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Revision of the Genera *Pseudatheta* Cameron and *Phymatura* Sahlberg (Coleoptera, Staphylinidae, Aleocharinae) from Japan

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Abstract

New taxonomic and distributional data for five species of the genera *Pseudatheta* Cameron, 1920 and *Phymatura* Sahlberg, 1876 from Japan are provided, and the following seven species are recognized: *Pseudatheta crenulicauda* (Bernhauer, 1907), **comb. nov.** (= *Pseudatheta similis* Pace, 2010, **syn. nov.**); *Pseudatheta taiwanensis* Pace, 2008; *Pseudatheta hilaris* (Sharp, 1888), **comb. nov.**; *Pseudatheta cooteri* Pace, 1998; *Pseudatheta elegans* Cameron, 1920; *Phymatura japonica* Cameron,1933, **stat. rev.** (= *Phymatura cooteri* Assing, 2005, **syn. nov.**); and *Phymatura russa* Assing, 2021. *Pseudatheta cooteri*, *Ps. elegans*, *Ps. taiwanensis*, and *Ph. russa*, are recorded from Japan for the first time. *Platyola oligotinula* (Sharp, 1888), **comb. rev.** is excluded from *Pseudatheta* and confirmed as a member of the genus *Platyola* Mulsant & Rey, 1875. Lectotypes are designated for two species, *Atheta crenulicauda* (= *Ps. crenulicauda* **comb. nov.**) and *Homalota oligotinula* (= *Platyola oligotinula* **comb. rev.**). Although the two genera were reviewed in this paper, there are some diagnostic problems in the two genera and in species classification and identification, and further studies, including DNA analysis, are required in the future. We also examined specimens from outside of Japan relevant to the taxonomic study of Japanese species.

Key words: East Asia, Homalotini, Bolitocharina, rove beetle, new combination, new synonymy

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Introduction

In Japan, the aleocharine subtribe Bolitocharina of the tribe Homalotini comprises 23 species in six genera, including *Pseudatheta* Cameron, 1920 and *Phymatura* Sahlberg, 1876 (Shibata *et al.*, 2013; Schülke & Smetana, 2015). Members of these two genera are similar in their external morphology, and species assigned to one have occasionally been subsequently transferred to the other (Pace 1992, 2010; Kim & Ahn, 2016). The type species of the genus *Pseudatheta*, *Ps. elegans* Cameron, 1920, were collected from fungi (Cameron, 1920), and fungal spores were found in their gut (Ashe, 1993). Other species of these genera are also found on fungi, but their identification has been challenging. Of the 27 species of *Pseudatheta* Cameron, 1920 known from the Old World (Newton 2022), 26 are distributed in Asia (Sharp, 1888; Cameron, 1920, 1939; Pace, 1987, 1988, 1989, 1992, 2007, 2008, 2010, 2012, 2014, 2016) and one is found in Africa (Cameron, 1932). From Japan, only one species, *Ps. oligotinula* (Sharp, 1888), is known (Pace, 1992; Schülke & Smetana, 2015) but is not considered to belong to this genus or to the tribe Homalotini.

Worldwide, 24 species of *Phymatura* Sahlberg, 1896 have thus far been reported (Newton, 2022), with only one species, *Ph. crenulicauda* (Bernhauer, 1907), from Japan (Schülke & Smetana 2015). However, *Ph. japonica* Cameron, 1933, regarded as a synonym of *Ph. crenulicauda*, is a valid species (Shibata *et al.*, 2013). Most Japanese species of the subfamily Aleocharinae were described by Sharp (1874, 1888), Cameron (1933), and Bernhauer (1907, 1939), but without sufficient line drawings or photographs, although a few species were later redescribed in detail (e.g., Maruyama *et al*., 2014; Yamamoto & Maruyama, 2016; Hashizume *et al*., 2023).

The type materials of Sharp (1888) and Cameron (1933) are housed at the Natural History Museum in London and were examined in 2011 by MM. The type materials of Bernhauer (1907) are housed at the Field Museum of Natural History in Chicago and were examined in August and September 2011 by SY and MM. Based on the results, *Oxypoda hilaris*, isolated in Honshu and described by Sharp (1888), should be considered as a member of the genus *Pseudatheta*. Judging from the original description (Pace, 2010), the aedeagus of *Pseudatheta similis* Pace, 2010 is identical to that of the lectotype of *Atheta crenulicauda*. Moreover, *Ph. japonica* Cameron, 1933 was found to not be a synonym of *Ph. crenulicauda*, whereas *Ph. cooteri*, described by Assing (2005) from China, should be considered a junior synonym of *Ph. japonica*.

In this study, the known Japanese species noted above are redescribed, with respect to taxonomic changes. In addition, the occurrence in Japan of three species of the genus *Pseudatheta* and one species of the genus *Phymatura* is recorded for the first time.

Materials and Methods

The materials examined in the present study are deposited in the following collections: the Natural History Museum (BMNH), London, UK, the Field Museum of Natural History (FMNH), Chicago, USA, the Ehime University Museum (EUM), Matsuyama, Japan, the Kyushu University Museum (KUM), Fukuoka, Japan, and Toshio Kishimoto private collection (TKc), Shizuoka, Japan, The label data of the type specimens are quoted verbatim, with the text in double quotation marks (“”); a slash (/) was used to separate lines on the same label, and a double slash (//) was used to separate different labels on the same pin. We refer to the side of the median lobe of the aedeagus containing the medial foramen as ventral; the opposite side is referred to as dorsal. For distributional data, we mainly referred to Schülke & Smetana (2015) and Newton (2022).

Dissected body parts were soaked in a 10% KOH solution and then heated in a hot water bath until the muscles and other soft tissues were dissolved and the specimens become suitable for observations. Later, they were embedded in Euparal and as permanent specimens on glass plates, following the procedure of Maruyama (2004). Morphological observations were conducted using Olympus SZX10, Leica S8AP0O and Nikon ECLIPSE Ci-L microscopes. Habitus photos were taken using a Sony α 7R IV digital camera with a Canon MP-E65 mm 1–5× macro lens. The photos were combined in Zerene Stacker software (Zerene System LLC, USA). Line drawings were made in Clip Studio Paint Pro (Celsys Inc., Tokyo, Japan) from photographs or sketches. Some line drawings were traced from MM’s line drawings of type specimens. Figures were edited using GIMP 2. 8. 22 software.

The following abbreviations were applied: BL—length of body from anterior margin of clypeus to posterior margin of tergite VII; FBL—length of forebody from anterior margin of clypeus to posterior margin of elytral suture; HL—length of head from anterior margin of clypeus to posterior margin of vertex; HW—maximum width of head, including eyes; HTL—length of hind tibia; PL—maximum length of pronotum; PW—maximum width of

pronotum; EL—length of elytra from apex of scutellar shield to posterior elytral margin; EW—maximum width of elytra. All measurements are in millimeters and are used in the format "minimum-maximum".

Taxonomy

Tribe Homalotini Heer, 1839

Subtribe Bolitocharina Thomson, 1859

Genus *Pseudatheta* Cameron, 1920

[Japanese name: Hime-kinokotsuyakeshi-hanekakushi-zoku]

Pseudatheta Cameron, 1920: 224 (original description; type species: *Pseudatheta elegans* Cameron, 1920).

Remarks. Species of this genus often have intraspecific variation in body coloration, the ratio of the length and width of each antennomere, and the processes on the posterior margin of the tergite VIII of males, which do not necessarily correspond to those described or illustrated in this paper. The genus *Pseudatheta* can be distinguished from the genus *Phymatura* by following character states: mesoventrite without longitudinal carina; number of setose lobes on flabellum of hind wing varies from zero to one.

Key to species of the genus *Pseudatheta* in Japan

1. Body larger, forebody length 1.00–1.25 mm; male sternite VI with small medial lobe on posterior margin (Fig. 4C); median lobe of aedeagus without ventral process; distal portion of spermatheca long, strongly curved (Fig. 5C, F) 2
- Body smaller, forebody length 0.86–1.01 mm; male sternite VI without medial lobe on posterior margin; median lobe of aedeagus with ventral process; distal portion of spermatheca short, not curved or slightly curved (Fig. 7D, G) 3
2. Apical process of aedeagus dilated apically in lateral view (Fig. 5B) . . . . . *Ps. crenulicauda* (Bernhauer), **comb. nov.**
- Apical process of aedeagus parallel to near apex, not dilated in lateral view (Fig. 5E) . . . . . *Ps. taiwanensis* Pace
3. Apical process of median lobe of aedeagus simply curved (Fig. 7B); ventral process of median lobe of aedeagus with a distinct angle on dorsal side (Fig. 7C); distal portion of spermatheca nearly conical shape (Fig. 7D) . . . . . *Ps. cooteri* Pace
- Apical process of median lobe of aedeagus sinuate (Fig. 7F); ventral process of median lobe of aedeagus sinuate; distal portion of spermatheca nearly reniform (Fig. 7G) . . . . . *Ps. elegans* Cameron

Remarks. *Pseudatheta hilaris* (Sharp), **comb. nov.**, is excluded from this key because only female specimens were available.

Pseudatheta crenulicauda (Bernhauer, 1907), comb. nov.

(Figs. 1A, 2C, 5A–C)

[Japanese name: Miiro-kinokotsuyakeshi-hanekakushi]

Atheta (*Datomicra*) *crenulicauda* Bernhauer, 1907: 398 (original description; type locality: "Bukenji" [Yokohama-shi, Kanagawa-ken, central Honshu, Japan]); Sawada, 1977: 217 (as a synonym of *Ph. oligotinula*).

Phymatura crenulicauda (Bernhauer, 1907); Pace, 1984: 54 (transferred to the genus *Phymatura* from the genus *Atheta*); Shibata *et al*., 2013: 115 (catalogue); Schülke & Smetana, 2015: 633 (catalogue).

"*Phymatura oligotinula*": Sawada, 1977: 217 (redescription; misidentification).

"*Pseudatheta oligotinula*": Pace, 1992: 242 (transferred to genus *Pseudatheta* from *Phymatura*; probably based on Sawada (1977)).

Pseudatheta similis Pace, 2010: 268 (original description; type locality: "China: Sichuan, Ganzi Prefecture, Daxue Shan, Gongga Shan, Hailougou glacier park, 102°04'E 29°36'N, river valley, ca. 1 km above camp I, 2100 m"); Schülke & Smetana, 2015: 634 (catalogue); Pace, 2016: 301 (Yunnan). **Syn. nov.**

Material examined. Type material. *Atheta* (*Datomicra*) *crenulicauda*: Lectotype: here designated, male "Hans Sauter 4000 / Bukenji 10 XI 05 / Unter Schilfhaufen [handwritten] // Bukenji / Japan. Sauter [handwritten] // crenulicauda / Brnh. Typ. [handwritten] // Chicago NHMus / M. Bernhauer / Collection" (abdominal segments VIII–X and aedeagus were dissected and mounted in Euparal by MM) (FMNH).

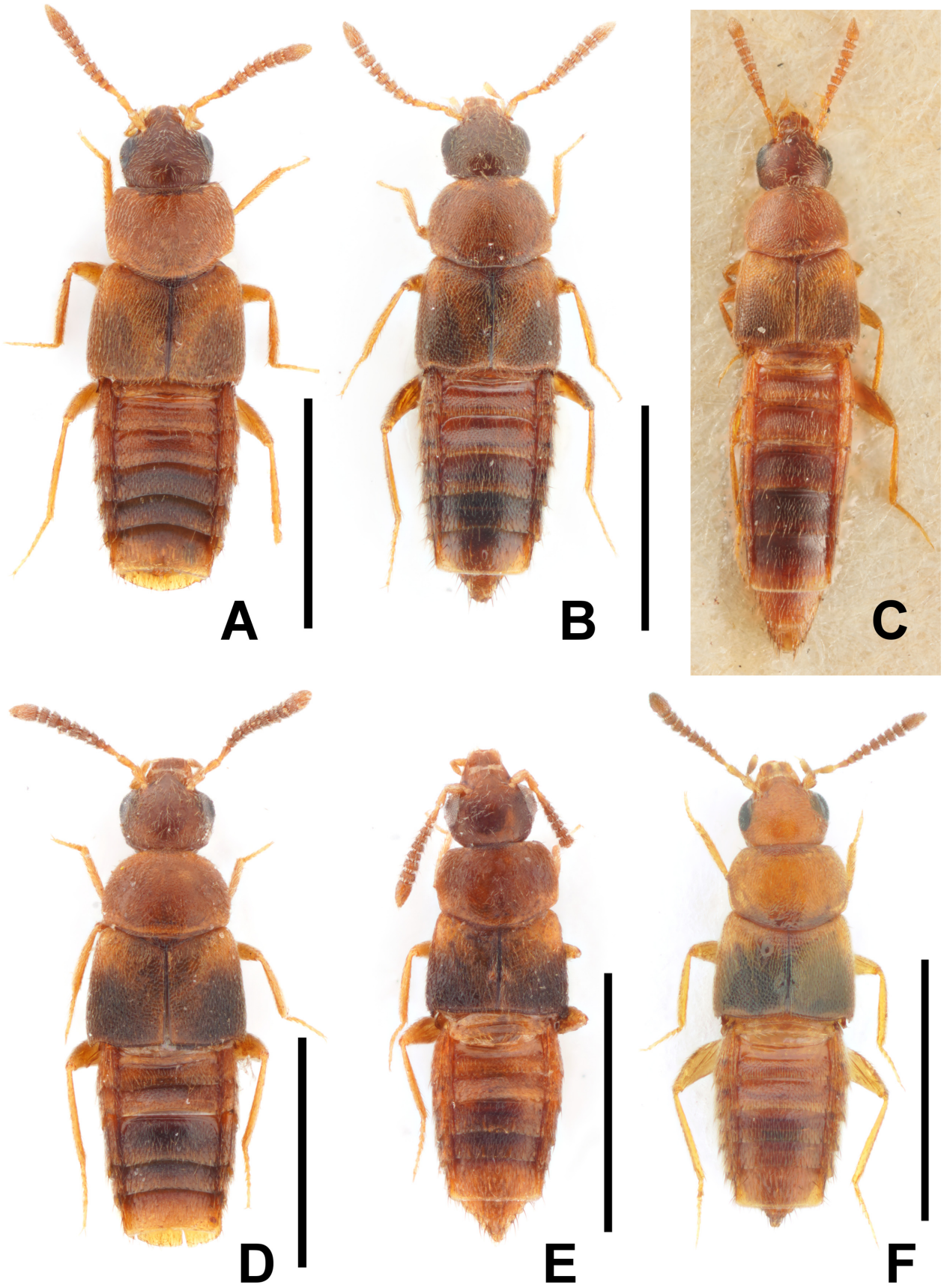

FIGURE 1. Habitus of *Pseudatheta* spp. A. *Pseudatheta crenulicauda* (Bernhauer, 1907), **comb. nov.**; B. *Pseudatheta taiwanensis* Pace, 2008; C. *Pseudatheta hilaris* (Sharp, 1888), **comb. nov.**, lectotype of *Oxypoda hiralis*; D. *Pseudatheta thailandensis* Pace, 1992; E. *Pseudatheta cooteri* Pace, 1998; F. *Pseudatheta elegans* Cameron, 1920. Scale bars: 1.0 mm.

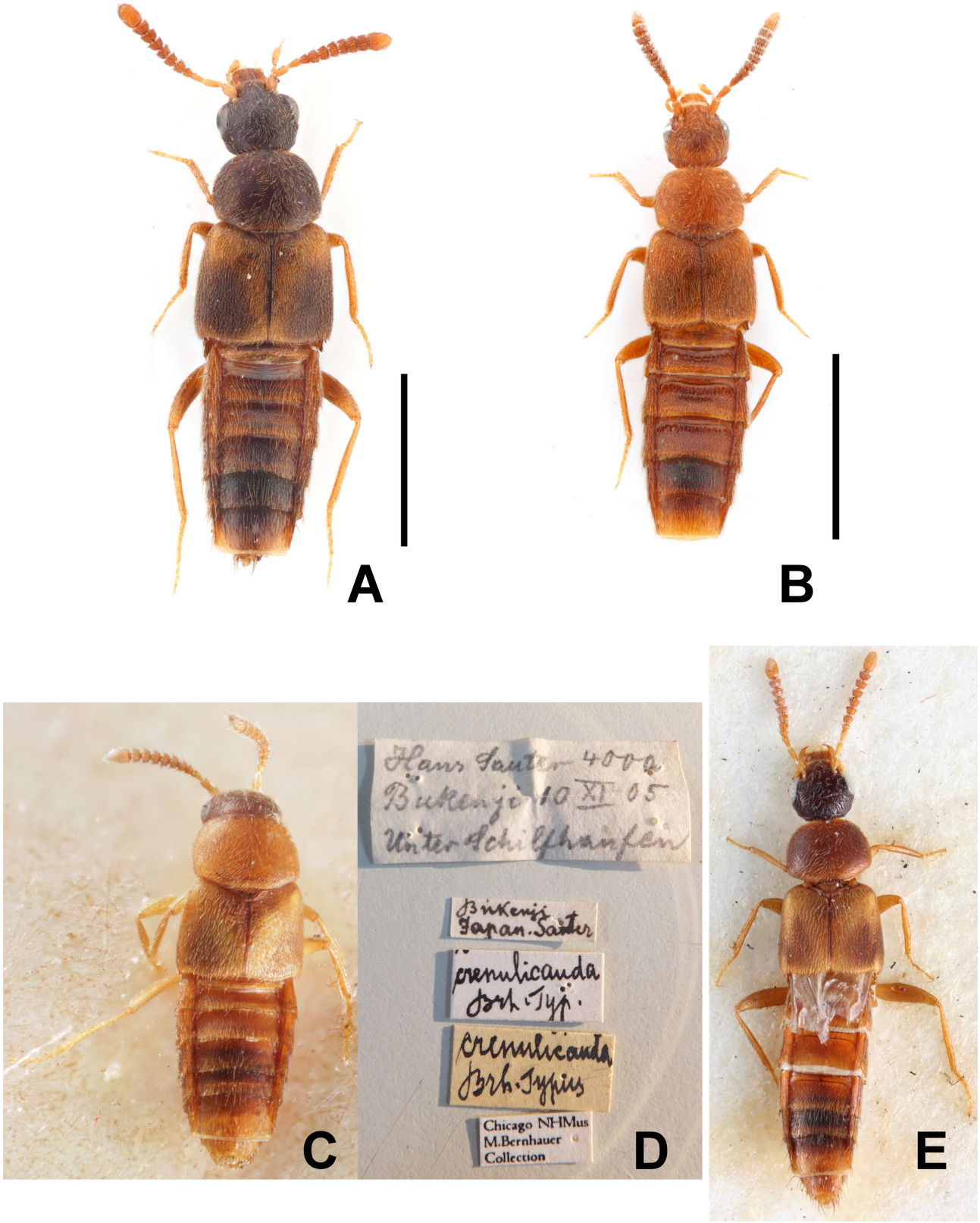

FIGURE 2. Habitus of *Phymatura* spp. and type specimens examined. A. *Phymatura japonica* Cameron, 1933, **stat. rev.**; B. *Phymatura russa* Assing, 2021; C. lectotype of *Atheta* (*Datomicra*) *crenulicauda* Bernhauer, 1907 (=*Pseudatheta crenulicauda* **comb. nov.**); D. labels of C; E. holotype of *Phymatura japonica* Cameron, 1933, **stat. rev.** Scale bars: 1.0 mm for A–B.

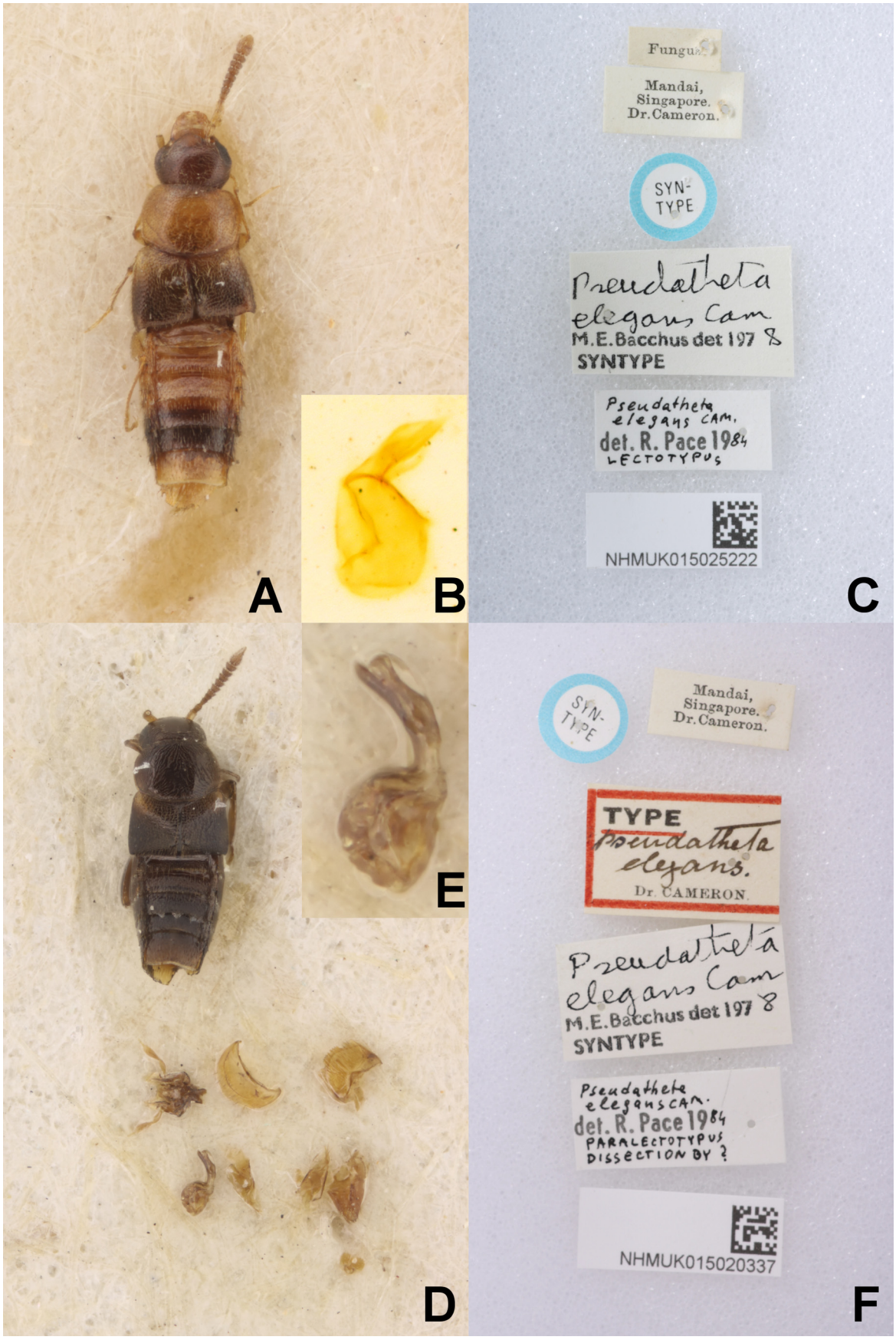

FIGURE 3. Syntypes of *Pseudatheta elegans* Cameron, 1920. A. habitus in dorsal view; B. median lobe of aedeagus of A; C. labels of A; D. habitus in dorsal view and dissected body parts; E. median lobe of aedeagus of D; F. labels of D. (photo by K. Matsumoto, used with permission).

Paralectotype: 1 female, “crenulicauda / Bernh. Cotypus [handwritten] // Unzen. 2600’ / Japan. Sauter [handwritten] // Chicago NHMus / M. Bernhauer / Collection” (abdominal segments VIII–X and spermatheca were dissected and mounted in Euparal by MM) (FMNH).

Additional material examined. JAPAN: [**Aomori-ken**]: 1 male, Yasumiya, Towada-shi, 4–5 VIII 1966, M. & M. T. Chûjô leg. (KUM); [**Miyagi-ken**]: 2 males, 1 female, Yoshida, Taiwa-chô, 20 VIII 2009, J. Aoki leg. (KUM); [**Fukushima-ken**]: 1 male, Shitokigawa-keikoku, Iwaki-shi, 24 V 1992, K. Haga leg. (KUM); [**Tochigi-ken**]: 1 male, 1 female, Watarase, 6 V 1979, M. Tao leg. (KUM); [**Gunma-ken**]: 1 male, Naganohara, Naganohara-machi, 9 VIII 1997, T. Kishimoto leg. (TKc); [**Saitama-ken**]: 1 male, 1 female, Yoshimi-machi, 16 VII 2000, K. Toyoda leg. (KUM); 3 males, 2 females, Mitsumine, Chichibu-shi, 28 V 1997, M. Maruyama leg. (KUM); [**Chiba-ken**]: 1 male, Noda-shi, 17 V 1991, T. Kishimoto leg. (TKc); [**Tokushima-ken**]: 1 male, Shikibidani, Naka-chô, 17 VII 2010, J. Aoki leg. (KUM); [**Ehime-ken**]: 1 male, Sara-ga-mine, 29 IV 1962, S. Hisamatsu leg. (EUM); Komenono, 18 VII 1975, A. Yonetsu leg. (EUM); 1 male, Sara-ga-mine, 27 VI 1959, M. Satô leg. (EUM); [**Kochi-ken**]: 1 male, 1 female, Yusuhara-chô, 5 V 2010, T. & T. Miyata leg. (KUM); 2 males, 1 female, Kamioriwatashi, Yusuhara-chô, 24 V 1997, M. Sakai leg. (EUM); [**Nagasaki-ken**]: Tsushima Is.: 1 male, Kamiagatamachi Sasuna, Tsushima-shi, 18 VI 2022, T. Hashizume leg. (KUM).

Redescription. Measurements (n = 5): BL ≈ 1.86–2.39; FBL, 1.00–1.22; HL, 0.34–0.38; HW, 0.38–0.44; PL, 0.35–0.42; PW, 0.50–0.59; EL, 0.38–0.48; EW, 0.60–0.73. (Lectotype of *Atheta crenulicauda*: BL ≈ 2.0; PL, 0.40; PW, 0.55; HTL, 0.41).

Relative length of antennomeres I–XI (n = 1): 25: 24: 21: 11: 11: 11: 11: 10: 11: 12: 37. Ratio of length/width of antennomeres I–XI (n = 1): 1.84: 2.07: 2.16: 0.88: 0.71: 0.68: 0.64: 0.55: 0.57: 0.63: 1.83.

Body (Figs. 1A, 2C) reddish brown; head darker; posterolateral areas of elytra darker; abdominal segments V–VII darker.

Head almost as long as wide, HW/HL: 1.11–1.26; surface densely covered with setae. Antenna with antennomeres I–III and XI longer than wide, antennomeres IV–X wider than long; antennomeres I and II with rounded distal end, antennomeres III–X strongly angulated near distal end, antennomere XI oval.

Pronotum transverse, PW/PL: 1.36–1.50, PW/HW: 1.32–1.41; surface densely covered with setae, finely punctured, without microsculpture; posterior margin slightly bisinuate. Elytra wider than long, EW/EL: 1.60–1.70, EL/PL: 1.00–1.10, EW/PW: 1.20–1.24; surface densely covered with setae and finely punctured; posterior margin sinuate near posterolateral corners. Hind wings well developed; flabellum with one seta. Mesoventrite without longitudinal carina; mesoventral process extended to slightly beyond middle of mesocoxal cavities, with pointed apex; metaventral process shorter than mesoventral process, with rounded apex; isthmus present.

Abdomen slightly narrowed posteriad; surface densely covered with setae.

Male. Elytra with a pair of small tubercles at about posterior 1/3 on sutural margin. Sternite VI with small medial lobe on posterior margin. Tergite VII with a tubercle on posteromedian area. Tergite VIII (Fig. 5A) with a tubercle on median area; three to five processes on each side of posterior margin, outer ones slightly curved, longer and sharper than the others. Aedeagus as in Fig. 5B; median lobe with large basal bulb; apical process broad, dilated in lateral view, apical end thin and elongated, apex pointed; flagellum moderately long.

Female. Spermatheca (Fig. 5C) curved twice, with a transverse band-like structure at base of distal portion; distal portion elongated, U-shaped; median portion elongated, slightly curved; proximal portion longer than wide.

Distribution. Japan (Honshu, Shikoku, Tsushima Is., Kyushu?); China (Sichuan, Yunnan).

Remarks. Sawada (1977) redescribed this species in detail as *Ph. oligotinula*. Based on its characteristics (e.g., small body size, absence of the longitudinal carina on the mesoventrite, and the shape of the median lobe of the aedeagus and the spermatheca), this species belongs to *Pseudatheta* rather than to *Phymatura*. The illustration of the median lobe of the aedeagus of *Ps. similis*, shown by Pace (2010), fully agrees with that of *Ps. crenulicauda* (as *Ps. similis* **syn. nov.**). Pace (2016) recorded this species from Yunnan as *Ps. similis*. Kim & Ahn (2014) listed *Ph. crenulicauda* as a Korean species, based on the record of “*Ph. japonica*” from North Korea in Paśnik (2001), but later found that the specimens examined in Paśnik (2001) were not *Ph. crenuicauda* (Kim & Ahn, 2016). While the true species identity of these specimens is unknown, we tentatively consider this record as a record of *Ph. japonica* from North Korea. This species can be distinguished from its congeners by the apically dilated apical process and the absence of a ventral process of the median lobe of the aedeagus. There is currently no practical key to distinguish the female of this species from the female of its allies [i.e., *Ps. hilaris*, *Ps. taiwanensis*, *Ps. thailandensis*, and *Ph. bigranipennis* (Bernhauer, 1915)]. Thus, despite our detailed morphological observations, these species could not

be distinguished based on female specimens. The paralectotype of this species was collected from Unzen, Nagasaki, Kyushu, and is the only record of this species from Kyushu; however, because it was a female, it could not be positively identified. Further study is needed to allow morphologically based species identification in *Pseudatheta* females, supported perhaps by DNA information (see also the remarks on *Ph. hilaris*).

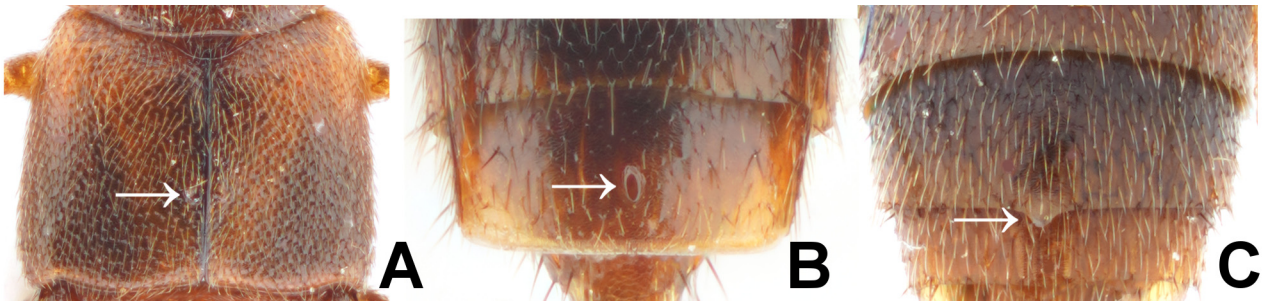

FIGURE 4. *Pseudatheta taiwanensis* Pace, 2008. A. male elytra (white arrow indicates granules); B. male tergite VII (white arrow indicates granule); C. male sternite VI (white arrow indicates medial lobe).

***Pseudatheta taiwanensis* Pace, 2008**

(Figs. 1B, 4, 5D–F)

[Japanese name: Taiwan-miiro-kinokotsuyakeshi-hanekakushi]

Pseudatheta taiwanensis Pace, 2008: 146 (original description; type locality: "Taiwan, Kaohsiung Hs., for. abv. Tona For. Sta. 1100 m").

Materials examined. JAPAN: [**Hokkaido**]: 2 males, Midorimachi, Assabu-chô, 8 IX 2022, T. Hashizume leg. (KUM); 2 males, Ôsawaguchi, Nopporo-shinrin-kôen, Ebetsu-shi, 16–19 VI 2001, S. Hori leg. (KUM); 1 male, 1 female, Kannonzawa-rindô, Minami-ku, Sapporo-shi, 8 VIII 2021, T. Nozaki leg. (KUM); [**Saitama-ken**]: 1 male, 2 females, Futago-yama, 28 VIII 1984, H. Oda leg. (KUM); [**Tokyo-to**]: 1 male, Nippara, Okutama-machi, 15 VI 1997, K. Haga leg. (KUM); 1 male, 1 female, same data, but 5 V 1998 (KUM); [**Tottori-ken**]: 1 male, Hyô-no-sen, Wakasa-chô, 6–9 VIII 1968, I. H. B. C. (EUM); [**Fukuoka-ken**]: 2 males, 1 female, Hiko-san, Soeda-machi, 23 V 2020, S. Inoue leg. (KUM); 1 male, 2 female, Hiko-san, 7 V 1971, K. Takeno leg. (KUM); 1 male, Hiko-san, 15 X 1968, M.-T. Chûjô leg. (KUM); [**Kumamoto-ken**]: 1 male, Shiratori-yama, Izumimachi Momigi, Yatsushiro-shi, 14 V 2021, S. Inoue leg. (KUM); [**Oita-ken**]: 1 male, Kyûsuikei, Kokonoe-machi, 31 V–10 VI 2011, S. Imasaka leg. (KUM).

Redescription. Measurements (n = 5): BL ≈ 1.90–2.13; FBL: 1.09–1.25; HL: 0.34–0.38; HW: 0.39–0.44; PL: 0.38–0.40; PW: 0.53–0.59; EL: 0.36–0.43; EW: 0.62–0.72.

Relative length of antennomeres I–XI (n = 1): 20: 22: 18: 10: 12: 13: 13: 11: 12: 12: 33. Ratio of length/width of antennomeres I–XI (n = 1): 1.90: 2.27: 1.86: 0.80: 0.73: 0.78: 0.77: 0.63: 0.73: 0.69: 1.79.

Body (Fig. 1B) reddish brown; head darker; posterolateral areas of elytra darker; abdominal segments V–VII darker.

Head almost as long as wide, HW/HL: 1.07–1.23; surface densely covered with setae. Antenna with antennomeres I–III and XI longer than wide, antennomeres IV–X wider than long; antennomeres I and II with rounded distal end, antennomeres III–X strongly angulated near distal end, antennomere XI oval.

Pronotum transverse, PW/PL: 1.35–1.45, PW/HW: 1.31–1.41; surface densely covered with setae, finely punctured, without microsculpture; posterior margin slightly bisinuate. Elytra wider than long, EW/EL: 1.60–1.79, EL/PL: 0.97–1.06, EW/PW: 1.14–1.22; surface densely covered with setae and finely punctured; posterior margin sinuate near posterolateral corners. Hind wings well developed; flabellum with one seta. Mesoventrite without longitudinal carina; mesoventral process extended to slightly beyond middle of mesocoxal cavities, with rounded apex; metaventral process shorter than mesoventral process, with rounded apex; isthmus present.

Abdomen slightly narrowed posteriad; surface densely covered with setae.

Male. Elytra with a pair of small tubercles at about posterior 1/3 on sutural margin. Sternite VI with small medial lobe on posterior margin. Tergite VII with a tubercle on posteromedian area. Tergite VIII (Fig. 5D) with a tubercle on median area; three to five processes on each side of posterior margin, outer ones slightly curved, longer

and sharper than the others. Aedeagus as in Fig. 5E; median lobe with large basal bulb; apical process broad, parallel to near apex, not dilated in lateral view, apical end thin and elongated, apex pointed; flagellum moderately long.

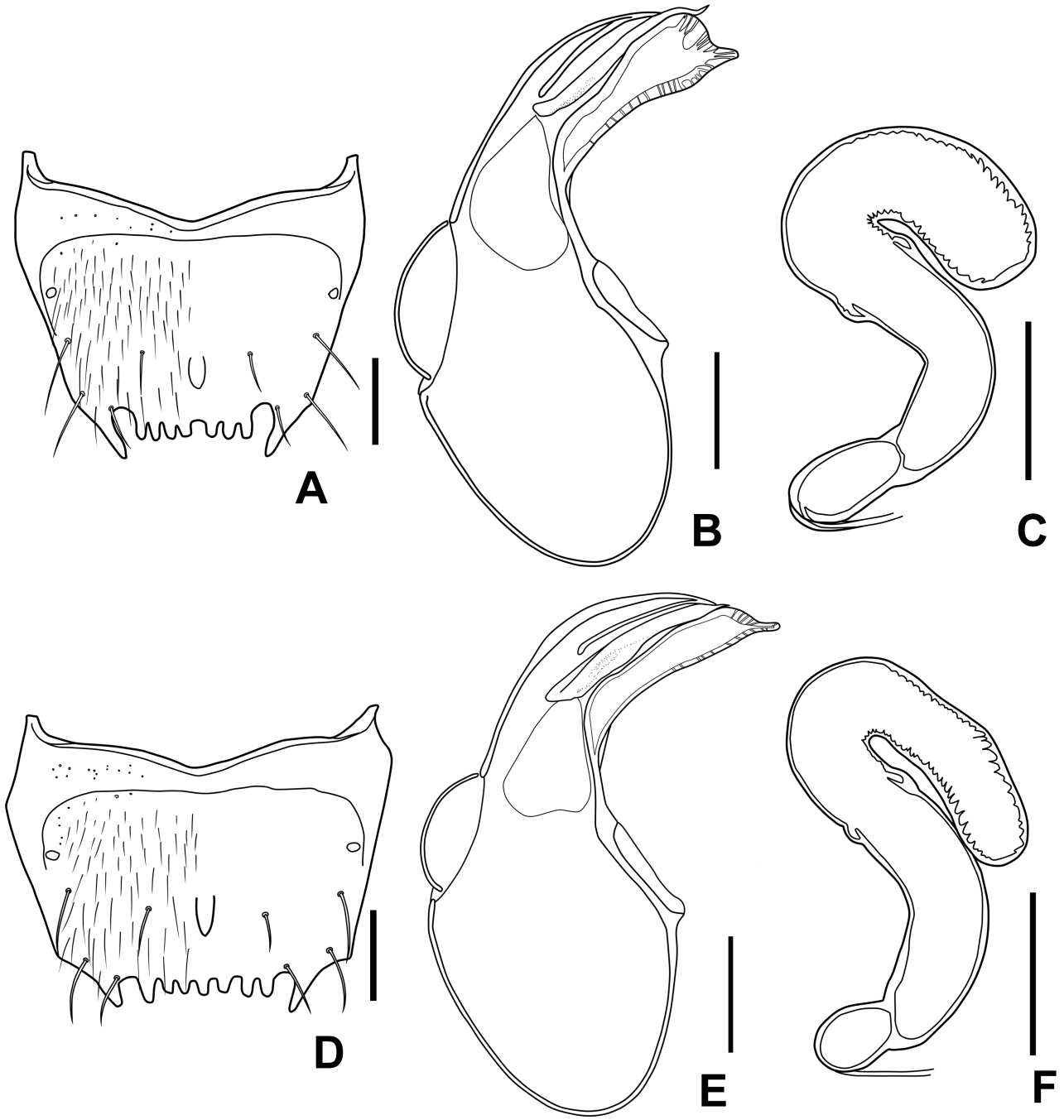

FIGURE 5. *Pseudatheta* spp. A–C: *Pseudatheta crenulicauda* (Bernhauer, 1907), **comb. nov.**, D–F: *Pseudatheta taiwanensis* Pace, 2008. A, D. male tergite VIII in dorsal view; B, E. median lobe of aedeagus in lateral view; C, F. spermatheca. Scale bars: 0.1 mm.

Female. Spermatheca (Fig. 5F) curved twice, with a transverse band-like structure at base of distal portion; distal portion elongated, U-shaped; median portion elongated, slightly curved; proximal portion longer than wide.

Distribution. Japan (Hokkaido, Honshu, Kyushu)—new record; Taiwan.

Remarks. This species can be distinguished from *Ps. crenulicauda* by the non-dilated, parallel-sided apical process of its aedeagus. Most of the aedeagi of specimens from Japan have an abruptly narrowed and protruding apical part on their apical process, which is not seen in Pace's illustrations of the specimen from Taiwan (2008).

Similar aedeagi are seen in a few Japanese specimens, but it is likely that they were damaged. While we cannot rule out the possibility that the original description of *Ps. taiwanensis* was based on a specimen with a damaged apical process of aedeagus, we nonetheless identified the Japanese specimen as *Ps. taiwanensis*. The female morphology is not informative for distinguishing this species from *Ps. crenulicauda* and other relatives.

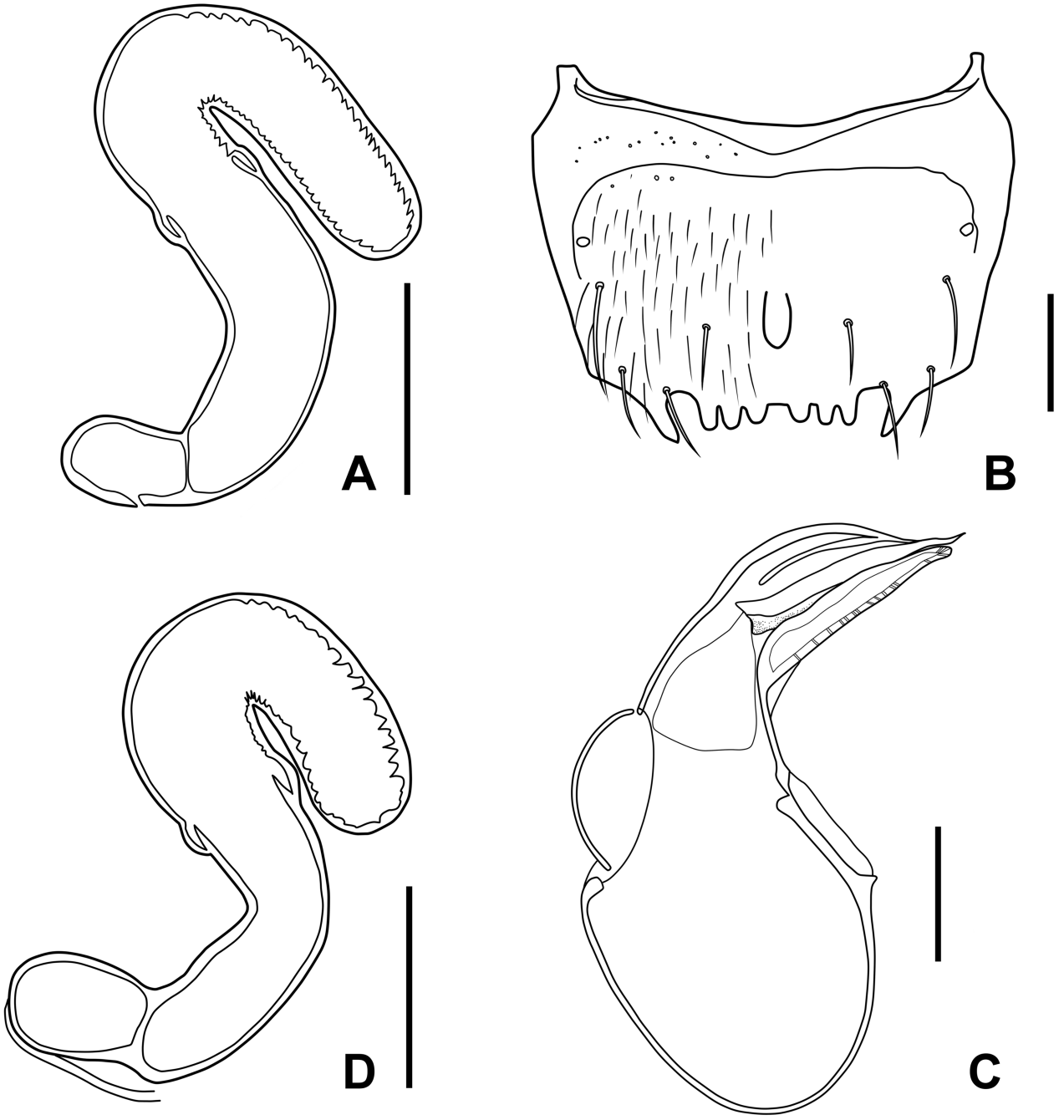

FIGURE 6. *Pseudatheta* spp. A: *Ps. hilaris* (Sharp, 1888), **comb. nov.**, B–D: *Ps. thailandensis* Pace, 1992. A, D. spermatheca; B. male tergite VIII in dorsal view; C. median lobe of aedeagus in lateral view. Scale bars: 0.1 mm.

***Pseudatheta hilaris* (Sharp, 1888), comb. nov.**
(Figs. 1C, 6A)

Oxypoda hilaris Sharp, 1888: 285 (original description; type locality: "Nikko" [Nikkô-shi, Tochigi-ken, central Honshu]); Schülke & Smetana, 2015: 711 (catalogue).

Type material. Lectotype: here designated, female, "Oxypoda hi- / laris Type / D.S. / Nikko. Japan. / 31.10.80. Lewis [handwritten, paper card] // Type [red round label pinned by a curator] // Japan. / G. Lewis. // Sharp Coll. / 1905-313." (abdominal segments VIII–X and spermatheca were dissected and glued on paper card, and labium and maxilla were mounted in Euparal by MM). (BMNH)
Paralectotypes: 2 females, "Kuro / matsu [handwritten, paper card, underside of label] // Japan. / G. Lewis. / 1910-320. // Oxypoda / hilaris [handwritten]" (BMNH). See remarks.

Redescription. Measurements of lectotype of *Oxypoda hilaris*: BL ≈ 2.6; PL, 0.39; PW, 0.56; HTL, 0.40.

Relative length of antennomeres I–XI (n = 1): 23: 24: 22: 10: 13: 13: 13: 12: 14: 13: 36. Ratio of length/width of antennomeres I–XI (n = 1): 1.95: 1.59: 1.96: 0.65: 0.70: 0.70: 0.67: 0.59: 0.64: 0.63: 1.64.

Body (Fig. 1C) reddish brown; head darker; posterolateral areas of elytra darker; abdominal segments V–VII darker.

Head. Surface densely covered with setae. Antenna with antennomeres I–III and XI longer than wide, antennomeres IV–X wider than long; antennomeres I and II with rounded distal end, antennomeres III–X strongly angulated near distal end, antennomere XI oval.

Pronotum transverse (PW/PL: 1.44); surface densely covered with setae, finely punctured; posterior margin slightly bisinuate. Elytra wider than long; surface densely covered with setae and finely punctured; posterior margin sinuate near posterolateral corners.

Abdomen slightly narrowed posteriad; surface densely covered with setae.

Male. Unknown.

Female. Spermatheca (Fig. 6A) curved twice, with a transverse band-like structure at base of distal portion; distal portion elongated, U-shaped; median portion elongated, slightly curved; proximal portion longer than wide.

Distribution. Japan (Honshu).

Remarks. This species clearly does not belong to the genus *Oxypoda*, judging from the shape of the spermatheca, but to the genus *Pseudatheta*. As the type series of *Oxypoda hilaris* consists only of females, there is currently no method to distinguish this species from its allies. It is unclear whether this species is identical to *Ps. crenulicauda*, *Ps. taiwanensis*, both known from Japan, or neither. There is no reason to believe that the paralectotypes are the same species as the lectotype. Since this species was described in 1888 (*hilaris* is the oldest name), one or more of the similar species are likely to be junior synonyms of this species.

Pseudatheta thailandensis Pace, 1992

(Figs. 1D, 6B–D)

Pseudatheta thailandensis Pace, 1992: 239 (original description; type locality: "Chiang Mai Prov., Doi Suthep"); Pace, 2004: 66 (China, Shaanxi); Schülke & Smetana, 2015: 634 (catalogue).

Material examined. THAILAND: 2 males, 1 female, Doi Inthanon, Chaing Mai, 1560 m, 20 X 1983, M. Sakai leg. (EUM).

Additional description. Measurements (n = 1): BL ≈ 2.07; FBL: 1.22; HL: 0.36; HW: 0.43; PL: 0.52; PW: 0.60; EL: 0.43; EW: 0.72. Ratios (n = 1): HW/HL: 1.18, PW/PL: 1.44, EW/EL: 1.67, PW/HW: 1.39, EL/PL: 1.03, EW/PW: 1.20.

Relative length of antennomeres I–XI (n = 1): 20: 24: 15: 10: 12: 10: 12: 12: 12: 11: 34. Ratio of length/width of antennomeres I–XI (n = 1): 1.79: 2.36: 1.50: 0.68: 0.76: 0.65: 0.66: 0.63: 0.58: 0.55: 1.61.

Male. Elytra with a pair of small tubercles at about posterior 1/3 on sutural margin. Sternite VI with small medial lobe on posterior margin. Tergite VII with a tubercle on posteromedian area. Tergite VIII (Fig. 6B) with a tubercle on median area; four processes on each side of posterior margin, outer ones slightly curved, longer and sharper than the others. Aedeagus as in Fig. 6C; median lobe with large basal bulb; apical process relatively slender, narrowed apically in lateral view, apex pointed; flagellum moderately long.

Distribution. Thailand, China (Shaanxi).

Remarks. This species was described only from a female and could not be distinguished from its allied species based on the spermatheca. According to the original description by Pace (1992), the median part of the spermatheca is short, but this description may have derived from a deformed specimen. In many aleocharine species, spermathecae are easily deformed immediately after mounting in mounting medium. Later, Pace (2004) recorded this species from China, but it was again a female specimen. In this study, we were able to examine specimens of both sexes of

the genus *Pseudatheta*, which were similar to *Ps. thailandensis* collected in an area close to the type locality of *Ps. thailandensis*. Since there are areas where more than one species of this genus is distributed, such as Japan, whether these specimens are *Ps. thailandensis* is unclear. Nonetheless, since this species is the only known *thailandensis*-like species from Thailand, we tentatively identified the specimens as *Ps. thailandensis* and described the aedeagus.

This species can be distinguished from its allies (*Ps. crenulicauda*, *Ps. taiwanensis*) by the apical process of the aedeagus, which tapers gradually toward the apex. However, *Ph. bigranipennis* (Bernhauer, 1915), redescribed by Benick (1980) and Kim & Ahn (2016), cannot be distinguished from *Ps. thailandensis* judging from the illustrations and description, and specimens described by the authors are considered identical. Since Benick (1980) and Kim & Ahn (2016) did not state that they examined the type specimen, we cannot rule out the possibility of a misidentification. Thus, we refrain from taxonomic treatment of *Ph. bigranipennis* at this time. The relationship between *Ps. thailandensis* and *Ps. hilaris* could not be determined.

Pseudatheta cooteri **Pace, 1998**

(Figs. 1E, 7A–D)

[Japanese name: Minami-hime-kinokotsuyakeshi-hanekakushi]

Pseudatheta cooteri Pace, 1998: 208 (original description; type locality: "China, Jiangsu Prov., Nanjing Zijinshan"): Schülke & Smetana, 2015: 634 (catalogue); Pace, 2016: 301 (Yunnan).

Material examined. JAPAN: [**Kagoshima-ken**]: Yaku-shima Is.: 1 male, Aiko-dake, Yakushima-chô, 25 IX–23 X 2006, T. Yamauchi *et al*. leg, (KUM); 1 male, 2 females, Kurio, Yakushima-chô, 21 VII 2021, T. Hashizume leg. (KUM); [**Okinawa-ken**]: Okinawa-jima Is.: 2 males, Takazato, Ôgimi-son, 3 XI 1993, M. Kimura leg. (KUM); 2 males, Yona, 25–27 V 1974, M. Sato leg. (KUM); Iriomote-jima Is.: 2 males, 2 females, Kampiree, 27 III 1984, S. Nomura leg. (KUM).

TAIWAN: 3 males, Wulai, Taipei Hsien, 17 V 1972, M, Sakai leg. (EUM).

Redescription. Measurements (n = 5): BL ≈ 1.65–1.84; FBL, 0.91–1.00; HL, 0.28–0.34; HW, 0.35–0.39; PL, 0.31–0.35; PW, 0.46–0.50; EL, 0.30–0.35; EW, 0.55–0.60.

Relative length of antennomeres I–XI (n = 1): 25: 27: 19: 10: 10: 10: 11: 11: 13: 13: 35. Ratio of length/width of antennomeres I–XI (n = 1): 1.94: 2.21: 1.80: 0.87: 0.66: 0.64: 0.59: 0.58: 0.63: 0.61: 1.62.

Body (Fig. 1E) reddish brown; head darker; elytra dark brown except for the anterior 1/4–1/3; abdominal segments V–VI darker.

Head slightly transverse, HW/HL: 1.12–1.36; surface densely covered with setae. Antenna with antennomeres I–III and XI longer than wide, antennomeres IV–X wider than long; antennomeres I and II with rounded distal end, antennomeres III–X strongly angulated near distal end, antennomere XI oval.

Pronotum transverse, PW/PL: 1.43–1.50, PW/HW: 1.29–1.33; surface densely covered with setae, finely punctured, without microsculpture; posterior margin arcuate. Elytra wider than long, EW/EL: 1.71–1.84, EL/PL: 0.92–1.00, EW/PW: 1.13–1.24; surface densely covered with setae and finely punctured; posterior margin sinuate near posterolateral corners. Mesoventrite without longitudinal carina; mesoventral process extended to slightly beyond middle of mesocoxal cavities, with pointed apex; metaventral process shorter than mesoventral process, with rounded apex; isthmus absent.

Abdomen slightly narrowed posteriad; surface densely covered with setae.

Male. Elytra with a pair of small tubercles at about posterior 1/3 on sutural margin. Tergite VII with a tubercle on anteromedian area. Tergite VIII (Fig. 7A) with a tubercle on median area; six processes on posterior margin. Aedeagus as in Fig. 7C; median lobe with large basal bulb; apical process elongated, simply curved ventrally, slightly widened at basal part; ventral process large, apex pointed, with a distinct angle on dorsa side; flagellum very long.

Female. Spermatheca (Fig. 7D) curved twice; distal portion large, nearly conical shape, slightly curved; median portion elongate, curved; proximal portion very small.

Distribution. Japan (Yaku-shima Is., Okinawa-jima Is., Iriomote-jima Is.), Taiwan—new record; China (Jiangsu, Yunnan).

Remarks. We report the first discovery of males of *Ps. cooteri* and describe them here. Variations in the shape of the ventral process of the median lobe of the aedeagus were observed (Fig. 7B). The aedeagus and spermatheca

of *Ps. spinosa*, a species from Taiwan described by Pace (2008), are similar to those of *Ps. cooteri*. However, judging from the illustrations in that report, *Ps. cooteri* can be distinguished from *Ps. spinosa* by the longer apical process of the median lobe of its aedeagus and by the longer, weakly curved distal portion of the spermatheca. We were able to examine specimens of *Pseudatheta* from Taiwan and found that the aedeagi were identical to those of *Ps. cooteri* from Japan. We consider the former specimens to be *Ps. cooteri* from Taiwan, although we were unable to compare the spermathecae because females were not collected with the male specimens. While it is possible that the two species are distributed in Taiwan, the slight differences may have instead been due to intraspecific variation, deformation of the specimens, or misinterpretations in sketching. Therefore, we cannot rule out the possibility that these two species are synonyms.

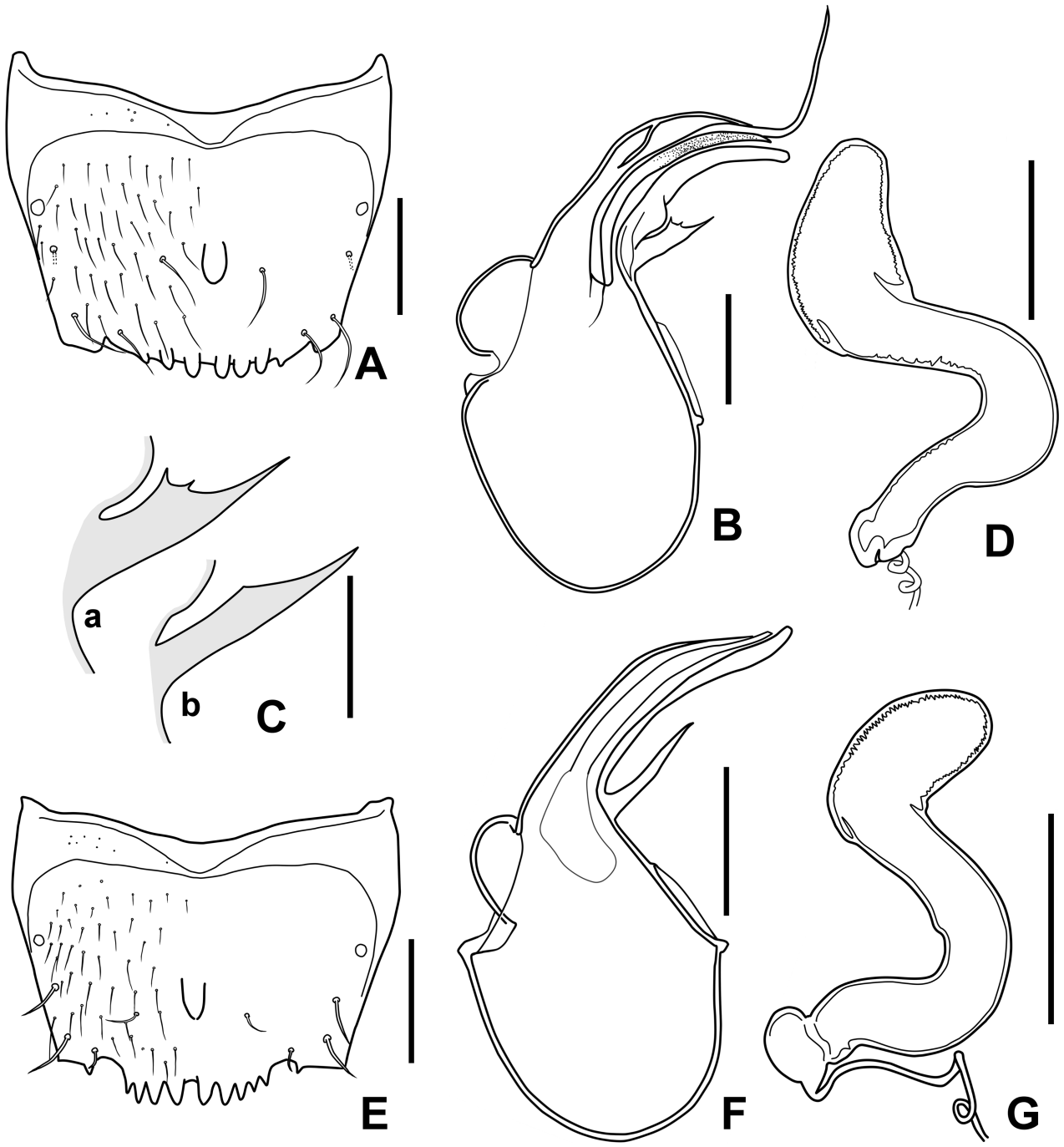

FIGURE 7. *Pseudatheta* spp. A–D: *Ps. cooteri* Pace, 1998, E–G: *Ps. elegans* Cameron, 1920. A, E. male tergite VIII in dorsal view; B, F. median lobe of aedeagus in lateral view; D, G. spermatheca; C. ventral process of median lobe of aedeagus in lateral view, a: Yaku-shima Is., b: Iriomote-jima Is. Scale bars: 0.1 mm.

***Pseudatheta elegans* Cameron, 1920**

(Figs. 1F, 3, 7E–G)

[Japanese name: Ko-hime-kinokotsuyakeshi-hanekakushi]

Pseudatheta elegans Cameron, 1920: 225 (original description; type locality: "Bukit Timah, woodlands, Mandai" [Singapore]): Cameron, 1939: 226 (Northern India); Schülke & Smetana, 2015: 634 (catalogue).

Material examined. Type materials compared. Syntypes: 1 male, "Fungus // Mandai, / Singapore. / Dr. Cameron. // SYN- / TYPE [blue round label pinned by a curator] // Pseudatheta / elegans Cam. / M. E. Bacchus det 1978 / SYNTYPE // *Pseudatheta* / *elegans* CAM. / det. R. Pace 1984 / LECTOTYPUS // NHMUK015025222" (BMNH); 1 male, "Fungus / (rotten) // Mandai, / Singapore. / Dr. Cameron. // SYN- / TYPE [blue round label pinned by a curator] // Pseudatheta / elegans Cam / M. E. Bacchus det 1978 / SYNTYPE // *Pseudatheta* / *elegans* CAM. / det. R. Pace 1984 / PARALECTOTYPUS // NHMUK015020370" (BMNH); 1 male, "SYN- / TYPE [blue round label pinned by a curator] // Mandai, / Singapore. / Dr. Cameron // TYPE / *Pseudatheta* / *elegans*. / Dr. CAMERON. // Pseudatheta / elegans Cam. / M. E. Bacchus det 1978 / SYNTYPE // *Pseudatheta* / *elegans* CAM. / det. R. Pace 1984 / PARALECTOTYPUS / Dissection By ? // NHMUK015020337" (BMNH): 1 male, "Fungus / (rotten) // Woodlands, / Singapore. / Dr. Cameron. // SYN- / TYPE [blue round label pinned by a curator] // *Pseudatheta* / *elegans* CAM. / det. R. Pace 1984 / PARALECTOTYPUS // Pseudatheta / elegans Cam. / M. E. Bacchus det 1978 / SYNTYPE / NHMUK015025223" (BMNH); 1 female, "Wood / (rotten) // Bukit Timah, / Singapore. / Dr. Cameron. / SYN- / TYPE [blue round label pinned by a curator] // Pseudatheta / elegans Cam. / M. E. Bacchus det 1978 / SYNTYPE // *Pseudatheta* / *elegans* CAM. / det. R. Pace 1984 / PARALECTOTYPUS // NHMUK015025224" (BMNH)

Additional materials studied. JAPAN: [Miyagi-ken]: 1 male, Yoshida, Taiwa-chô, 20 VIII 2009, J. Aoki leg. (KUM); [**Fukuoka-ken**]: 1 male, Tonoue-yama, Moji-ku, Kitakyûshû-shi, 15 V 2022, J.-H. Park leg. (KUM); 1 male, 1 female, Hiko-san, Soeda-machi, 24 VII 2020, T. Nozaki leg. (KUM); 1 male, Ryôgenji, Munakata-shi, 15 V 2022, T. Hashizume leg. (KUM); [**Saga-ken**]: 1 male, 2 females, Uki-dake, Nanayama, Karatsu-shi, 6 X 2022, N. Tsuji leg. (KUM); [**Nagasaki-ken**]: Tsushima Is.: 1 male, 1 female, Kamiagatamachi Sagohigashisato, Tsushima-shi, 18 VI 2022, T. Hashizume leg. (KUM); 1 male, Kamiagatamachi Sasuna, 19 VI 2022, T. Hashizume leg. (KUM); Fukue-jima Is.: 1 female, Kishikumachi Nakadake, Gotô-shi, 11 X 2022, T. Hashizume leg. (KUM); [**Oita-ken**]: 1 male, Takatoriya-yama, Minamitabaru, Ume, Saeki-shi, 14 XI 2020, S. Inoue leg. (KUM); [**Kagoshima-ken**]: 1 female, Sata-misaki, 5 V 1985, Y. Takai leg. (KUM); Yaku-shima Is.: 2 males, 1 female, Koseda, Yakushima-chô, 22 VII 2021, T. Hashizume leg. (KUM); Amami-Ôshima Is.: 1 male, Sumiyôchô Nishinakama, Amami-shi, 27 VI 2021, T. Hashizume leg. (KUM); 1 male, Shinmura, 11 IV 1971, M. Sakai leg. (EUM); Tokuno-shima Is.: 1 female, Mikyo, 12 IV 1968, M. Tomokuni leg. (EUM); [**Okinawa-ken**] Ishigaki-jima Is.: 1 male, Omoto-dake, Hirae, Ishigaki-shi, 24 III 2022, S. Inoue leg. (KUM).

Redescription. Measurements (n = 5): BL ≈ 1.49–1.94; FBL, 0.86–0.96; HL, 0.29–0.30; HW, 0.34–0.36; PL, 0.30–0.34; PW, 0.44–0.48; EL, 0.30–0.35; EW, 0.51–0.56.

Relative length of antennomeres I–XI (n = 1): 23: 25: 18: 11: 10: 11: 10: 10: 11: 11: 31. Ratio of length/width of antennomeres I–XI (n = 1): 1.88: 2.35: 2.10: 0.96: 0.77: 0.75: 0.96: 0.58: 0.63: 0.57: 1.46.

Body (Fig. 1F) reddish brown; head darker; elytra dark brown except for the anterior 1/4–1/3; abdominal segments V–VI darker.

Head almost as long as wide, HW/HL: 1.17–1.21; surface densely covered with setae. Antenna with antennomeres I–III and XI longer than wide, antennomeres IV–X wider than long; antennomeres I and II with rounded distal end, antennomeres III–X strongly angulated near distal end, antennomere XI oval.

Pronotum transverse, PW/PL: 1.30–1.46, PW/HW: 1.30–1.31; surface densely covered with setae, finely punctured, without microsculpture; posterior margin arcuate. Elytra wider than long, EW/EL: 1.54–1.71, EL/PL: 1.00–1.04, EW/PW: 1.17–1.29; surface densely covered with setae and finely punctured; posterior margin sinuate near posterolateral corners. Hind wings well developed; without flabellum. Mesoventrite without longitudinal carina; mesoventral process extended to slightly beyond middle of mesocoxal cavities, with pointed apex; metaventral process shorter than mesoventral process, with rounded apex; isthmus absent.

Abdomen slightly narrowed posteriad; surface densely covered with setae.

Male. Elytra with a pair of small tubercles at about posterior 1/3 on sutural margin. Tergite VII with a tubercle on anteromedian area. Tergite VIII (Fig. 7E) with a tubercle on median area; eight to ten processes on posterior

margin. Aedeagus as in Fig. 7F; median lobe with large basal bulb; apical process elongated, sinuated, apical half slightly widened; ventral process narrow, sinuated; flagellum moderately long.

Female. Spermatheca (Fig. 7G) curved twice; distal portion nearly reniform; median portion elongate, curved; proximal portion round, wider than long; constriction between median and proximal portion distinct.

Distribution. Japan (Honshu, Kyushu, Tsushima Is., Gotô-rettô Isls. (Fukue-jima Is.), Yaku-shima Is., Amami-Ôshima Is., Tokuno-shima Is., Ishigaki-jima Is.)—new record; Singapore, India.

Remarks. We compared photographs of the habitus and the aedeagi of the type series with those of the specimens collected from Japan, and determined them to be the same species based on the similarity of dorsal habitus, the slightly sinuate apical process of the median lobe of aedeagus, and moderately long flagellum of the aedeagus. This species is similar in the shapes of the aedeagus and the spermatheca to *Ps. tronqueti,* described from Sri Lanka by Pace (1988), *Ps. mendica*, described from Nepal by Pace (1989), *Ps. rougemonti*, described from Sabah in East Malaysia by Pace (2014), *Ps. borneensis,* described from Sabah by Pace (2007), *Ps. kinabaluensis*, described from Sabah by Pace (2007), and *Ps. pahangensis*, described from Peninsular Malaysia by Pace (2012). These similar species, except for *Ps. mendica*, can be distinguished from *Ps. elegans* as follows:

in *Ps. rougemonti*, the ventral process of the median lobe of aedeagus is almost straight;

in *Ps. borneensis* the flagellum of the median lobe of aedeagus is longer, and the proximal portion of the spermatheca is slightly smaller;

in *Ps. kinabaluensis*, the ventral process of the median lobe of aedeagus is simply slightly curved dorsally, and the shape of the proximal portion of the spermatheca is different;

in *Ps. tronqueti*, the apical process of the median lobe of aedeagus is almost straight, and the proximal portion of the spermatheca is slightly smaller;

in *Ps. pahangensis*, the distal portion of the spermatheca is slightly broader and shorter. It is desirable to find males of *Ps. pahangensis* because the spermatheca is very similar to that of *Ps. elegans*.

Unfortunately, *Ps. mendica* cannot be distinguished from the Japanese *Ps. elegans* based on the information in the original description based on the female holotype (Pace, 1989).

Some of species compared here are difficult to distinguish and we cannot refute the possibility that they are geographic or individual variation of this species. In fact, the aedeagus of the *Pseudatheta* sp. from Taiwan we examined is almost identical to those of specimens from Japan, but the distal portion of the spermatheca is slightly shorter. In this study, we were not able to examine the spermatheca of the type series of *Ps. elegans* and it is desirable to do so in the future.

Species excluded from the genus *Pseudatheta*

Platyola oligotinula (Sharp, 1888), comb. rev.

[Japanese name: Hime-tobimushi-hanekakushi]

Homalota oligotinula: Sharp, 1888: 293 (original description; type locality: "Kumamoto" [Kumamto-shi, Kumamoto-ken, Kyushu]).

Atheta (*Microdota*) *oligotinula*: Bernhauer & Scheerpeltz, 1926: 634 (catalogue).

Platyola oligotinula: Pace, 1984: 54 (transferred to the genus *Platyola* from the genus *Phymatura*).

Pseudatheta oligotinula; Pace, 1992: 242 (transferred to the genus *Pseudatheta* from the genus *Phymatura*; probably based on Sawada (1977)); Schülke & Smetana, 2015: 634 (catalogue).

nec. *Phymatura oligotinula* sensu Sawada, 1977: 217 (transferred to the genus *Phymatura* from the genus *Homalota*).

Material examined. Type material. Lectotype: here designated, female, "Homalota / oligotinula / Type D.S. / Kumamoto / 26.IV.81. Lewis [paper card, handwritten] // SYN- / TYPE [blue round label pinned by a curator] // Type [red round label pinned by a curator] // Japan. / G. Lewis. // Kumamoto / 23.IV.-26.IV.81. // Sharp Coll. / 1905-313 // Platyola / oligotinula (SH.) // det. R. Pace, 1982" (spermatheca is mounted in glycerin by previous researcher) (BMNH).

Remarks. This species was redescribed based on misidentified specimens of *Ps. crenulicauda* by Sawada (1977) and transferred to the genus *Phymatura*. However, as Pace (1984) stated that this species belongs to the genus *Platyola* of the tribe Athetini, not Homalotini. Later, Pace (1992) probably forgot this arrangement (Pace, 1984) and moved this species from the genus *Phymatura* to the genus *Pseudatheta*, and this treatment was followed in the later catalogs (e.g., Schülke & Smetana 2015; Newton 2022). We here place this species again in the genus *Platyola*.

Genus *Phymatura* Sahlberg, 1876

[Japanese name: Kinokotsuyakeshi-hanekakushi-zoku]

Phymatura Sahlberg, 1876: 85 (original description; type species: *Bolitochara brevicollis* Kraatz, 1856, fixed by subsequent designation by Casey, 1906: 264).

Venusa Casey, 1906: 272 (original description; type species: *Venusa picta* Casey, 1906, fixed by subsequent designation by Fenyes, 1918: 26); Ashe, 1992: 371 (as a synonym of *Phymatura*).

Remarks. The genus *Phymatura* can be distinguished from the genus *Pseudatheta* by the following character states: mesoventrite with a longitudinal carina; flabellum of hind wing with at least three setose lobes.

Key to species of the genus *Phymatura* in Japan

1. Body nearly uniformly reddish; eyes smaller, length shorter than 40% length of head. . . . . *Ph. russa* Assing
- Body uniformly darker; eyes larger, length longer than 40% length of head. . . . . *Ph. japonica* Cameron **stat. rev.**

Phymatura japonica Cameron, 1933, stat. rev.

(Figs. 2A, E, 8A–C)

[Japanese name: Nihon-kinokotsuyakeshi-hanekakushi]

Phymatura japonica Cameron, 1933: 210 (original description; type locality; "Chuzenji" [Chûzenji, Nikkô-shi, Tochigi-ken, central Honshu]); Sawada, 1977: 217 (as a synonym of *Ps. oligotinula*); Schülke & Smetana, 2015: 633 (catalogue, as a synonym of *Ph. crenulicauda*).

Phymatura cooteri Assing, 2005: 24 (original description; type locality: "Bai He [Baihe], Jilin Prov., China"); Schülke & Smetana, 2015: 633 (catalogue); Assing, 2021: 330 (Japan: Amami-Ôshima Is.; Russia). **Syn. nov.**

Material examined. Type material. *Phymatura japonica*: Holotype: male, "Holo- / type [red round label pinned by a curator] // JAPAN / CHUZENJI // AT FT J. E. A. Lewis // Cameron / Bequest. / B. M. 1955-147. // Phymatura / japonica / TYPE Cam. [handwritten] // Phymatura / japonica Cam. / P. M. Hammond / det. 1973 / HOLOTYPE" (abdominal segments VIII–X and aedeagus are dissected and mounted in Euparal by MM) (BMNH).

Additional materials studied. JAPAN: [Hokkaido]: 1 ex., Akan-chô, 2 VIII 1988, K. Haga leg. (KUM); 1 ex., Akan N. Park, 6 VII 1958, M. Miyatake leg. (EUM); 1 male, Taiki-chô, 2 IX 1990, K. Haga leg. (KUM); 7 exs., Sounkyô, 17–18 VII 1970, S. Kinoshita leg. (EUM); **[Fukushima-ken]**: 1 male, 3 females, Shindenpara, Minamiaizu-machi, 13 VII 1996, K. Haga leg. (KUM); **[Saitama-ken]**: 1 male, 3 females, Mitsumine, Chichibu-shi, 28 V 1997, M. Maruyama leg. (KUM); 10 males, 10 females, Taki-gawa, Chichibu-shi, 30 V 1997, M. Maruyama leg. (KUM); **[Tokyo-to]**: 1 male, 1 female, Nippara, Okutama-machi, 8 VI 1991, K. Haga leg. (KUM): 1 female, same data, but 9 VI 1991 (KUM); 1 male, 1 female, Nippara, Okutama-machi, 7 V 1997, T. Shimada leg. (KUM); **[Kanagawa-ken]**: 1 male, 2 females, Hakone, 1 V 1974, Y. Hirano leg. (KUM); 1 female, Nishi Tanzawa, 8 IX 1984, Y. Hirano leg. (KUM); **[Niigata-ken]:** 1 female, Yuzawa-machi, 1 X 1995, K. Haga leg. (KUM); **[Yamanashi-ken]**: 1 male, Sentouboshi-yama, Minaniarupusu-shi, 2 VIII 1992, K. Haga leg. (KUM); **[Shizuoka-ken]**: 1 female, Sessokyo, Kawanehon-chô, 9–10 V 1992, T. Kishimoto leg. (TKc); 1 femle, Amagi-tôge, Kawazu-chô, 14–16 III 1996, S. Naomi leg. (KUM); **[Nara-ken]**: 1 female, Ôdaigahara, 29 V 1985, S. Nomura leg. (KUM); **[Hiroshima-ken]**: 1 male, Kure-shi, 2 XII 1995, I. Okamoto leg. (KUM); **[Tokushima-ken]**: 1 female, Tsurugi-san, 27 VII 1961, M.T. Chûjô leg. (KUM); 5 males, 2 females, same data, but 28 VII 1961 (KUM); 1 ex., Tsurugi-san, 11 VII 1993, M. Sakai leg. (EUM); 1 male, Iyadani, Tsurugi-san, 19 VIII 1989, K. Matsumoto leg. (KUM); 1 female, Shikibidani, Naka-chô, 17 VII 2010, J. Aoki leg. (KUM); **[Ehime-ken]**: 1 ex., Omogo-kei, 2 V 1976, A. Oda leg. (EUM); 1 ex., Omogo-kei, 4 VI 1983, K. Ishida leg. (EUM); 1 ex., Banshodani, Omogo, 11 VI 1988, M. Sakai leg. (EUM); 1 ex., Ôhira, Tôon-shi, 27 IV 2007, T. Kitano leg. (EUM); **[Fukuoka-ken]**: 1 female, Tachibana-yama, Fukuoka-shi, 27 XI 1983, S. Naomi leg. (KUM); 1 male, 1 female, Hiko-san, 24 IX 1938, Hori & Fujino leg. (KUM); 2 males, Hiko-san, 7 V 1971, K. Takano leg. (KUM); 1 female, Hiko-san, Soeda-machi, 23 V 2020, S. Inoue leg. (KUM); **[Saga-ken]**: 1 female, Sefuri-san, 3 X 1976, H. Oishi leg. (KUM); **[Kumamoto-ken]**: 1 male, 1 female, Izumimachi Momigi, 14 V 2021, S. Inoue leg. (KUM); 1 male, Gokanoshô, 17 X 1988, S. Naomi leg. (KUM); 4 males, 8 females, Aso-shi, 3 X 1995, Y. Tomishima leg. (KUM); 1 male, Ichifusa-yama, Mizukami-mura, 13 X 1995, Y. Tomishima leg.

(KUM); 2 exs., Ichifusa-yama, 11 VI 1972, S. Hisamatsu leg. (EUM); 1 male, Kirihagi, Yamato-chô, 15 X 1993, Y. Tomishima leg. (KUM); **[Oita-ken]**: 1 male, Shônaichô Asono, Yufu-shi, 20 V 2021, T. Hashizume leg. (KUM); **[Kagoshima-ken]**: Amami-Ôshima Is.: 12 exs., Hatsuno, 2 V 1977, A. Oda leg. (EUM); 3 exs., same data, but M. Sakai & A. Oda leg. (EUM); 1 ex., same data, but M. Sakai leg. (EUM); 3 exs., Yuwan, 3 IV 1968, M. Tomokuni leg. (EUM); Tokuno-shima Is.: 6 exs., Mikyo, 12 IV 1968, M. Tomokuni leg. (EUM).

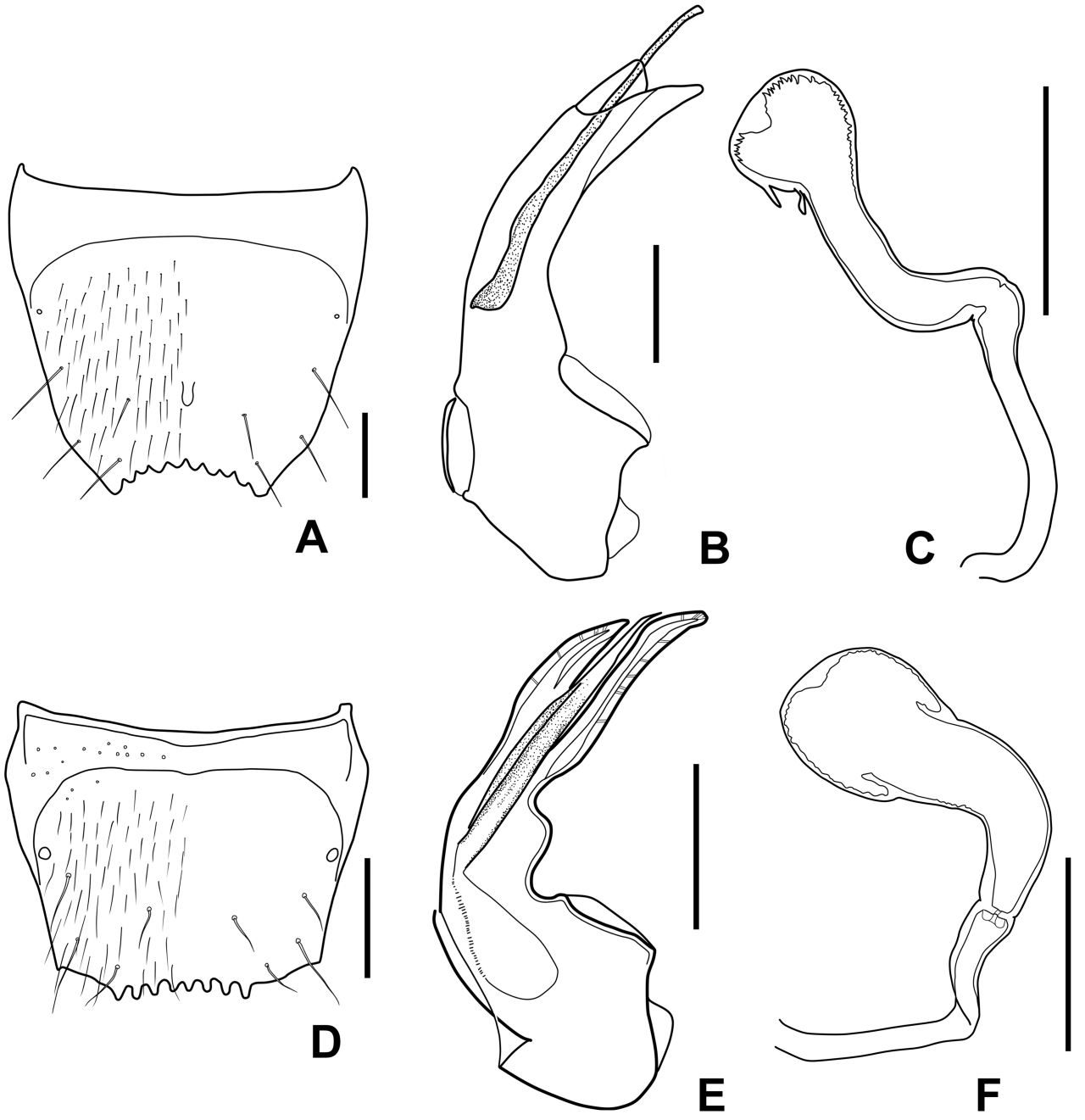

FIGURE 8. *Phymatura* spp. A–C: *Ph. japonica* Cameron, 1933, D–F: *Ph. russa* Assing, 2021. A, D. male tergite VIII in dorsal view; B, E. median lobe of aedeagus in lateral view; C, F. spermatheca. Scale bars: 0.1 mm.

Redescription. Measurements (n = 5): BL ≈ 2.69–3.05; FBL, 1.35–1.65; HL, 0.38–0.46; HW, 0.45–0.51; PL, 0.43–0.51; PW, 0.58–0.69; EL, 0.49–0.61; EW, 0.75–0.86.

(Holotype: BL ≈ 3.2; PL, 0.46; PW, 0.63; HTL, 0.51)

Relative length of antennomeres I–XI (n = 1): 21: 21: 19: 10: 13: 12: 13: 13: 12: 14: 31. Ratio of length/width of antennomeres I–XI (n = 1): 1.88: 2.22: 1.94: 0.82: 0.85: 0.71: 0.76: 0.77: 0.68: 0.73: 1.58.

Body (Fig. 2A, D) relatively large. Head dark brown; pronotum brown; posterolateral areas of elytra dark

brown, anterior 1/4–1/3, sutural area, and narrow area of posterior margin yellowish brown; abdomen reddish brown, around midline of tergite III–V dark brown, segments VI–VII dark brown.

Head almost as long as wide, HW/HL: 1.11–1.20; surface densely covered with setae. Antenna with antennomeres I–III and XI longer than wide, antennomeres IV–X wider than long; antennomeres I and II with rounded distal end, antennomeres III–X strongly angulated near distal end, antennomere XI oval.

Pronotum transverse, PW/PL: 1.32–1.35, PW/HW: 1.28–1.34; surface densely covered with setae, finely punctured, without microsculpture; posterior margin slightly bisinuate. Elytra wider than long, EW/EL: 1.34–1.54, EL/PL: 1.12–1.21, EW/PW: 1.18–1.30; surface densely covered with setae and finely punctured; posterior margin sinuate near posterolateral corners. Hind wings well developed; flabellum with several setae. Mesoventrite with short longitudinal carina from anterior margin; mesoventral process extended to slightly beyond middle of mesocoxal cavities, with pointed apex; metaventral process shorter than mesoventral process, with rounded apex; listhmus absent.

Abdomen slightly narrowed posteriad; surface densely covered with setae.

Male. Tergite VII with a tubercle on posteromedian area. Tergite VIII (Fig. 8A) broadly emarginate; one tubercle on median area; eight to ten small processes on posterior margin. Aedeagus as in Fig. 8B; median lobe with relatively narrow basal bulb; apex of apical process pointed; flagellum well sclerotized, very long.

Female. Spermatheca as in Fig. 8C; distal portion large; wall of distal end protrudes inward; median portion and proximal portion small.

Distribution. Japan (Hokkaido, Honshu, Shikoku, Kyushu, Amami-Ôshima Is., Tokuno-shima Is.); China (Jilin, Heilongjiang), North Korea, Russia.

Remarks. There is only the male holotype of *Ph. japonica* in BMNH. The original description of *Phymatura cooteri* agrees with the feature of the type specimen of *Ph. japonica* in the shapes of the tergite VIII, sternite VIII and the aedeagus. Therefore, *Ph. cooteri* is here synonymized with *Ph. japonica*. Assing (2021) recorded this species from Southwestern Japan (Amami-Ôshima) and Russia. Paśnik (2001) recorded this species from North Korea (see Assing (2005) for more detailed description of *Ph. japonica* (as *Ph. cooteri*)).

Phymatura russa Assing, 2021

(Figs. 2B, 8D–F)

[Japanese name: Aka-kinokotsuyakeshi-hanekakushi]

Phymatura russa Assing, 2021: 331 (original description; type locality: "CHINA: S-Shaanxi (Qinling Shan), pass on rd. Zhouzhi—Foping, 105 km SW Xi′an, N-slope, 1990 m, 33°44′N, 107°59′E").

Material examined. JAPAN: [Hokkaido]: 1 female, Nopporo-shinrin-kôen, Ebetsu-shi, 16–19 VI 2001, S. Hori leg. (KUM); 1 ex., Kamibisei, Memuro-chô, 25 VIII 1995, M. Sakai leg. (EUM); [**Ehime-ken**]: 2 males, Komenomachi, Matsuyama-shi, 8 V 1999, T. Kan leg. (EUM).

Measurements. (n = 3): BL ≈ 1.98–2.31; FBL: 1.08–1.19; HL: 0.31–0.36; HW: 0.35–0.36; PL: 0.38–0.40; PW: 0.48 ; EL: 0.39–0.41; EW: 0.59–0.62. Ratios (n = 3): HW/HL: 1.04–1.13, PW/PL: 1.20–1.28, EW/EL: 1.50, PW/HW: 1.32–1.37, EL/PL: 1.00–1.03, EW/PW: 1.22–1.29.

Relative length of antennomeres I–XI (n = 1): 26: 25: 15: 10: 12: 11: 12: 12: 13: 13: 30. Ratio of length/width of antennomeres I–XI (n = 1): 2.09: 2.08: 1.21: 0.71: 0.75: 0.62: 0.60: 0.55: 0.61: 0.55: 1.46.

Distribution. Japan (Hokkaido, Shikoku)—new record; China (Shaanxi).

Remarks. *Phymatura russa* is recorded from Japan for the first time. This species can be distinguished from the other *Phymatura* species recorded from Japan by its nearly uniformly reddish coloration, the smaller eyes, and the shapes of the aedeagus and the spermatheca. This species has been collected from Hokkaido and Shikoku, and may be widely distributed in mainland Japan (see Assing (2021) for detailed description of *Ph. russa*).

Discussion

The external morphological characteristics of *Pseudatheta* and *Phymatura* are remarkably similar, which has led to considerable taxonomic confusion in recent decades. The diagnosis of these two genera by Ashe (1992) seems to make little sense considering the various species belonging to these genera. Some exceptions of the generic

definitions of Ashe (1992) were found, for example, in the degree of development of the longitudinal carina of the mesoventrite, the presence or absence of a posterior marginal lobe of male sternite VI, and the number of setose lobes of the flabellum. The Japanese taxa are no exceptions. For example, here we propose a new combination of a previously Japan-endemic species, *Pseudatheta crenulicauda*, **comb. nov.**, which we have transferred to the genus *Pseudatheta* from the genus *Phymatura* based on the absence of the longitudinal carina on the mesoventrite. However, each of its hind wings has one setose lobe on the flabellum, characteristics not shared by *Ps. elegans*, the type species of the genus *Pseudatheta* (Ashe, 1992). Thus, comprehensive studies are needed to verify the generic placement of *Ps. crenulicauda*, **comb. nov.** as well as the generic definitions, preferably with the aid of molecular phylogenetic analyses. Genus-level classification of the subtribe Bolitocharina poses significant challenges and necessitates a precise understanding of the phylogenetic relationships to distinguish reliable morphological traits for use in identification.

Furthermore, the genus *Pseudatheta* includes several species with minor intraspecific differences, which makes their species-level identification difficult. Despite our detailed morphological observations, four similar species (*Ps. hilaris*, *Ps. crenulicauda*, *Ps. taiwanensis*, and *Ps. thailandensis*) could not be distinguished using female specimens. It was therefore difficult to accurately identify *Ps. hilaris* and *Ps. thailandensis* described based on female specimens only. While we described a male tentatively identified as *Ps. thailandensis*, the male of *Ps. hilaris* is still unknown. Further morphological information for females allowing their species identification, perhaps supported by DNA data (see the Remarks for *Ph. hilaris*), is needed. Some species of the widely distributed Aleocharinae show geographic variations in the male and female genitalia (e.g., *Pella*: Maruyama 2006). *Pseudatheta elegans* and *Ps. cooteri* also cannot be resolved by examining only a few specimens, resulting in a lack of taxonomic clarity. In the species of the genus *Pseudatheta* described in this paper, body color is generally as shown in Figs. 1A–F, but with individual variations. Body color can be useful for identification but should not be relied upon completely. It is also problematic that for several species only males or females are known.

Four species of *Pseudatheta* and two species of *Phymatura* from Japan are also distributed in continental East, South, and Southeast Asia. These species might be found in wider areas in the future.

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References

Ashe, J.S. (1992) Phylogeny and revision of genera of the subtribe Bolitocharina (Coleoptera: Staphylinidae: Aleocharinae). *University of Kansas science bulletin*, 54 (10), 335–406.
https://doi.org/10.5962/bhl.part.19642

Ashe, J.S. (1993) Mouthpart modifications correlated with fungivory among aleocharine staphylinids (Coleoptera: Staphylinidae: Aleocharinae). *In*: Schaefer, C.W. & Leschen, R.A.B. (Eds.), *Functional morphology of insect feeding. Proceedings: Thomas Say Publications in Entomology*. Entomological Society of America, Lanham, Maryland, pp. 105–130.

Assing, V. (2005) New species and records of Staphylinidae from China (Coleoptera). *Entomologische Blätter*, 101 (1), 21–42.

Assing, V. (2021) Two new species of *Phymatura* from China (Coleoptera: Staphylinidae: Aleocharinae). *Acta Musei Moraviae,*

Science biologocae, 106 (2), 329–334.
Benick, G. (1980) Weitere neue Atheten aus Sowjet-Russland (Col. Staphyl.). *Nouvelle Revue d'Entomologie*, 10 (4), 335–340.
Bernhauer, M. (1907) Zur Staphylinidenfauna von Japan. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 57, 371–414.
Bernhauer, M. (1939) Zur Staphylinidenfauna von China u. Japan. *Entomologisches Nachrichtenblatt (Troppau)*, 12, 97–109 + 145–158. [1938]
Cameron, M. (1920) New species of Staphylinidae from Singapore. Part III. *Transactions of the Entomological Society of London*, 1920, 212–284.
https://doi.org/10.1111/j.1365-2311.1920.tb00214.x
Cameron, M. (1932) New species of Staphylinidae from the Belgian Congo. *Bulletin & Annales de la Société royale d'entomologie de Belgique*, 72, 131–146.
Cameron, M. (1933) New species of Staphylinidae (Col.) from Japan. *Entomologist's Monthly Magazine*, 69, 168–175 + 208–219.
Cameron, M. (1939) *Fauna of British India including Ceylon and Burma. Coleoptera Staphylinidae. Vol. IV. Part I*. Taylor and Francis, London, xviii + 410 pp.
Casey, T.L. (1906) Observations on the staphylinid groups Aleocharinae and Xantholinini, chiefly of America. *Transactions of the Academy of Science of St. Louis*, 16, 125–434.
https://doi.org/10.5962/bhl.title.48654
Fenyes, J.S. (1918) Coleoptera. Fam. Staphylinidae, Subfam. Aleocharinae. *In*: Wytsmam, P.A. (Ed.), *Genera Insectorum. Vol. XXVII*. M. Nijhoff, The Hague, pp. 1–110.
Hashizume, T., Yamamoto, S. & Maruyama, M. (2023) Taxonomic notes on the genus *Pseudoligota* Cameron (Coleoptera: Staphylinidae: Aleocharinae) from Japan. *Zootaxa*, 5227 (1), 100–108.
https://doi.org/10.11646/zootaxa.5227.1.4
Kim, Y.-H. & Ahn, K.-J. (2014) *Insect Fauna of Korea. Vol. 12. No. 17. Arthropoda: Insecta; Coleoptera: Staphylinidae: Aleocharinae: Homalotini.* National Institute of Biological Resources, Incheon, 113 pp.
Kim, Y.-H. & Ahn, K.-J. (2016) Taxonomy of the genus *Phymatura* J. Sahlberg (Coleoptera: Staphylinidae: Aleocharinae) in the Korean Peninsula. *Zootaxa*, 4061 (2), 189–196.
https://doi.org/10.11646/zootaxa.4061.2.9
Maruyama, M. (2004) A permanent slide pinned under a specimen. *Elytra*, *Tokyo*, 32 (2), 276.
Maruyama, M. (2006) Revision of the Palearctic species of the myrmecophilous genus *Pella* (Coleoptera, Staphylinidae, Aleocharinae). *National Science Museum Monographs*, 32, 1–207.
Maruyama, M., Yamamoto, S. & Eldredge, T.K. (2014) Synopsis of the Japanese species of Aleocharinae (Coleoptera: Staphylinidae), with review of the type specimens I. Tribes Himalusini and Leucocraspedini. *Zootaxa*, 3887 (3), 393–400.
https://doi.org/10.11646/zootaxa.3887.3.6
Newton, A. (2022) Staphyliniformia world catalog database. *In*: Bánki, O., Roskov, Y., Döring, M., Ower, G., Vandepitte, L., Hobern, D., Remsen, D., Schalk, P., DeWalt, R.E., Keping, M., Miller, J., Orrell, T., Aalbu, R., Adlard, R., Adriaenssens, E.M., Aedo, C., Aescht, E., Akkari, N., Alexander, S. *et al*., *Catalogue of Life Checklist*, August 2022. Available from: https://doi.org/10.48580/dfqf-3gk (accessed 5 February 2023)
Pace, R. (1984) Note su alcune specie del genere *Platyola* Muls. & Rey e generi affini del Giappone e del Gabon (Coleoptera Staphylinidae). *Lavori della Società veneziana di scienze naturali*, 9, 51–57.
Pace, R. (1987) Aleocharinae dell'Asia sudorientale raccolte da G. de Rougemont (Coleoptera, Staphylinidae). *Bollettino del Museo Civico di Storia Naturale di Verona*, 13, 139–237.
Pace, R. (1988) Aleocharinae dello Sri Lanka raccolte da Marc Tronquet (Coleoptera Staphylinidae). *Bollettino del Museo Civico di Storia Naturale di Verona*, 14, 315–338.
Pace, R. (1989) Aleocharinae nepalesi del Museo di Ginevra. Parte I (Coleoptera Staphylinidae). *Revue suisse de Zoologie*, 96 (3), 483–539.
https://doi.org/10.5962/bhl.part.82045
Pace, R. (1992) Aleocharinae della Thailandia (Coleoptera Staphylinidae). *Bollettino del Museo Civico di Storia Naturale di Verona*, 16, 227–268.
Pace, R. (1998) Aleocharinae della Cina: Parte I (Coleoptera, Staphylinidae). *Revue suisse de Zoologie*, 105 (1), 139–220.
https://doi.org/10.5962/bhl.part.80035
Pace, R. (2004) Specie nuove o poco note di Homalotini, Silusini, Bolitocharini, Diestotini e Autaliini della Cina e della Thailandia (Coleoptera, Staphylinidae). *Revue suisse de Zoologie*, 111 (1), 63–76.
https://doi.org/10.5962/bhl.part.80227
Pace, R. (2007) Le specie di Oligotini, Leucocraspedini, Hygrinomini, Placusini, Bolitocharini e Diestotini nel Borneo (Coleoptera, Staphylinidae). *Revue suisse de Zoologie*, 114 (4), 771–815.
https://doi.org/10.5962/bhl.part.80415
Pace, R. (2008) Pronomaeini, Homalotini, Bolitocharini, Diestotini e Falagriini di Taiwan (Coleoptera, Staphylinidae). *Bollettino del Museo Civico di Storia Naturale di Verona. Botanica Zoologia*, 32, 137–156.
Pace, R. (2010) Biodiversità delle Aleocharinae della Cina: Placusini, Homalotini, Bolitocharini, Eusteniamorphini e Falagriini1

(Coleoptera, Staphylinidae). *Beiträge zur entomologie*, 60 (2), 259–280.
https://doi.org/10.21248/contrib.entomol.60.2.259-280
Pace, R. (2012) New data, new species, and two new genera of Aleocharinae from the Oriental Region (Insecta: Coleoptera: Staphylinidae). *Veröffentlichungen des Naturkundemuseums Erfurt—VERNATE*, 31, 319–360.
Pace, R. (2014) Aleocharinae from Sabah (Borneo) collected by Guillaume de Rougemont (Coleoptera, Staphylinidae). *Linzer biologische Beiträge*, 46 (1), 727–794.
Pace, R. (2016) Aleocharinae della Cina al "Naturkundemuseum" di Erfurt (Insecta: Coleoptera: Staphyinidae). *Veröffentlichungen des Naturkundemuseums Erfurt - VERNATE*, 35, 295–336.
Paśnik, G. (2001) The North Korean Aleocharinae (Coleoptera, Staphylinidae): diversity and biogeography. *Acta zoologica cracoviensia*, 44 (3), 185–234.
Sawada, K. (1977) Studies on the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae) III: Japanese species described by the previous authors. *Contributions from the Biological Laboratory*, *Kyoto University*, 25 (2), 171–222.
Sahlberg, J. (1876) Enumeratio Coleopterorum brachelytrorum Fenniae. Systematisk förteckning öfver de inom Finlands naturalhistoriska område hittills funna Coleoptera Brachelytra jemte uppgift om arternas utbredning och beskrifningar af nya och mindre kända species. I. Staphylinidae. *Acta Societatis pro Fauna et Flora Fennica*, 1 (3), 1–248.
Schülke, M. & Smetana, A. (2015) Staphylinidae. *In*: Löbl, I. & Löbl, D. (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 2*. *Hydrophiloidea—Staphylinoidea*. *Revised and updated edition*. Brill, Leiden/Boston, pp. 304–1134.
Sharp, D.S. (1874) The Staphylinidae of Japan. *Transactions of the Entomological Society of London*, 1874, 1–103.
https://doi.org/10.1111/j.1365-2311.1874.tb00159.x
Sharp, D.S. (1888) The Staphylinidae of Japan. *Annales and Magazine of Natural History*, Series 6, 3, 277–295 + 369–387 + 451–464.
https://doi.org/10.1080/00222938809487515
Shibata, Y., Maruyama, M., Hoshina, H., Kishimoto, T., Naomi, S.-I., Nomura, S., Puthz, V, Shimada, T., Watanabe, Y. & Yamamoto, S. (2013) Catalogue of Japanese Staphylinidae (Insecta: Coleoptera). *Bulletin of the Kyushu University Museum*, 11, 69–218.
Yamamoto, S. & Maruyama, M. (2016) Revision of the subgenus *Aleochara* Gravenhorst of the parasitoid rove beetle genus *Aleochara* Gravenhorst of Japan (Coleoptera: Staphylinidae: Aleocharinae). *Zootaxa*, 4101 (1), 1–68.
https://doi.org/10.11646/zootaxa.4101.1.1