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New genera and species of the Oriental mirine plant bugs from Southeast Asia, with six new combinations (Insecta: Heteroptera: Miridae: Mirinae: Mirini)

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Abstract. Four new Oriental mirine plant bug species accommodated by three new genera, *Malayamiridius nigrotenuis*, new species (from Brunei, Indonesia, Malaysia, Thailand and Vietnam), *Sundacapsus flavonitidus*, new species (Sumatra, Indonesia), *S. kinabaluensis*, new species (Sarawak, E Malaysia), and *Tondomiris puguis*, new species (Luzon, Philippines), are diagnosed and described. The phylogenetic relationships of the new genera to superficially similar taxa are discussed. Six Asian species originally described in *Megacoelum* Fieber are transferred to *Orientomiris* Yasunaga; accordingly the following six new combinations are proposed: *Orientomiris brunnetii* (Distant, 1909), *O. marginandus* (Distant, 1909), *O. patruus* (Distant, 1909), *O. pervalidus* (Distant, 1909), *O. straminipes* (Distant, 1909), and *O. tibialis* (Distant, 1909). A key is provided to distinguish superficially confusing mirine genera analysed in the present work.

Key words. distributions, relationships, genitalic documentation, scanning electronic micrographs

INTRODUCTION

The plant bug tribe Mirini (Miridae: Mirinae) is a huge and diverse group with many genera and species awaiting description particularly in subtropical and tropical forest zones, or biodiversity hotspots. From the late 19th to the early 20th century, numerous mirine taxa were described from the Oriental Region predominantly by European researchers (e.g., Reuter, 1891, 1903, 1906; Distant, 1904, 1911; Poppius, 1911, 1914, 1915a, b). However, most of these original descriptions did not provide sufficient information on unequivocal diagnostic characters and/or illustrations, therefore, many genera and species are still in need of proper diagnosis and redescription (cf. Schwartz & Chérot, 2005; Yasunaga et al., 2018).

Although recent taxonomic work by Chérot & Malipatil (2016) comprehensively reviewed the taxa of the *Adelphocoris-Creontiades-Megacoelum* complex of Mirini, there remain quite a few undescribed species of this group in the Oriental Region (e.g., Yasunaga & Schwartz, 2015; Yasunaga, 2016). Based on specimens collected from Indonesia, Malaysia, Philippines, and Thailand mostly in 1980–90s, the present paper documents four unique species which cannot be assigned to any known mirine genus of the ACM complex.

We herein describe three new genera to accommodate these species, *Malayamiridius*, new genus for *M. nigrotenuis*, new species from Brunei, Peninsular Malaysia, Thailand and Vietnam, *Sundacapsus*, new genus for *S. flavonitidus* from North Sumatra, Indonesia and *S. kinabaluensis* from Sarawak, Malaysia, and *Tondomiris*, new genus for *T. puguis* from Luzon, Philippines. The phylogenetic position and zoogeography are also discussed for each taxon, and a key is provided to facilitate identification of the related Oriental genera discussed.

MATERIAL AND METHODS

Type specimens are, unless otherwise stated, deposited in American Museum of Natural History, New York (AMNH); Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Ontario (CNC); Muséum National d'Histoire Naturelle, Paris, France (MNHN); National Institute of Agro-Environmental Sciences, Tsukuba, Ibaraki, Japan (NIAES); National Science Museum, Tsukuba, Japan (NSMT); T. Yasunaga collection, Nagasaki, Japan (TYCN); or Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore (ZRC); several additional specimens from Borneo (Brunei) recently collected by C. Damken (UBDM: Universiti Brunei Darussalam Museum) were also examined by the

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second author. Some relevant materials deposited in Natural History Museum, London, UK (BMNH) were also examined.

Matrix code labels, which uniquely identify each specimen and are referred to as 'unique specimen identifier' (USI), are attached to the holotypes and some representative specimens. The USI codes [e.g., AMNH_PBI 00123456] comprise an institution and project code (AMNH_PBI) and a unique number (00123456). These data were digitised 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 (by species name) on 'Heteroptera Species Pages' (http://research.amnh.org/pbi/heteropteraspeciespage/).

Measurements are given in millimetres; for some of the SEM images, scale bars are shown in micrometres (μm). Maps were built using the online free resource Simplemappr (Shorthouse, 2010). The plates were edited in Photoshop CS2 or CS4. Photographs of *Sundacapsus kinabaluensis*, new species, were taken with a Leica M205C with a Plan Apo 1.6X objective, using LAS 4.12 software (Leica Microsystems, Wetzlar, Germany). Images were stacked using Zerene Stacker (Zerene Systems, Richland, WA). Terminology of the male genitalia follows Schwartz & Foottit (1998), Yasunaga & Schwartz (2007), and Yasunaga (2016). Scanning electron micrographs were taken with Hitachi Tabletop Microscope® TM3030; Nikon Eclipse-Ci upright microscope with a phase-contrast unit was used to observe and photograph the genitalic structures.

SEM documentation of the internal genitalia is currently developing (Symonds & Cassis, 2018). After our observations with dissection microscopy, the delicate, fragile minute organs are dipped and washed in 60% ethyl alcohol, placed on filter paper until dry, carefully attached to cards using water soluble wood glue, and finally placed in the TM3030 Tabletop SEM chamber for examination (without vapour deposition of metals).

TAXONOMY

Malayamiridius, new genus

Type species. *Malayamiridius nigrotenuis* Yasunaga, Chérot & Schwartz, new species.

Diagnosis. Distinguished from superficially similar mirine genera (e.g., *Adelphocoris* Reuter, *Creontiades* Distant, *Megacoelum* Fieber, *Orientomiris* Yasunaga) by the following combination of characters: Remarkably slender, parallel-sided body more than 3.5× as long as maximum width; moderate size (4.8−6.6 mm in total length); uniformly fuscous, shagreened, almost glabrous dorsum (Fig. 1A) with minute, reticular surface structure (cf. Fig. 2C, L); smooth, roundly vertical head with a longitudinal mesal sulcation on vertex (Fig. 2I, J); a sharp spine at base of each claw (Fig. 2E−G); developed, lamellate parempodia (Fig. 2E); narrow pygophore with apical spine ventrally (Fig. 2D); generally short parameres (Fig. 3A, B); membranous endosoma with pair of narrow sclerotised supports on posterior surface and pair of small spiculate fields on membrane basad of secondary gonopore (Fig. 3C, D); broad, spade-shaped apex of gonapophysis I (Fig. 9B); and wide, broadly ovoid interramal lobe (Figs. 3F, 8A).

Description. *Male.* Body medium-sized, remarkably slender and elongate, parallel-sided, not sexually dimorphic in general shape. COLOURATION: Dorsum generally fuscous. SURFACE AND VESTITURE: Dorsum somewhat matte, weakly shining, covered with micro-reticulate structure, almost glabrous, pronotum, scutellum, hemelytron, and thoracic pleura with similar reticular structure (Fig. 2L); sparsely distributed, minute sensory setae, or trichobothria (which are invisible using light microscopy, cf. Fig. 2C). STRUCTURE: **Head**: Somewhat bulbous, vertical in lateral view; eyes removed from anterior margin of pronotal collar; vertex with a shallow, longitudinal sulcus mesally; frons and clypeus flattened. **Antenna**: Longer than body, almost linear, not incrassate; segment I about as long as width of head across eyes, slightly longer than IV; segments II–IV almost uniform in thickness; segment III slightly shorter than II. **Labium**: Relatively short, reaching or slightly surpassing apex of mesocoxa, slightly shorter than antennal segment II. **Thorax**: Pronotum moderately rounded posteriorly; calli reduced, indistinct, with slightly raised posterior half; collar flattened, about as thick as base of antennal segment I; propleuron not margined nor carinate; metathoracic scent efferent system subtriangular, with narrow mesothoracic evaporatorium (or accessory evaporatorium, sensu Yasunaga & Duwal, 2019) (Fig. 2B, K); scutellum rather flat; mesoscutum without reticulation, only roughened. **Hemelytron**: Parallel-sided, weakly constricted at middle; cuneus small, about 1.5× as long as basal width. **Legs**: Long, generally slender; tibial spines short, sparse; meta-tarsomere I shorter than II or III; pretarsus with noticeable spine subbasally on each claw (Fig. 2E–G); parempodia lanceolate, lamellate, rather widened; pulvilli absent. **Abdomen**: Slender, parallel-sided, with apex reaching middle of forewing membrane (at level of apex of cuneus) in ventral view (as in Fig. 1B, C). **Genitalia** (Fig. 3A–D): Pygophore short, slender, narrowly produced, somewhat flattened apically, with flat apical spine ventrally (Fig. 2D). Parameres generally short (Fig. 3A, B); left paramere C-shaped, with stout sensory lobe and L-shaped hypophysis terminated in a blunt, flattened tip. Phallotheca smooth; endosoma (vesica) membranous, supported on posterior surface by pair of long, narrow sclerites; anterior surface of membrane with pair of small spiculate or dentate fields basad of either side of secondary gonopore, membrane with larger basal field of spicules and with some apical spicules (Fig. 3C, D); ductus seminis weakly expanded apicad.

Female. As in male. **Genitalia** (Figs. 3E, F, 8A−C, 9A, B): Ovipositors generally stout (Fig. 9A, B); gonapophysis I with apical part significantly broadened, spade-shaped (Fig. 9B); gonapophysis II (Figs. 8C, 9A) with apical half expanded towards minutely teethed, sword-shaped apex. Lateral oviduct obscure. Sclerotised ring (Fig. 3E) crescent,

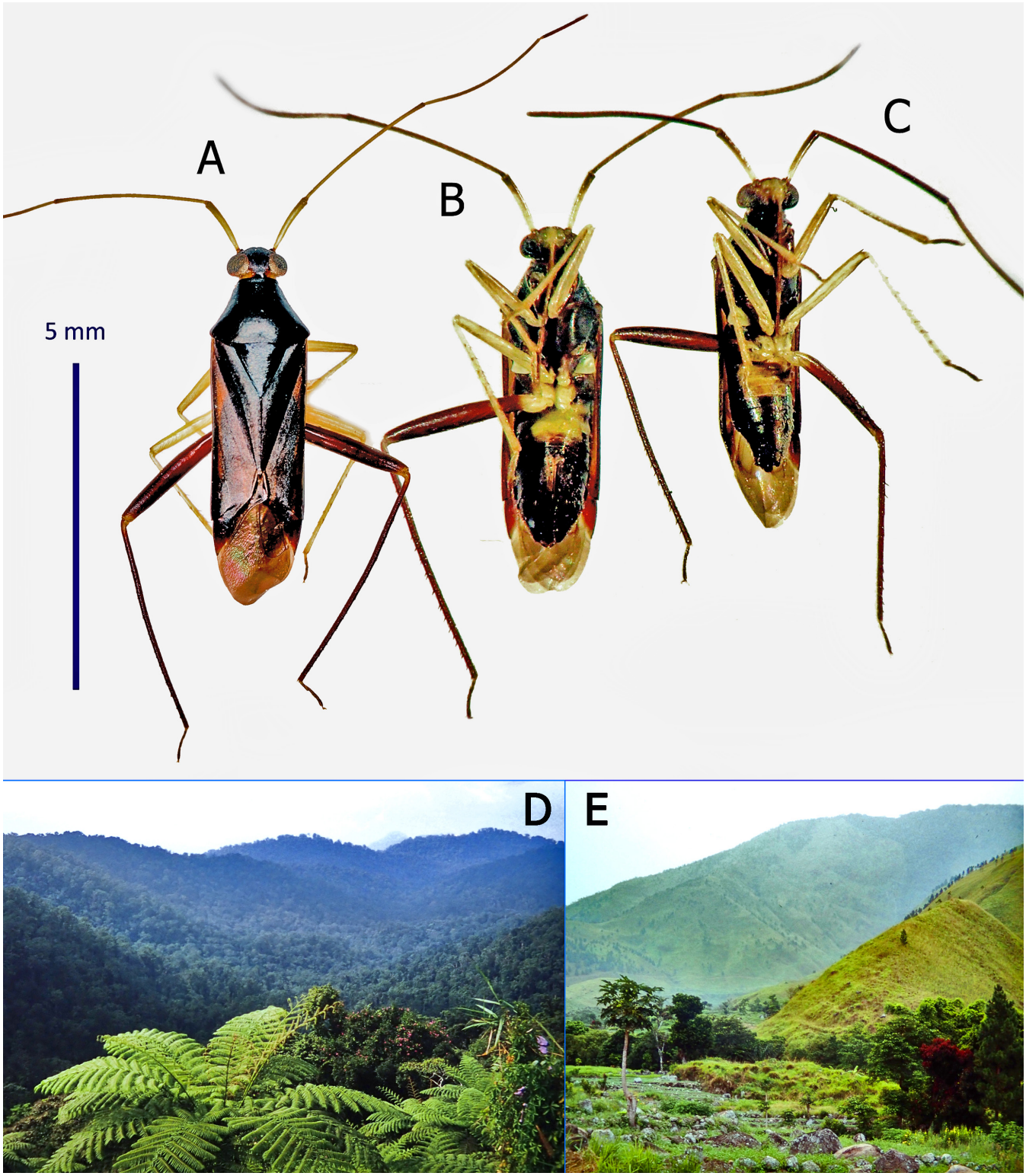

Fig. 1. Habitus images (A–C) of *Malayamiridius nigrotenuis* and environments on which the (UV lighting) sampling sites of the new mirines faced (D–E). A, *M. nigrotenuis*, holotype male from Perak, Malaysia; B, ditto, female in ventral view; C, ditto, male in ventral view; D, tropical rain forest of the type locality (Bukit Larut, Perak, Malaysia in January 1990); F, Brastagi, N. Sumatra, type locality of *Sundacapsus flavonitidus* (December 1989).

rather thin-rimmed, with broadened posterolateral corner; dorsal labiate plate with spiculate posterior sclerite spanning bursa copulatix; ventral labiate plate broad laterally, narrow in middle, supporting spiculate intersegmental membrane continuous with dorsal structure of posterior wall. Posterior wall (Figs. 3F, 8A, B) with thick, broadly ovoid interramal lobe; dorsal structure reduced.

Etymology. Named for Malaya, combined with mirine genus *Miridius* Fieber (with similarly slender-bodied representatives); most of the specimens of the type species were collected in Malaysia and neighbouring areas; gender masculine.

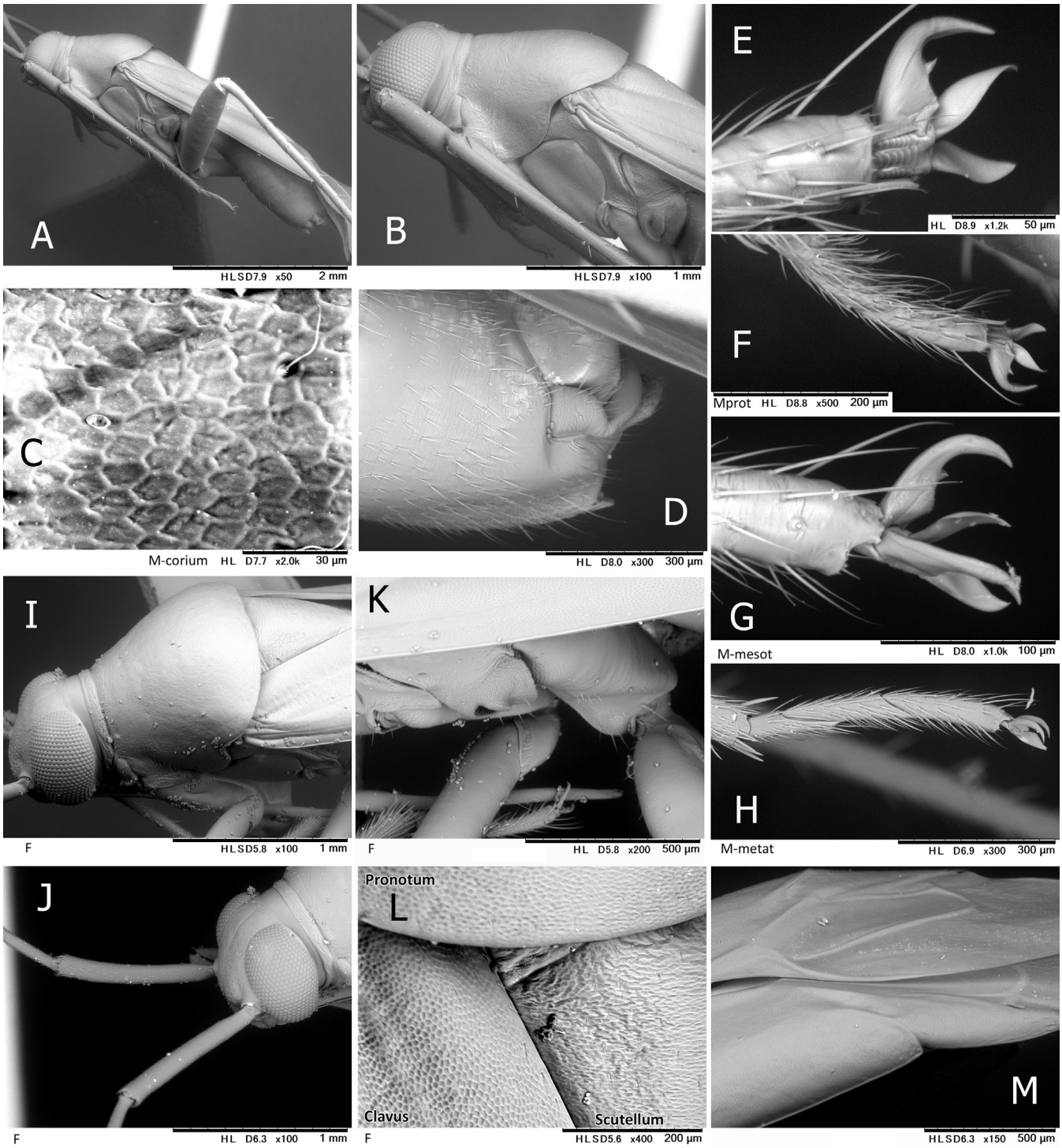

Fig. 2. Scanning electron micrographs for male (A–H) and female (I–M) of *Malayamiridius nigrotenuis*. A, left lateral habitus; B, ditto, anterior body; C, surface of corium; D, pygophore; E, pretarsal structure of proleg; F, protarsus; G, pretarsal structure of mesoleg; H, metatarsus; I, head and pronotum; J, head; K, scent efferent system; L, surface of pronotum, scutellum, and clavus; M, apical part of forewing.

Discussion. This unique genus is herein established for a single representative which has the following combination of distinct characters: Body fuscous, remarkably slender; dorsum shagreened, impunctate, nearly glabrous; ventral basal surface of each claw with noticeable spine; pygophore with flat ventral spine; endosoma [vesica] small-sized, almost entirely membranous, with a row of sharp spicules along gonoporal rim; female genitalia with apical region of gonapophysis I broadened, arrowed; dorsal labiate plate with spiculate sclerite on posterior margin spanning bursa copulatrix and interramal lobe of posterior wall wide, strongly developed, broadly ovoid.

Malayamiridius is most similar in general appearance to *Creontiades* Distant or *Orientomiris* Yasunaga, from which the present new genus can be distinguished by the above-mentioned characters. Judging from the male and female genitalic structures, relationships between these three genera

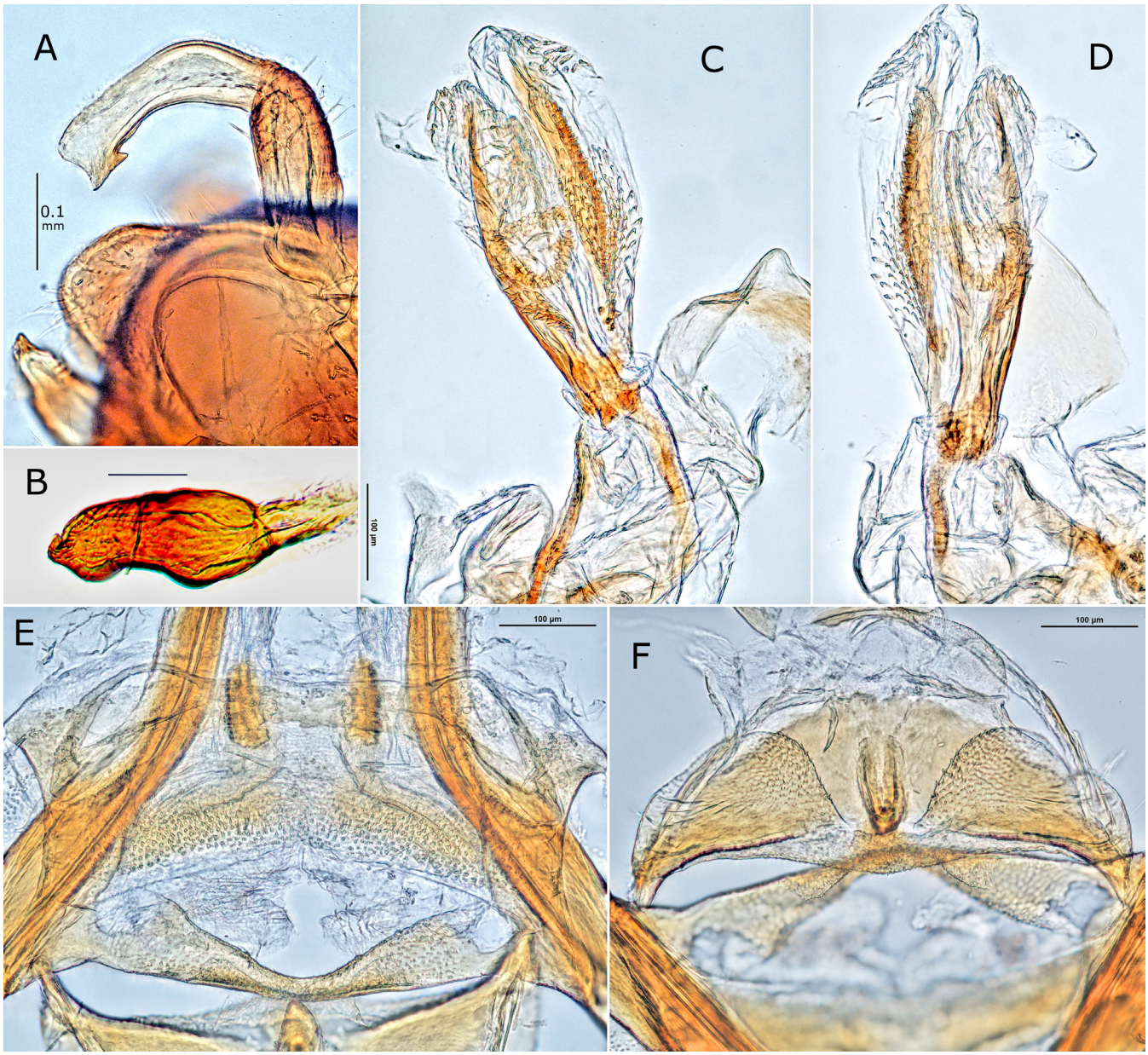

Fig. 3. Male (A–D) and female (E–F) genitalia of *Malayamiridius nigrotenuis*. A, apex of pygophore in dorsal view; B, right paramere; C, D, endosoma; E, genital chamber, ventral view; F, posterior wall of bursae, anterior view. Scale bars = 0.1 mm.

are considered to be only superficial (cf. Yasunaga, 1997; Yasunaga et al., 2001; Chérot & Malipatil, 2016).

The shagreened dorsal surface in *Malayamiridius* is formed by reticulated cuticle ultrastructure (cf. Fig. 2C, L). *Ficinus* Distant, 1893 and *Jornandes* Distant, 1884, two genera of New World Orthotylini (Schaffner & Schwartz, 2008) have similar dorsal sculpturation, caused rather by minute punctation (see Schaffner & Schwartz, 2008: figs. 6A, 17A, 20A, 28A).

Malayamiridius nigrotenuis, new species
(Figs. 1A–C, 2, 3, 8A–C, 9A, B, 12)

Type material. Holotype: male, **MALAYSIA:** Perak, Taiping, Bukit Larut (Maxwell Hill), 4.8624°N, 100.7999°E, 1,100 m, MV light trap, T. Yasunaga, 4 January 1990 (AMNH_PBI 00380626) (ZRC). Paratypes: **INDONESIA:** Sulawesi Utara (North Sulawesi): 1 male, Lake Mala (Mooat), E of Kotamobagu [CL 2113], 0.73333°N, 124.45°E, 1,000 m, 10 September 1985, D. A. & J. T. Polhemus (00418894) (CNC). North Sumatra: 1 male, Prapat (1,000 m), 50 km E of Pematang Siantar, 2.88°N, 99.52°E, MV light trap, E. W. Diehl, October 1989 (00380627) (TYCN). **MALAYSIA:** 1 male, 4 females, same data as for holotype, except for date: 13 July 1989 (1 female), 14 July 1989 (1 male), 29 December 1989 (1 female), and 3 January 1990 (1 female) (TYCN); 3 females, 20 km NW of Barus on Pakkat-Barus Road [CL 2195], 2.12641°N 98.45196°E, 551 m, 10 November 1985, D. A. & J. T. Polhemus, Light Trap (00418896–00418897) (CNC). **THAILAND:** 1 male, Chiang Mai, Doi Pui, 18.82, 98.89, M. Takakuwa, 3 May 1984 (00380628) (NIAES). **VIETNAM:** 1 male, 1 female, Sa Pa, 1,900 m alt., 22.35, 103.82, UV light trap, Y. Nakatani, 20 May 1999 (NIAES) (1 female with USI label: 00380682). **Additional specimens examined: BRUNEI:** 1 female, Temburong

Table 1. Measurements for Oriental mirine species. Abbreviations: L = length, W = width.

	Body	Head	Vertex	Pronotum		Max	Antennomere L				Labium	Hind leg segments L		
	L	W	W	L	W	W	I	II	III	IV	L	Femur	Tibia	Tarsus
***Malayamiridius nigrotenuis* male** (n = 3)														
max	5.13	0.95	0.29	1.03	1.38	1.41	0.95	2.34	2.09	0.93	2.22	2.28	3.61	0.55
min	4.80	0.93	0.23	0.95	1.32	1.35	0.87	2.13	1.84	0.82	1.90	2.09	3.23	0.51
mean	4.98	0.94	0.25	0.98	1.36	1.37	0.92	2.22	1.94	0.87	2.01	2.17	3.41	0.53
***Malayamiridius nigrotenuis* female** (n = 3)														
max	6.06	0.99	0.34	1.15	1.65	1.71	0.99	2.57	2.30	0.95	2.24	2.57	3.99	0.59
min	5.49	0.97	0.30	1.03	1.58	1.58	0.84	2.32	1.98	0.93	1.82	2.28	3.57	0.55
mean	5.78	0.98	0.33	1.11	1.62	1.63	0.93	2.46	2.09	0.94	2.08	2.44	3.82	0.57
***Sumatracapsus flavonitidus* male** (n = 4)														
max	5.88	1.08	0.35	1.24	1.79	2.01	1.14	2.89	1.73	0.61	2.09	2.34	3.90	0.76
min	4.86	0.99	0.32	1.12	1.69	1.79	1.01	2.66	1.56	0.57	2.05	2.15	3.33	0.68
mean	5.33	1.03	0.34	1.15	1.72	1.88	1.09	2.79	1.66	0.59	2.03	2.22	3.60	0.73
***Sumatracapsus flavonitidus* female** (n = 3)														
max	6.48	1.14	0.40	1.35	2.09	2.32	0.95	2.32	1.52	0.61	2.20	2.34	3.25	0.74
min	5.76	1.06	0.38	1.31	1.92	2.20	0.82	2.28	1.39	0.59	2.05	2.26	3.19	0.70
mean	6.09	1.10	0.39	1.32	2.02	2.26	0.87	2.30	1.45	0.60	2.12	2.29	3.22	0.72
***Sumatracapsus kinabaluensis* male** (n = 4)														
max	7.10	1.14	0.34	1.28	2.13	2.30	1.23	2.85	1.28	0.65	2.40	2.75	3.98	0.88
min	5.90	1.04	0.30	1.13	1.88	2.04	1.00	2.44	1.23	0.60	2.18	2.33	3.50	0.85
mean	6.58	1.09	0.32	1.20	1.99	2.17	1.10	2.60	1.26	0.63	2.28	2.49	3.68	0.87
***Sumatracapsus kinabaluensis* female** (n = 5)														
max	7.93	1.20	0.43	1.50	2.54	2.80	1.00	2.34	1.30	0.68	2.48	2.75	4.10	0.88
min	7.60	1.15	0.39	1.43	2.48	2.65	0.98	2.10	1.16	0.63	2.36	2.50	3.70	0.80
mean	7.78	1.17	0.40	1.46	2.50	2.72	0.99	2.21	1.23	0.65	2.42	2.59	3.80	0.82
***Tondomiris puguis* male**														
Holotype	6.30	1.08	0.32	1.25	2.01	2.28	1.25	2.62	2.09	–	3.10	3.14	4.66	0.76

NP, mixed dipterocarp forest, Ashton trail, summit of trail, MVP light, heavy rain, 3 January 2014, 7–9 pm, leg. C. Damken, 4°32′35″N, 115°9′11″E (Belagong.02191, image 0.75*) (UBDM, Universiti Brunei Darussalam Museum, temporary preserved in Damken collection, Dunedin, New Zealand). **INDONESIA:** 1 female, North Sumatra, Brastagi, Mt Sibayak, 1,500–2,000 m, 02–04 April 1998 (P. Magnien collection, Paris, France). **MALAYSIA:** 1 female, Pahang Province, Tanah Rata env., 9–23 April 1999, VLT Kabourek leg. (P. Magnien collection, Paris, France).

Diagnosis. Recognised by fuscous chestnut brown basic colouration; creamy yellow clypeus, pro- and mesofemora, pro- and mesotibia, and abdominal sternites IV−VI, in addition to the characters mentioned in generic diagnosis.

Description. COLOURATION: Body chocolate brown to fuscous (Fig. 1A−C). Head blackish brown, with creamy clypeus (Fig. 1B); vertex about as wide as an eye in dorsal view, with a faint, narrow, longitudinal, mesal sulcus; frons shallowly and obliquely striolate. Antenna uniformly yellow dorsally, dark ventrally; segment II about as long as metafemur; segment III about as long as labium. Labium shiny dark brown, slightly suffused with red (Fig. 1B, C). Pronotum uniformly dark, smooth; pleura widely darkened, rather shining, with creamy yellow ostiolar peritreme (Fig. 1B); scutellum nearly flat, transversely rugose medially. Hemelytron concolorously fuscous; apical inner part of cuneus slightly tinged with red; membrane smoky brown. All coxae dark brown, except for apical part of metacoxa creamy yellow; trochanters and legs creamy yellow; metafemur chocolate brown, except for pale extreme base and apex; metatibia smoky brown; all tarsi pale brown. Abdomen fuscous; sternites IV−VI pale brown or creamy brown (Fig. 1B, C). Surface, vestiture, and structure as in generic description.

Measurements. See Table 1.

Etymology. From Latin, niger (= black) combined with tenuis (= slender), referring to the darkened, slender body of this new species; an adjective.

Distribution. Brunei, Indonesia (northern Sulawesi and northwestern highlands of Sumatra), Malaysia, Thailand, and Vietnam (Fig. 12).

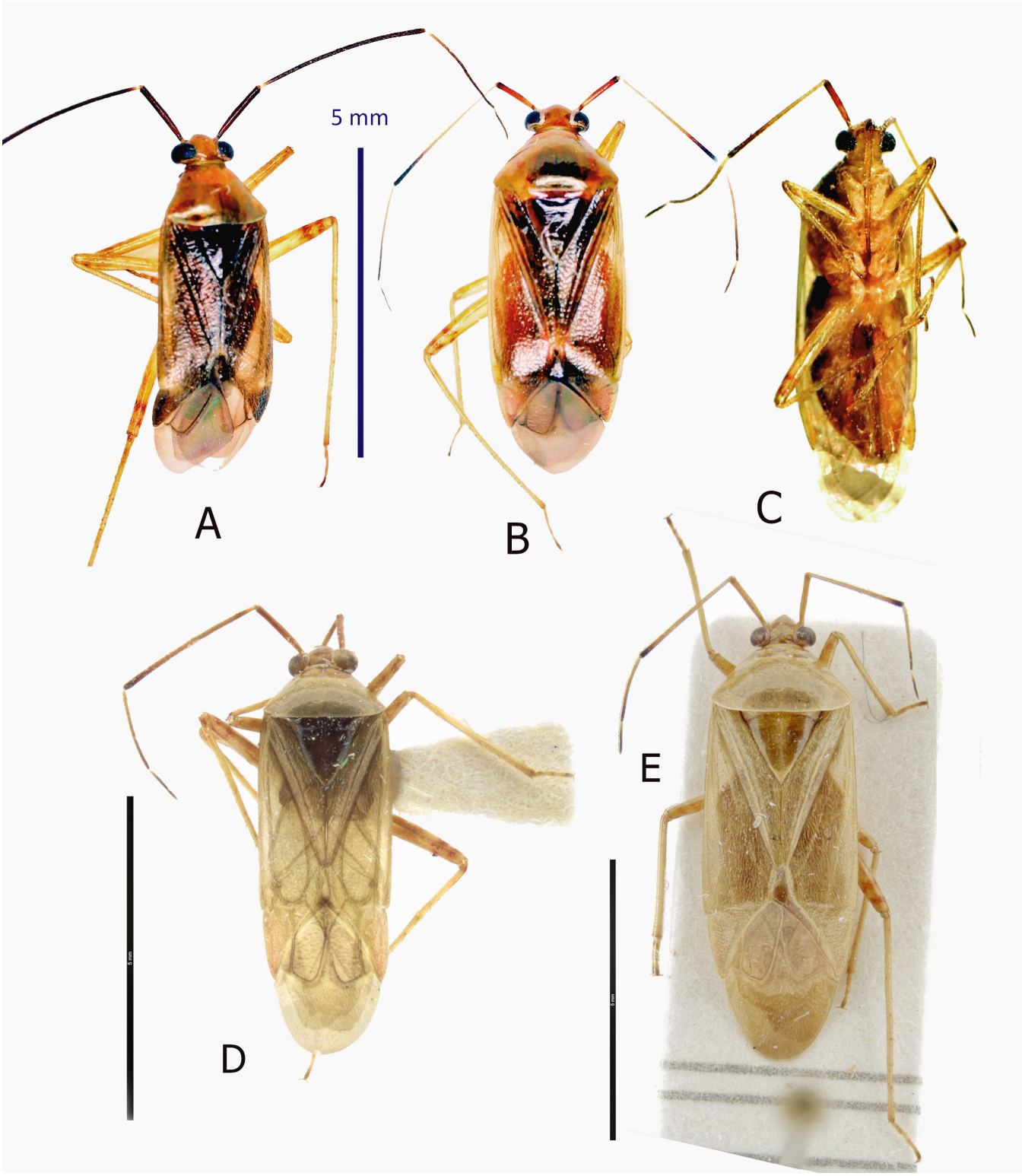

Fig. 4. Habitus images of *Sundacapsus flavonitidus* (A–C) and *S. kinabaluensis* (D–E). A, D, male in dorsal view; B, E, female in dorsal view; C, female in ventral view.

Biology. All available specimens collected using UV light traps were found to be covered partly with pollen (cf. Fig. 2K). This mirid is assumed to inhabit inflorescence of (most probably broadleaf) angiosperms and appears to be a pollinator in the Asian tropical forest-zone ecosystem (cf. Fig. 1D). Collection records suggest that this mirid has at least two generations per year.

Sundacapsus, new genus

Type species. *Sundacapsus flavonitidus* Yasunaga, Chérot & Schwartz, new species.

Diagnosis. Distinguished from other mirine genera by the following combination of characters: Moderate size (4.8−6.0 mm in total length); yellowish brown basic colouration;

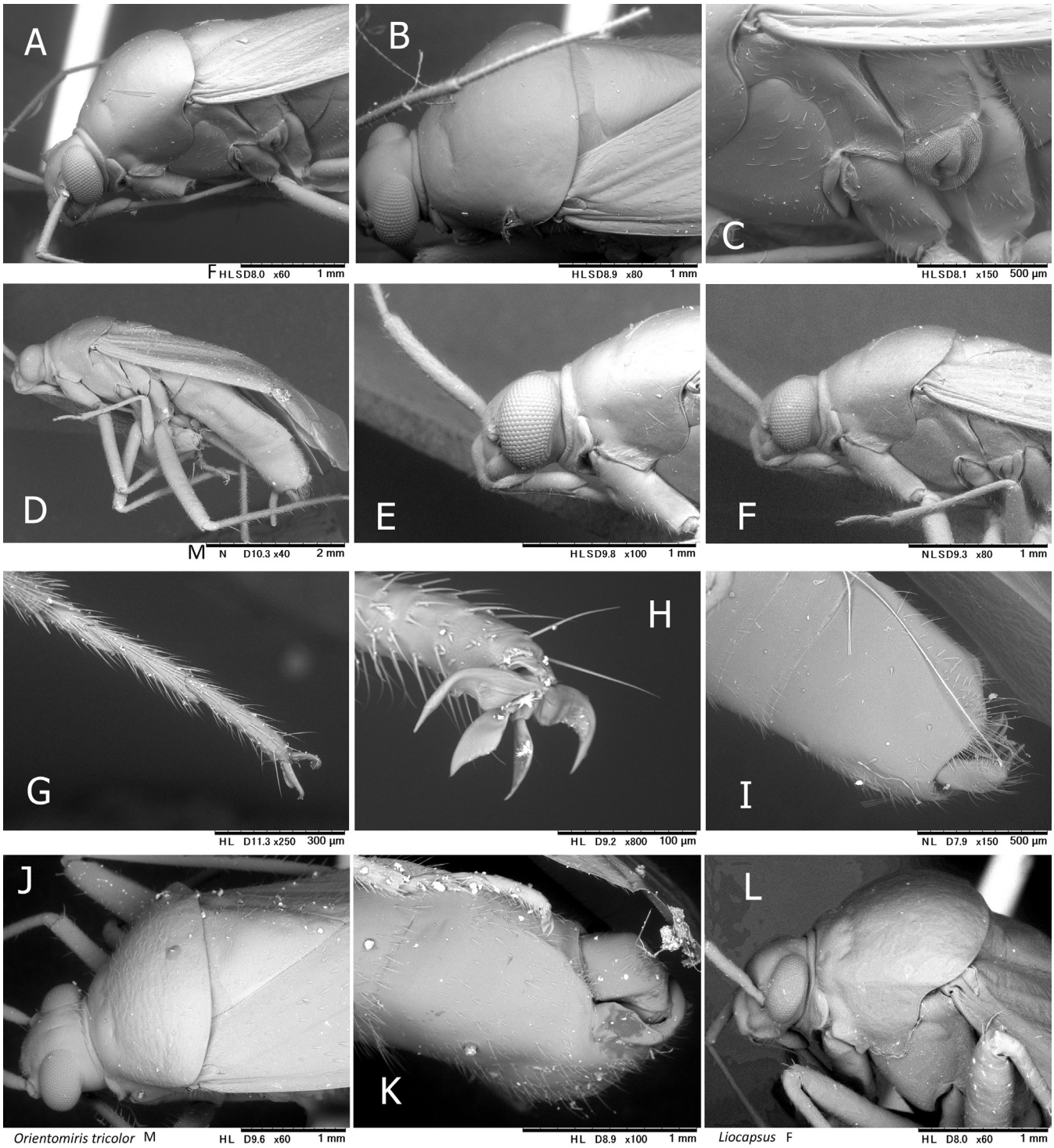

Fig. 5. Scanning electron micrographs for female (A–C, L) and male (D–K) of *Sundacapsus flavonitidus*, (A–I), *Orientomiris tricolor* Scott from Nagasaki, Japan (J–K) and *Liocapsus langtang* Yasunaga & Schwartz from Rasuwa, Nepal (L). A, B, J, L, anterior body; C, thoracic pleura; D, left lateral habitus; E, head and pronotum; F, anterior body; G, metatarsus; H, pretarsal structure of metaleg; I, K, pygophore.

highly polished, oily shiny dorsum with sparse vestiture (Figs. 4A, B, 5B); long, almost linear antenna longer than body; slender, short labium not exceeding apex of mesocoxa (Fig. 5A); smooth, impunctate, glabrous pronotum (Fig. 5A, B, E, F); weakly inflated scutellum (Fig. 5A, B); shiny hemelytron with uniformly distributed, simple, reclining setae; trapeziform pygophore (Fig. 5I); left paramere with stout sensory lobe covered in long setae and slender, hooked hypophysis with axe-shaped apex (Figs. 6B, 8H); endosoma (vesica) membranous, with long, narrow spicule-like support on posterior surface and lobal sclerite on right side (Fig. 6C); noticeably straight gonapophyses (Fig. 9C) with rounded apices (Figs. 8F, 9D); and posterior wall with paired, spinulate dorsal structure (Figs. 6D, 8D, E).

Description. *Male.* Body elongate oval. COLOURATION: Generally yellowish brown; partly suffused with red, with more or less darkened scutellum and hemelytron (Fig. 4A, B). SURFACE AND VESTITURE: Dorsum highly polished, oily shiny, head smooth glabrous, pronotum glabrous, impunctate,

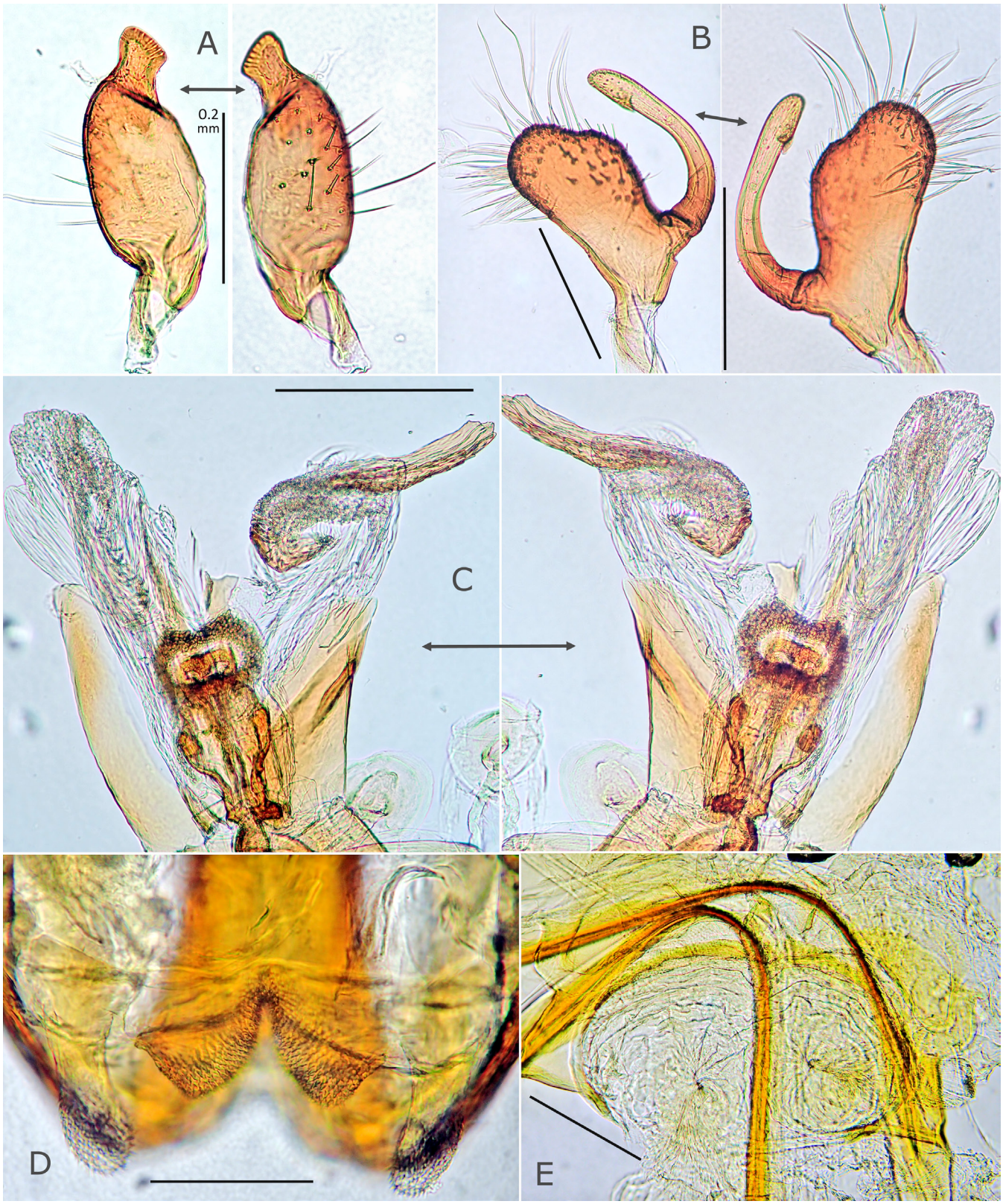

Fig. 6. Male (A–C) and female (D–E) genitalia of *Sundacapsus flavonitidus*. A, right paramere; B, left paramere; C, endosoma; D, posterior wall; E, genital chamber. Scale bars = 0.2 mm.

scutellum somewhat swollen, shallowly and transversely rugose, hemelytron smooth, with uniformly distributed, pale, simple, reclining setae (Fig. 5B). STRUCTURE: **Head:** Subvertical (Fig. 5E, F), without sulcation, groove, or carina on vertex and frons (Fig. 5B); clypeus weakly projected. **Antenna:** Subequal in length to body, generally slender, almost linear, not incrassate; segments II–IV almost uniform in thickness; segment I slightly longer than width of head across eyes, longer than IV; segment II longer than maximum width across hemelytron; antennal segment III longer than head width across eyes; segment III slightly shorter than II; segments III and IV filiform. **Labium:** Relatively slender,

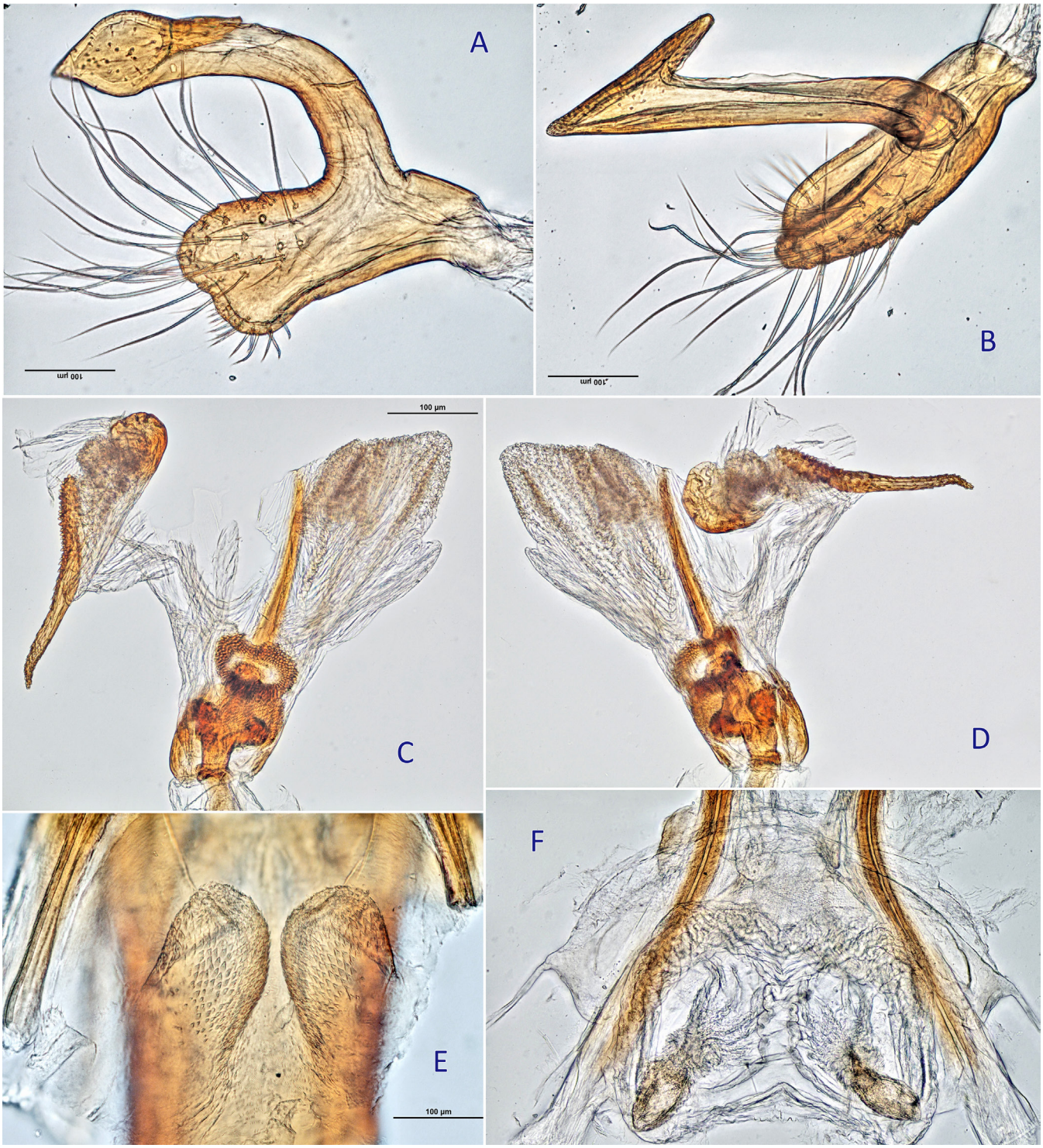

Fig. 7. Male (A–C) and female (D–E) genitalia of *Sundacapsus kinabaluensis*. A, left paramere, right lateral view; B, same, dorsal view; C, endosoma, anterior view; D, same, caudal view; E, posterior wall, anterior view; F, genital chamber, dorsal view. Scale bars = 0.1 mm.

reaching but not exceeding apex of mesocoxa, slightly shorter than metafemur (Fig. 4C). **Thorax:** Pronotum with weakly demarcated calli (Fig. 5B); scutellum somewhat swollen. **Hemelytron:** Obovate. **Legs:** Long, generally slender; tibial spines short, sparse; meta-tarsomere I shorter than II or III; pretarsus with parempodia lamellate, wedge-shaped; pulvilli absent (Fig. 5H). **Genitalia** (Figs. 6A–C, 7A–D, 8G–I): Pygophore rather long, not much narrowed towards apex, with smooth apical margin (Fig. 5I). Parameres as in Figs. 6A, B, 8G–I; left paramere with developed, bulbous, strongly setose sensory lobe and slender, J-shaped hypophysis with axe-shaped apex (Figs. 6B, 8H); right paramere short, somewhat ovoid, with flat, widened apex (Figs. 6A, 8I); endosoma (vesica) widely membranous, with lobal-sclerite on right side; posterior surface with long, narrow supporting sclerite (Fig. 6C); ductus seminis with U-shaped sclerite at middle; gonopore ovate, thick-rimmed.

Female. Not significantly different from male in general appearance (Fig. 4B). **Genitalia** (Figs. 6D, E, 7E, F, 8D–F,

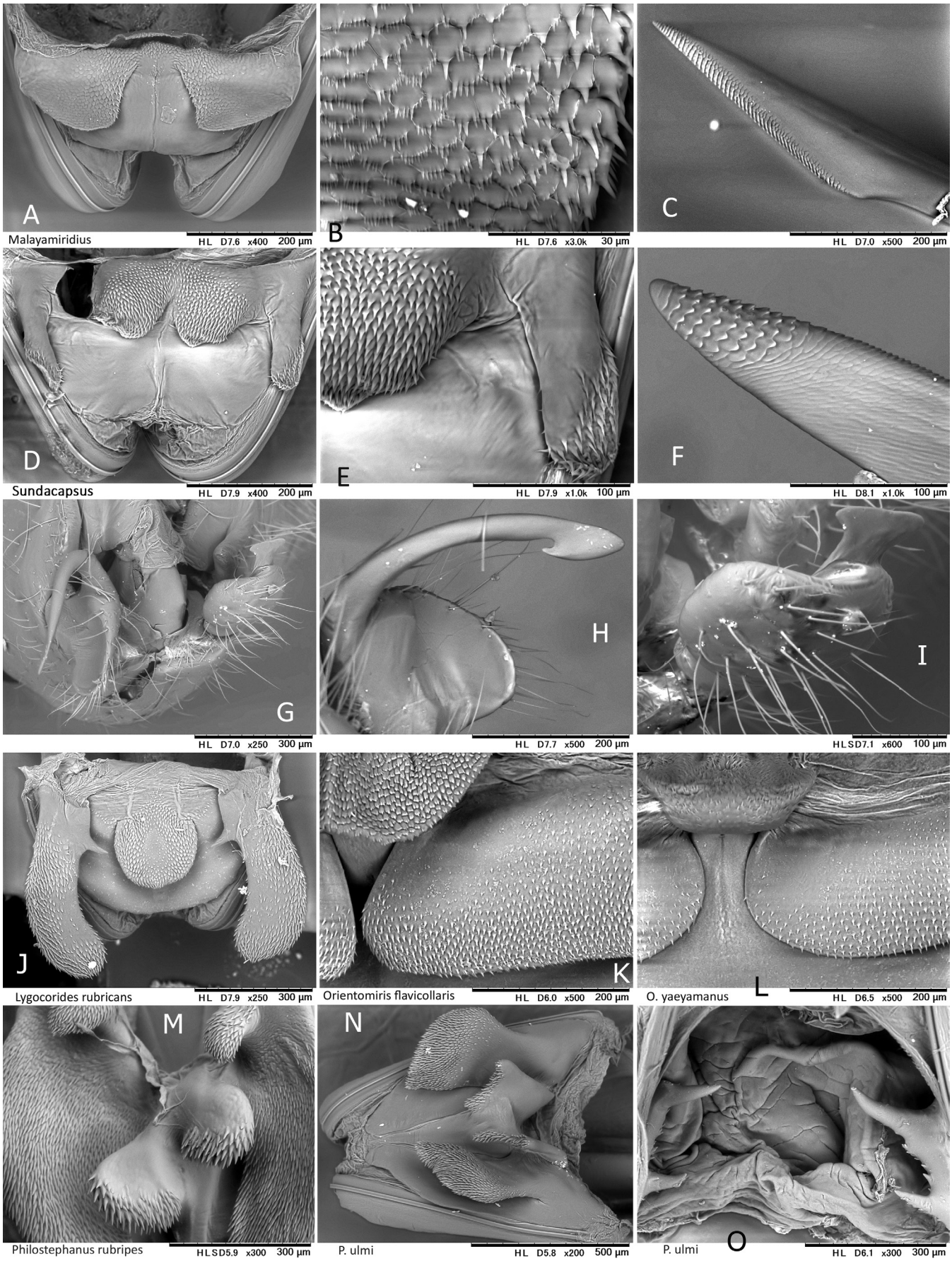

Fig. 8. Scanning electron micrographs of female and male (G–I) genitalia. A–C, *Malayamiridius nigrotenuis*; D–I, *Sundacapsus flavonitidus*; J, *Lygocorides rubricans* Yasunaga from Ryukyus, Japan; K, *Orientomiris flavicollaris* Yasunaga from Ryukyus; L, *O. yaeyamanus* Yasunaga from Ryukyus; M, *Philostephanus rubripes* (Jakovlev) from Nagasaki, Japan; N, O, *P. ulmi* (Kerzhner) from Russian Primorsky. A, D, E, J, M, N, posterior wall; B, K, L, interramal lobe; C, F, ovipositor (gonapophysis) I; G, apex of pygophore, caudal view; H, left paramere; I, right paramere; O, genital chamber.

9C, D): Ovipositors uniquely round- or blunt-tipped, not sharpened (Figs. 7F, 8F, 9C, D); gonapophysis II straight, rather slender (Fig. 9C); apex of gonapophysis I minutely toothed (Figs. 8F, 9D); sclerotised ring elongate oval (Fig. 6E, 7F); posterior wall with obscure, narrow median process, paired, spinulate dorsal structure and slender, projecting interramal lobes (Figs. 6D, 8D, E) but sometimes interramal lobes very short (Fig. 7E).

Etymology. Named for the Sunda[land], combined with the mirine generic name *Capsus* Fabricius; gender masculine.

Discussion. The present new genus is reminiscent of *Poppiocapsidea* Yasunaga which is composed of two Oriental species, *P. biserratense* (Distant, 1903) (Fig. 10E) and *P. clypeale* (Poppius, 1915), by the similar facies (e.g., medium-sized, elongate ovoid body, pale brown basic colouration, shiny dorsum, long antenna). However, our new genus can be easily distinguished from *Poppiocapsidea* by the following characters: head rather oblique; vertex smooth, without mesal sulcus; pronotum, scutellum, and hemelytron highly polished, oily shiny; left paramere with developed, bulbous sensory lobe and slender hypophysis J-shaped, apex axe-shaped; endosoma lacking hair-like membranous processes along secondary gonopore; ovipositors with blunt-tipped, rounded apices; and elongate, finger-like interramal lobe.

The structure of the ovipositors in *Sundacapsus* are unusual, as the apices are rounded and not sharply pointed, being different from those in other mirid bugs which usually have sword-like ovipositors with sharp apices (cf. Figs. 8C, 9A, B). The single representative of *Sundacapsus* described below is assumed to lay eggs into rather soft plant tissue. Based on this character (apical shape of the gonapophyses), we cannot imagine any reliable close relative for *Sundacapsus*. Comparison with *Liocapsus* Poppius, *Orientocapsus* Yasunaga & Schwartz, or *Philostephanus* Distant may merit careful consideration, as some members of these genera have similarly well-polished, glabrous dorsum and are known to occur in the Oriental Region. Nonetheless, they are considered to have remote relationships to *Sundacapsus*, judging from the completely different form of the male and female genitalia including the ovipositors (see Yasunaga & Schwartz, 2007).

The general appearance and elongate interramal lobes (Figs. 6D, 8E) of *Sundacapsus* are similar to those possessed by members of *Lygocorides* Yasunaga, 1991 known from eastern Asia. However, in the latter genus, the dorsal surface uniformly bears simple setae (cf. Yasunaga, 1996) and the interramal lobes are remarkably longer and broader (Fig. 8J). Based on the structure of the male genitalia, the two lineages (genera) are apparently remote from each other. We currently cannot suggest any candidate taxon definitely related to *Sundacapsus*.

***Sundacapsus flavonitidus*, new species**
(Figs. 4A–C, 5A–I, 6, 8D–I, 9C, D, 12)

Type material. Holotype: male, **INDONESIA**: North Sumatra, Prapat (1,000 m), 50 km E of Pematang Siantar, 2.88°N, 99.52°E, UV light trap, T. Yasunaga, 29 November 1989 (AMNH_PBI 00380629) (AMNH). Paratypes: INDONESIA: North Sumatra: 1 male, same data as for holotype (CNC); 3 males, same data (TYCN); 2 males, 10 females, Brastagi, North of Toba Lake, 3.18°N, 98.50°E, 1,400 m, UV light trap, T. Yasunaga, 5–9 December 1989 (1 male with USI label: 00380630) (TYCN); 2 females, same data (CNC); 2 females, same data (ZRC); 1 male, 2 females, same locality, E. W. Diehl, 24 March 1974 (AMNH); 1 female, same locality and collector, 23 November 1973 (AMNH); 1 male, Simalungun, Dolok Merangir, 3.12°N, 99.12°E, light trap, E. W. Diehl, April–June 1970 (AMNH); 1 female, same locality and collector, April 1970 (AMNH); 2 males, 4 females, same locality and collector, without date (AMNH).

Diagnosis. Recognised by moderate size and yellowish brown, oily shiny, glabrous, impunctate dorsum, with darkened scutellum, clavus and cuneus (male only) (Fig. 4A, B), in addition to the male and female genitalic structures mentioned in the above generic description. The male antenna is generally longer and cuneus is darker than those of female.

Description. *Male*. COLOURATION: Body yellowish brown; dorsum more or less tinged with red (Fig. 4A). Antenna dark brown; extreme bases of segments III and IV pale. Labium yellowish brown; apical half of segment IV darkened. Pronotum somewhat shining, widely pale brown, narrowly darkened posteriorly, with yellowish white collar and posterior margin. Thoracic pleura chestnut brown, with yellowish brown ostiolar peritreme; mesoscutum and scutellum shiny dark brown. Hemelytron pale brown; clavus and cuneus usually chestnut brown; membrane pale smoky brown, semitransparent, with dark brown veins. All coxae and legs yellowish brown; metafemur with two reddish rings subapically. Abdomen shiny chocolate brown, except for median part of sternites II–VII and base of pygophore pale brown. Surface, vestiture, and structure as in generic description.

Female. Almost similar to male, but body larger and stouter (Fig. 4B). Antenna pale yellowish to reddish brown; apex of segment I and apical ¼ of II and apical ⅓ of III dark reddish brown. Labium shiny pale reddish brown. Mesoscutum and cuneus pale reddish brown. Ventral surface generally pale brown, not significantly darkened (Fig. 4C).

Male (Figs. 6A–C, 8G–I) and female (Figs. 6D, E, 8D–F) genitalia as mentioned in generic description.

Measurements. See Table 1.

Etymology. From Latin, flavus (yellow) + nitidus (shiny, polished), referring to the shiny yellowish basic colouration of this new species; an adjective.

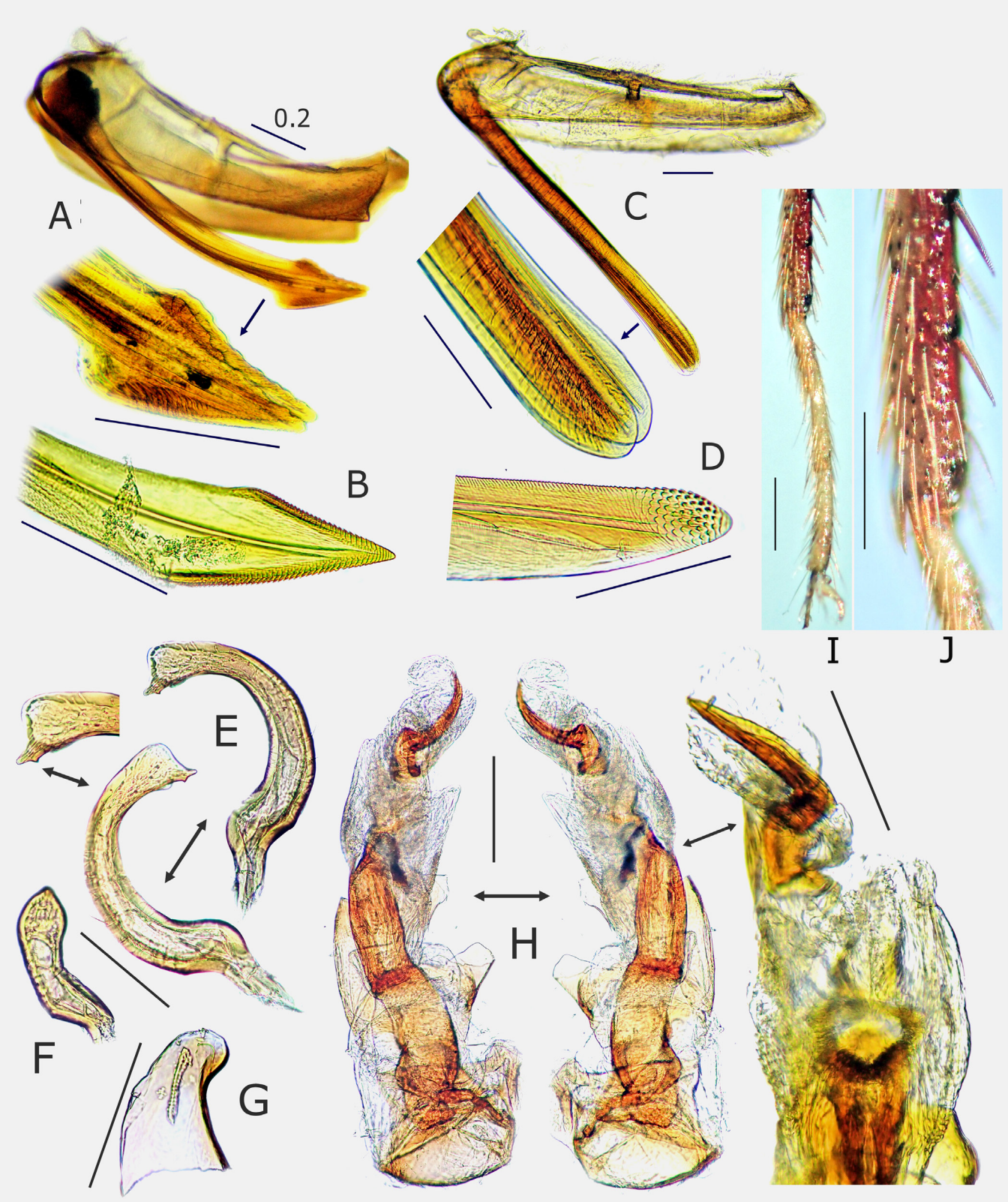

Fig. 9. Female (A–D) and male (E–H) genitalia, and apical part of metaleg (I–J) of *Malayamiridius nigrotenuis* (A, B); *Sundacapsus flavonitidus* (C, D) and *Tondomiris puguis* (E–J). A, C, gonapophysis II; B, D, gonapophysis I; E, left paramere; F, right paramere; G, phallotheca; H, endosoma. Scale bars = 0.2 mm.

Distribution. Indonesia (northwestern highlands of Sumatra) (Fig. 12).

Biology. Unknown; all known specimens were collected at mercury or fluorescence lights.

Sundacapsus kinabaluensis, new species
(Figs. 4D, E, 7, 12)

Type material. Holotype: male, **MALAYSIA**: Sabah, Borneo, Sabah Mt. Kinabalu National Park, HQ, 1,560 m, 6.00574, 116.54268, 15 May 1987, A. Smetana (AMNH_PBI 00418901) (CNC). Paratypes: **MALAYSIA**: Sabah, 3 males, 31 females, same data as for holotype (AMNH_PBI 00418900, 00418902–36) (CNC); 2 females, Mt. Kinabalu National Park, HQ, Mempening Trail, 1,600 m, 6.01209, 116.54112, A. Smetana, 17 May 1987 (AMNH_PBI 00418937–38) (CNC).

Diagnosis. Distinguished by its larger size and overall dusky greenish tan colouration with dark brown apical portions of antenna segments II–IV and scutellum (except for corners), clavus and endocorium faintly darkened, cuneus with faint reddish brown tinge (Fig. 4D); endosoma with long narrow, apically pointed lobal sclerite and supporting basal sclerite extending to apical margin of membrane and pointed; interramal lobes of posterior wall very short and fin-shaped.

Description. *Male*. COLOURATION: Body practically uniform dusky greenish tan for pinned specimens (Fig. 4D). Antenna pale yellowish tan; variable dark brown on apical portion of segment II and on most of segments III–IV except bases. Labium with apical one-third of segment IV darkened. Head with portion ventral to antennal insertions dark brown. Pronotum anterior of calli diffusely dark brown, collar contrasting yellowish white. Thoracic pleura dark brown, with yellowish white ostiolar peritreme; mesoscutum shiny dark brown, except lateral margins tan, scutellum shiny dark brown except for tan apex. Hemelytron with clavus and endocorium variably and diffusely brown, darkest lateral of anal vein; cuneus with faint reddish brown tinge; membrane pale brown, translucent, with concolourous veins. All coxae and legs yellowish tan; bases of tibiae with dark mark; metafemora with two subapical, poorly defined, reddish brown rings. Abdomen shiny reddish brown, except for tan on median parts of sternites II−VII and base and ventral portions of pygophore. Surface, vestiture, and structure as in generic description. Genitalia (Fig. 7A–D): Hypophysis of left paramere developed, with sharply arrowed apex (Fig. 7B); distal lobal-sclerite of endosoma slender, tapered towards apex (Fig. 7D). Surface, vestiture, and structure as in generic description.

Female. Similar to male, but body somewhat longer and wider (Fig. 4E). COLOURATION: Generally paler than male, with dark markings restricted to maxillary plate, ventral margin of tylus, apex of antennal segment II, apical ¼ of III and apical ½ of IV; reddish markings as in male. Genitalia (Fig. 7E, F): Posterior wall with short interramal lobe (Fig. 7E).

Measurements. See Table 1.

Etymology. Named for its occurrence in Kinabalu National Park, a World Heritage Site.

Distribution. Currently known only from Sabah, East Malaysia (northern highlands of Borneo) (Fig. 12).

Biology. Unknown; all known specimens were taken from foliage near park headquarters.

Tondomiris, new genus

Type species. *Tondomiris puguis* Yasunaga, Chérot & Schwartz, new species.

Diagnosis. Distinguished from other known mirine genera by the following combination of characters: generally reddish brown, elongate, parallel-sided body; moderate size (6.3 mm in total length); almost glabrous dorsum; shiny, polished head and pronotum; shallow, indistinct longitudinal sulcus on vertex; long labium exceeding apex of metacoxa and reaching abdominal sternum VI (Fig. 11A); distinctly elevated scutellum (Fig. 11B); dark spots or annulations at bases of tibial spines; unique micro-spines on apical metatibia (Fig. 11D, E); almost smooth margin of pygophore without sharp process at base of left paramere (Fig. 11G); and a single, lobal-sclerite at apex of endosoma (Fig. 9H).

Description. *Male*. Body elongate, nearly parallel-sided. COLOURATION: Generally dark reddish brown. SURFACE AND VESTITURE: Dorsal surface almost glabrous (Fig. 10A, B); head polished, glabrous; pronotum shiny, glabrous, impunctate; scutellum transversely rugose; hemelytron somewhat matte, almost glabrous, impunctate. STRUCTURE: **Head**: Vertical (Figs. 10C, 11B), vertex with a shallow, faint median sulcus (Fig. 10B); clypeus weakly projected. **Antenna**: Segments I–III almost uniform in thickness, not incrassate; segment I longer than width of head across eyes, equal to mesal length of pronotum; segment III slightly longer than pronotal width. **Labium**: Relatively thick exceeding apex of metacoxa, reaching abdominal sternum VI, slightly shorter than metafemur (Fig. 11A). **Thorax**: Pronotum with flat but distinct calli (Fig. 10B); scutellum distinctly elevated anteriorly with rather flattened apex; scent efferent system subtriangular, with ear-like peritreme (Fig. 11C). **Hemelytron**: Cuneus narrow. **Legs**: Long; tibia with dark spots or annulations at bases of dark spines; apical part (outer surface) of metatibia densely covered with scaly spinules, or microspines (Fig. 11D, E); meta-tarsomere II as long as III; with wide, lamellate parempodia and pulvilli (Fig. 11F). **Genitalia** (Fig. 9E–H): Pygophore with almost smooth margin, lacking process at base of left paramere (Fig. 11G). Parameres as in Fig. 9E, F; left paramere C-shaped, with widened apex (Fig. 9E); right paramere short, less than half as long as left (Fig. 9F); apex of phallotheca rounded; endosoma widely membranous, with a single, lobal sclerite that is twisted subbasally (Fig. 9H); ductus seminis almost cylindrical.

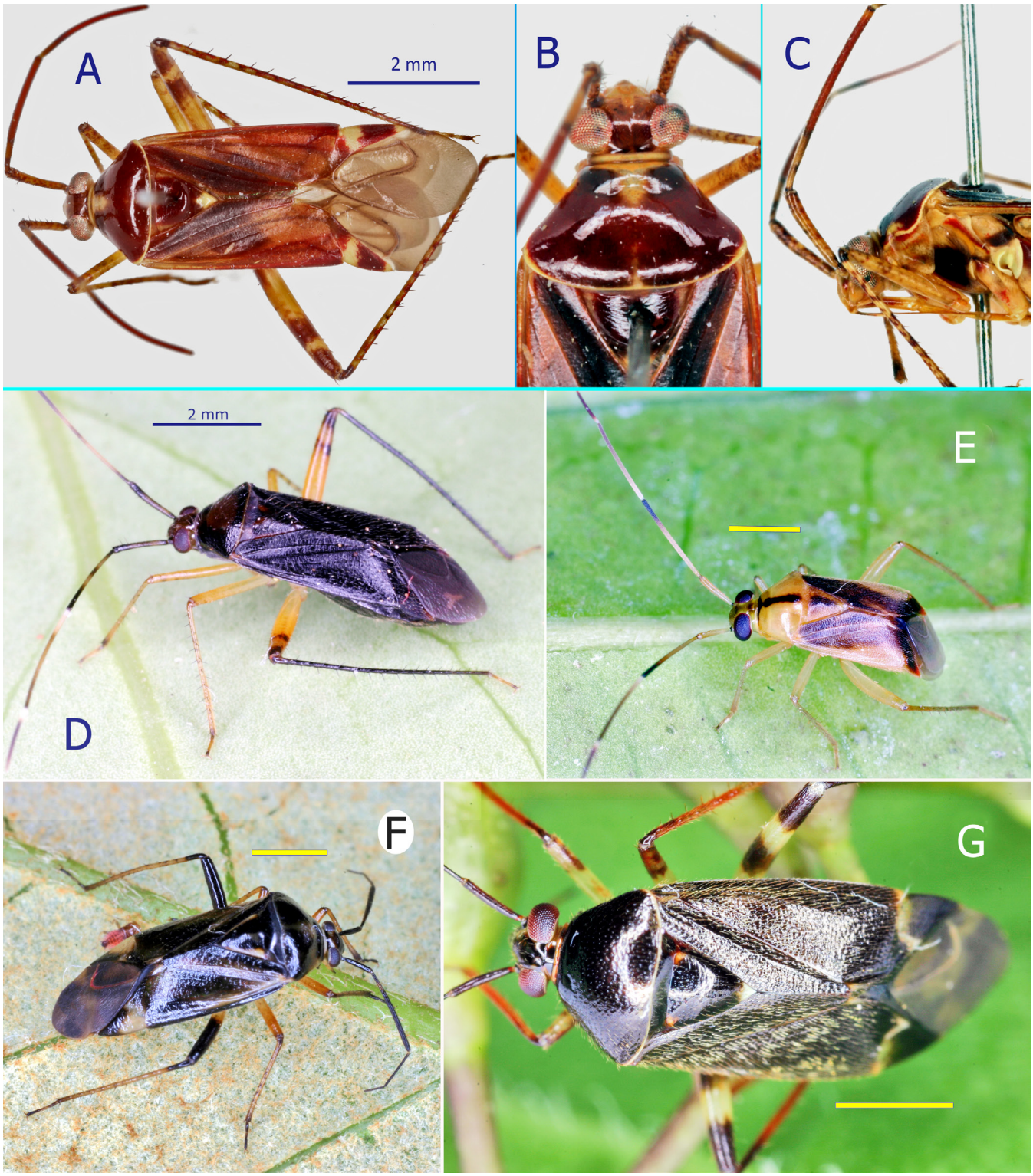

Fig. 10. Habitus images of *Tondomiris puguis* (A–C) and other Asian mirines superficially similar to the present new taxa. A, *T. puguis*, holotype male, dorsal view; B, anterior body; C, left lateral view; D, *Orientomiris straminipes* (Distant) from Kasuki, Nepal; E, *Poppiocapsidea biseratensis* (Distant) from Ayutthaya, Thailand; F, *Liocapsus langtang* Yasunaga & Schwartz from Rasuwa, Nepal; G, *Philostephanus rubripes* (Jakovlev) from Nagasaki, Japan. Scale bars = 2 mm.

Female. Unknown.

Etymology. Named for Tondo (or Tundu), an ancient polity that existed in Luzon before colonisation of the Spanish Empire, combined with the mirine generic name *Miris* Fabricius; gender masculine.

Discussion. The present new genus is externally similar to *Liocapsus* Poppius, *Orientocapsus* Yasunaga & Schwartz, or *Philostephanus* Distant, in having the similar colour pattern and polished, glabrous dorsal surface. Based on the male genitalic structure (e.g., an apical lobal-sclerite on the endosoma), however, *Tondomiris* is presumed to be related

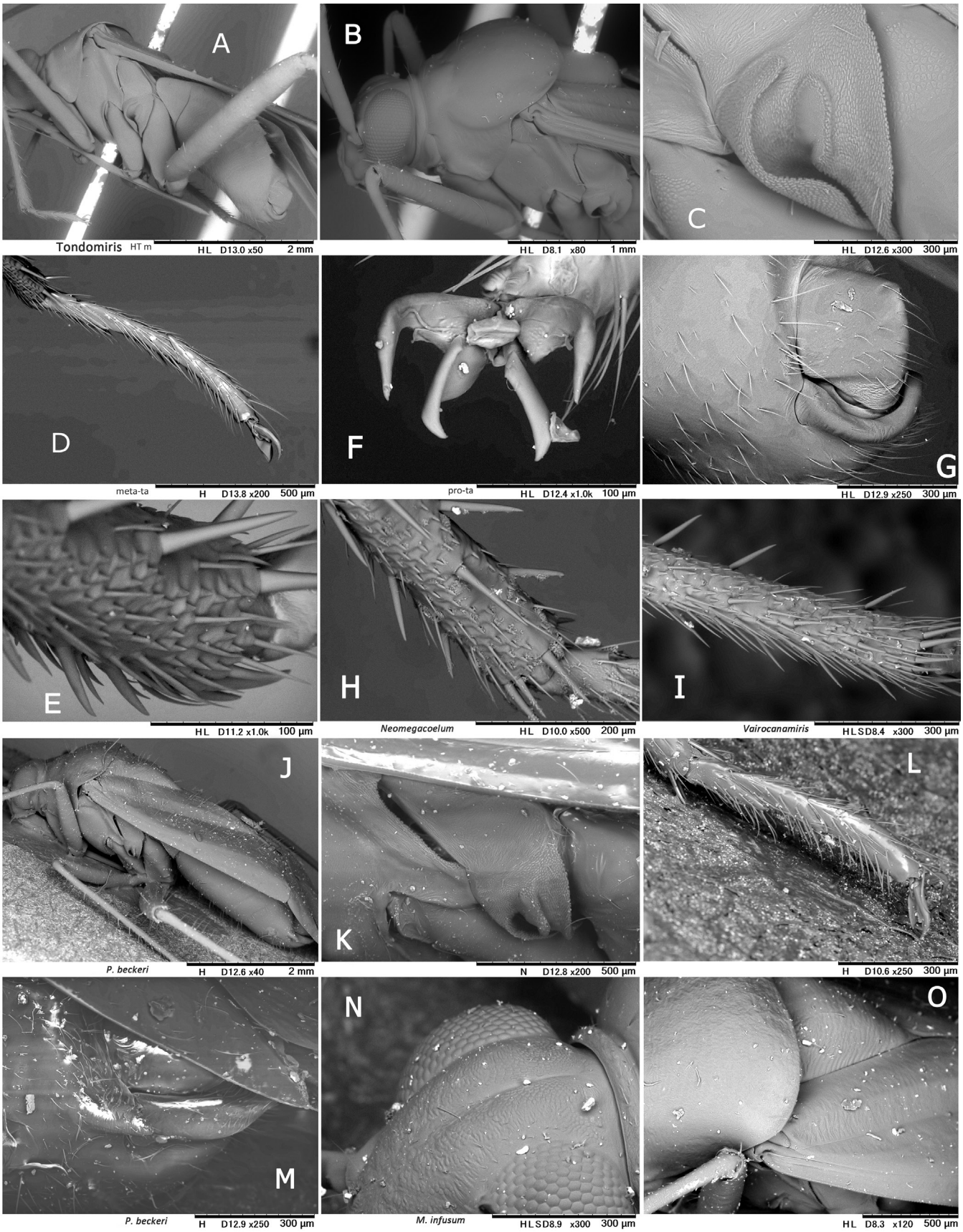

Fig. 11. Scanning electron micrographs of *Tondomiris puguis*, holotype male (A–G), *Neomegacoelum vitreum*, female (H), *Vairocanamiris jordiribesi*, holotype male (I), *Pseudomegacoelum beckeri* (Fieber), male from Bulgaria (J–M), and *Megacoelum infusum* (Herrich-Schaeffer), male from Romania (N, O, J). A, J, left lateral habitus; B, anterior body, left lateral view; C, K, scent efferent system; D, apex of metaleg (outer side); E, apex of metatibia (outer side); F, pretarsal structure of proleg; G, pygophore, left lateral view; H, I, apex of metaleg (outer side); L, metatarsus; M, apex of pygophore, left lateral view; N, head; O, pronotum, scutellum, and anterior forewing.

to *Megacoelum* Fieber. The former is distinguished from the latter by the oily, shiny head and pronotum, the long labium extending beyond apex of the metacoxa, the bulbously elevated anterior ⅔ of the scutellum, the clear dark spots or annulations on the tibiae, and the smooth pygophore lacking any spine or process at the base of left paramere, in addition to the unique, scaly micro-spines at apical part of the metatibia. The apical metatibial micro-spines (Fig. 10D, E) are currently considered as an autapomorphy for *Tondomiris*, as we have not recognised its presence in any other mirine genera. This structure is hardly visible by compound or stereoscopic microscopes (Fig. 7I, J) and can be observed only by scanning electron microscopes. The micro-spines are also furnished on the metatibiae of *Neomegacoelum* Yasunaga, including a single eastern Palearctic element *N. vitreum* (Kerzhner, 1988), and *Vairocanamiris* Yasunaga but are obviously sparser and structurally different from those found in *Tondomiris* (Fig. 11H, I).

Vairocanamiris Yasunaga is also similar in general appearance to our new genus. However, this unique genus currently known only by *V. jordiribesi* Yasunaga, 2011 from Indian Sikkim is different from *Tondomiris* in the following characters: body even larger (9–11 mm in total length); vertex wider, with a narrow but recognisable longitudinal mesal sulcation; antenna slenderer; labium shorter, not exceeding apex of metacoxa; apical part of metatibia with sparsely distributed micro-spines; pygophore with a prominent, conical process at base of left paramere; and endosoma with a short lobal-sclerite and a bundle of hair-like appendages behind secondary gonopore (cf. Yasunaga, 2011).

Incidentally, *Megacoelum* currently comprises more than 50 species in the Old World (Schuh, 2002–2013; Aukema, 2018). However, at least 35 of these species are in all likelihood members of other genera (e.g., *Adelphocorisella*, *Creontiades*, *Orientomiris*) as indicated by Chérot & Malipatil (2016). In the Oriental Region and eastern Asia, only *Megacoelum formosanum* Poppius, 1915 [China, Taiwan] may be regarded as a true member of the genus (cf. Yasunaga, 1998), and all other taxa placed in *Megacoelum* require further verification. Our examinations on taxa described by Distant (1909) (deposited in BMNH) revealed that the following five species doubtlessly are members of *Orientomiris*; accordingly, new combinations are herein proposed (all transferred from *Megacoelum*): *Orientomiris brunnetii* (Distant, 1909), new combination [India: Uttar Pradesh]; *O. marginandus* (Distant, 1909), new combination [Sri Lanka], *O. patruus* (Distant, 1909) new combination [Sri Lanka], *O. pervalidus* (Distant, 1909) new combination [India: Darjeeling, Nepal: Bagmati-zone]; *O. straminipes* (Distant, 1909), new combination [India: Himachal Pradesh, Nepal: Kasuki (new record, cf. Fig. 10D)]; and *O. tibialis* (Distant, 1909), new combination [India: Himachal Pradesh] Images of all relevant type materials are available on BMNH 'Data Portal' site (https://data.nhm.ac.uk), except for the damaged holotype of *O. tibialis*.

On the other hand, the following seven Oriental species are currently regarded as 'incertae sedis' and need further verification: *Megacoelum annulicorne* Reuter, 1891 [Indonesia: Java], *M. celebense* Poppius, 1915 [Indonesia: Sulawesi], *M. esmedorae* Ballard, 1927 [India: Tamil Nadu], *M. hampsoni* Distant, 1904 [India: Tamil Nadu], *M. horni* Poppius, 1911 [Sri Lanka], *M. oberthuri* Poppius, 1915 [India: Karnataka], and *M. picturatum* Distant, 1904 [Myanmar].

***Tondomiris puguis*, new species**

(Figs. 9E−J, 10A–C, 11A–I, 12)

Type material. Holotype: male, **PHILIPPINES**: North Luzon, Mountain Prov., Mt. Puguis, 1,800–2,000 m alt., 17°03′N 121°03′E, M. Sakai, 18 July 1985 (AMNH_PBI 00380681) (NSMT).

Diagnosis. Recognised by the characters mentioned in generic diagnosis (see above) and key (see below).

Description. Male. COLOURATION: As in generic description. Body widely dark reddish brown (Fig. 10A); lateral and ventral surface widely yellowish brown. Head shiny dark brown dorsally, with pale brown below level of antennal insertions (Fig. 10C); vertex about as wide as an eye in dorsal view; frons and clypeus partly suffused with red; eye in lateral view occupying of head height. Antenna reddish brown; segment I yellowish brown, speckled with dark spots, slightly thicker than II; basal ¼ of segment II grayish yellow, with an obscure ring subbasally. Labium pale grayish brown; apical half of segment IV darkened. Pronotum shiny dark reddish brown, with creamy yellow collar, anterior median part, and posterior to lateral margins; pleura widely yellowish brown, weakly shining; mesepisternum reddish brown; dorsal margin of propleuron and posterior margin of mesepimeron suffused with red (Fig. 10C); scent efferent system yellow; scutellum shiny reddish brown, bulbous at anterior ⅔, with yellow apex. Hemelytron dark reddish brown; base and apex of cuneus yellowish brown, partly tinged with red; membrane including veins and areolar cells pale smoky brown, with pale, semitransparent border to inner margin of cuneus. Coxae and legs pale brown, except for reddish basal half of metacoxa; pro- and mesofemora with obscure spots apically; metafemur with dark base and two apical bands; all tibiae with dark annulations or spots; all tarsi pale brown, with darkened apical halves of distal tarsomeres. Abdomen pale brown, with reddish brown stripes ventrolaterally and darkened genital segment. Surface, vestiture and structure as in generic description.

Measurements. See Table 1.

Etymology. Named for the type locality, Mt. Puguis in Luzon; a noun in apposition.

Distribution. Only known from holotype taken in Philippines (northern highlands of Luzon) (Fig. 12).

Biology. Unknown.

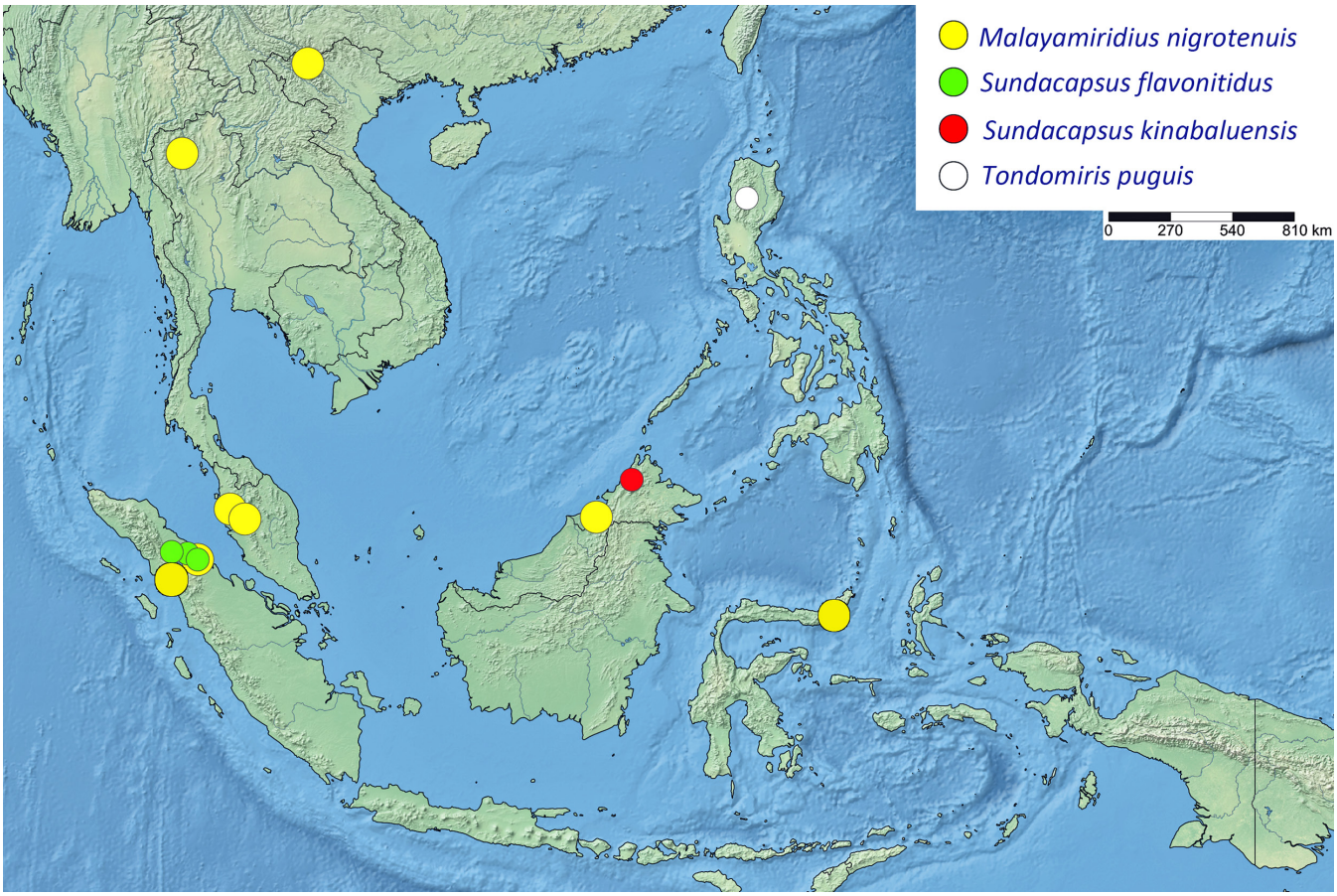

Fig. 12. Map showing distributions of four new mirine species.

Key to the Oriental genera discussed

1. Vertex with a recognisable, longitudinal, mesal sulcation (cf. Figs. 2J, 11N) 2
– Vertex smooth, lacking mesal sulcation; if present, sulcation faint, shallow, or hardly visible (due to highly polished surface structure as in Fig. 10B) 7
2. Body generally pale stramineous or pale brown, sometimes with a dark mesal stripe on pronotum, or with reddish or orange stripe on scutellum 3
– Basic colouration castaneous to fuscous; pronotum and scutellum without such striped pattern 4
3. Body elongate; antenna uniformly pale brown, not significantly darkened; pronotum weakly shining, partly roughened or matte, pubescent (Yasunaga, 1997) ..... *Creontiades* Distant
– Body elongate oval (cf. Fig. 10E); antenna at least partly darkened; pronotum shiny, almost impunctate and glabrous ..... *Poppiocapsidea* Yasunaga
4. Medium- or rather small-sized (total body length < 6.2 mm); body remarkably slender, more than 3.5 times as long as maximum width (Fig. 1A–C); pygophore with a mesal spine at ventral apical part but lacking spine at base of left paramere (Fig. 2D) ..... *Malayamiridius*, new genus
– Large-sized (body length > 7 mm, usually more than 8 mm); body elongate but total length less than 3.2 times as long as maximum width; pygophore smooth, lacking such ventral spine but usually with a spine or conical process at base of left paramere (Fig. 11J, M) 5
5. Pronotum, scutellum, and hemelytron usually with uniformly distributed, semierect setae (Figs. 5J, 10D); scutellum rather flat or weakly arched ..... *Orientomiris* Yasunaga
– Pronotum, scutellum, and hemelytron almost glabrous or with very sparsely distributed, upright setae (Figs. 9B, 11B); scutellum usually arched, tumid (Fig. 11B) 6
6. Body smaller, less than 8 mm in length; dorsum moderately shining ..... *Megacoelum* Fieber
– Body more than 9 mm; dorsum well-polished, oily shiny ..... *Vairocanamiris* Yasunaga
7. Dorsal surface highly polished, oily shiny; pronotum impunctate and very smooth; vestiture on dorsum absent or only sparsely distributed 8
– Dorsal surface more or less shining, but with punctures at least on pronotum and scutellum; one or both of pronotum and hemelytron as a rule with uniformly distributed simple setae 10
8. Labium very short, not surpassing apex of procoxa ..... *Liocapsus* Poppius
– Labium longer 9
9. Labium reaching but not exceeding apex of mesocoxa ..... *Sundacapsus*, new genus
– Labium very long, exceeding apex of metacoxa, reaching abdominal sternum VI ..... *Tondomiris*, new genus
10. Labium shorter than metafemur; endosoma with inner elongate sclerite and apical sclerite; female genital chamber nearly symmetrical, dorsally with a sclerotised, median keel dividing each lateral oviduct ..... *Orientocapsus* Yasunaga
– Labium as long as or longer than metafemur; endosoma principally composed of four sclerites; female genital chamber and posterior wall heavily sclerotised and asymmetrical (Fig. 8M–O) ..... *Philostephanus* Distant

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