorsal view; G, style; H–L, *H. brunnifacialis*; H, aedeagus and connective, lateral view; I, aedeagus, caudal view; J, style; K, connective, ventral view; L, female pregenital sternite; M–Q, *H. knighti*; M, aedeagus, ventral view; N, connective, ventral view; O, style; P, aedeagus and connective, lateral view; Q, female pregenital sternite.

Etymology. This species is named in honour of Dr. William J. Knight, the second author's mentor at the BMNH and organiser of the Project Wallace Expedition (see Material and methods).

Material examined. Holotype: ♂, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, Fog. 13, Plot A, 230m, 11.vii.1985, RESL-Project Wallace, NHMUK 010591764 (BMNH). Paratypes: 1♂1♀, Indonesia, Sulawesi Utara, Dumoga-Bone National Park, ii.1985, RESL-Project Wallace (BMNH).

Other material. 1♀, Indonesia, Sulawesi Tengah, nr Morowali, Ranu Lakes, 7-10.iii.1980, at light, M.J.D. Brendell (BMNH).

Remarks. This species can be distinguished from other *H. quadripicta* group species by the aedeagus without processes.

H. quadripicta Zhang & Webb sp. nov.

Figs. 1Q, 8A–D

Description. Body length (including tegmina), male: 5.2–5.5mm; female: 5.5mm.

Colour as in *H. brunnifacialis*.

Male genitalia similar to *H. brunnifacialis* but style lateral lobe more produced (Fig. 8C).

Female pregenital sternite with posterior margin conically rounded (Fig. 8D).

Material examined. Holotype: ♂, Malaysia, Sarawak, Foot of Mt Dulit, junction of rivers Tinjar and Lejok, at light, 29.viii.1932, B.M. Hobby & A.W. Moore, Oxford University Expedition (BMNH). Paratypes: 1♂, same data as holotype except 29.viii.1932, NHMUK 010591760; 1♀, same data as holotype except old secondary forest; 1♀, same data as holotype except 2.ix.1932 (BMNH).

Etymology. This species is named after the four spots on the mesonotum.

Remarks. This species is very similar to *H. brunnifacialis* but is considered distinct as it has a more produced style lateral lobe and the female pregenital sternite is conical rather than with the posterior margin produced medially.

H. sandakanensis Zhang & Webb sp. nov.

Figs. 1R, 8E–H

Description. Body length (including tegmina), male: 5.3mm; female: 5.6mm.

Colour as in *H. brunnifacialis*.

Male genitalia similar to *H. brunnifacialis* but aedeagus with very long basal apodeme; shaft abruptly tapered subapically in lateral view with two pairs of closely appressed processes, gonopore arising subapically on ventral surface.

Female pregenital sternite with posterior margin produced medially.

Material examined. Holotype: ♂, Borneo, Sandakan, Baker (NMNH). Paratype: 1♀, same data as holotype (NMNH).

Etymology. This species is named after the type locality.

Remarks. This species can be distinguished from other *H. quadripicta* group species by the two pairs of closely appressed apical aedeagal processes.

H. singaporensis Zhang & Webb sp. nov.

Figs. 1S, 8I–L

Description. Body length (including tegmina), male: 4.9–5.1mm; female: 5.2–5.3mm.

Colour as in *H. brunnifacialis*.

Male genitalia similar to *H. brunnifacialis*. Aedeagus with shaft narrow in lateral view, with a pair of bifurcate widely divergent apical processes and a pair of processes at mid-length of shaft on dorsal surface.

Female pregenital sternite with posterior margin conically rounded.

Material examined. Holotype: ♂, Singapore, Baker (NMNH). Paratypes: 1♂4♀1? (abdomen missing), same data as holotype (NMNH).

Etymology. This species is named after the type locality.

Remarks. This species is similar to *H. brunifacialis* and *H. quadripicta* but the aedeagal shaft is narrower in lateral view with apical processes bifurcate.

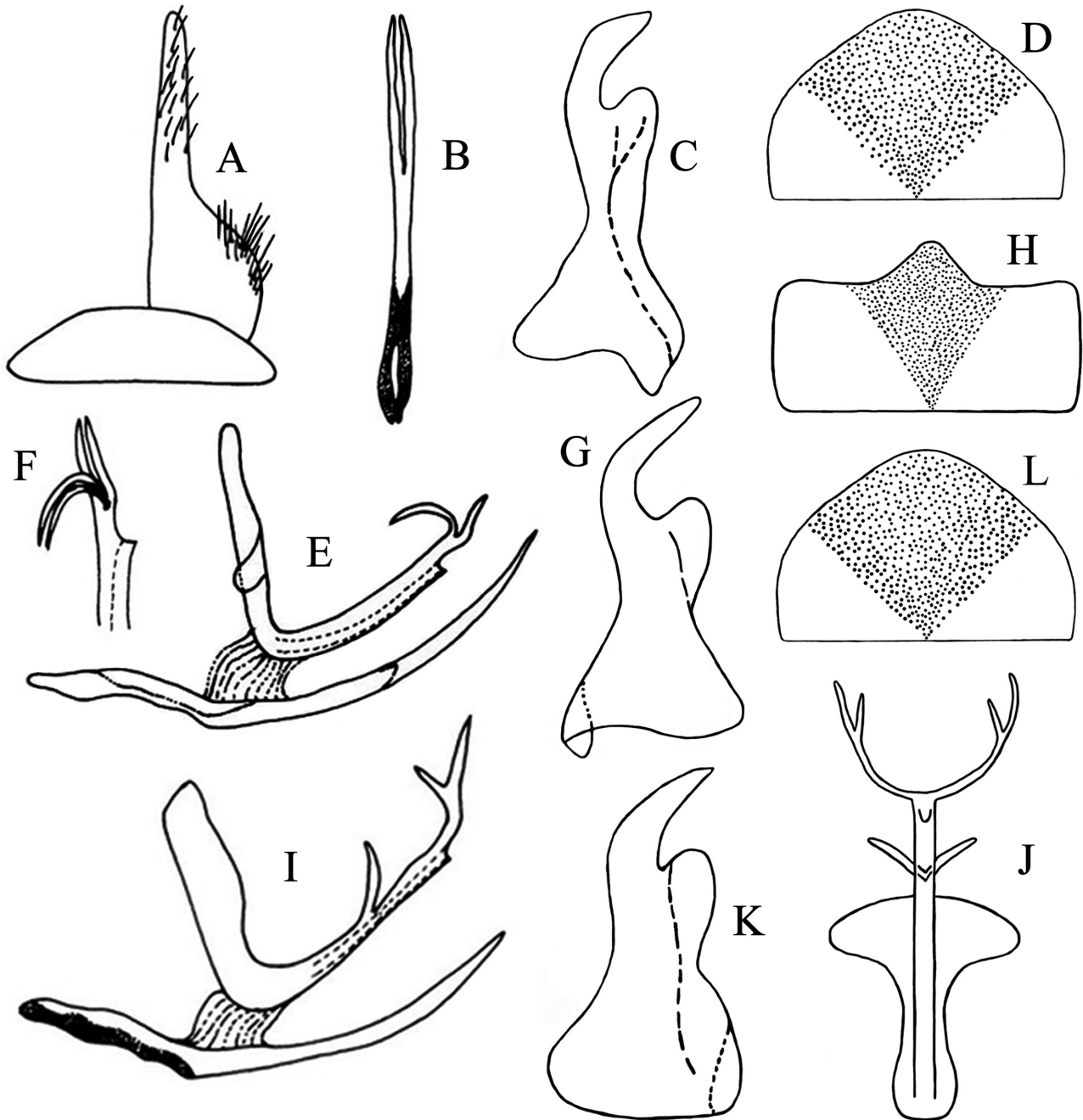


FIGURE 8. Male genitalia and female pregenital sternite of *H. quadripicta* species group. A–D, *H. quadripicta*; A, valve and subgenital plate, dorsal view; B, connective, ventral view; C, style; D, female pregenital sternite; E–H, *H. sandakanensis*; E, aedeagus and connective, lateral view; F, apex of aedeagus, lateral view; G, style; H, female pregenital sternite; I–L, *H. singaporensis*; I, aedeagus and connective, lateral view; J, aedeagus, caudal view; K, style; L, female pregenital sternite.

Incertae sedis

H. brunifasciata Zhang & Webb sp. nov.

Figs. 1T, 9A–L

Description. Body length (including tegmina), male: 8.9–9.0mm.

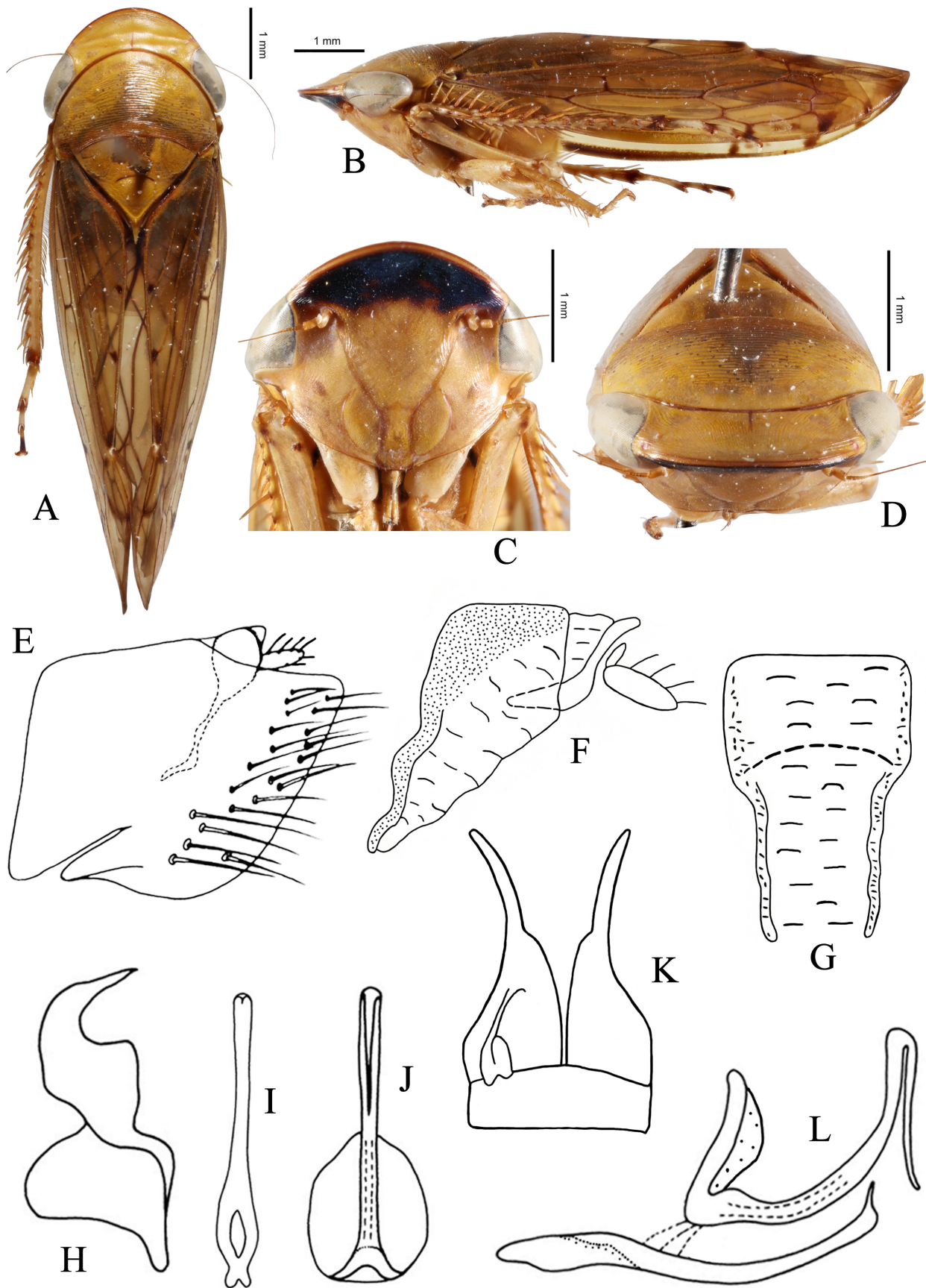


FIGURE 9. *H. brunifasciata*; A–B, habitus, dorsal and lateral view; C, face; D, head and thorax, anterior view; E, male pygofer and anal tube, lateral view; F–G, male Xth segment, lateral and caudal view; H, style; I, connective, dorsal view; J, aedeagus, caudal view; K, valve and subgenital plates, dorsal view; L, aedeagus and connective, lateral view.

Head and thorax stramineous; face dark brown dorsally from above antennae to marginal rim. Forewings brownish hyaline; veins darker brown, concolorous with wing in clavus, a small dark brown spot on apex of clavus and on apex of claval veins and veins of 4th and fifth apical cells.

Head very slightly wider than pronotum, anteriorly foliaceous with anterior margin rim-like with a pair of marginal carina; vertex slightly transversely sulcate between anterior corners of eyes, finely obliquely striate; ocelli just above marginal rim approximate twice diameter from corresponding eye; face nearly flat in profile, dorsally slightly concave with fine transverse striations extending laterally onto ocellular area and then ventrally to antennal ledge, remaining ventral part of face shagreen; antennae short, arising approximately two thirds distance to upper corner of eyes in facial view. Pronotum with sides short, carinate; finely transversely striate basally and centrally. Forewing with three subapical cells, inner open; outer subapical cell slightly narrowed basally. Fore femur with few basal ventral setae. Fore tibia with dorsal setal formula 1+4. Hind femur with apical setal formula 2+2+1.

Male genitalia with pygofer tapered to conically rounded apex with several macrosetae distally, without processes. Segment X extended ventrally. Subgenital plates wide basally, there-after strongly incurved to mid-length with apex digitate, without macrosetae. Style with apical process hook-like, lateral lobe large. Connective with apices of arms fused, stem long, extended caudally into a long distal process, upturned apically. Aedeagus situated dorsad of connective and connected to it by membrane; shaft recurved apically and extended into a long ventrally directed process, tapered to acute apex; gonopore at base of process; basal apodeme long, expanded laterally.

Material examined. Holotype: ♂, Brunei, Temburong District, ridge NE of Kuala Belalong, approx. 300m alt., xi.1992, J.H. Martin, m.v. light trap, NHMUK 010591765 (BMNH). Paratype: 1♂, same data as holotype (BMNH).

Etymology. This species is named after the brown transverse band dorsally on the face.

Remarks. This species superficially resembles other species of *Hecaloidella* but is only tentatively included in the genus as the anterior margin of the vertex is more evenly rounded in dorsal view, it lacks the distinctly convex face in profile (Fig. 9B); the antennae arise slightly higher on the face (Fig. 9C) and the male segment X is extended ventrally (Figs. 9F–G). It is also significantly larger than other species of the genus.

Acknowledgements

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