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RESEARCH PAPER

Revision of the intertidal rove beetle genus *Bryothinusa* from Japan (Coleoptera: Staphylinidae: Aleocharinae)

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Abstract. The Japanese species of the intertidal rove beetle genus *Bryothinusa* Casey, 1904 are revised. Of 17 recognized species in total, six known species (*B. algarum* Sawada, 1971, *B. gangjinensis* Ahn & Jeon, 2004, *B. minuta* (Sawada, 1955), *B. nakanei* (Sawada, 1955), *B. sakishimana* Sawada, 1991, *B. tsutsuii* (Sawada, 1955)) are redescribed and nine new species (*B. aikoae* sp. nov. from Honshû, *B. constricta* sp. nov. from Honshû, *B. fulvipennis* sp. nov. from Honshû and Shikoku, *B. hokkaidensis* sp. nov. from Hokkaidô and Kyûshû, *B. itsuroi* sp. nov. from Honshû, Kyûshû and Nansei-shotô, *B. moriguchii* sp. nov. from Nansei-shotô, *B. nigra* sp. nov. from Honshû, Shikoku, Kyûshû and Nansei-shotô, *B. okinawana* sp. nov. from Nansei-shotô, *B. yoshigoui* sp. nov. from Honshû) are described. Additional descriptions and records for the two species (*B. koreana* Ahn & Jeon, 2004 and *B. japonica* Liu, Ono & Maruyama, 2020) which are currently described/redescribed are given. Mouthparts and sexual organs of both sexes of all species are illustrated. A key to the Japanese species and distribution map of these species are provided. The habitats and behaviour of some representatives are reported, and the distributional range related to flight ability is discussed.

Key words. Coleoptera, Staphylinidae, Aleocharinae, Myllaenini, new species, taxonomy, intertidal, seashore, Oriental Region, Palearctic Region

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:27EA8466-6B29-40F4-8236-DD49061C523B

Introduction

The intertidal rove beetle genus *Bryothinusa* Casey, 1904 belongs to the tribe Myllaenini of the subfamily Aleocharinae. Members of *Bryothinusa* occur in the intertidal zones of muddy, sandy or gravel beaches throughout the Pacific and Indian Ocean. They inhabit gaps in substrate or under stones except when they walk on the surface of substrate to find prey (Moore & Legner 1971, Moore et al. 1973, Wong & Chan 1977, Ashe 2004; Liu, Ono & Maruyama, personal observation).

Bryothinusa was established by Casey (1904) based on the species *B. catalinae* Casey, 1904 from southern California in the United States (eastern Pacific Coast). Later, Bernhauer (1929) described the subgenus *Anopsisus* Bernhauer, 1929 of the genus *Phytosus* Curtis, 1838 for *P. microphthalmus* Bernhauer, 1929 (= *B. cameroni* (Fauvel, 1904)) from Perim Island, Yemen (Red Sea). Sawada (1955) established the genus *Halesthenus* Sawada, 1955 for *Halesthenus minutus* Sawada, 1955 from Nansei-shotô, Japan (western Pacific Coast). However, the two latter genera were synonymized with *Bryothinusa* by the subsequent studies (Sawada 1971, Pace 1987, Haghebaert 1990).

Regarding the Japanese species, Sawada (1955) described four species: *Halesthenus minutus*, *H. nakanei*, *H. tsutsuii* and *H. serpentis* from Nansei-shotô. Sawada (1971) synonymized *H. serpentis* with *B. tsutsuii*, and with the synonymy of *Halesthenus,* transferred three species, *B. minuta*, *B. nakanei* and *B. tsutsuii*, from *Halesthenus* to *Bryothinusa*. In the same paper, Sawada (1971) also described *B. algarum* from Wakayama-ken of Honshû and moved *Bryothinusa* from the tribe Phytosini to the tribe Myllaenini. Sawada (1991) described *B. sakishimana* from

Nansei-shotô of Japan. Asano & Kojima (2010) recorded *B. gangjinensis* Ahn & Jeon, 2004 from Nansei-shotô in Japan. Liu et al. (2020) described *B. japonica* Liu, Ono & Maruyama, 2020 and recorded *B. koreana* Ahn & Jeon, 2004 from the mainland of Japan. Therefore, up to now, eight species are known from Japan.

Japan has a long territory stretching from the subarctic Hokkaidô to the subtropical Nansei-shotô, and its biogeographic region covers both the Palearctic and Oriental Regions, giving it an extremely rich biodiversity. The diversity of intertidal rove beetles is also very high, and many species were added recently, during the last two decades (e.g., Maruyama 2011a,b; Maruyama & Ahn 2000a,b; Maruyama & Hayashi 2009; Maruyama et al. 2008; Ono & Maruyama 2014, 2015; Song et al. 2018). Recently, in our faunistic survey of Japanese intertidal beetles, we found nine new species and numerous new locality records of *Bryothinusa*. It is surprising that all these new species were discovered in Japan considering the genus contains only 32 known species in the world (Frank & Ahn 2011; Shibata et al. 2013; Liu et al. 2020). In this paper, we revise the Japanese species of the genus *Bryothinusa* and provide a key to the Japanese species and a map of their geographic distribution in Japan.

Material and methods

Most of the specimens examined are from the Kyushu University Museum, which were collected by the authors and several entomologists in Japan. All of them were found under stones or among gravel in intertidal zones and in estuarine habitats. They were then collected using an aspirator, killed in a plastic tube (35 or 50 ml) with some drops of ethyl acetate and preserved as dry specimens. The specimens were dissected under a stereoscopic microscope (Nikon SMZ-U). The whole body was soaked in hot water about 10 minutes to macerate, and abdominal segments VIII–X containing the sexual organs were removed from the body and soaked in 10% KOH for 2 hours at 60°C or overnight at room temperature. After that they were cleaned with water for a few minutes, moved to 80% ethanol solution for 5 minutes and dehydrated in 99% ethanol. Then, those parts were placed in Euparal and mounted on a small slide glass (5 × 10 mm) and glued on a thick card paper (5 × 7 mm) for permanent preservation (Maruyama 2004).

Habitus photos were taken using a Canon 7D Mark II camera with a Canon MP-E 65mm 1–5X macro photo lens and these series of images were later combined using the software Zerene Stacker 1.04. Scanning electron microscope photographs were taken using a JCM-6000Plus. Drawing was done using a Nikon Eclipse 50i microscope and Adobe Illustrator CS2.

The holotypes and paratypes of the new species are deposited in the Kyushu University Museum (KUM), but several paratypes will be deposited in National Museum, Prague, Czech Republic (NMPC), and the Natural History Museum, London (BMNH).

Japanese place names are romanized as they are in Japanese. However, the word, which is included in the name of the place and means environment, was separated by a hyphen. For example, "Obitsugawa" is changed to "Obitsu-gawa" to recongnise "-gawa" which means a river or creek. Words representing administrative districts are also separated by hyphens. The meanings of those words are listed in the Appendix 1.

The following abbreviations are used for measurements (all measurements in mm):

AL	maximum length of antenna;
AS	antennal segment length;
BL	body length (from apex of clypeus to apex of abdomen);
EL	elytral length;
EW	elytral width;
FBL	fore body length (from apex of clypeus to apices of elytra);
HL	head length;
HTL	hind tibial length;
HW	head width;
PL	pronotal length;
PW	pronotal width.

Key to the Japanese species of *Bryothinusa*

1 Hind wings present. 2
– Hind wings completely absent. 12
2 Hind wings reduced (small, evidently not functional). 3
– Hind wings fully developed (large, evidently functional). 7
3 Elytra narrowed anteriorly, shorter than pronotum. ..... ***B. constricta* sp. nov.**
– Elytra subquadrate, longer than pronotum. 4
4 Number of facets 29 or more. ..... ***B. itsuroi* sp. nov.**
– Number of facets 25 or less. 5
5 Spermatheca complicated in shape (2 times coiled or more). ..... ***B. fulvipennis* sp. nov.**
– Spermatheca simplified in shape (1.5 times coiled or less). 6
6 Antennal segment I longer than II; spermatheca 1.5 times coiled near base. ***B. sakishimana*** Sawada, 1991
– Antennal segment I almost as long as II; spermatheca 1 times coiled near base. ..... ***B. hokkaidensis* sp. nov.**
7 Number of facets 24 or less. ..... ***B. aikoae* sp. nov.**
– Number of facets 29 or more. 8
8 Female tergite X with posterior margin protruded medially. 9
– Female tergite X with posterior margin rounded or truncated. 10
9 Antennal segment I longer than II; body almost black, elytra clearly bicolour. ..... ***B. nakanei*** (Sawada, 1955)
– Antennal segment I almost as long as II; body pale brown, elytra almost unicolour. ..... ***B. moriguchii* sp. nov.**
10 Labrum with large, spiniform seta antero-laterally. ..... ***B. nigra* sp. nov.**
– Labrum with normal-shaped spiniform seta antero -laterally. 11
11 Antennal segment I longer than II; elytra bicolour. ..... ***B. gangjinensis*** Ahn & Jeon, 2004
– Antennal segment I almost as long as II; elytra almost unicolour. ..... ***B. okinawana* sp. nov.**
12 Female tergite X with posterior margin protruded medially. ..... ***B. minuta*** (Sawada, 1955)

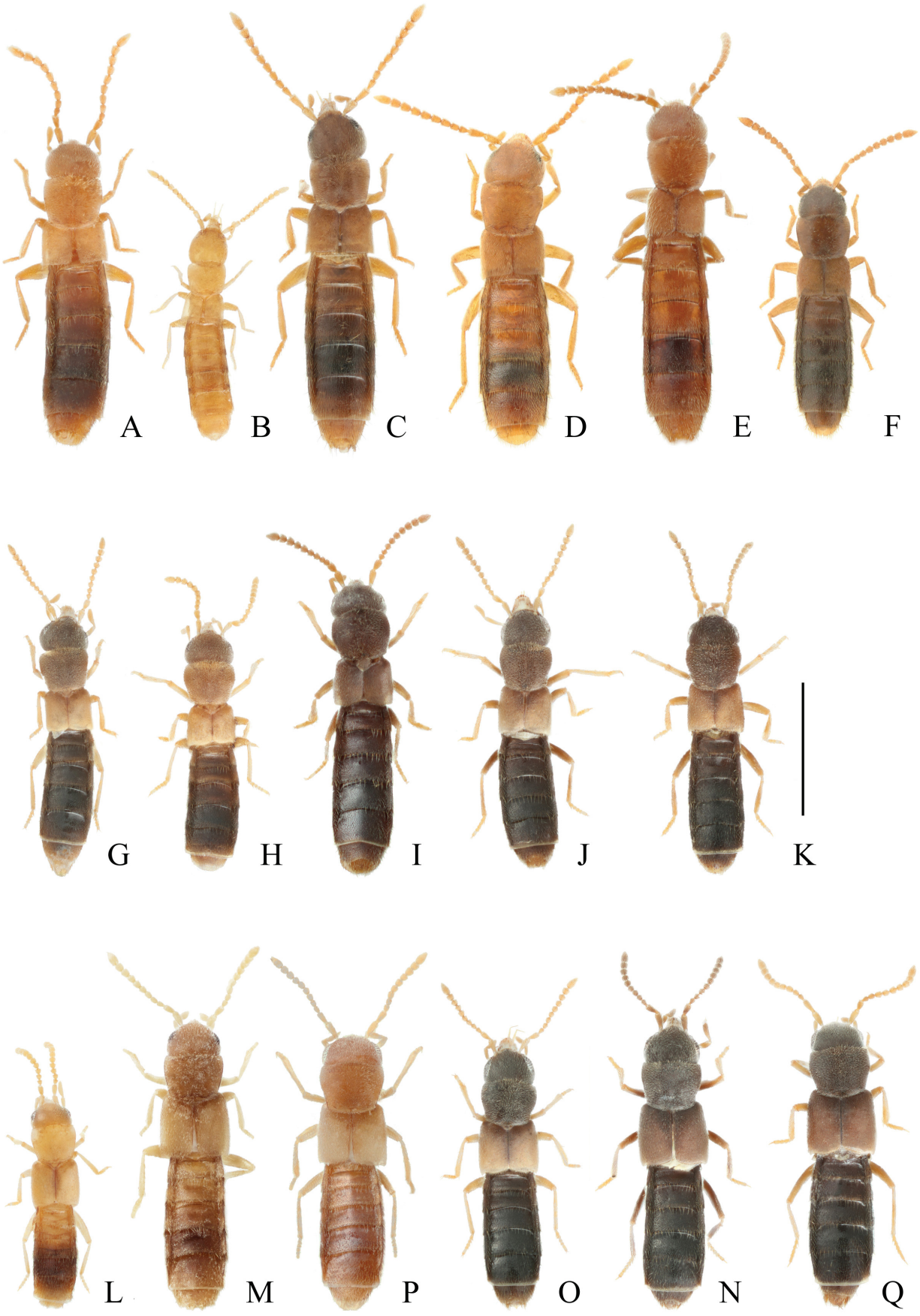

Fig. 1. Habitus of *Bryothinusa* spp. A – *B. algarum* Sawada, 1971; B – *B. minuta* (Sawada, 1955); C – *B. tsutsuii* (Sawada, 1955); D – *B. koreana* Ahn & Jeon, 2004; E – *B. yoshigoui* sp. nov.; F – *B. japonica* Liu, Ono & Maruyama, 2020; G – *B. sakishimana* Sawada, 1991; H – *B. constricta* sp. nov.; I – *B. hokkaidensis* sp. nov.; J – *B. fulvipennis* sp. nov.; K – *B. itsuroi* sp. nov.; L – *B. aikoae* sp. nov.; M – *B. okinawana* sp. nov.; N – *B. nigra* sp. nov.; O – *B. nakanei* (Sawada, 1955); P – *B. moriguchii* sp. nov.; Q – *B. gangjinensis* Ahn & Jeon, 2004. Scale bars: 1.00 mm.

– Female tergite X with posterior margin rounded or truncated. 13
13 Inner wall of spermatheca roughly wrinkled. .... ***B. japonica*** Liu, Ono & Maruyama, 2020
– Inner wall of spermatheca not wrinkled. 14
14 Spermatheca complicated in shape (2 times coiled or more). ..... ***B. algarum*** Sawada, 1971
– Spermatheca simplified in shape (1.5 times coiled or less). 15
15 Median lobe of aedeagus without granule-like projections. ..... ***B. tsutsuii*** (Sawada, 1955)
– Median lobe of aedeagus with several granule-like projections. 16
16 Number of facets usually 17 or more. .... ***B. koreana*** Ahn & Jeon, 2004
– Number of facets 14 or less. ..... ***B. yoshigoui* sp. nov.**

Taxonomy

Genus *Bryothinusa* Casey, 1904

(Japanese name: Nagisa-hanekakushi-zoku)

Bryothinusa Casey, 1904: 312 (original description; type species: *Bryothinusa catalinae* Casey, 1904, by monotypy); Ahn & Jeon (2004): 29 (key to Korean species); Ahn & Ashe (2004): 123–138 (phylogeny of Myllaenini and related taxa); Ashe (2004): 581–597 (annotated catalogue of world species); Smetana (2004): 463 (catalogue of Palearctic species); Frank & Ahn (2011): 1–98 (checklist; biogeography; natural history); Schülke & Smetana (2015): 676 (catalogue of Palearctic species); Liu et al. (2020): 585–593 (key to Japanese species; checklist).

Anopsisus Bernhauer, 1929: 187 (original description; type species: *Phytosus microphthalmus* Bernhauer, 1929 (= *Diglossa cameroni* Fauvel, 1904), fixed by monotypy). Synonymised by Haghebaert (1990: 133).

Halesthenus Sawada, 1955: 83 (original description; type species: *Halesthenus minutus* Sawada, 1955, by original designation). Synonymised by Sawada (1971: 81).

See Ashe (2004: 589) for the detailed citations before 2004.

Diagnosis. Body small (1.6–2.6 mm), more or less parallel-sided; body surface densely covered with minute setae. Head capsule without neck and infraorbital carina; eyes variable in size, with small setae among facets. Antenna with 11 segments. Mouthparts: labrum with long setae 7+7; mandibles asymmetrical, right mandible with median tooth, left mandible without tooth, blunt at apex; maxilla with galea and lacinia elongate; galea styliform, ciliate apically; apex of lacinia with several spines like a comb and with some larger setae around base; maxillary palpus with 4 segments, elongate, segment IV very short, membranous at apex; labial palpus elongate, with 2 segments; most setae located basally; mentum with antero-lateral angles prolonged into spinose processes; anterior margin deeply emarginated to truncate at bottom, and with small "v seta" (Sawada 1971) on antero-lateral margin. Pronotum slightly wider than long, narrowest at base; basal margin slightly rounded; hypomera entirely visible in lateral aspect. Tarsal formula 4-4-5. Paramere of aedeagus with distinctive velum and 4 (3 longer + 1 shorter) setae near tip. Spermatheca with short apical part and long, more or less coiled basal part.

Distinguishing species. The species of this genus can be divided into some main groups based on presence/absence of hind wings and the degree of their development as mentioned in the key. The condition of the hind wings can be estimated to some extent by the appearance of elytra, which are square shaped in species with fully developed hind wings or anteriorly narrowed elytra in species with reduced or absent hind wings. Species of this genus may exhibit slight geographical variation in colouration, but this may not be an important characteristic in distinguishing species, since colouration also varies with condition of the specimen. Morphology of the spermatheca is the most useful character for distinguishing species in this genus. Except for some species, there is no great interspecific variation in male genitalia which is normally the most useful species-diagnostic character in Aleocharinae. Body size, the number of facets of the eye and character states of the mouthparts and abdominal terminalia are also informative. In case more than one species is found at a single site, the best way to identify species is to collect as large number of specimens as possible, examine them closely for body size, condition of hind wings and number of facets, dissect some representatives of each morphotype, and confirm species identity based on spermathecal shape.

Bryothinusa algarum Sawada, 1971

(Figs 1A; 2A; 3; 20A; 21G; 22)

(Japanese name: Usuaka-nagisa-hanekakushi)

Bryothinusa algarum Sawada, 1971: 90–92 (original description, illustrated, type locality: Kirimezaki, Wakayama-ken, 15.iv.1970, K. Sawada); Sawada (1972): unnumbered table at end of article (characters); Moore et al. (1973): 74 (in key to species of *Bryothinusa*), 77 (nomenclatorial history, diagnosis); Moore & Legner (1975): 109–110 (in key to species of *Bryothinusa*), 111 (in tabular key to known species of *Bryothinusa*); Ashe (2004): 590 (in annotated catalogue of world species); Smetana (2004): 463 (in catalogue of Palearctic species); Kawakami (2008): 69–73 (life cycle report at the Osaka Nanko Bird Sanctuary); Frank & Ahn (2011): 26 (in checklist); Schülke & Smetana (2015): 676 (catalogue of Palearctic species); Liu et al. (2020): 589 (in key to Japanese species), 591 (in checklist).

Type material. Not examined.

Material examined. JAPAN: Hokkaidô: 1 ♂ 1 ♀, 9 unsexed spec., Notori-ko, Abashiri-shi, Hokkaidô, 11.ix.2008, T. Kato; 1 ♂ 1 ♀, 8 unsexed spec., Usu-chô, Date-shi, Hokkaidô, 12.iv.2020, Y. Tasaku. **Honshû:** 4 unsexed spec., Nemoto, Shirahama-machi, Chiba-ken, 1.iv.2005, H. Ono; 1 ♂ 2 ♀♀, 6 unsexed spec., Fujimi, Tateyama-shi, Okino-shima, Chiba-ken, 15.ii.2008, H. Ono; 4 unsexed spec., Ito, Tateyama-shi, Chiba-ken, 15.iv.2008, H. Ono; 2 unsexed spec., Hara, Kamega-saki, Tomiyama-machi, Chiba-ken, 1.iv.2005, H. Ono; 1 ♂ 2 unsexed spec., Nagasaki-bana, Chôshi-shi, Chiba-ken, 2.iv.2009, H. Ono; 1 ♀, same locality, 16.ix.2009, H. Ono; 4 unsexed spec., same locality, 13.x.2009, H. Ono; 1 ♀, Shibasaki-bashi, Kanaya, Futtsu-shi, Chiba-ken, 14.vi.2009, H. Ono; 22 unsexed spec., Tsumeki-zaki, Shimoda-shi, Shizuoka-ken, 21.iv.2003, M. Maruyama; 1 ♂ 2 unsexed spec., Mouth of Kô-gawa, Numazu-shi, Shizuoka-ken, 1.x.2000, T. Kurihara; 2 ♂♂ 1 ♀, 7 unsexed spec., Hannan 2-ku, Kishiwada-shi, Ôsaka-fu, 7.x.2010, Y. Kawakami; 2 unsexed spec., Naruga-shima, Sumoto-shi, Hyôgo-ken, 20.iv.2012, Y. Kawakami; 4 unsexed spec., Hatake-jima, Shirahama-chô, Wakayama-ken, 29.iii.2006, Y. Nakase; 13 unsexed spec., Kusumibana, Ôbatake, Ko-jima, Kurashiki-shi, Okayama-ken, 21.iii.2009, O. Yamaji; 4 unsexed spec., Manabe-jima, Kasaoka-shi, Okayama-ken, 18.v.2008, Y. Fujitani; 4 unsexed spec., Kanaburo, Kitagi-shima, Kasaoka-shi, Okayama-ken, 11.x.2008, O. Yamaji; 2 unsexed spec., Naga-shima, Kaminoseki-chô, Yamaguchi-ken, 5.v.2005, Y. Nakase; 2 ♂♂ 55 unsexed spec., same locality, 23.vii.2005, Y. Nakase; 1 unsexed spec., same locality, 1.v.2008, M. Moriguchi. **Shikoku:** 1 unsexed spec., Koura-kaigan, Koiso, Higashi-kagawa-shi, Kagawa-ken, 12.v.2012, T. Taki; 2 unsexed spec., same

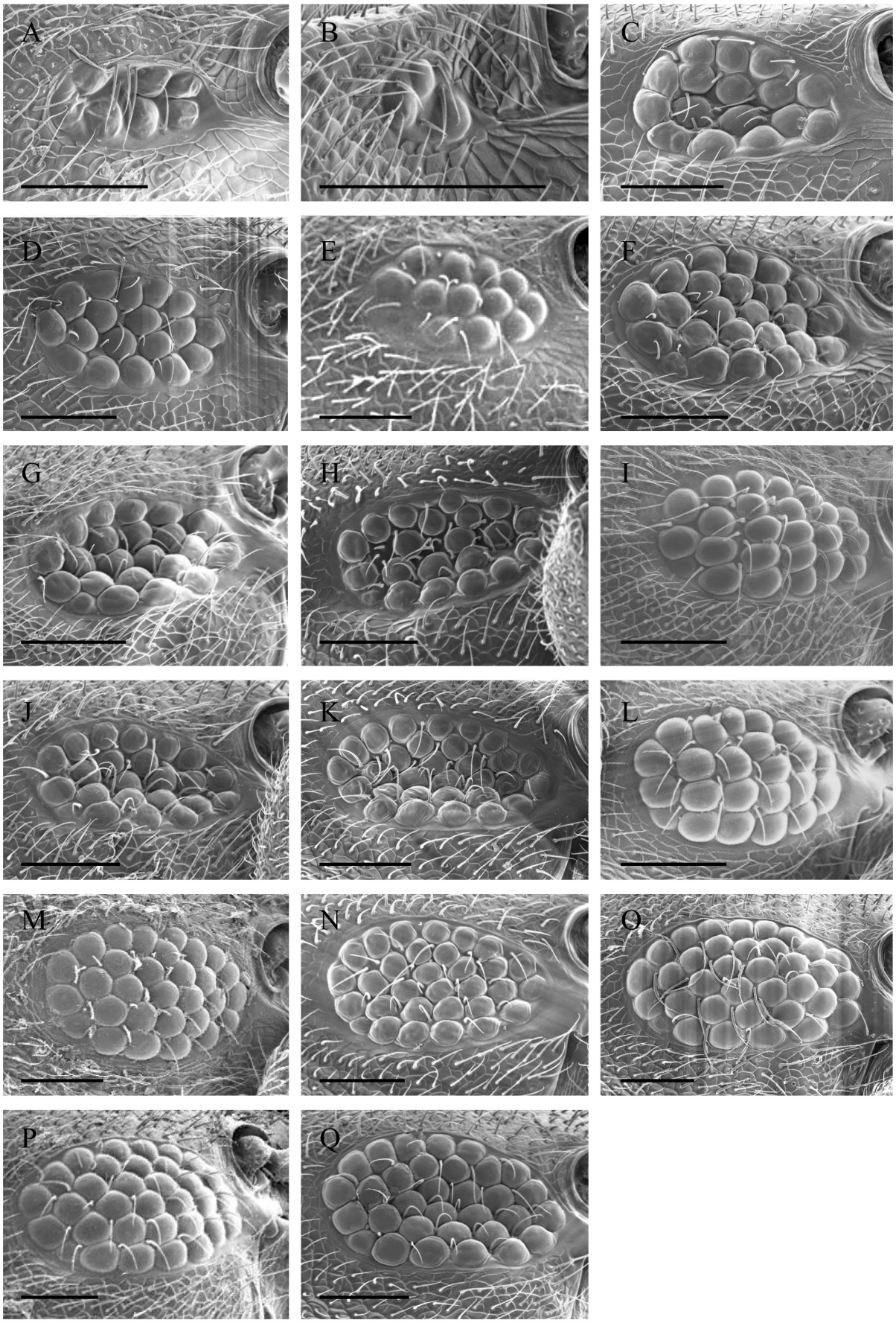

Fig. 2. Compound eyes of *Bryothinusa* spp. A – *B. algarum* Sawada, 1971; B – *B. minuta* (Sawada, 1955); C – *B. tsutsuii* (Sawada, 1955); D – *B. koreana* Ahn & Jeon, 2004; E – *B. yoshigoui* sp. nov.; F – *B. japonica* Liu, Ono & Maruyama, 2020; G – *B. sakishimana* Sawada, 1991; H – *B. constricta* sp. nov.; I – *B. hokkaidensis* sp. nov.; J – *B. fulvipennis* sp. nov.; K – *B. itsuroi* sp. nov.; L – *B. aikoae* sp. nov.; M – *B. okinawana* sp. nov.; N – *B. nigra* sp. nov.; O – *B. nakanei* (Sawada, 1955); P – *B. moriguchii* sp. nov.; Q – *B. gangjinensis* Ahn & Jeon, 2004. Scale bars: 0.05 mm.

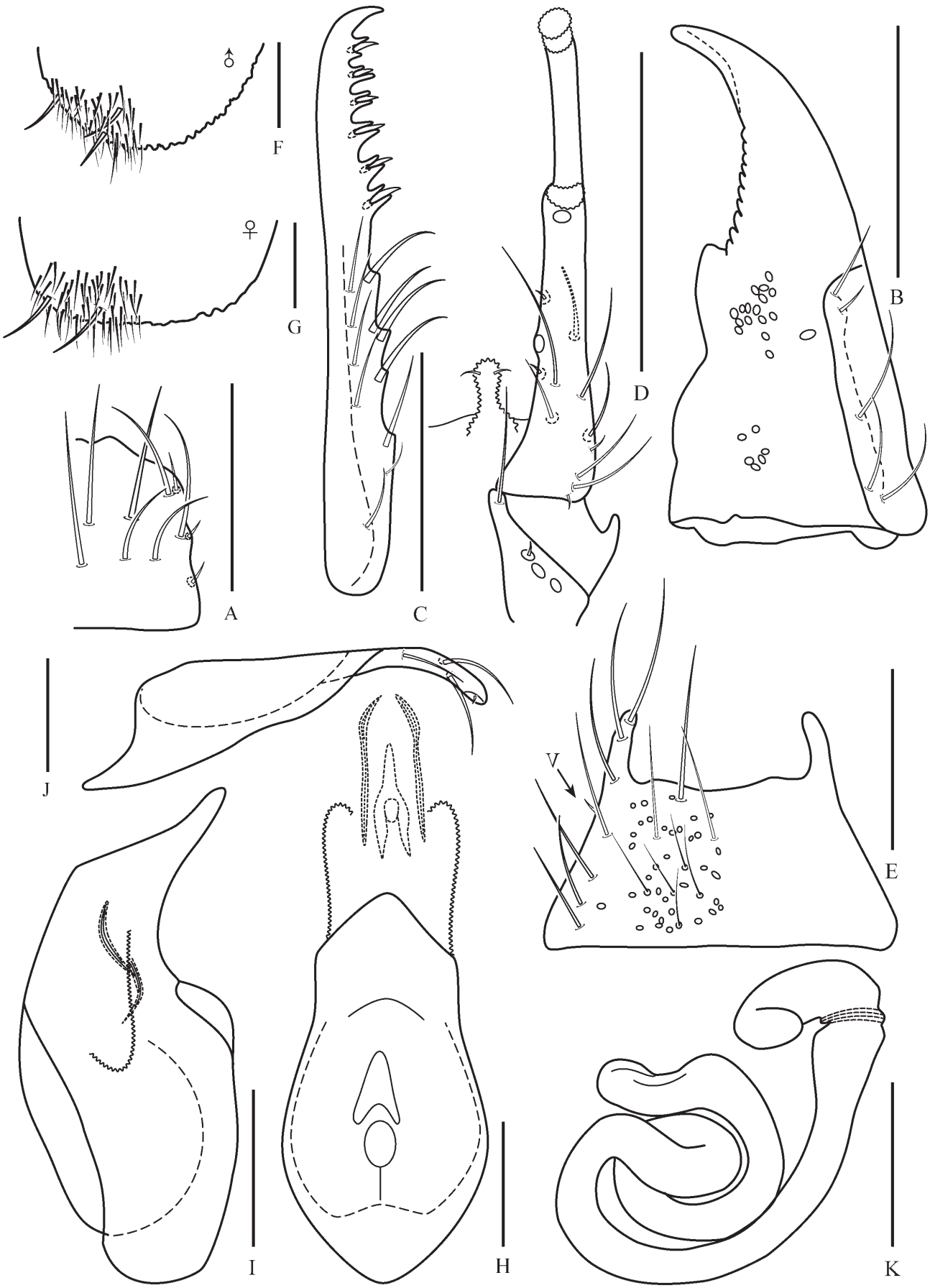

Fig. 3. *Bryothinusa algarum* Sawada, 1971. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

locality, 16.iii.2013, T. Taki; 2 ♂♂ 14 unsexed spec., same locality, 21.iv.2013, T. Taki; 5 unsexed spec., same locality, 29.iv.2014, T. Taki; 2 ♂♂ 2 ♀♀, 16 unsexed spec., Komatsubara, Matsubara, Higashi-kagawa -shi, Kagawa-ken, 5.iv.2008, H. Fujimoto; 5 ♂♂ 1 ♀, 12 unsexed spec., Kaburagoshi, Matsubara, Higashi-kagawa-shi, Kagawa-ken, 7.ix.2015, T. Taki; 2 unsexed spec., same locality, 14.v.2006, Y. Nakase; 1 unsexed spec., Mouth of Umayado-gawa, Umayado, Higashikagawa-shi, Kagawa-ken, 11.v.2014, T. Taki; 11 unsexed spec., Hojô-Ôura, Matsuyama-shi, Ehime-ken, 15–16.iv.2010, M. Maruyama. **Kyûshû:** 1 ♀, 5 unsexed spec., Sunosaki, Imazu, Nishi-ku, Fukuoka-shi, Fukuoka-ken, 26.vi.2020, Y. Hisasue; 12 unsexed spec., same locality, 16.x.2020, T. Liu & T. Nozaki. **Nansei-shotô:** 1 unsexed spec., Shimokushi, Tokunoshima-chô, Tokuno-shima, Kagoshima-ken, 8.vi.2008, M. Maruyama; 9 unsexed spec., You, Kasari-chô, Amami-Ôshima, Ôshima-gun, Kagoshima-ken, 27.ii.2004, H. Kamezawa. Deposited at KUM but some will be distributed to NMPC and BMNH.

Redescription. Body (Fig. 1A) small, about 2.3–2.8 mm in length, covered with minute setae. Head, pronotum and elytra yellowish brown; abdominal tergites V–VII infuscate; antenna, mouthparts and legs similarly coloured, lightly paler than head colour and paler toward apex.

Head oval, wider than long, shorter than pronotum, almost as long as elytra; eyes (Fig. 2A) small, reniform, shorter than 1/3 of head length, with 7–8 facets; antennal length little shorter than distance from anterior margin of head to posterior margin of elytra; antennal segment all longer than wide; segment I 1.4 times longer than II, almost 2 times longer than III, and as long as XI.

Mouthparts (Figs 3A–E) with distribution of labral setae as in Figure 3A; mandibles (Fig. 3B) elongate triangle, asymmetrical, right with median tooth; median tooth longer than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 3C) with two spines not closely interdigitating; 4 setae on inner margin of lacinia; labial palpus (Fig. 3D) with most setae located basally; mentum (Fig. 3E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" of mentum lower than level of anterior margin.

Pronotum longer than elytra, almost as wide as head.

Elytra widened apically, wider than long, wider than pronotum; hind wings absent.

Male sternite VIII (Fig. 3F) with posterior margin slightly serrate. Median lobe of aedeagus as in Figs 3H, I; paramere (Fig. 3J) elongate.

Female abdominal sternite VIII (Fig. 3G) with posterior margin slightly serrate but smoother than in male. Spermatheca (Fig. 3K) with apical part curved and narrowed at apex; basal part complicated in shape; coiled several times near base.

Measurements. BL 2.30–2.80, FBL 1.00–1.60, HL 0.33–0.36, HW 0.41–0.46, PL 0.37–0.41, PW 0.41–0.46, EL 0.33–0.37, EW 0.43–0.52, HTL 0.31–0.43, AL 0.87–0.99, AS-I 0.13–0.15, AS-II 0.09–0.10, AS-III 0.06–0.07.

Differential diagnosis. In general appearance, the species is very similar to *B. koreana*, *B. tsutsuii*, *B. yoshigoui* sp. nov. and *B. japonica*, but easily distinguished from them by the number of facets and the spermathecal shape.

Distribution. Japan (**Hokkaidô**; **Honshû:** Chiba-ken, Tôkyô-to, Kanagawa-ken, Shizuoka-ken, Ôsaka-fu, Hyôgo-ken, Wakayama-ken, Okayama-ken, Yamaguchi-ken; **Shikoku:** Kagawa-ken, Ehime-ken; **Kyûshû:** Fukuoka-ken, Miyazaki-ken, Kagoshima-ken: Shimokoshiki-jima; **Nansei-shotô:** Kagoshima-ken: Amami-Ôshima, Tokuno-shima).

Remarks. This species is widely distributed in Japan, and as well as *B. minuta* and *B. hokkaidensis* sp. nov., it was collected at the highest latitude (about 44N in Hokkaidô) recorded for this genus. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22. The voucher specimens of previous records should be re-examined; the specimens from mainland Japan could be confused with the other similar species, such as *B. japonica* and *B. koreana*.

Bryothinusa minuta (Sawada, 1955)

(Figs 1B; 2B; 4; 20B–D; 21G; 22)

(Japanese name: Hoso-nagisa-hanekakushi)

Halesthenus minutus Sawada, 1955: 83–84, plate 16 (original description, illustrated, type locality: Yoriki, Nakano-shima, 4.vi.1953, S. Uéno).

Bryothinusa minuta: Sawada (1971): 82 (transferred from *Halesthenus*; redescription; new distribution records); Sawada (1972): unnumbered table at end of article (characters); Moore et al. (1973): 74 (in key to species of *Bryothinusa*), 77 (nomenclatorial history; diagnosis); Moore & Legner (1975): 109–110 (in key to species of *Bryothinusa*), 111 (in tabular key to known species of *Bryothinusa*); Ahn & Ashe (2004): 123–138 (phylogeny of Myllaenini and related taxa); Ahn & Jeon (2004): 34 (new record of Korea); Ashe (2004): 592 (in annotated catalogue of world species); Frank & Ahn (2011): 27 (in checklist); Schülke & Smetana (2015): 676 (in catalogue of Palearctic species); Ahn et al. (2017): 307 (in checklist of Staphylinidae in Korea); Liu et al. (2020): 589 (in key of Japanese species), 591 (in checklist).

Type material. Not examined.

Material examined. JAPAN: Hokkaidô: 2 ♀♀, Usu-chô, Date-shi, Hokkaidô, 12.iv.2020, Y. Tasaku. **Honshû:** 44 unsexed spec., Sunosaki-kaigan, Sunosaki, Tateyama-shi, Chiba-ken, 6.ii.2007, H. Ono; 1 unsexed spec., Kanaya, Futtsu-shi, Chiba-ken, 9.iv.2007, H. Ono; 2 unsexed spec., Shibasaki-bashi, Kanaya, Futtsu-shi, Chiba-ken, 14.vi.2009, H. Ono; 2 unsexed spec., Nagasakibana, Chôshi-shi, Chiba-ken, 16.ix.2009, H. Ono; 2 unsexed spec., same locality, 13.x.2009, H. Ono; 1 unsexed spec., Kuruwa-kaigan, Akiya, Yokosuka-shi, Kanagawa-ken, 14.ix.2013, H. Ono; 3 ♂♂ 5 unsexed spec., Mouth of Kô-gawa, Numazu-shi, Shizuoka-ken, 1.x.2000, T. Kurihara; 3 ♀♀, 5 unsexed spec., Tsumeki-zaki, Shimoda-shi, Shizuoka-ken, 21.iv.2003, M. Maruyama; 1 ♂, Wakamatsu-zaki, Numazu -shi, Shizuoka-ken, 1.x.2000, T. Kurihara; 2 unsexed spec., Kusumibana, Ôbatake, Kojima, Kurashiki-shi, Okayama-ken, 21.iii.2009, O. Yamaji; 3 unsexed spec., Ta-no-ura, Naga-shima, Kaminoseki-chô, Yamaguchi-ken, 15.x.2005, Y. Nakase. **Shikoku:** 1 ♂, Kaigan-ji, Nishishirakata, Tadotsu-chô, Kagawa-ken, 31.iii.2008, H. Fujimoto; 2 ♂♂ 2 ♀♀, 3 unsexed spec., Ôyatomi-machi, Sakaide-shi, Kagawa-ken, 29.iii.2008, H. Fujimoto; 1 ♂ 2 ♀♀, 10 unsexed spec., Mouth of Umayado-gawa, Umayado, Higashi-kagawa-shi, Kagawa-ken, 11.v.2014, T. Taki; 7 unsexed spec., Ado-ike, Hiketa, Higashi-kagawa-shi, Kagawa-ken, 28.vii.2013, T. Taki; 17 unsexed spec., same locality, 11.v.2014, T. Taki; 2 unsexed spec., Koura-kaigan, Koiso, Higashi-kagawa-shi, Kagawa-ken, 29.iv.2014, T. Taki; 1 unsexed spec., same locality, 21.iv.2014, T. Taki. **Kyûshû:** 1 ♂, Suno-saki, Imazu, Nishi-ku, Fukuoka-shi, Fukuoka-ken, 26.vi.2020, Y. Hisasue; 31 unsexed spec., same locality, 16.x.2020, T. Liu & T. Nozaki; 1 unsexed spec., Miyaga-hama, Ibusuki-shi, Kagoshima-ken, 19.iv.2008, M. Maruyama; 2 unsexed spec., Ko-ura, Kasasa-machi, Minamisatsuma-shi, Kagoshima-ken, 20.iv.2008, M. Maruyama; 3 unsexed spec., Aiboshi-gawa, Aiboshi, Minamisatsuma-shi, Kagoshima-ken, 20.iv.2008, M. Maruyama. **Nansei-shotô:** 6 unsexed spec., Ôgomori, Takara-jima, Tokara-rettô, Kagoshima-ken, 6.vii.2019, T. Liu, N. Tsuji & H. Ono; 3 ♂♂ 1 ♀, 27 unsexed spec., Yoriki (a gravel beach), Nakano-shima, Tokara-rettô, Kagoshima-ken, 7.vii.2019, T. Liu, N. Tsuji & H. Ono; 15 unsexed spec., same locality, 8.vii.2019, T. Liu, N. Tsuji & H. Ono; 1 unsexed spec., You, Kasari-chô, Amami-Ôshima, Ôshima-

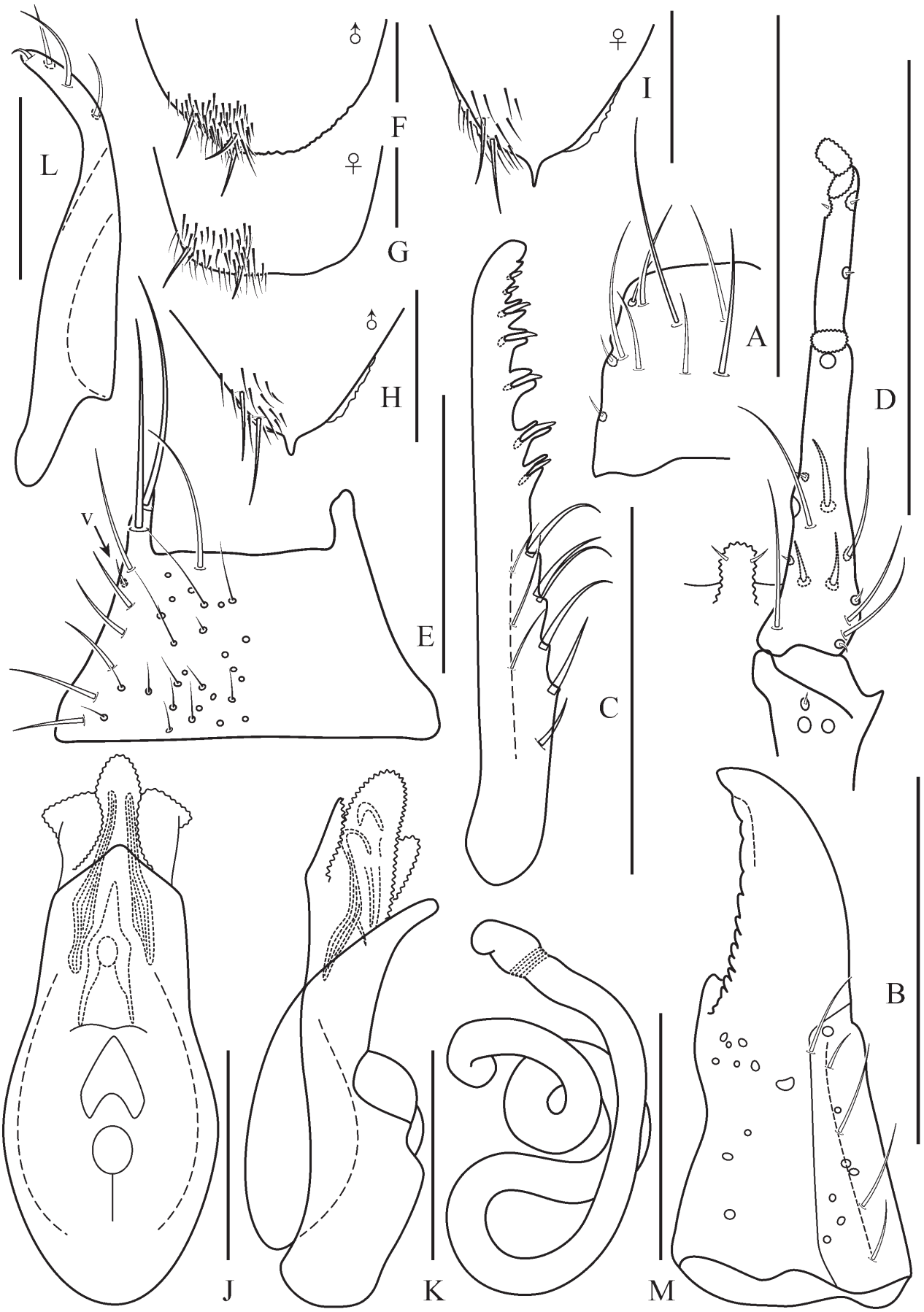

Fig. 4. *Bryothinusa minuta* (Sawada, 1955). A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – male tergite X; I – female tergite X; J – medin lobe, ventral view; K – medin lobe, lateral view; L – paramere; M – spermatheca. Scale bars: 0.1 mm.

gun, Kagoshima-ken, 27.ii.2004, H. Kamezawa; 2 ♀♀, 2 unsexed spec., Kasari-wan, Kasari-chô, Amami-Ôshima, Kagoshima-ken, 4.vi.2008, M. Maruyama; 4 unsexed spec., Yuwan, Uken-son, Amami-Ôshima, Kagoshima-ken, 5.vi.2008, M. Maruyama; 1 ♂ 1 ♀, 3 unsexed spec., Shokazu, Setouchi-chô, Kakeroma-jima, Kagoshima-ken, 6.vi.2008, M. Maruyama; 1 ♀, Onna-son, Inbu-gun, Okinawa-ken, 11–13.v.2005, M. Sugimoto; 3 ♂♂, Teruma, Yonagusuku-son, Okinawa-ken,14.ix.2003, M. Moriguchi ; 2 unsexed spec., Fûne, Ishigaki-shi, Okinawa-ken, 7.iii.2000, T. Kurihara; 6 ♂♂ 8 unsexed spec., same locality, 8.iii.2000, T. Kurihara; 3 unsexed spec., same locality, 12.iii.2000, T. Kurihara; 10 unsexed spec., Nagura-Anparu, Nagura, Ishigaki-shi, Okinawa-ken, 4.ii.2009, H. Ono; 2 ♂♂ 2 ♀♀, 42 unsexed spec., Mouth of Honera-gawa, Iriomote-jima, Takana, Taketomi-chô, Okinawa-ken, 2.iv.2019, T. Nozaki; 3 unsexed spec., Mouth of Honera-gawa, Takana, Taketomi-chô, Iriomote-jima, Okinawa-ken, 24.vi.2019, T. Liu & N. Tsuji. **Ogasawara-shotô:** 2 ♂♂ 1 ♀, 6 unsexed spec., Ô-mura, Chichi-jima, Ogasawara-shotô, Tôkyô-to, 1.x.1977, Y. Watanabe. Deposited at KUM but some will be distributed to NMPC and BMNH.

Redescription. Body (Fig. 1B) small, about 1.6–1.7 mm long, densely covered with minute setae. Head, pronotum and elytra light yellow; abdominal tergites VI–VII almost infuscate posteriorly; antenna, mouthparts and legs similarly coloured, lightly paler than head colour and paler toward apex.

Head oval, wider than long, longer than pronotum and elytra; eyes (Fig. 2B) small, reniform, shorter than 1/4 head length, with 3 or 4 facets; antennal length shorter than distance from anterior margin of head to posterior margin of elytra; all antennal segments longer than wide; segment I 1.5 times longer than II, almost 2.5 times longer than III, and shorter than XI.

Mouthparts (Figs 4A–E) with distribution of labral setae as in Figure 4A; mandibles (Fig. 4B) elongate triangle, asymmetrical, right mandible with median tooth; median tooth longer than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 4C) with two spines interdigitating close; 2–3 setae on inner margin of lacinia; labial palpus (Fig. 4D) with most setae located basally; mentum (Fig. 4E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" of mentum distant from apical setae.

Pronotum longer than elytra, narrower than head.

Elytra widened apically, wider than long, narrower than pronotum; hind wings absent.

Male abdominal sternite VIII (Fig. 4F) with posterior margin slightly serrate. Medial posterior margin protruded sharp in form on tergite X of male (Fig. 4H). Median lobe of aedeagus as in Figs 4J, K; paramere (Fig. 4L) elongate.

Female abdominal sternite VIII (Fig. 4G) with posterior margin slightly serrate but rounder and smoother than in male. Medial posterior margin protruded sharp in form on tergite X of female (Fig. 4I), and sharper than in male. Spermatheca (Fig. 4M) small and apical part very short; basal part complicated in shape; several times coiled near base.

Measurements. BL 1.60–1.70, FBL 0.70–0.80, HL 0.25–0.28, HW 0.25–0.34, PL 0.24–0.26, PW 0.25–0.28, EL 0.20–0.23, EW 0.24–0.25, HTL 0.23–0.26, AL 0.55–0.65, AS-I 0.08–0.09, AS-II 0.05–0.06, AS-III 0.03–0.04.

Differential diagnosis. This species is easily distinguished from the other Japanese species of *Bryothinusa* by the smaller body and strongly reduced eyes, each consisting of 3 or 4 facets only.

Distribution. Japan (**Hokkaidô**; **Honshû:** Chiba-ken, Tôkyô-to, Kanagawa-ken, Shizuoka-ken, Wakayama-ken, Okayama-ken, Yamaguchi-ken; **Shikoku:** Kagawa-ken; **Kyûshû:** Fukuoka-ken, Kagoshima-ken; **Nansei-shotô:** Kagoshima-ken: Takara-jima, Nakano-shima, Amami-Ôshima, Kakeroma-jima; Okinawa-ken: Okinawa-jima, Ishigaki-jima, Iriomote-jima; **Ogasawara-shotô:** Chichi-jima); Korea.

Remarks. This species is very small, currently the smallest species in Japan, and the specimens were collected under stones. In the Japanese species of *Bryothinusa*, *B. minuta* is most widely distributed, from Hokkaidô to Iriomote-jima. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa tsutsuii (Sawada, 1955)

(Figs 1C; 2C; 5; 20E–G; 21D; 22)

(Japanese name: Kiiro-nagisa-hanekakushi)

Halesthenus tsutsuii Sawada, 1955: 84 (original description; type locality: Japan: Nansei-shotô, Tokara-rettô, Takara-jima).

Halesthenus serpentis Sawada, 1955: 84–85 (original description); Sawada (1971): 85 (placed as a junior synonym of *B. tsutsuii*); Smetana (2004): 464 (catalogue of Palearctic species; as a valid species); Schülke & Smetana (2015): 676 (catalogue of Palearctic species; as a valid species). Synonymized by Sawada (1971: 85).

Bryothinusa tsutsuii: Sawada (1971): 85–87 (transferred from *Halesthenus*; redescription); Sawada (1972): unnumbered table at end of article (characters); Moore et al. (1973): 74 (in key to species of *Bryothinusa*), 77 (nomenclatorial history; diagnosis); Moore & Legner (1975): 109–110 (in key to species of *Bryothinusa*), 111 (in tabular key to known species of *Bryothinusa*); Ashe (2004): 595 (in annotated catalogue of world species); Smetana (2004): 464 (in catalogue of Palearctic species); Frank & Ahn (2011): 27 (in checklist); Schülke & Smetana (2015): 676 (in catalogue of Palearctic species); Liu et al. (2020): 589 (in key of Japanese species), 592 (in checklist).

Type material. Not examined.

Material examined. JAPAN: Nansei-shotô: 3 ♂♂ 2 ♀♀, 9 unsexed spec., Mage-shima (near Tanega-shima), Kagoshima-ken, 14.x.2000, M. Maruyama (under stone on sandy beach, in a port); 5 ♂♂ 3 ♀♀, 18 unsexed spec., Ama-domari (a gravel beach), Nakano-shima, Tokara-rettô, Kagoshima-ken, 7.vii.2019, T. Liu & H. Ono; 1 ♂ 6 ♀♀, 19 unsexed spec., Uken-son, Edateku-jima (near Amami-Ôshima), Kagoshima-ken, 5.vi.2008, M. Maruyama; 6 unsexed spec., Izena, Izena-son, Shimajiri-gun, Okinawa-ken, 5.v.2013, M. Asano; 4 ♂♂ 5 ♀♀, 66 unsexed spec., Mihama (Sunset Beach), Chatan-chô, Okinawa-jima, Okinawa-ken, 27.iii.2009, H. Suenaga; 1 ♀, 7 unsexed spec., Chatan-chô, Okinawa, Okinawa-ken, Nansei-shotô, 26.v.2002, M. Moriguchi; 1 ♂ 2 ♀♀, 7 unsexed spec., Teruma, Yonagusuku-son, Okinawa-ken, 14.ix.2003, M. Moriguchi; 1 ♀, 3 unsexed spec., Ou-jima, Nago-shi, Okinawa-ken, 30.iv.2006, M. Moriguchi; 2 ♂♂ 1 ♀, 2 unsexed spec., Inbu-gun, Onna-son, Okinawa-ken, 11–13.v.2005, M. Sugimoto; 3 ♂♂ 1 ♀, 7 unsexed spec., Kadena-Marina, Kadena-chô, Okinawa-ken, 25.iv.2005, M. Moriguchi (under stone on sandy beach in estuary); 1 unsexed spec., Nakasuji, Ishigaki-shi, Ishigaki-jima, Okinawa-ken, 14.iii.2000, T. Kurihara; 1 ♂ 2 ♀♀, 8 unsexed spec., Inoda, Ishigaki-jima, Okinawa-ken, 31.v.2003, M. Moriguchi; 2 ♂♂ 1 ♀, 13 unsexed spec., Fûne, Ishigaki-shi, Ishigaki-jima, Okinawa-ken, 8.iii.2000, T. Kurihara; 2 unsexed spec., Akaishi, Ishigaki-shi, Ishigaki-jima, Okinawa-ken, 30–31.iii.2010, T. Hayama; 1 unsexed spec., Haemida, Taketomi-chô, Iriomote-jima, Okinawa-ken, 19.iii.2000, T. Kurihara; 2 ♀♀, 7 unsexed spec., same locality, 24.x.2020, T. Nozaki; 1 ♂ 1 ♀, 7 unsexed spec., Mouth of Nakama-gawa, Haiminaka, Iriomote-jima, Yaeyama-gun, Okinawa-ken, 4.ix.2020, S. Inoue & Y. Hisasue. Deposited at KUM but some will be distributed to NMPC and BMNH.

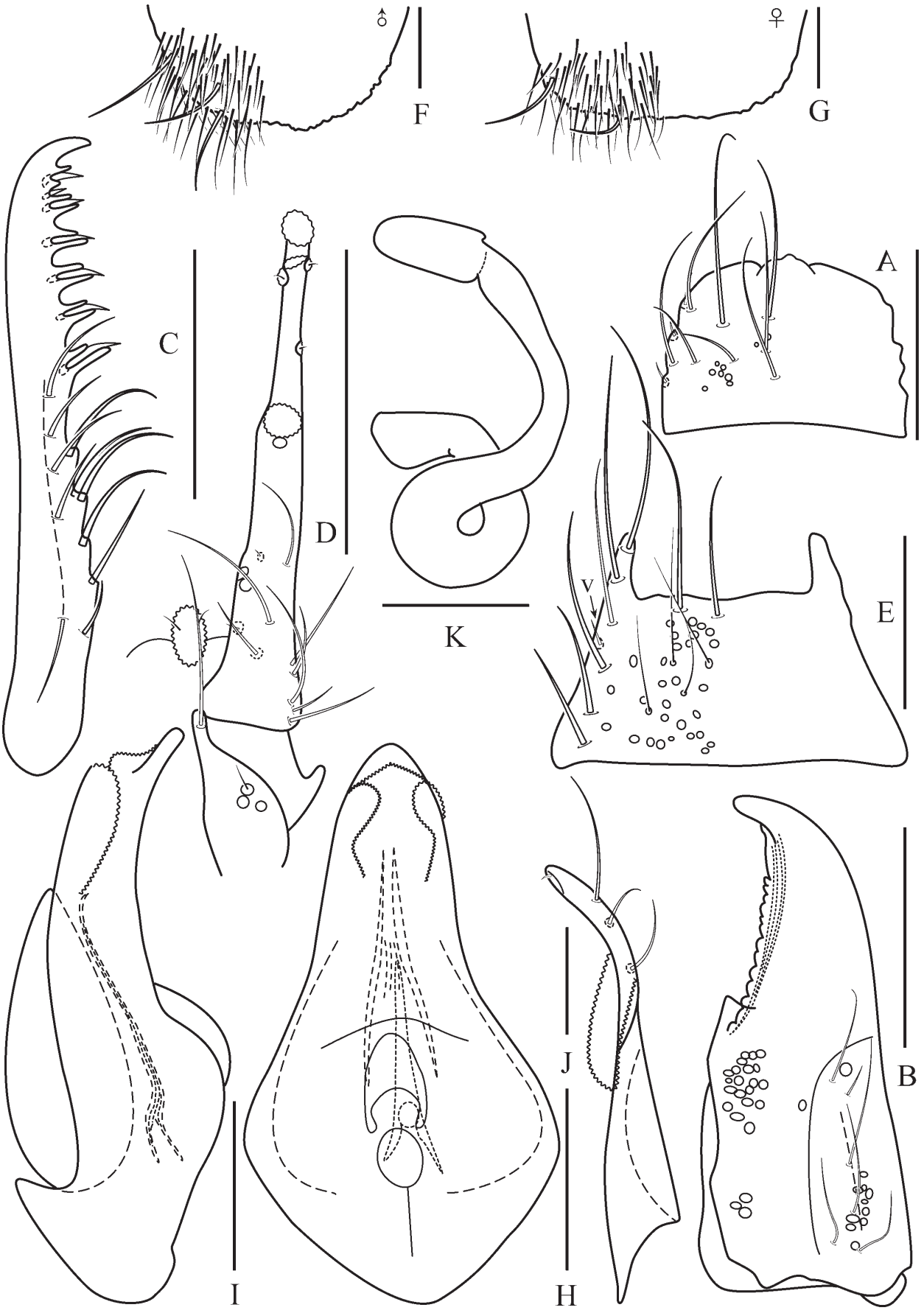

Fig. 5. *Bryothinusa tsutsuii* (Sawada, 1955). A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

Redescription. Body (Fig. 1C) small about 1.9–2.2 mm long, covered with minute setae. Head, pronotum and elytra yellowish brown; abdominal tergites IV–VII infuscate posteriorly; antenna, mouthparts and legs similarly coloured, slightly paler than head colour and paler toward apex.

Head oval, slightly wider than long, longer than pronotum and elytra; eyes (Fig. 2C) small, reniform, shorter than tempora length, setae present between about 15–17 facets; antennal length little shorter than distance from anterior margin of head to posterior margin of elytra; all antennal segments longer than wide; segment I 1.3 times longer than II, almost 2 times longer than III, and as long as XI.

Mouthparts (Figs 5A–E) with distribution of labral setae as in Figure 5A; mandibles (Fig. 5B) elongate triangle, asymmetrical, right mandible with median tooth; median tooth longer than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 5C) with three spines closely interdigitating and second spine very small, not obvious; 4 setae on inner margin of lacinia; labial palpus (Fig. 5D) with most setae located basally; mentum (Fig. 5E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" of mentum lower than level of anterior margin.

Pronotum almost as long as elytra, slightly wider than head.

Elytra wider than long, almost as wide as pronotum; hind wings absent.

Male abdominal sternite VIII (Fig. 5F) with posterior margin slightly serrate. Median lobe of aedeagus as in Figures 5H, I; paramere (Fig. 5J) elongate.

Female abdominal sternite VIII (Fig. 5G) with posterior margin slightly serrate but smoother than in male. Spermatheca (Fig. 5K) about 1.5 times coiled near base.

Measurements. BL 1.90–2.20, FBL 1.00–1.20, HL 0.33–0.45, HW 0.43–0.45, PL 0.35–0.40, PW 0.40–0.46, EL 0.38–0.40, EW 0.45–0.46, HTL 0.33–0.38, AL 0.83–1.05, AS-I 0.11–0.14, AS-II 0.08–0.11, AS-III 0.05–0.07.

Differential diagnosis. In general appearance the species is closely allied to *B. algarum*, *B. japonica*, *B. koreana* and *B. yoshigoui* sp. nov., but easily distinguished from *B. japonica*, *B. koreana* and *B. yoshigoui* sp. nov. by the shape of the spermatheca and the median lobe of the aedeagus without granule-like projections and from *B. algarum* by the simplified shape of the spermatheca.

Distribution. Japan (**Nansei-shotô:** Kagoshima-ken: Tanega-shima, Takara-jima, Nakano-shima, Edateku-jima; Okinawa-ken: Izena-jima, Okinawa-jima, Ou-jima, Ishigaki-jima, Iriomote-jima).

Remarks. The number of facets is different from the original description, but other morphological characters completely coincide with it. The type specimen was not found despite the efforts of Mr. Shigehiko Shiyake of Ôsaka Museum of Natural History, to which Dr. Kohei Sawada donated the collection.

This species is mainly found in Nansei-shotô but probably found also in mainland Kyûshû. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa koreana Ahn & Jeon, 2004

(Figs 1D; 2D; 6; 20H; 21A; 22)

(Japanese name: Chôsen-nagisa-hanekakushi)

Bryothinusa koreana Ahn & Jeon, 2004: 31 (original description; type locality: Korea: Jeonnam); Ashe (2004): 592 (in annotated catalogue of world species); Jeon & Ahn (2009): 367–373 (larval description); Frank & Ahn (2011): 27 (in checklist); Park et al. (2013): 163 (in checklist from Korea); Schülke & Smetana (2015): 676 (catalogue of Palearctic species); Ahn et al. (2017): 307 (in checklist of the Staphylinidae in Korea); Liu et al. (2020): 585–593 (new record from Japan; redescription), 589 (in key of Japanese species), 592 (in checklist).

Type material. Not examined.

Material examined. JAPAN: Honshû: 1 ♂ 1 ♀, Kusumi-bana, Ôbatake, Ko-jima, Kurashiki-shi, Okayama-ken, 21.iii.2009, O. Yamaji; 3 ♂♂ 2 ♀♀, Miya-jima, Hiroshima-ken, 23.iv.1997, K. Sawada & R. Sawada; 5 ♂♂ 2 ♀♀, 6 unsexed spec., Tanoura, Naga-shima, Kaminoseki-chô, Yamaguchi-ken, 15.x.2005, Y. Nakase; 1 ♀, same locality, 1.v.2008, M. Moriguchi. **Shikoku:** 2 ♀♀, 7 unsexed spec., Koura-kaigan, Koiso, Higashi-kagawa-shi, Kagawa-ken, 21.iv.2013, T. Taki; 1 ♀, 2 unsexed spec., same locality, 29.iv.2014, T. Taki; 4 ♀♀, 6 unsexed spec., Kaburagoshi, Matsubara, Higashi-kagawa-shi, Kagawa-ken, 7.ix.2015, T. Taki. **Kyûshû:** 6 unsexed spec., Mouth of Sakurai-gawa, Shima-nogita, Itoshima-shi, Fukuoka-ken, 21.iv.2020, Y. Hisasue; 2 ♀♀, 4 unsexed spec., Kakise, Takashima, Nagasaki-shi, Nagasaki-ken, 4.viii.2020, Y. Hisasue. Deposited at KUM but some will be distributed to NMPC and BMNH.

Additional description. Number of facets is 17–19 as in Figure 2D. Antennal segment I 1.1 times longer than II, almost 2 times longer than III, and as long as XI. Mouthparts with median tooth longer than 1/4 of mandibles; 6 setae on inner margin of lacinia; male and female abdominal sternite VIII, spermatheca and aedeagus as in Figure 6 (edited from Liu et al. (2020)). See also Liu et al. (2020).

Differential diagnosis. In general appearance, the species is closely similar to *B. algarum*, *B. japonica*, *B. tsutsuii* and *B. yoshigoui* sp. nov., but is easily distinguished from *B. japonica* by the apical part of the spermatheca without granule-like projections, and from *B. tsutsuii* by the median lobe of the aedeagus with granule-like projections while that of *B. tsutsuii* and *B. algarum* median lobe of aedeagus without granule-like projections, and differs from *B. yoshigoui* sp. nov. in the number of facets and body colour.

Distribution. Japan (**Honshû:** Okayama-ken, Hiroshima-ken, Yamaguchi-ken; **Shikoku:** Kagawa-ken; **Kyûshû:** Fukuoka-ken, Nagasaki-ken); Korea (Jeonnam).

Remarks. Presumably this species occurs also in other areas, especially Japan Sea coast of western Japan and Seto Inland Sea coast of Japan. A distribution map of examined specimens of this species in Japan is illustrated in Fig. 22.

Bryothinusa yoshigoui sp. nov.

(Figs 1E; 2E; 7; 22)

(Japanese name: Hiroshima-nagisa-hanekakushi)

Type material. Holotype: ♂, **JAPAN: Honshû:** Mitsuguchi-kaigan, Yasuura-chô, Kure, Hiroshima-ken, 28.vii.2019, H. Yoshigou (KUM). Paratypes: **Honshû:** 6 ♂♂ 1 ♀, 2 unsexed spec., same data as holotype (KUM, NMPC).

Description. Body (Fig. 1E) small about 2.3–2.4 mm long, covered with minute setae; background colour deep reddish brown, head, pronotum and elytra reddish brown; posteriorly abdominal tergite VI infuscate; antenna and legs similarly reddish-brown coloured, lightly paler than body colour and paler toward apex.

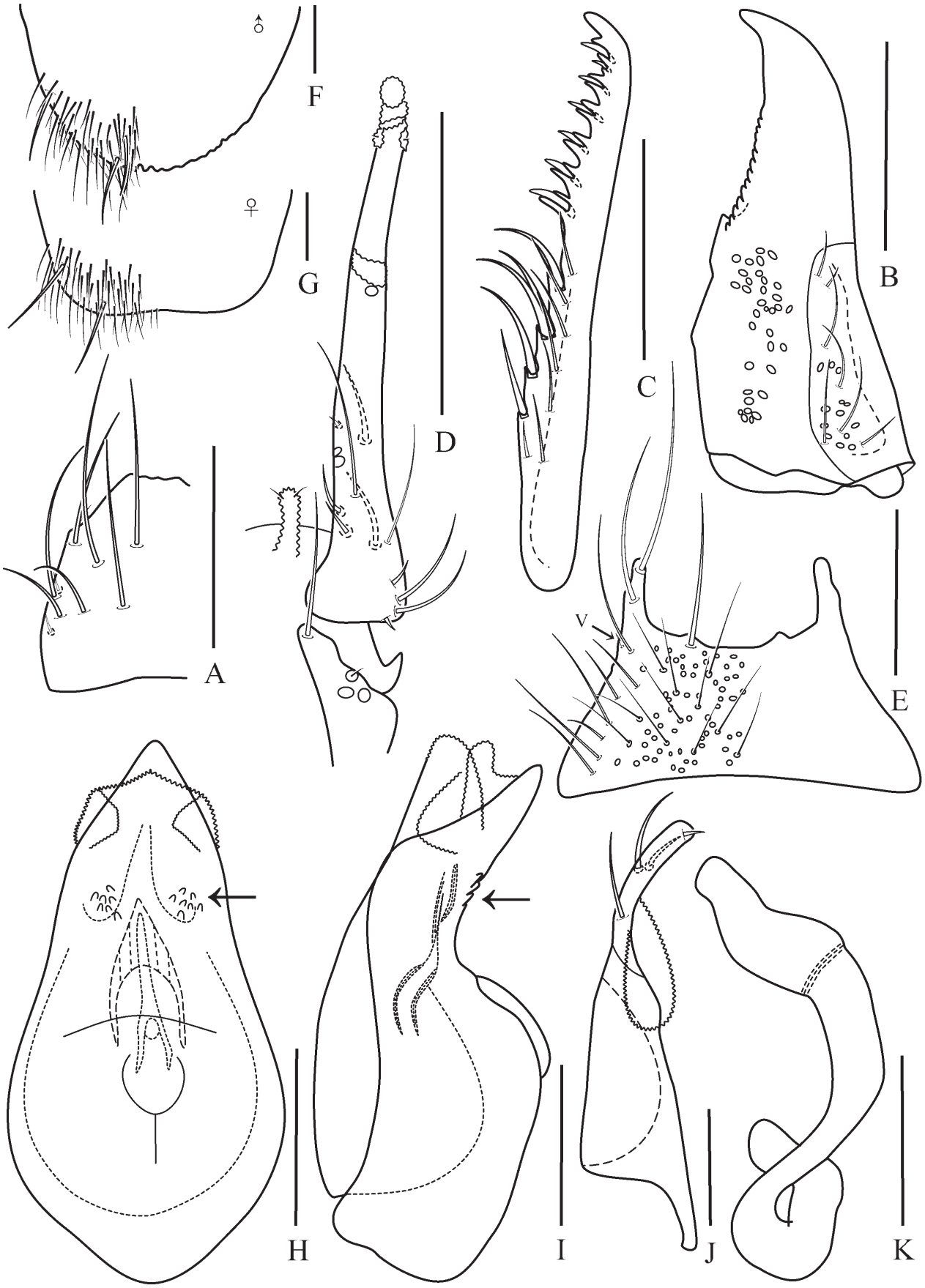

Fig. 6. *Bryothinusa koreana* Ahn & Jeon, 2004. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm. Modified from Liu et al. (2020).

Fig. 7. *Bryothinusa yoshigoui* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

Head oval, wider than long, longer than pronotum and elytra; eyes (Fig. 2E) small, reniform, shorter than 1/2 of head length, with 12–14 facets; antennal length a little shorter than distance from anterior margin of head to posterior margin of elytra; antennal segments all longer than wide; segment I as long as II, 1.2 times longer than III, and shorter than XI; posterior margin of antennal segment III narrower than anterior margin.

Mouthparts (Figs 7A-E) with distribution of labral setae as in Figure 7A; mandibles (Fig. 7B) elongate triangle, asymmetrical, right with median tooth; median tooth longer than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 7C) with second spines very small and not obvious, at tip with two spines not closely interdigitating; 4 setae on inner margin of lacinia; labial palpus (Fig. 7D) with most setae located basally; mentum (Fig. 7E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" of mentum near the level of anterior margin.

Pronotum almost as long as elytra, slightly narrower than head.

Elytra widened apically, wider than long, almost as wide as pronotum; hind wings absent.

Male abdominal sternite VIII (Fig. 7F) with posterior margin slightly serrate. Median lobe of aedeagus (Figs 7H, I) with some granules on apical lobe, and not clearly visible in dorsal view; paramere elongate, as in Figure 7J.

Female abdominal sternite VIII (Fig. 7G) with posterior margin slightly serrate but smoother than in male. Spermatheca (Fig. 7K) small, simplified in shape, about half times coiled near base.

Measurements. BL 2.30–2.40, FBL 1.00–1.20, HL 0.38–0.45, HW 0.43–0.48, PL 0.35–0.38, PW 0.40–0.43, EL 0.35–0.38, EW 0.41–0.43, HTL 0.34–0.39, AL 0.88–0.97, AS-I 0.09–0.10, AS-II 0.09–0.10, AS-III 0.07–0.08.

Differential diagnosis. In general appearance, the species is closely similar to *B. tsutsuii*, *B. algarum*, *B. koreana* and *B. japonica*, in but easily distinguished from *B. tsutsuii* and *B. algarum* by the spermathecal shape and the median lobe of the aedeagus with granule-like projections, from *B. koreana* at the number of facets and the darker body colour, and from *B. japonica* by the apical part of spermatheca without granule-like projections.

Distribution. Japan (**Honshû:** Hiroshima).

Etymology. This new species is named after Mr. Hidenori Yoshigou, a famous ichthyologist and the collector of the type series.

Remarks. The specimens were collected on the coastline of Setonaikai (inland sea between Honshû and Shikoku), Japan. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa japonica Liu, Ono & Maruyama, 2020

(Figs 1F; 2F; 8; 21A–B, G; 22)
(Japanese name: Nippon-nagisa-hanekakushi)

Bryothinusa japonica Liu, Ono & Maruyama, 2020: 586 (original description; type locality: Japan, Kyûshû, Fukuoka).

Material examined. JAPAN: Honshû: 7 ♂♂ 1 ♀, 22 unsexed spec., Matsumi-ga-ura, Ôchiba, Kosai-shi, Shizuoka-ken, 11.iv.2004, Y. Tahira; 8 unsexed spec., Miya-gawa, Iso-chô, Ise-shi, Mie-ken, 8.vi.2008, K. Akita; 4 ♂♂ 2 ♀♀, 67 unsexed spec., Kumozu-gawa, Karasu-chô, Mie-ken, 15.v.2004, K. Akita; 2 ♂♂ 1 ♀, 26 unsexed spec., Mouth of Kansa-gawa, Nansei-chô, Mie-ken, 5.v.2008, K. Akita; 4 ♂♂ 4 unsexed spec., Mouth of Yoshii-gawa, Nishikôzai, Okayama-shi, Okayama-ken, 24.x.2004, O. Yamaji; 2 ♂♂ 4 ♀♀, 6 unsexed spec., Mitsuguchi-kaigan, Yasuura-chô, Kure, Hiroshima-ken, 28.vii.2019, H. Yoshigou. **Shikoku:** 2 ♂♂ 5 ♀♀, 112 unsexed spec., Shimoda, Shimanto-shi, Kôchi-ken, 21.iv.2012, M. Maruyama; 1 ♂ 4 ♀♀, 2 unsexed spec., Kagami-gawa, Takajô-machi, Kôchi-shi, Kôchi-ken, 20.vi.2008, H. Fujimoto. **Kyûshû:** 3 ♂♂ 1 ♀, 4 unsexed spec., Sunosaki, Imazu, Nishi-ku, Fukuoka-shi, Fukuoka-ken, 16.x.2020, T. Liu & T. Nozaki; 8 unsexed spec., Mouth of Sakurai-gawa, Shima-Nogita, Itoshima-shi, Fukuoka-ken, 21.iv.2020, Y. Hisasue; 1 ♀, same locality, 11.x.2018, Liu et al. Deposited at KUM but some will be distributed to NMPC and BMNH.

Additional description. Number of facets 23–25 as Fig. 2F. Antennal segment I 1.2 times longer than II, almost 2.4 times longer than III, and longer than XI. Mouthparts with median tooth longer than 1/4 of mandibles; 6 setae on inner margin of lacinia; male and female abdominal sternite VIII, spermatheca and aedeagus as in Figure 8. See also Liu et al. (2020).

Differential diagnosis. In general appearance, the species is closely allied to *B. tsutsuii*, *B. algarum*, *B. koreana* and *B. yoshigoui* sp. nov., but easily distinguished from them by the apical part of spermatheca without granule-like projections.

Distribution. Japan (**Honshû:** Chiba-ken, Shizuoka-ken, Mie-ken, Ôsaka-fu, Hyôgo-ken, Wakayama-ken, Okayama-ken, Hiroshima-ken, Yamaguchi-ken; **Shikoku:** Kagawa-ken, Ehime-ken, Kôchi-ken; **Kyûshû:** Fukuoka-ken).

Remarks. About 200 specimens were collected before the original description but they were not included in the type series due to the difficulty of identification. There was considerable variation in the colouration of the specimens, ranging from light brown to brown, but it is unclear whether this is due to geographical variation or to the methods in which the specimens were preserved.

This species is quite common in sandy to mud flats in estuaries in Japan, mainly west of Kantô District. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa sakishimana Sawada, 1991

(Figs 1G; 2G; 9; 21B, D; 22)
(Japanese name: Sakishima-nagisa-hanekakushi)

Bryothinusa sakishimana Sawada, 1991: 144 (original description; type locality: Japan, Nansei-shotô, Iriomote-jima), 145 (compared with *B. nakanei* Sawada); Ashe (2004): 594 (in annotated catalogue of world species); Smetana (2004): 464 (in catalogue of Palearctic species); Frank & Ahn (2011): 27 (in checklist); Schülke & Smetana (2015): 676 (in catalogue of Palearctic species); Liu et al. (2020): 589 (in key of Japanese species), 592 (in checklist).

Type material. Not examined.

Material examined. JAPAN: Nansei-shotô: 3 ♂♂ 2 ♀♀, 11 unsexed spec., Ôgomori, Takara-jima, Tokara-rettô, Kagoshima-ken, 3.vii.2019, T. Liu, N. Tsuji & H. Ono; 1 unsexed spec., Mouth of Honera-gawa, Takana, Taketomi-chô, Iriomote-jima, Okinawa-ken, 2.iv.2019, T. Nozaki. Deposited at KUM but some will be distributed to NMPC and BMNH.

Redescription. Body (Fig. 1G) small, about 1.6–1.9 mm in length, covered with minute setae. Abdomen almost black and darker than head and pronotum; elytra lighter than pronotum; antenna and legs yellowish brown.

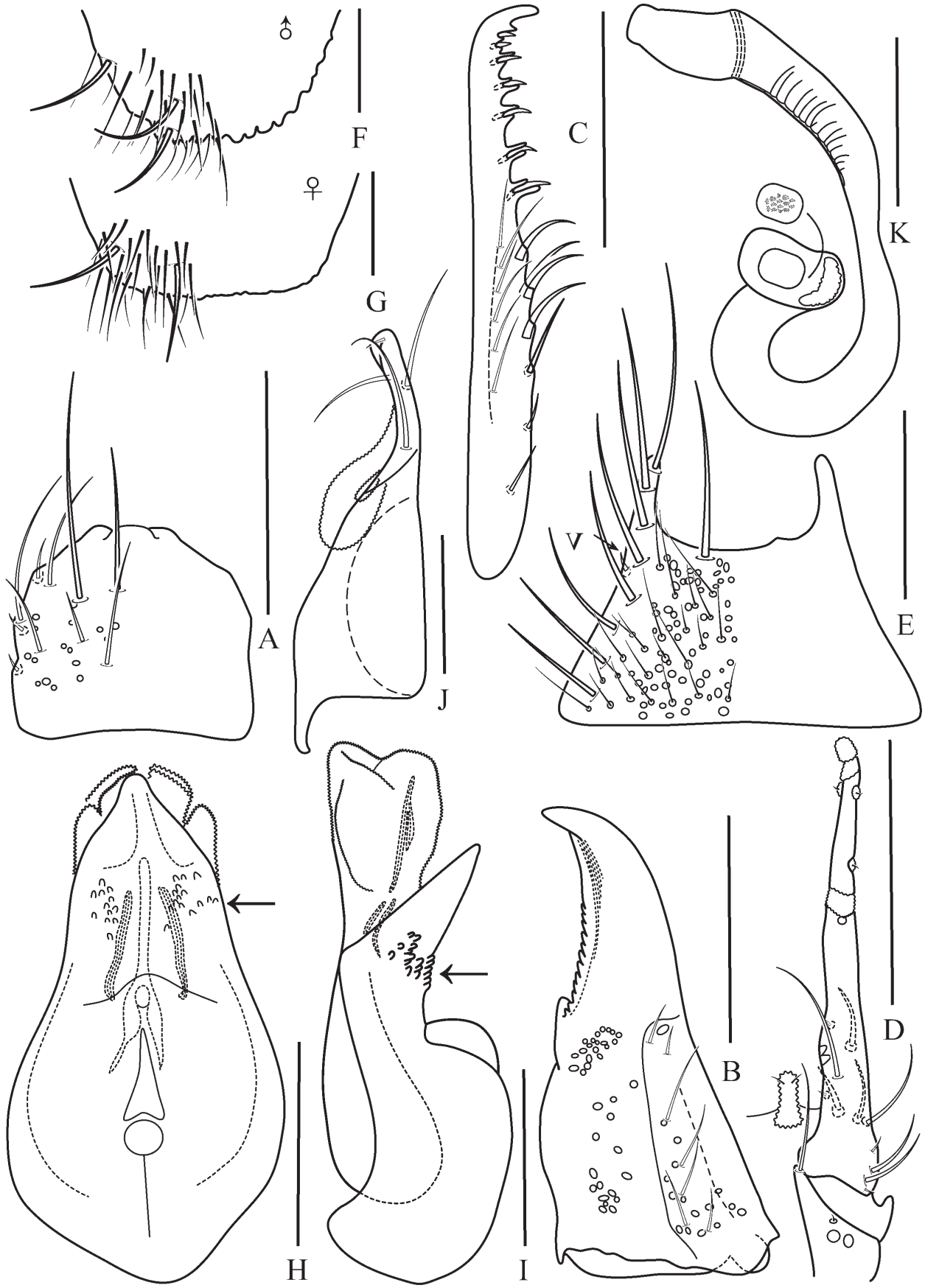

Fig. 8. *Bryothinusa japonica* Liu, Ono & Maruyama, 2020. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm. Modified from Liu et al. (2020).

Fig. 9. *Bryothinusa sakishimana* Sawada, 1991. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

Head evenly rounded, more or less produced anteriorly, wider than long, shorter than pronotum and elytra; eyes (Fig. 2G) large, setae present between about 21–23 facets, slightly longer than tempora length; antenna yellowish brown, longer than total length of head and pronotum; segment I 1.4 times longer than II, almost 3.8 times longer than III, and longer than XI; antennal segments V–X almost as long as wide.

Mouthparts (Figs 9A–E) with distribution of labral setae as in Fig. 9A, with large and thick spiniform seta antero-laterally; mandibles (Fig. 9B) elongate triangle, asymmetrical, right mandible with median tooth; median tooth shorter than 1/4 of mandibles; left without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 9C) with second spine very small, not obvious; 3 setae on inner margin of lacinia; labial palpus (Fig. 9D) with most setae located basally; mentum (Fig. 9E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum shorter than elytra, wider than head.

Elytra subquadrate, narrower than pronotum; almost unicolour and hind wings present but small, apparently flightless.

Male abdominal sternite VIII (Fig. 9F) with posterior margin slightly serrate. Median lobe of aedeagus as in Figures 9H, I; paramere (Fig. 9J) elongate.

Female abdominal sternite VIII (Fig. 9G) slightly serrate alike male on posterior margin. Spermatheca (Fig. 9K) about 1.5 times coiled near base, apical part elongate.

Measurements. BL 1.60–1.90, FBL 0.70–1.00, HL 0.28–0.33, HW 0.35–0.40, PL 0.33–0.38, PW 0.40–0.45, EL 0.35–0.40, EW 0.38–0.40, HTL 0.33–0.35, AL 0.70–0.83, AS-I 0.12–0.15, AS-II 0.09–0.10, AS-III 0.03–0.04.

Differential diagnosis. In Nansei-shotô, this species is especially similar to *B. nakanei*, but easily distinguished from it by the paler elytral colour, the number of facets, the spermathecal shape and the posterior margin of the tergite X rounded medially. This species is also similar to *B. constricta* sp. nov. in general appearance but differentiated from it by the elytral shape not being almost square and the shape of the spermatheca.

Distribution. Japan (**Nansei-shotô:** Kagoshima-ken: Takara-jima; Okinawa-ken: Iriomote-jima).

Remarks. This species is distributed in Nansei-shotô of Japan. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa constricta sp. nov.

(Figs 1H; 2H; 10; 22)

(Japanese name: Kubire-nagisa-hanekakushi)

Type material. Holotype: ♂, **JAPAN: Honshû:** Futtsu-misaki, Futtsu-shi, Chiba-ken, 1.v.2014, H. Ono (KUM). Paratypes: **Honshû:** 3 ♀♀, 6 unsexed spec., same locality as holotype, 28.v.2010, H. Ono (KUM); 2 ♂♂ 5 ♀♀, 10 unsexed spec., same data as holotype (KUM, NMPC, BMNH); 1 ♀, 4 unsexed spec., Izumo, Koryô-chô, Shimane-ken, 3.ix.2007, T. Hayama (KUM).

Description. Body (Fig. 1H) small, about 1.7–2.0 mm in length, covered with minute setae. Abdomen almost black and darker than head and pronotum; elytra lighter than pronotum; legs yellowish brown.

Head evenly rounded, more or less produced anteriorly, wider than long, shorter than pronotum and as long as elytra; eyes (Fig. 2H) large, setae present between about 20–22 facets, slightly longer than tempora length; antenna yellowish brown, equal to total length of head and pronotum; segment I 1.6 times longer than II, almost 3.5 times longer than III, and longer than XI; antennal segments III–X almost wider than long, and VI–VII wider than width of III–IV.

Mouthparts (Figs 10A–E) with distribution of labral setae as in Figure 10A, with large and thick spiniform seta at antero-laterally; mandibles (Fig. 10B) elongate triangle, asymmetrical, right mandible with median tooth; median tooth shorter than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 10C) at right angle; at tip with two spines very small and not closely interdigitating; 3 setae on inner margin of lacinia; labial palpus (Fig. 10D) with most setae located basally; mentum (Fig. 10E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum longer than elytra, wider than head.

Elytra widened apically, wider than long, almost as wide as pronotum; hind wings present but very small, apparently flightless.

Male abdominal sternite VIII (Fig. 10F) with posterior margin slightly serrate. Median lobe of aedeagus as in Figures 10H, I; paramere (Fig. 10J) elongate.

Female abdominal sternite VIII (Fig. 10G) slightly serrate alike male on posterior margin. Spermatheca (Fig. 10K) simplified in shape, about 1.5 times coiled near base.

Measurements. BL 1.70–2.00, FBL 0.80–1.00, HL 0.30–0.31, HW 0.35–0.39, PL 0.30–0.33, PW 0.38–0.40, EL 0.29–0.30, EW 0.36–0.40, HTL 0.30–0.31, AL 0.61–0.67, AS-I 0.11–0.14, AS-II 0.06–0.09, AS-III 0.03–0.04.

Differential diagnosis. In general appearance, the species is similar to *B. sakishimana*, but easily distinguished from it by the elytral shape being narrowed anteriorly and the shape of the spermatheca.

Etymology. Bringing attention to the constricted body shape; adjective.

Distribution. Japan (**Honshû:** Chiba-ken, Shimane-ken).

Remarks. This species is found mainly on the Japan Sea coast of western Japan and east of Tôkyô Bay, but it is probably occurring in other areas of mainland Japan. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa hokkaidensis sp. nov.

(Figs 1I; 2I; 11; 21C; 22)

(Japanese name: Hokkai-nagisa-hanekakushi)

Type material. Holotype: ♂, **JAPAN: Hokkaidô:** Shunkunitai, 43.2725 N, 145.472 E, Nemuro-shi, Hokkaidô, 11.ix.1999, M. Maruyama (KUM). Paratypes: **Hokkaidô:** 3 ♂♂ 4 ♀♀, 96 unsexed spec., same data as holotype (KUM, NMPC, BMNH); 1 ♀, 4 unsexed spec., Usu-chô, Date-shi, Hokkaidô, 12.iv.2020, Y. Tasaku (KUM). **Kyûshû:** 1 ♀, Nokono-shima, Fukuoka-shi, Fukuoka-ken, 21.iv.2018, T. Hashizume (KUM).

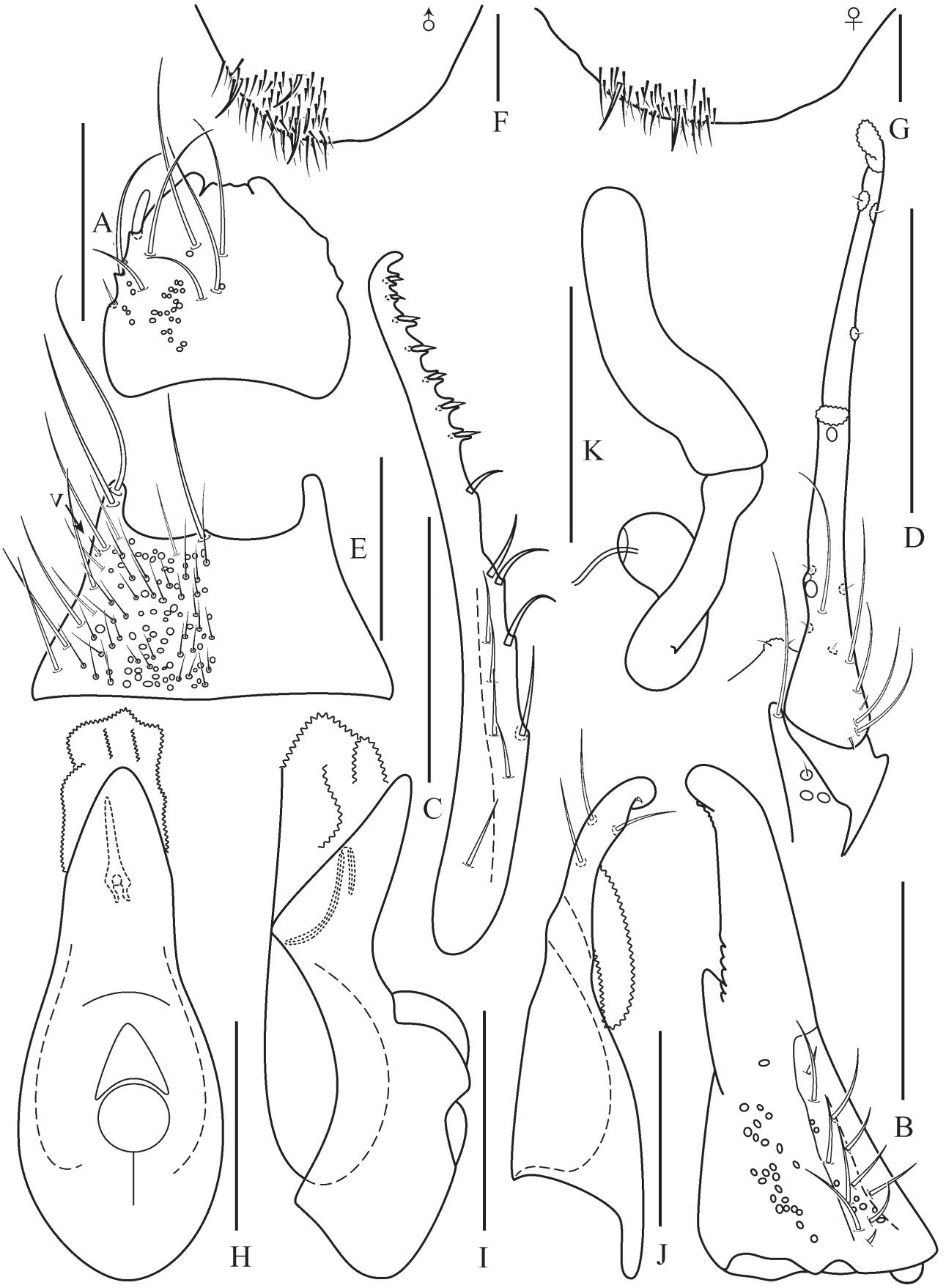

Fig. 10. *Bryothinusa constricta* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

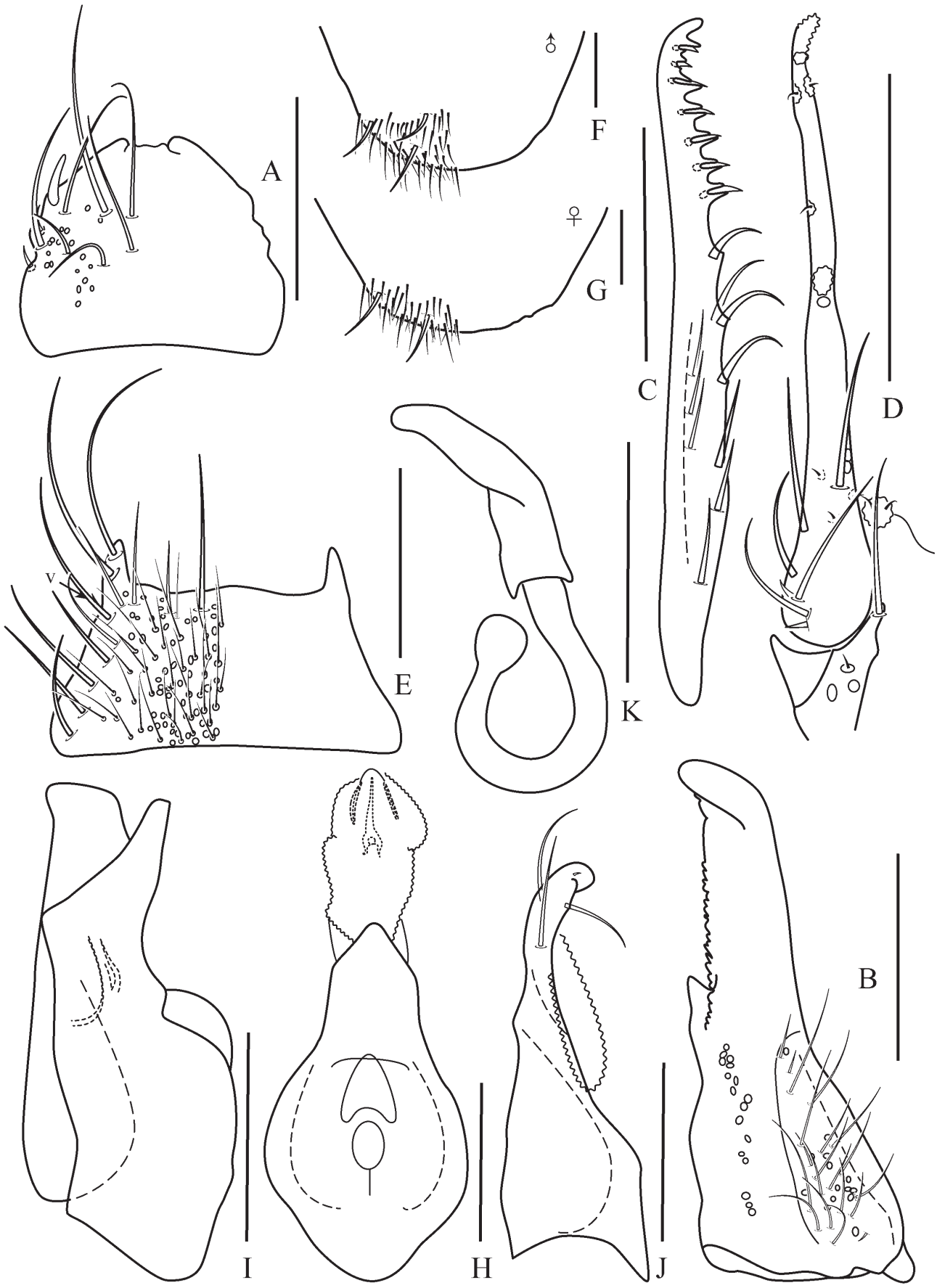

Fig. 11. *Bryothinusa hokkaidensis* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

Description. Body (Fig. 1I) small, about 1.8–2.2 mm in length, covered with minute setae. Abdomen almost dark brown and darker than head and pronotum; elytra lighter than pronotum; legs yellowish brown; antenna brown, similar coloured with mouthparts and legs, lightly paler than body colour.

Head evenly oval, wider than long, shorter than pronotum and elytra; eyes (Fig. 2I) large, setae present between about 22–25 facets, slightly longer than tempora length; antenna brown, equals to total length of head and pronotum; segment I as long as II, almost 2.3 times longer than III, and as long as XI; antennal segments III–IV subquadrate, V–X almost same length and wider than long.

Mouthparts (Figs 11A–E) with distribution of labral setae as in Figure 11A, with large and thick spiniform seta at antero-laterally; mandibles (Fig. 11B) elongate triangle, asymmetrical, right mandible with some median tooth and irregular; median tooth longer than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 11C) at obtuse angle; at tip with two spines very small and not closely interdigitating; 2–3 setae on inner margin of lacinia; labial palpus (Fig. 11D) with most setae located basally, small ligula; mentum (Fig. 11E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum shorter than elytra, wider than head.

Elytra subquadrate but wider than long, slightly narrower than pronotum; hind wings present but very small, apparently flightless.

Male abdominal sternite VIII (Fig. 11F) with posterior margin slightly serrate. Median lobe of aedeagus as in Figures 11H, I; paramere (Fig. 11J) elongate.

Female abdominal sternite VIII (Fig. 11G) slightly serrate similar male on posterior margin. Spermatheca (Fig. 11K) simplified in shape, about 1 time coiled near base.

Measurements. BL 1.80–2.20, FBL 0.90–1.00, HL 0.25–0.30, HW 0.38–0.40, PL 0.33–0.35, PW 0.40–0.43, EL 0.35–0.38, EW 0.35–0.40, HTL 0.25–0.35, AL 0.60–0.68, AS-I 0.10–0.11, AS-II 0.09–0.10, AS-III 0.04–0.05.

Differential diagnosis. In general appearance, the species is similar to *B. fulvipennis* sp. nov. and *B. itsuroi* sp. nov. but distinguished from them by the combination of the following character states: the body colour (especially head and pronotum colour) and the spermathecal shape.

Etymology. Toponym. Named after Hokkaidô, the type locality of this new species; adjective.

Distribution. Japan (**Hokkaidô**; **Kyûshû:** Fukuoka-ken).

Remarks. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa fulvipennis sp. nov.

(Figs 1J; 2J; 12; 21B; 22)

(Japanese name: Usucha-nagisa-hanekakushi)

Type material. Holotype: ♂, **JAPAN: Honshû:** Mouth of Obitsu-gawa, Kuzuma, Kisarazu-shi, Chiba-ken, 2.iii.2007, H. Ono (KUM).

Paratypes: **Honshû:** 1 ♀, same data as holotype (KUM); 1 unsexed spec., same locality as holotype, 19.ii.2007, H. Ono (KUM); 1 ♂ 2 unsexed spec., Mouth of Obitsu-gawa, Kuroto, Kisarazu-shi, Chiba-ken, 19.ii.2007, H. Ono (KUM); 1 unsexed spec., same locality, 12.iii.2009, H. Ono (KUM); 1 ♀, 3 unsexed spec., same locality, 16.iii.2009, H. Ono (KUM); 1 ♂, same locality, 4.i.2010, H. Ono (KUM); 1 unsexed spec., same locality, 12.i.2011, H. Ono (KUM); 1 unsexed spec., same locality, 14.i.2011, H. Ono (KUM); 1 unsexed spec., Kushida-gawa, Matsuzaka-shi, Mie-ken, 28.iv.2002, Y. Kawakami (KUM); 10 unsexed spec., Himeshima, Yodo-gawa, Nishiyodo-gawa-ku, Ôsaka-fu, 12.iv.2002, Y. Kawakami (KUM, MNPC, BMNH); 3 unsexed spec., Hanakawa Yodo-gawa, Nishiyodo-gawa-ku, Ôsaka-fu, 25.iv.2002, Y. Kawakami (KUM); 4 unsexed spec., same locality, 28.iii.2002, Y. Kawakami (KUM); 1 unsexed spec., Kinburo, Kitagi-shima, Kasaoka-shi, Okayama-ken, 11.x.2008, O. Yamaji (KUM); 3 unsexed spec., Kurahashi-jima (Umikoshi), Kurahashi-chô, Kure-shi, Hiroshima-ken, 1.ii.2009, K. Nakano (KUM). **Shikoku:** 11 unsexed spec., Kaigan-ji, Nishishirakata, Tadotsu-chô, Kagawa-ken, 31.iii.2008, H. Fujimoto (KUM); 1 unsexed spec., Ôyatomi-machi, Sakaide-shi, Kagawa-ken, 29.iii.2008, H. Fujimoto (KUM); 1 unsexed spec., Kôtô-gawa, Gôtô-chô, Takamatsu-shi, Kagawa-ken, 12.iv.2008, H. Fujimoto (KUM).

Description. Body (Fig. 1J) small, about 1.6–2.0 mm in length, covered with minute setae. Abdomen almost black and darker than head and pronotum; elytra lighter than pronotum; antenna and legs yellowish brown.

Head evenly rounded, more or less produced anteriorly, wider than long, shorter than pronotum and elytra; eyes (Fig. 2J) large, setae present between about 22–24 facets, slightly longer than tempora length; antenna yellowish brown, almost equals to total length of head and pronotum; segment I 1.7 times longer than II, almost 4 times longer than III, and longer than XI; antennal segments IV–X almost as long as wide.

Mouthparts (Figs 12A–E) with distribution of labral setae as in Figure 12A, with large and thick spiniform seta antero-laterally; mandibles (Fig. 12B) elongate triangle, asymmetrical, right with median tooth; median tooth shorter than 1/4 of mandibles; left without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 12C) second spine very small, not obvious; 3 setae on inner margin of lacinia; labial palpus (Fig. 12D) with most setae located basally; mentum (Fig. 12E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum almost as long as elytra, wider than head.

Elytra subquadrate but wider than long, almost as wide as pronotum; hind wings present but very small, apparently flightless.

Male abdominal sternite VIII (Fig. 12F) with posterior margin slightly serrate. Median lobe of aedeagus (Fig. 12H) and dorsal view as in Figure 12I; paramere (Fig. 12J) elongate.

Female abdominal sternite VIII (Fig. 12G) slightly serrate alike male on posterior margin. Spermatheca (Fig. 12K) about 2 times coiled near base.

Measurements. BL 1.60–2.00, FBL 0.90–1.00, HL 0.28–0.30, HW 0.36–0.43, PL 0.36–0.40, PW 0.40–0.45, EL 0.35–0.41, EW 0.36–0.45, HTL 0.23–0.33, AL 0.61–0.76, AS-I 0.13–0.14, AS-II 0.07–0.08, AS-III 0.03–0.04.

Differential diagnosis. In general appearance the species is very similar to *B. hokkaidensis* sp. nov. and *B. itsuroi* sp.

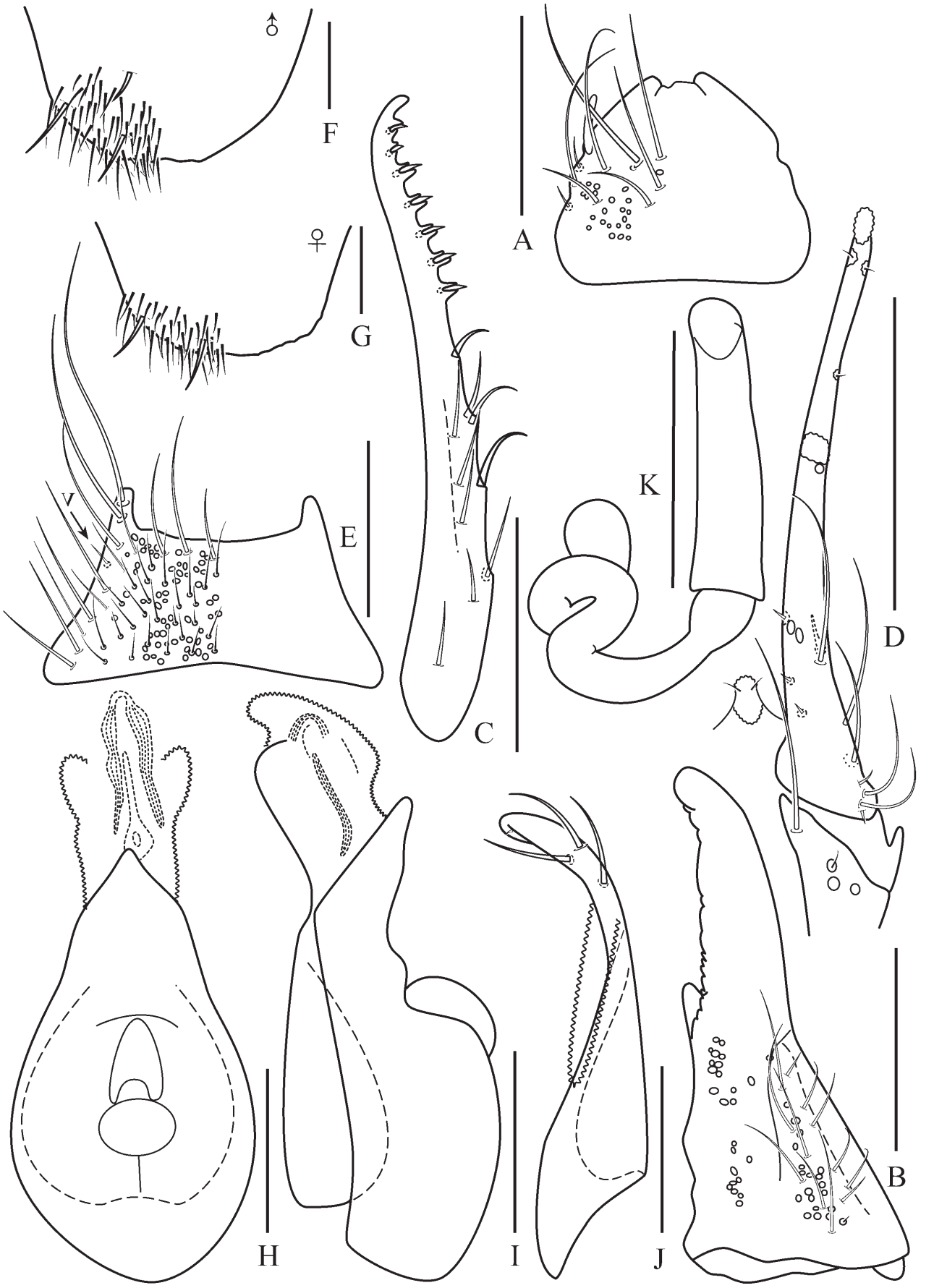

Fig. 12. *Bryothinusa fulvipennis* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

nov., but easily distinguished from *B. hokkaidensis* sp. nov. by the paler body colour and the shape of the spermatheca, and from *B. itsuroi* sp. nov. by the number of facets and the shape of the spermatheca.

Etymology. The species epithet refers to the yellowish -brown elytra; adjective.

Distribution. Japan (**Honshû:** Chiba-ken, Mie-ken, Ôsaka-fu, Okayama-ken, Hiroshima-ken; **Shikoku:** Kagawa-ken).

Remarks. This species has been found mainly in coasts of bay and inland sea such as Tôkyô-wan, Ise-wan and Setonaikai. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa itsuroi sp. nov.

(Figs 1K; 2K; 13; 20H; 22)
(Japanese name: Niseusucha-nagisa-hanekakushi)

Type material. Holotype: ♂, **JAPAN: Honshû:** Kuruwa-kaigan, Akiya, Yokosuka-shi, Kanagawa-ken, 14.ix.2013, H. Ono (KUM). Paratypes: **Honshû:** 1 ♀, 18 unsexed spec., Uraga-wan, Nishi-uraga, Yokosuka-shi, Kanagawa-ken, 4.iii.2013, H. Ono & I. Kawashima (KUM, NMPC, BMNH); 7 ♂♂ 3 ♀♀, 9 unsexed spec., same data as holotype (KUM). **Kyûshû:** 1 ♂ 1 ♀, 16 unsexed spec., Kakise, Takashima, Nagasaki-shi, Nagasaki-ken, 4.iii.2020, Y. Hisasue (KUM). **Nansei-shotô:** 1 ♂ 1 ♀, 1 unsexed spec., Mage-shima (near Tanega-shima), Kagoshima-ken, 14.x.2000, M. Maruyama (under stone on sandy beach, in a port) (KUM).

Description. Body (Fig. 1K) small, about 1.7–1.9 mm in length, covered with minute setae. Abdomen almost black and darker than head and pronotum; elytra lighter than pronotum; legs yellowish brown.

Head evenly rounded, more or less produced anteriorly, wider than long, shorter than pronotum and elytra; eyes (Fig. 2K) large, setae present between about 29–31 facets, longer than tempora; antenna yellowish brown, almost equals to total length of head and pronotum; segment I as long as II, almost 3 times longer than III, and longer than XI; antennal segments VII–X almost wider than long.

Mouthparts (Figs 13A–E) with distribution of labral setae as in Figure 13A, with large and thick spiniform seta antero-laterally; mandibles (Fig. 13B) elongate triangle, asymmetrical, right with median tooth; median tooth shorter than 1/4 of mandibles; left without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 13C) at right angle; at tip second spine very small, not obvious; 3 setae on inner margin of lacinia; labial palpus (Fig. 13D) with most setae located basally; mentum (Fig. 13E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum shorter than elytra, as wide as head.

Elytra subquadrate, wider than pronotum; hind wings present but small, apparently flightless.

Male abdominal sternite VIII (Fig. 13F) with posterior margin slightly serrate. Median lobe of aedeagus (Fig. 13H) and dorsal view as in Figure 13I; paramere (Fig. 13J) elongate.

Female abdominal sternite VIII (Fig. 13G) slightly serrate alike male on posterior margin. Spermatheca (Fig. 13K) of complicated shape, very small, shorter than 0.25 mm and several times coiled near base.

Measurements. BL 1.70–1.90, FBL 0.80–1.00, HL 0.31–0.33, HW 0.38–0.41, PL 0.33–0.38, PW 0.40–0.41, EL 0.42–0.43, EW 0.41–0.43, HTL 0.33–0.39, AL 0.61–0.66, AS-I 0.10–0.11, AS-II 0.09–0.10, AS-III 0.03–0.04.

Differential diagnosis. In general appearance the species is very similar to *B. fulvipennis* sp. nov. and *B. hokkaidensis* sp. nov., but can be easily distinguished from them by the number of facets, the shape of the spermatheca, and the antennal segment I as long as II.

Etymology. The new species is named after Mr. Itsuro Kawashima, a scientific illustrator and researcher of fireflies, who helped collect the type series of this species in Kanagawa.

Distribution. Japan (**Honshû:** Kanagawa-ken; **Kyûshû:** Nagasaki-ken; **Nansei-shotô:** Kagoshima-ken: Tanega -shima).

Remarks. Unfortunately, one of the habitats in Uraga-wan, Kanagawa Prefecture has likely disappeared due to recent seawall construction. This species has a wide distribution but is found very locally where it occurs. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa aikoae sp. nov.

(Figs 1L; 2L; 14; 21B; 22)
(Japanese name: Hime-nagisa-hanekakushi)

Type material. Holotype: ♀, **JAPAN: Honshû:** Mouth of Obitsu-gawa, Kuroto, Kisarazu-shi, Chiba-ken, 12.iii.2009, H. Ono (KUM). Paratypes: **Honshû:** 3 ♀♀, same data as holotype (KUM); 1 ♀, same locality as holotype, 16.iii.2009, H. Ono (KUM).

Description. Body (Fig. 1L) small, about 1.5–1.8 mm in length, covered with minute setae. Basically brown, head darker than pronotum and elytra, pronotum and elytra similarly coloured, from lower part of posteriorly abdominal tergite V to upper part of tergite VII infuscate; antenna, mouthparts and legs similarly coloured, lightly paler than head colour and paler toward apex.

Head oval, wider than long, shorter than elytra; eyes (Fig. 2L) large, reniform, longer than 1/2 of head length, with 22–24 facets; antennal length little shorter than distance from anterior margin of head to posterior margin of elytra; segment I 1.4 times longer than II, almost 3 times longer than III, and longer than XI; antennal segments I–III and XI longer than wide, antennal segments IV–VI almost as long as wide, antennal segments VII–X wider than long.

Mouthparts (Figs 14A–E) with distribution of labral setae as in Figure 14A, with large and thick spiniform seta at antero-laterally; mandibles (Fig. 14B) elongate triangle, asymmetrical, right with median tooth; median tooth shorter than 1/4 of mandibles; left without tooth, blunt at apex; maxilla with apical apex of lacinia (Fig. 14C) with second spines small, at tip with two spines not closely interdigitating; 3 setae on inner margin of lacinia; labial palpus (Fig. 14D) with most setae located basally; mentum (Fig. 14E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" of mentum slightly lower than level of anterior margin.

Pronotum shorter than elytra, wider than head.

Fig. 13. *Bryothinusa itsuroi* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

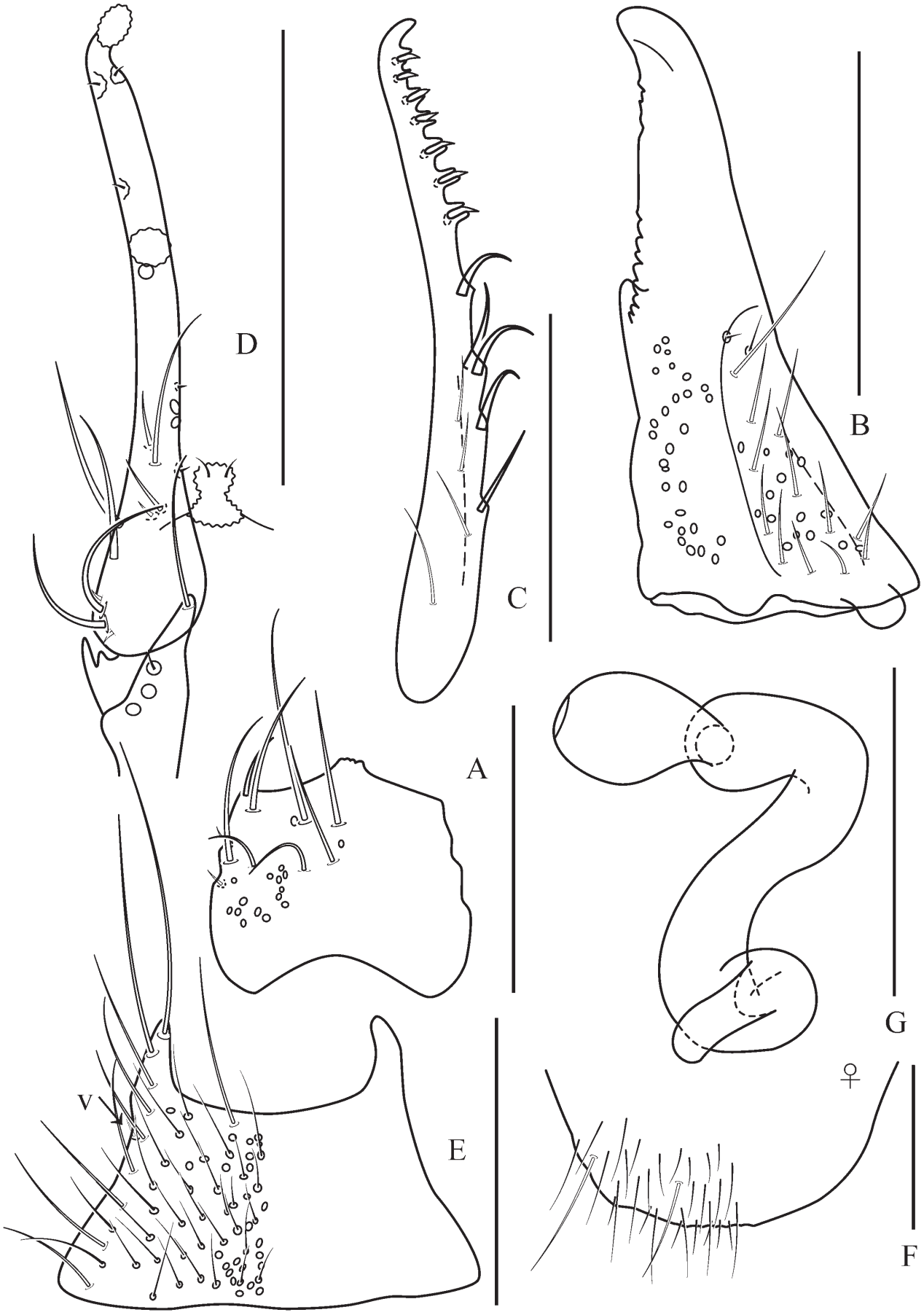

Fig. 14. *Bryothinusa aikoae* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – female sternite VIII; G – spermatheca. Scale bars: 0.1 mm.

Elytra subquadrate, almost as wide as pronotum; hind wings fully developed.

Male unknown.

Female abdominal sternite VIII in Figure 14F. Spermatheca (Fig. 14G) very small, simplified in shape, about one time coiled near base.

Measurements. BL 1.50–1.80, FBL 0.83–0.85, HL 0.23–0.28, HW 0.31–0.32, PL 0.29–0.30, PW 0.34–0.35, EL 0.35–0.36, EW 0.35–0.36, HTL 0.28–0.30, AL 0.58–0.63, AS-I 0.10–0.11, AS-II 0.07–0.08, AS-III 0.03–0.04.

Differential diagnosis. The species is distinct based on the body colour and shape. In body size this species is close to *B. minuta* but easily distinguished from it by the number of facets and by the fully developed hind wings.

Etymology. This new species is named after Mrs. Aiko Ono for supporting the entomological life of her husband H. Ono, the second author of this paper.

Distribution. Japan (**Honshû:** Chiba-ken).

Remarks. The type series consists of only female specimens. The second author repeatedly searched for this species in the type locality, but no additional specimens were found. Nevertheless, we describe it because of its very distinct general appearance. This species was only found in Chiba-ken. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa okinawana sp. nov.

(Figs 1M; 2M; 15; 22)

(Japanese name: Okinawa-nagisa-hanekakushi)

Type material. Holotype: ♂, **JAPAN: Nansei-shotô:** Gesashi, Higashison, Okinawa-jima, Okinawa-ken, 15.viii.2004, M. Moriguchi (KUM). Paratypes: 1 ♀, Mage-shima (near Tanega-shima), Kagoshima-ken, 14.x.2000, M. Maruyama (under stone on sandy beach, in a port) (KUM); 3 ♀♀, 3 unsexed spec., same data as holotype. (KUM).

Description. Body (Fig. 1M) small, about 2.1–2.2 mm in length, covered with minute setae. Basically, yellowish brown. head and pronotum similarly coloured, elytra lightly paler than body colour, abdomen darkest; antenna, mouthparts and legs similarly coloured, lightly paler than head colour and paler toward apex.

Head oval, wider than long, shorter than pronotum and elytra; eyes (Fig. 2M) small, reniform, longer than 1/2 of head length, with 29–31 facets; antennal length shorter than distance from anterior margin of head to posterior margin of elytra; segment I as long as II, almost 2 times longer than III, and as long as XI; antennal segments I–IV and XI longer than wide; antennal segments V–X almost as long as wide.

Mouthparts (Figs 15A–E) with distribution of labral setae as in Figure 15A; mandibles (Fig. 15B) elongate triangle, asymmetrical, right mandible with median tooth; median tooth shorter than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 15C) at right angle and second spines not very small, at tip with two spines not closely interdigitating; 4 setae on inner margin of lacinia; labial palpus (Fig. 15D) with most setae located basally; mentum (Fig. 15E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" of mentum lower than level of anterior margin.

Pronotum shorter than elytra, wider than head.

Elytra subquadrate, wider than pronotum; hind wings fully developed.

Male abdominal sternite VIII (Fig. 15F) with posterior margin obviously serrate. Median lobe of aedeagus (Fig. 15H) and dorsal view in Figure 15I; paramere (Fig. 15J) elongate.

Female abdominal sternite VIII (Fig. 15G) with posterior margin slightly serrate but obviously smoother than in male. Spermatheca (Fig. 15K) simplified in shape, about half times coiled near base.

Measurements. BL 2.10–2.20, FBL 1.00–1.10, HL 0.33–0.38, HW 0.40–0.43, PL 0.38–0.40, PW 0.43–0.45, EL 0.48–0.50, EW 0.50–0.51, HTL 0.33–0.36, AL 0.78–0.85, AS-I 0.10–0.13, AS-II 0.09–0.11, AS-III 0.05–0.06.

Differential diagnosis. In general appearance the species in is closely allied to *B. moriguchii* sp. nov., but easily distinguished from it by the shape of the spermatheca, and lack of large, thick spiniform seta at the antero-lateral part of the labrum, and the posterior margin of the tergite X being rounded medially.

Etymology. Toponym. Named after Okinawa, the type locality of this new species; adjective.

Distribution. Japan (**Nansei-shotô:** Kagoshima-ken: Tanega-shima; Okinawa-ken: Okinawa-jima).

Remarks. This species probably occurs in other areas, especially the coastline of southwest Japan. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa nigra sp. nov.

(Figs 1N; 16; 21B, D; 22)

(Japanese name: Kuro-nagisa-hanekakushi)

"*Bryothinusa nakanei*": Sawada (1971): 88 (misidentification); Ahn & Jeon (2004): 34 (misidentification; illustration of spermatheca); Ahn et al. (2017): 307 (misidentification; in checklist of Staphylinidae in Korea).

Type material. Holotype: ♂, **JAPAN: Honshû:** Mouth of Obitsu-gawa, Kuroto, Kisarazu-shi, Chiba-ken, 24.i.2011, H. Ono (KUM). Paratypes: **Honshû:** 1 unsexed spec., same locality as holotype, 19.ii.2007, H. Ono (KUM); 2 ♂♂ 4 ♀♀, 15 unsexed spec., same locality as holotype, 12.iii.2009, H. Ono (KUM, NMPC, BMNH); 1 ♂ 1 ♀, 5 unsexed spec., same locality as holotype, 16.iii.2009, H. Ono (KUM); 1 ♂ 5 unsexed spec., same locality as holotype, 4.i.2010, H. Ono (KUM); 2 unsexed spec., same locality as holotype, 14.i.2011, H. Ono (KUM); 3 ♂♂ 2 ♀♀, 17 unsexed spec., same data as holotype (KUM); 1 ♀, 3 unsexed spec., Edo-gawa, Gyôtoku, Ichikawa-shi, Chiba-ken, 18.vi.2012, H. Ono (KUM); 1 unsexed spec., Kushida-gawa, Matsunase-chô, Matsuzaka-shi, Mie-ken, 2.iv.2002, T. Wada (KUM). **Shikoku:** 1 ♀, 7 unsexed spec., Nio, Nio-chô, Kagawa-ken, 20.iv.2008, H. Fujimoto (KUM); 2 ♂♂ 1 ♀, Kaigan-ji, Nishishirakata, Tadotsu-chô, Kagawa-ken, 31.iii.2008, H. Fujimoto (KUM). **Kyûshû:** 2 ♂♂ 1 ♀, 7 unsexed spec., Aiboshi-gawa, Aiboshi, Minamisatsuma-shi, Kagoshima-ken, 20.iv.2008, M. Maruyama (KUM). **Nansei-shotô:** 1 ♂ 6 ♀♀, 19 unsexed spec., Uken-son, Edateku-jima (near Amami-Ôshima), Kagoshima-ken, 5.vi.2008, M. Maruyama (KUM).

Description. Body (Fig. 1N) small about 2.0–2.5 mm in length, covered with minute setae. Body almost black; elytra lighter than other parts; antenna and legs brown.

Head evenly rounded, more or less produced anteriorly, wider than long, almost as long as pronotum, shorter than elytra; eyes (Fig. 2N) large, setae present between about

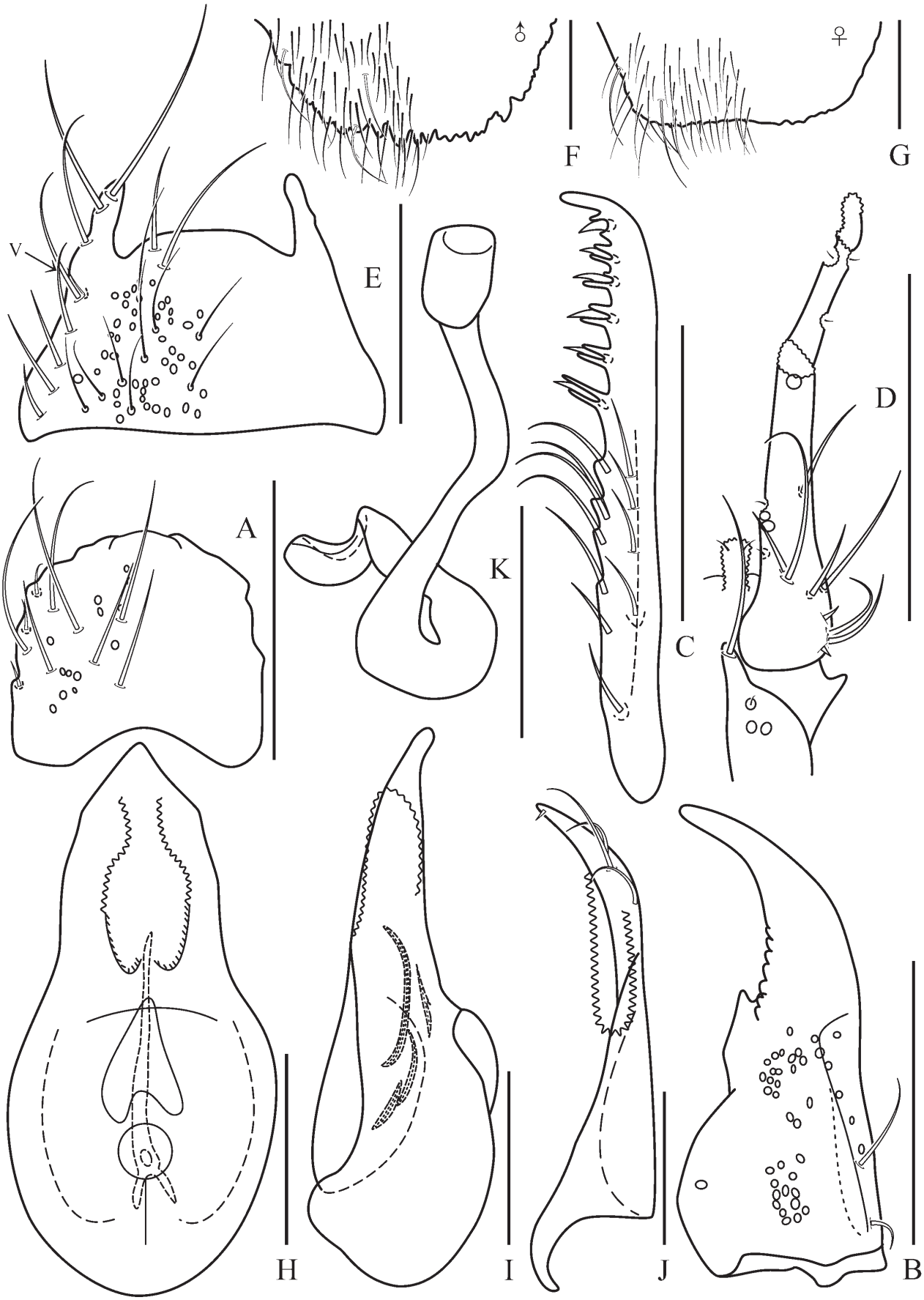

Fig. 15. *Bryothinusa okinawana* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

Fig. 16. *Bryothinusa nigra* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

32–33 facets, longer than 2/3 head length; antenna almost as long as distance from anterior margin of head to posterior margin of pronotum; segment I 1.3 times longer than II, almost 2.7 times longer than III, and longer than XI; antennal segments V–X almost as long as wide.

Mouthparts (Figs 16A–E) with distribution of labral setae as in Figure 16A, with large and thick spiniform seta at antero-laterally; mandibles (Fig. 16B) elongate triangle, asymmetrical, right mandible with median tooth; median tooth almost as long as 1/4 of mandibles; left without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 16C) at tip with two spines very small and not closely interdigitating; 4 setae on inner margin of lacinia; labial palpus (Fig. 16D) with most setae located basally; mentum (Fig. 16E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum shorter than elytra, wider than head.

Elytra subquadrate but wider than long, wider than pronotum; hind wings fully developed.

Male abdominal sternite VIII (Fig. 16F) with posterior margin slightly serrate. Median lobe of aedeagus (Fig. 16H) and dorsal view as in Figure 16I; paramere (Fig. 16J) elongate.

Female abdominal sternite VIII (Fig. 16G) with posterior margin slightly serrate alike male. Spermatheca (Fig. 16K) very small, shorter than 0.25 mm.

Measurements. BL 2.00–2.50, FBL 1.00–1.30, HL 0.35–0.40, HW 0.41–0.44, PL 0.31–0.42, PW 0.40–0.54, EL 0.41–0.46, EW 0.50–0.56, HTL 0.37–0.39, AL 0.65–0.70, AS-I 0.11–0.14, AS-II 0.08–0.10, AS-III 0.04–0.05.

Differential diagnosis. In general appearance, the species is closely similar to *B. nakanei* and *B. gangjinensis*, but it is easily distinguished from them by a different shape and size of spermatheca. It differs from *B. nakanei* also by the shape of the posterior margin of tergite X (rounded medially in the new species).

Etymology. The species epithet, the Latin adjective *niger* (*-a*, *-um*), refers to the blackish colour of the body.

Distribution. Japan (**Honshû:** Chiba-ken, Kanagawa-ken, Mie-ken; **Shikoku:** Kagawa-ken; **Kyûshû**: Kagoshima-ken; **Nansei-shotô:** Kagoshima-ken: Edateku-jima); Korea.

Remarks. Sawada (1971) illustrated the mouthparts and sexual organs of "*B. nakanei*" but the large, thick spiniform seta at the antero-lateral part of the labrum and the shape of aedeagus is very similar to those of *B. nigra* sp. nov. Therefore, we consider that the Figure 3 (Sawada 1971) is of *B. nigra* sp. nov.

Ahn & Jeon (2004) illustrated the spermatheca of "*B. nakanei*" based on the Korean specimens but its shape agrees well with that of *B. nigra* sp. nov.. Therefore, we consider that their figure (Ahn & Jeon 2004: Fig. 18) represents the spermatheca of *B. nigra* sp. nov. The misidentification by Ahn & Jeon (2004) was probably caused by the redescription of Sawada (1971). See also the Remarks of *B. nakanei* below.

This species is found mainly west of Kantô District. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa nakanei (Sawada, 1955)

(Figs 1O; 2O; 17; 21B, D-F; 22)

(Japanese name: Nakane-nagisa-hanekakushi)

Halesthenus nakanei Sawada, 1955: 85 (original description; type locality: Japan, Nansei-shotô, Tokara-rettô, Takara-jima).

Bryothinusa nakanei: Sawada (1971): 87 (transferred from *Halesthenus*; redescription); Sawada (1972): unnumbered table at end of article (characters); Moore et al. (1973): 74 (in key to species of *Bryothinusa*), 77 (nomenclatorial history; diagnosis); Moore & Legner (1975): 109–110 (in key to species of *Bryothinusa*), 111 (in tabular key to known species of *Bryothinusa*); Ashe (2004): 592 (in annotated catalogue of world species); Smetana (2004): 464 (in catalogue of Palearctic species); Frank & Ahn (2011): 27 (in checklist); Schülke & Smetana (2015): 676 (in catalogue of Palearctic species); Liu et al. (2020): 589 (in key to Japanese species), 592 (in checklist).

Type material examined. Holotype: unsexed specimen (not dissected), **JAPAN: Nansei-shotô:** "Halesthenus / nakanei / Sawada. // TAKARA-JIMA / (TOKARA Is.) / 29.v.1953 / coll. S. Uéno / Holotype / 49-16". Deposited in the Hokkaido University Museum.

Additional material examined. JAPAN: Nansei-shotô: 1 ♂, Mage -shima (near Tanega-shima), Kagoshima-ken, 14.x.2000, M. Maruyama (under stone on sandy beach, in a port); 8 ♂♂ 6 ♀♀, 57 unsexed spec., Ôgomori, Takara-jima, Tokara-rettô, Kagoshima-ken, 3.vii.2019, T. Liu, N. Tsuji & H. Ono; 1 unsexed spec., same locality, 6.vii.2019, T. Liu, N. Tsuji & H. Ono; 2 ♀♀, 9 unsexed spec., Tean, Setouchi-chô, Amami -Ôshima, Kagoshima-ken, 19.vii.2007, M. Moriguchi; 2 ♂♂ 2 unsexed spec., Chatan-chô, Okinawa-jima, Nansei-shôtô, Okinawa-ken, 26.v.2002, M. Moriguchi; 3 ♀♀, 9 unsexed spec., Senaha, Yomitani-son, Okinawa-jima, Okinawa-ken, 21.v.2004, M. Moriguchi; 1 ♂ 1 ♀, 2 unsexed spec., Fuchaku, Onna-son, Okinawa-ken, 8.iv.2000, T. Watanabe; 2 ♂♂ 3 ♀♀, 31 unsexed spec., Todoroki-gawa, Shiraho, Ishigaki-shi, Okinawa-ken, 29.iii.2010, T. Hayama; 2 ♀♀, 10 unsexed spec., Hira-kawa, Ishigaki-shi, Ishigaki-jima, Okinawa-ken, 29.iii.2010, T. Hayama; 2 ♀♀, 5 unsexed spec., Kabira-wan, Ôtake, Ishigaki-jima, Okinawa-ken, 3-11.vi.2000, S. Hori; 2 ♀♀, 11 unsexed spec., same locality, 1.vi.2003, M. Moriguchi; 2 ♂♂ 1 ♀, 9 unsexed spec., same locality, 26.iii.2015, Y. Hisasue; 1 ♀, 2 unsexed spec., same locality, 11.iii.2000, T. Kurihara; 2 ♂♂ 1 ♀, 50 unsexed spec., Nagura, Ishigaki-jima, Okinawa-ken, 21.iv.2009, M. Maruyama; 3 ♀♀, 5 unsexed spec., Nagura-anparu, Nagura, Ishigaki-shi, Ishigaki-jima, Okinawa-ken, 4.ii.2009, H. Ono; 1 ♂ 1 unsexed spec., Nakasuji, Ishigaki-shi, Ishigaki-jima, Okinawa-ken, 12.iii.2000, T. Kurihara; 4 ♀♀, 8 unsexed spec., Nakama-gawa, Ôtomi, Iriomote-jima, Okinawa-ken, 19–20.iv.2009, M. Maruyama; 1 ♀, Mouth of Honera-gawa, Takana, Taketomi-chô, Iriomote-jima, Okinawa-ken, 24.vi.2019, T. Liu & N. Tsuji; 2 unsexed spec., Mouth of Maira-gawa, Taketomi-chô, Iriomote-jima, Okinawa-ken, 21.iii.2000, T. Kurihara; 2 ♀♀, 53 unsexed spec., Haemida, Taketomi-chô, Iriomote-jima, Okinawa-ken, 19.iii.2000, T. Kurihara. Deposited at KUM but some will be distributed to NMPC and BMNH.

Redescription. Body (Fig. 1O) small, about 2.0–2.2 mm in length, covered with minute setae. Abdomen almost black and darker than head and pronotum; elytra lighter than pronotum, clearly bicolour, base darker than apex; legs yellowish brown.

Head evenly rounded, more or less produced anteriorly, wider than long, shorter than pronotum and elytra; eyes (Fig. 2O) large, setae present between about 34–36 facets, slightly longer than 2/3 of head length; antenna almost as long as distance from anterior margin of head to posterior margin of pronotum; segment I 1.3 times longer than II, almost 2.8 times longer than III, and longer than XI; antennal segments VII–X slightly wider than long.

Mouthparts (Figs 17A–E) with distribution of labral setae as in Figure 17A, with large and thick spiniform seta at antero-laterally; mandibles (Fig. 17B) elongate triangle, asymmetrical, right with median tooth; median

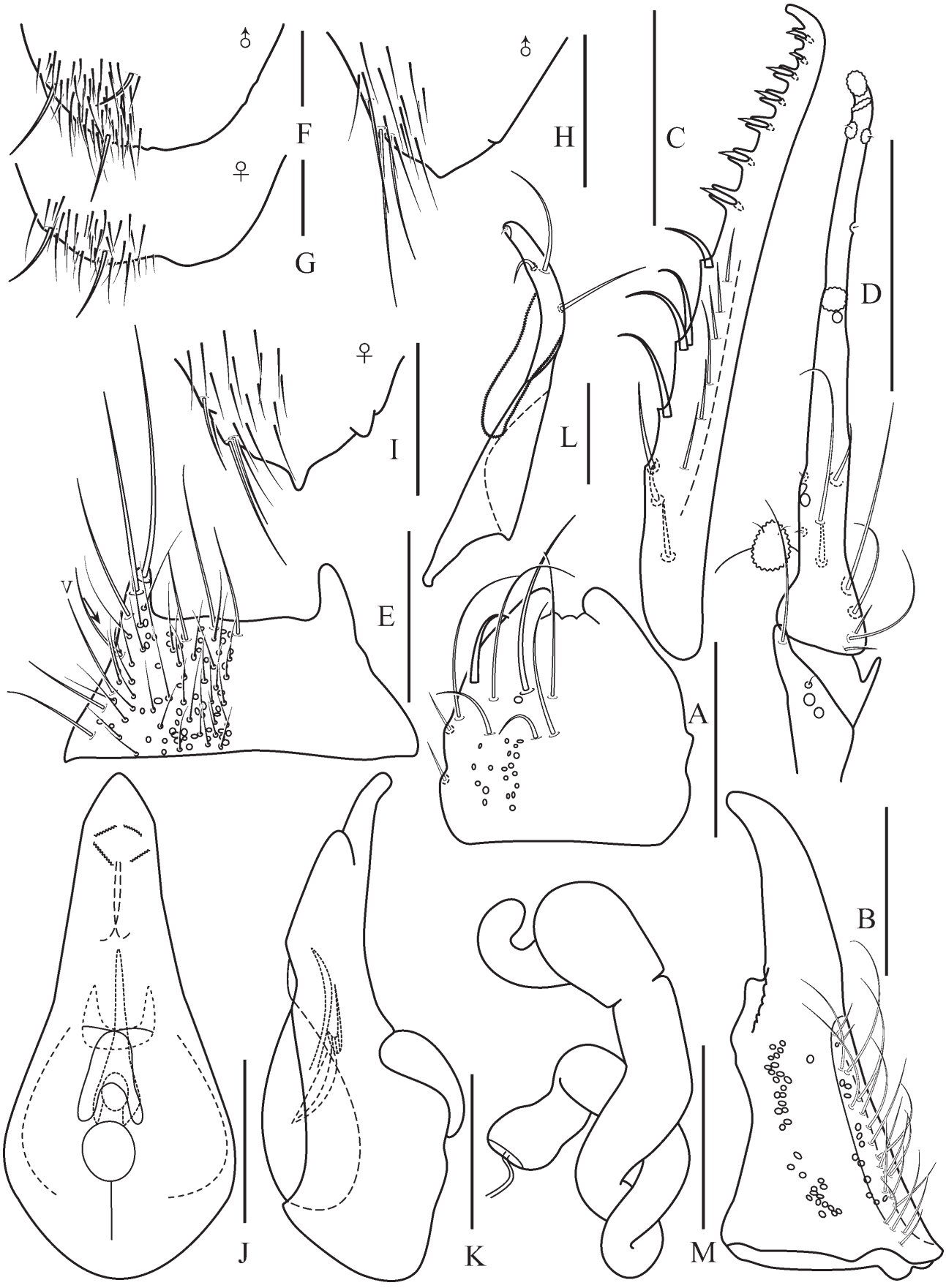

Fig. 17. *Bryothinusa nakanei* (Sawada, 1955). A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – male tergite X; I – female tergite X; J – median lobe, ventral view; K – median lobe, lateral view; L – paramere; M – spermatheca. . Scale bars: 0.1 mm.

tooth shorter than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 17C) at right angle; at tip with two spines not closely and second spine very small, not obvious; 6 setae on inner margin of lacinia; labial palpus (Fig. 17D) with most setae located basally; mentum (Fig. 17E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum shorter than elytra, almost as wide as head.

Elytra subquadrate but wider than long, wider than pronotum; hind wings fully developed.

Male abdominal sternite VIII (Fig. 17F) with posterior margin slightly serrate; medial posterior margin of tergite X protruded (Fig. 17H). Median lobe of aedeagus and dorsal view as in Figures 17J, K; paramere (Fig. 17L) elongate.

Female abdominal sternite VIII (Fig. 17G) slightly sunken at median posterior margin but wider and smoother than in male; medial posterior margin of tergite X more protruded than in male (Fig. 17I). Spermatheca (Fig. 17M) of complicated shape, about 2.5 times coiled near base.

Measurements. BL 2.00–2.20, FBL 1.10–1.20, HL 0.35–0.38, HW 0.45–0.50, PL 0.40–0.41, PW 0.45–0.50, EL 0.48–0.50, EW 0.45–0.54, HTL 0.35–0.38, AL 0.75–0.80, AS-I 0.11–0.15, AS-II 0.09–0.11, AS-III 0.04–0.05.

Differential diagnosis. In general appearance the species is very similar to *B. nigra* sp. nov. and *B. gangjinensis*. In the shape of the spermatheca, the species is closely similar to *B. moriguchii* sp. nov. However, the new species is easily distinguished from *B. nigra* sp. nov. and *B. gangjinensis* by the medial posterior margin of tergite X being protruded and is different from *B. moriguchii* sp. nov. in the body colour being darker.

Distribution. Japan (**Nansei-shotô:** Kagoshima-ken: Tanega-shima, Takara-jima, Amami-Ôshima; Okinawa-ken: Okinawa-jima, Ishigaki-jima, Iriomote-jima).

Remarks. Sawada (1955) originally described *B. nakanei* based on a single specimen from Takara-jima, Tokara-rettô, Nansei-shotô, without illustrating any sexual characters. Sawada (1971) redescribed "*B. nakanei*" in detail including the male aedeagus based on the "holotype." However, we examined the holotype of *B. nakanei* deposited in the late Dr. Takehiko Nakane collection of the Hokkaido University Museum and confirmed it was not dissected. Sawada (1971) also examined a male specimen of this species from Aburatsubo of Kanagawa, Honshû. The redescription is probably based on the specimen from Kanagawa. Moreover, the redescription does not coincide with the holotype but actually agrees well with the characteristics of *B. nigra* sp. nov. *Bryothinusa nakanei* is very similar to *B. nigra* sp. nov. in general appearance and Sawada (1971) probably confused them. As discussed in the Remarks of *B. nigra* sp. nov., Ahn & Jeon (2004) described the spermatheca of "*B. nakanei"* from Korea but it was of the same shape as that of *B. nigra* sp. nov. *Bryothinusa nakanei* may not occur in Korea because it has not been found in temperate zones in Japan, but in Nansei-shotô, a subtropical zone.

This species likely occurs in other areas, mainly in Nansei-shotô. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa moriguchii sp. nov.

(Figs 1P; 2P; 18; 22)

(Japanese name: Moriguchi-nagisa-hanekakushi)

Type material. Holotype: ♂, **JAPAN: Nansei-shotô:** Yagaji-jima, Nago-shi, Okinawa-ken, 21.iii.2005, M. Moriguchi (KUM). Paratypes: 3 ♂♂ 3 ♀♀, 4 unsexed spec., same data as holotype (KUM, NMPC, BNMH); 2 ♀♀, 4 unsexed spec., Uehara, Iriomote-jima, 2.iv.2004, M. Moriguchi (KUM).

Description. Body (Fig. 1P) small, about 1.9–2.2 mm in length, covered with minute setae. Basically, dark brown, elytra brown palest, head and pronotum similarly coloured, paler than abdomen; antenna, mouthparts and legs similarly coloured, lightly paler than head colour and paler toward apex.

Head oval, wider than long, almost as long as pronotum, shorter than elytra; eyes (Fig. 2P) small, reniform, longer than 2/3 of head length, with 32–34 facets; antennal length slightly longer than distance from anterior margin of head to posterior margin of pronotum; segment I as long as II, almost 2.5 times longer than III, and as long as XI; antennal segments I–III and XI longer than wide, antennal segments IV–X almost as long as wide.

Mouthparts (Figs 18A-E) with distribution of labral setae as in Figure 18A, with large and thick spiniform seta antero-laterally; mandibles (Fig. 18B) elongate triangle, asymmetrical, right with median tooth; median tooth shorter than 1/4 of mandibles; left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 18C) with second spines very small and not obvious, at tip with two spines not closely interdigitating; 3 setae on inner margin of lacinia; labial palpus (Fig. 18D) with most setae located basally; mentum (Fig. 18E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" of mentum lower than level of anterior margin.

Pronotum shorter than elytra, almost as wide as head.

Elytra subquadrate but wider than long, wider than pronotum; hind wings fully developed.

Male abdominal sternite VIII (Fig. 18F) with posterior margin slightly serrate. Medial posterior margin not protruded, sharp in form on tergite X of male (Fig. 18H). Median lobe of aedeagus (Fig. 18J) and dorsal view in Figure 18K; paramere (Fig. 18L) elongate.

Female abdominal sternite VIII (Fig. 18G) with posterior margin slightly sunken but smoother than in male. Medial posterior margin protruded sharp in form on tergite X of female (Fig. 18I). Spermatheca (Fig. 18M) of complicated shape, about 2.5 times coiled near base.

Measurements. BL 1.90–2.20, FBL 1.00–1.10, HL 0.35–0.40, HW 0.43–0.45, PL 0.38–0.40, PW 0.45–0.46, EL 0.45–0.48, EW 0.50–0.55, HTL 0.33–0.38, AL 0.75–0.85, AS-I 0.10–0.13, AS-II 0.10–0.13, AS-III 0.04–0.05.

Differential diagnosis. In general appearance the species is very similar to *B. okinawana* sp. nov., but easily distinguished from it by having large, thick spiniform seta at the antero-lateral part of the labrum, and the coil number of the spermathecal basal part and of the posterior margin of the tergite X being protruded.

Etymology. This new species is named after Mr. Mitsuru Moriguchi, the collector of the type series.

Fig. 18. *Bryothinusa moriguchii* sp. nov. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – male tergite X; I – female tergite X; J – median lobe, ventral view; K – median lobe, lateral view; L – paramere; M – spermatheca. Scale bars: 0.1 mm.

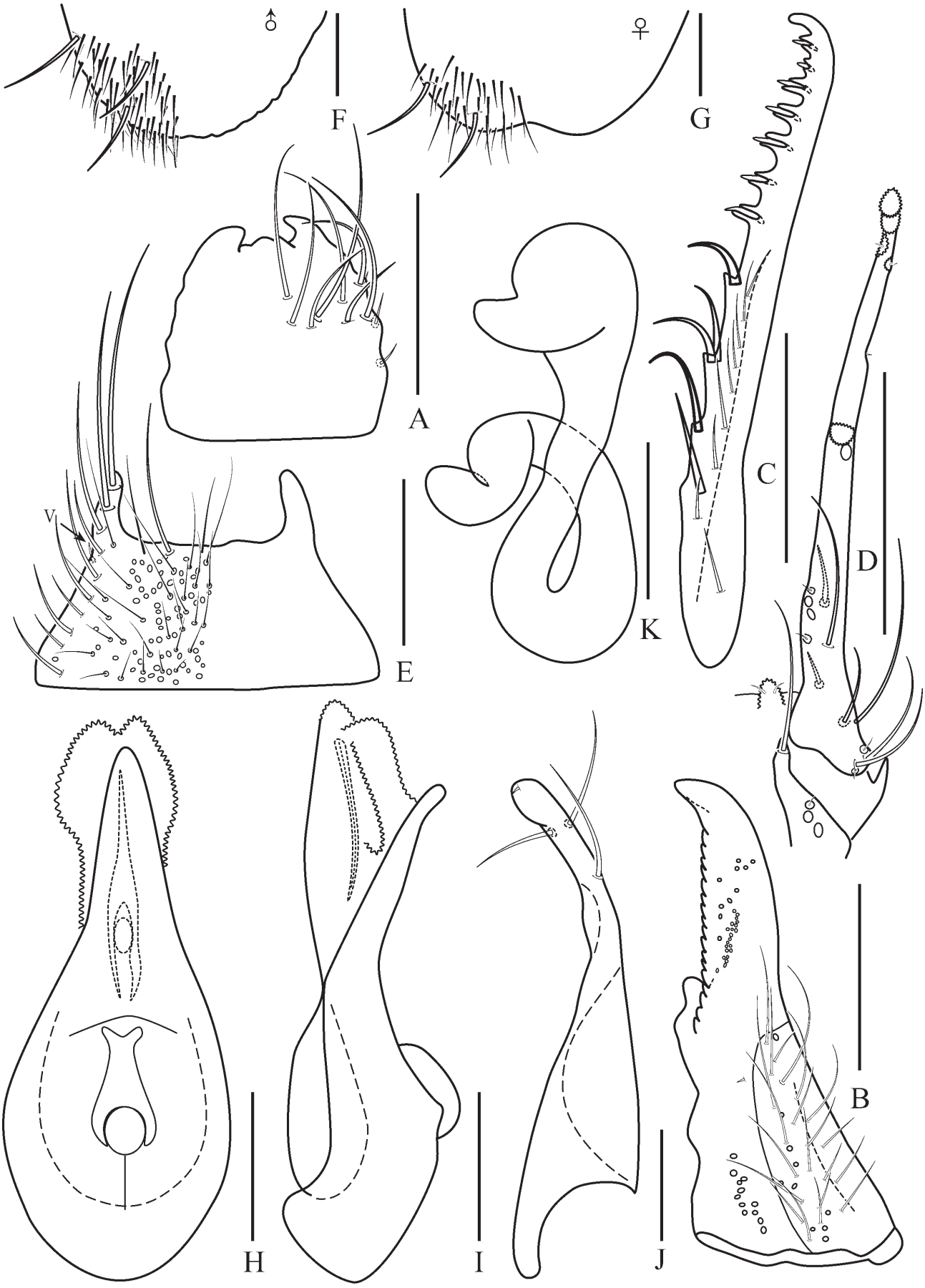

Fig. 19. *Bryothinusa gangjinensis* Ahn & Jeon, 2004. A – labrum; B – mandible, dorsal view; C – lacinia, dorsal view; D – labium; E – mentum; F – male sternite VIII; G – female sternite VIII; H – median lobe, ventral view; I – median lobe, lateral view; J – paramere; K – spermatheca. Scale bars: 0.1 mm.

Distribution. Japan (**Nansei-shotô:** Okinawa-ken: Yagaji-jima, Iriomote-jima).

Remarks. This species may occur in other areas, especially the coastline of western Japan. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Bryothinusa gangjinensis Ahn & Jeon, 2004

(Figs 1Q; 1Q; 19; 21F; 22)

(Japanese name: Kanjin-nagisa-hanekakushi)

Bryothinusa gangjinensis Ahn & Jeon, 2004: 29 (original description; type locality: Korea: Jeonnam); Ashe (2004): 591 (in annotated catalogue of world species); Asano & Kojima (2010): 297 (new record from Japan: Tanega-shima); Frank & Ahn (2011): 26 (in checklist); Schülke & Smetana (2015): 676 (in catalogue of Palearctic species); Ahn et al. (2017): 307 (in checklist of the Staphylinidae in Korea); Liu et al. (2020): 589 (in key of Japanese species), 592 (in checklist).

Type material. Not examined.

Material examined. JAPAN: Honshû: 2 ♂♂ 17 unsexed spec., Mouth of Minato-gawa, Minato, Futtsu-shi, Chiba-ken, 27.v.2013, H. Ono; 4 ♂♂ 1 ♀, 24 unsexed spec., same locality, 24.viii.2009 H. Ono; 2 ♂♂ 2 ♀♀, 7 unsexed spec., Koajiro-wan, Koajiro, Misaki-machi, Miura-shi, Kanagawa-ken, 23.v.2013, H. Ono; 1 ♂ 2 ♀♀, 67 unsexed spec., Miya-gawa, Iso-chô, Ise-shi, Mie-ken, 8.vi.2008, K. Akita; 2 ♀♀, 6 unsexed spec., Hannan 2-ku, Kishiwada-shi, Ôsaka-fu, 11.vi.2010, Y. Kawakami; 1 ♀, 5 unsexed spec., same locality, 7.x.2010, Y. Kawakami; 1 ♀, Arida-gawa, Miyazaki-chô, Arida-shi, Wakayama-ken, 28.v.2002, Y. Kawakami. **Shikoku:** 1 ♀, 1 unsexed spec., Kabe-gawa, Kamoshô, Sanuki-shi, Kagawa-ken, 13.iv.2008, H. Fujimoto; 1 ♀, 2 unsexed spec., Kôtô-gawa, Gôtô-chô, Takamatsu-shi, Kagawa-ken, 12.iv.2008, H. Fujimoto; 1 ♂ 3 unsexed spec., Kamobe-gawa, Kamoshô, Sanuki-shi, Kagawa-ken, 12.iv.2008, H. Fujimoto; 1 ♂, Aya-gawa, Ejiri-chô, Sakaide-shi, Kagawa-ken, 12.iv.2008, H. Fujimoto; 2 unsexed spec., Nishihabu-machi, Matsuyama-shi, Ehime-ken, 19.iv.2009, H. Suenaga. **Kyûshû:** 1 ♂, Iki-no-matsubara, Nishi-ku, Fukuoka-shi, Fukuoka-ken, 1.vii.2018, Y. Hisasue; 1 ♂ 1 ♀, 13 unsexed spec., Chichibu-ga-ura, Shimabara, Nagasaki-ken, 10.v.2001, T. Watanabe; 1 ♀, 3 unsexed spec., Kawashima, Nobeoka-shi, Miyazaki-ken, 24.vii.2006, J. Nakajima ; 1 ♀, 4 unsexed spec., Nagayoshi-kawa, Fukiage-chô, Hioki-shi, Kagoshima-ken, 9.xii.2007, K. Nakamura; 1 ♀, 6 unsexed spec., Manose-gawa, Masukawa, Kaseda, Minamisatsuma-shi, Kagoshima-ken, 20.iv.2008, M. Maruyama; 1 ♂ 2 ♀♀, 11 unsexed spec., Aiboshi-gawa, Aiboshi, Minamisatsuma-shi, Kagoshima-ken, 20.iv.2008, M. Maruyama. **Nansei-shotô:** 3 ♂♂ 6 unsexed spec., Ou-jima, Nago-shi, Okinawa-ken, 30.iv.2006, M. Moriguchi; 2 unsexed spec., Awase-Higata, Okinawa-shi, Okinawa-ken, 30.iv.2006, M. Moriguchi; 11 unsexed spec., Makiya, Nago-shi, Okinawa-jima, Okinawa-ken, 4.vii.2010, M. Moriguchi. Deposited at KUM but some will be distributed to NMPC and BMNH.

Redescription. Body (Fig. 1Q) small, about 1.9–2.4 mm in length, covered with minute setae. Abdomen almost black, darker than head and pronotum; elytra darker than pronotum, bicoloured but not clearly, base darker than apex; antenna and legs yellowish brown.

Head evenly rounded, more or less produced anteriorly, wider than long, shorter than elytra; eyes (Fig. 2Q) large, setae present between about 32–34 facets, slightly longer than 2/3 of head length; antennal length slightly longer than distance from anterior margin of head to posterior margin of pronotum; segment I 1.5 times longer than II, almost 2.8 times longer than III, and longer than XI; antennal segments V–X almost as long as wide.

Mouthparts (Figs 19A–E) with distribution of labral setae as in Figure 19A; mandibles (Fig. 19B) elongate triangle, asymmetrical, right with densely median tooth, left mandible without tooth, blunt at apex; maxilla with apical margin of lacinia (Fig. 19C) at right angle; at tip with two spines not clearly; 7 setae on inner margin of lacinia; labial palpus (Fig. 19D) with most setae located basally; mentum (Fig. 19E) with antero-lateral angles prolonged into spinose processes; anterior margin deeply truncate; small "v seta" far away from apical setae.

Pronotum shorter than elytra, wider than head.

Elytra subquadrate, wider than pronotum; hind wings fully developed.

Male abdominal sternite VIII (Fig. 19F) with posterior margin slightly serrate. Median lobe of aedeagus and dorsal view as in Figures 19H, I; paramere (Fig. 19J) with apical lobe elongate.

Female abdominal sternite VIII (Fig. 19G) slightly sunken at median posterior margin but wider and smoother than in male. Spermatheca (Fig. 19K) large, about 1.5 times coiled near base and larger than 0.25 mm.

Measurements. BL 1.90–2.40, FBL 0.90–1.20, HL 0.29–0.30, HW 0.36–0.45, PL 0.31–0.45, PW 0.37–0.49, EL 0.36–0.55, EW 0.43–0.56, HTL 0.28–0.43, AL 0.60–0.75, AS-I 0.11–0.14, AS-II 0.06–0.11, AS-III 0.04–0.05.

Differential diagnosis. In general appearance, the species closely resembles *B. nigra* sp. nov. and *B. nakanei* but is easily distinguished from *B. nigra* sp. nov. in the shape and size of the spermatheca and is different from *B. nakanei* in having the posterior margin of the tergite X rounded medially.

Distribution. Japan (**Honshû:** Chiba, Kanagawa, Mie, Ôsaka, Wakayama; **Shikoku:** Kagawa, Ehime; **Kyûshû:** Fukuoka, Nagasaki, Miyazaki, Kagoshima; **Nansei-shotô:** Tanega-shima, Okinawa: Ou-jima, Okinawa-jima); Korea (Jeonnam).

Remarks. This species is mainly found west of Kantô District and Okinawa Island. A distribution map of examined specimens of this species in Japan is illustrated in Figure 22.

Biology

Collecting circumstances. Most of the specimens of *Bryothinusa* were found under stones on sandy beaches or estuaries, or among gravel in the intertidal zone. Habitat varies slightly between species. Some species prefer estuaries, while others live on sandy beaches facing the open sea. In this section, we describe the collecting circumstances of each species to provide information for future research.

Bryothinusa algarum was collected from under stones of an estuary near the sea at Nemoto of Chiba-ken in Honshû (Fig. 20A).

Bryothinusa minuta, B. sakishimana and *B. nakanei* were collected together under stones at Ôgomori sandy beach at Takara-jima of Tokara-rettô in Nansei-shotô (Fig. 20B), also Yoriki gravel beach at Nakano-shima of Tokara-rettô (Fig. 20C) and an estuary of Honera-gawa near the sea at Iriomote-jima in Nansei-shotô (Fig. 20D).

Bryothinusa tsutsuii was collected at Amadomari, a gravel beach at Nakano-shima of Tokara-rettô in Nansei-shotô (Fig. 20E). This species was collected together with *B.*

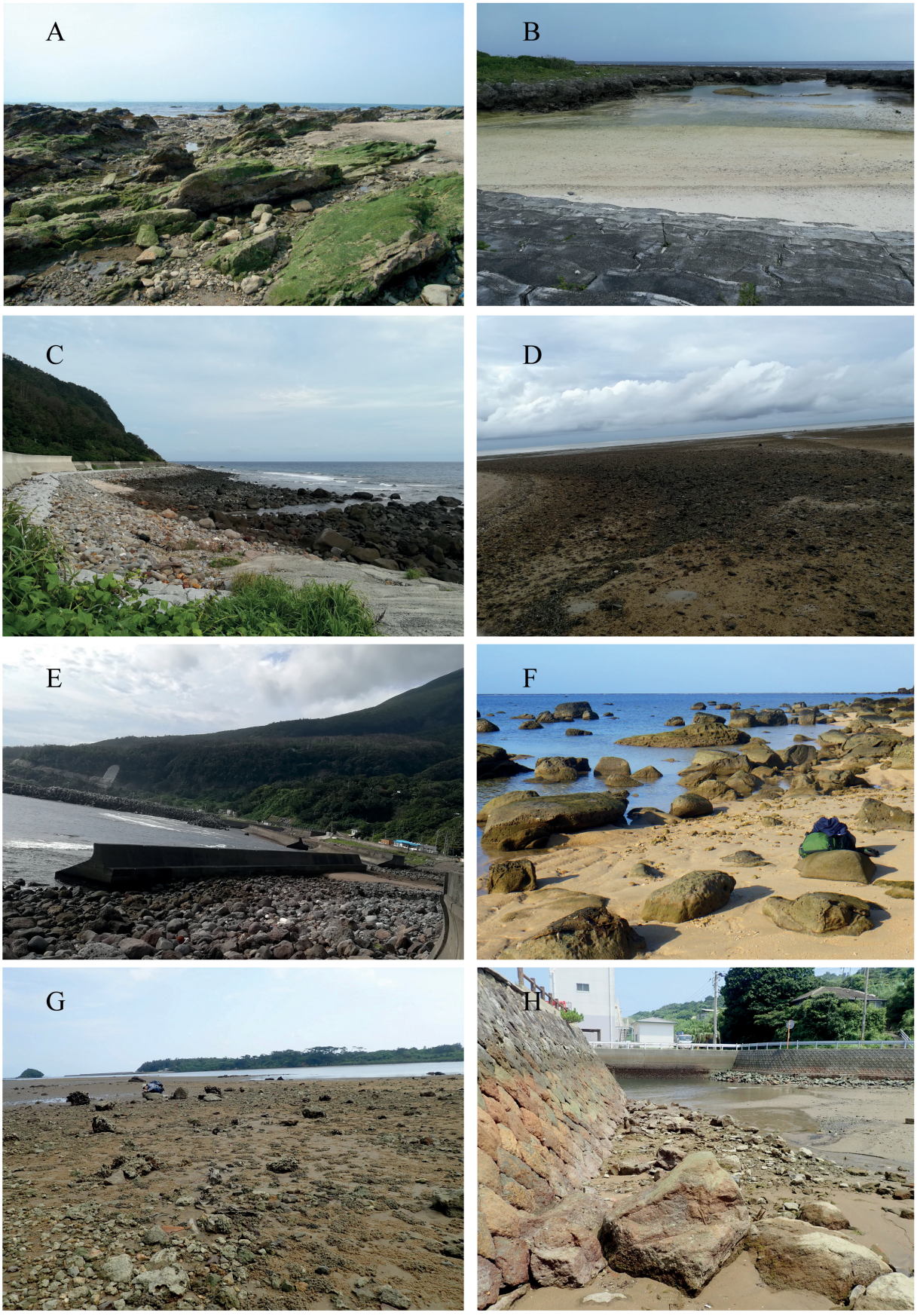

Fig. 20. Collection localities of *Bryothinusa* species in Japan: A – *B. algarum* Sawada, 1971 in Nemoto, Chiba; B – *B. minuta* (Sawada, 1955), *B. nakanei* (Sawada, 1955) and *B. sakishimana* Sawada, 1991 in Takara-jima (Ôgomori beach), Tokara-rettô; C – *B. minuta* in Nakano-shima (Yoriki), Tokara-rettô; D – *B. minuta*, *B. nakanei* and *B. sakishimana* in Iriomote-jima (mouth of Honera-gawa); E – *B. tsutsuii* (Sawada, 1955) in Nakano-shima (Amadomari), Tokara-rettô; F – *B. nakanei* and *B. tsutsuii* in Iriomote-jima (Haemida); G – *B. tsutsuii* in Iriomote-jima (mouth of Nakama-gawa); H – *B. itsuroi* sp. nov. and *B. koreana* Ahn & Jeon, 2004 in Kakise, Taka-shima, Nagasaki.

Fig. 21. Collection localities of *Bryothinusa* species in Japan: A – *B. koreana* Ahn & Jeon, 2004 and *B. japonica* Liu, Ono & Maruyama, 2020 in Shima-nogita, Fukuoka; B – *B. aikoae* sp. nov., *B. fulvipennis* sp. nov., *B. japonica* and *B. nigra* sp. nov. in Kuroto, Chiba; C – *B. hokkaidensis* sp. nov. in Shunkunitai, Hokkaidô; D – *B. nigra* sp. nov. and *B. tsutsuii* (Sawada, 1955) in Edateku-jima; E – *B. nakanei* (Sawada, 1955) in Nagura-anparu, Ishigaki-jima; F – *B. gangjinensis* Ahn & Jeon, 2004 in Iki-no-matsubara, Fukuoka; G – *B. algarum* Sawada, 1971, *B. japonica* and *B. minuta* (Sawada, 1955) in Sunosaki, Fukuoka.

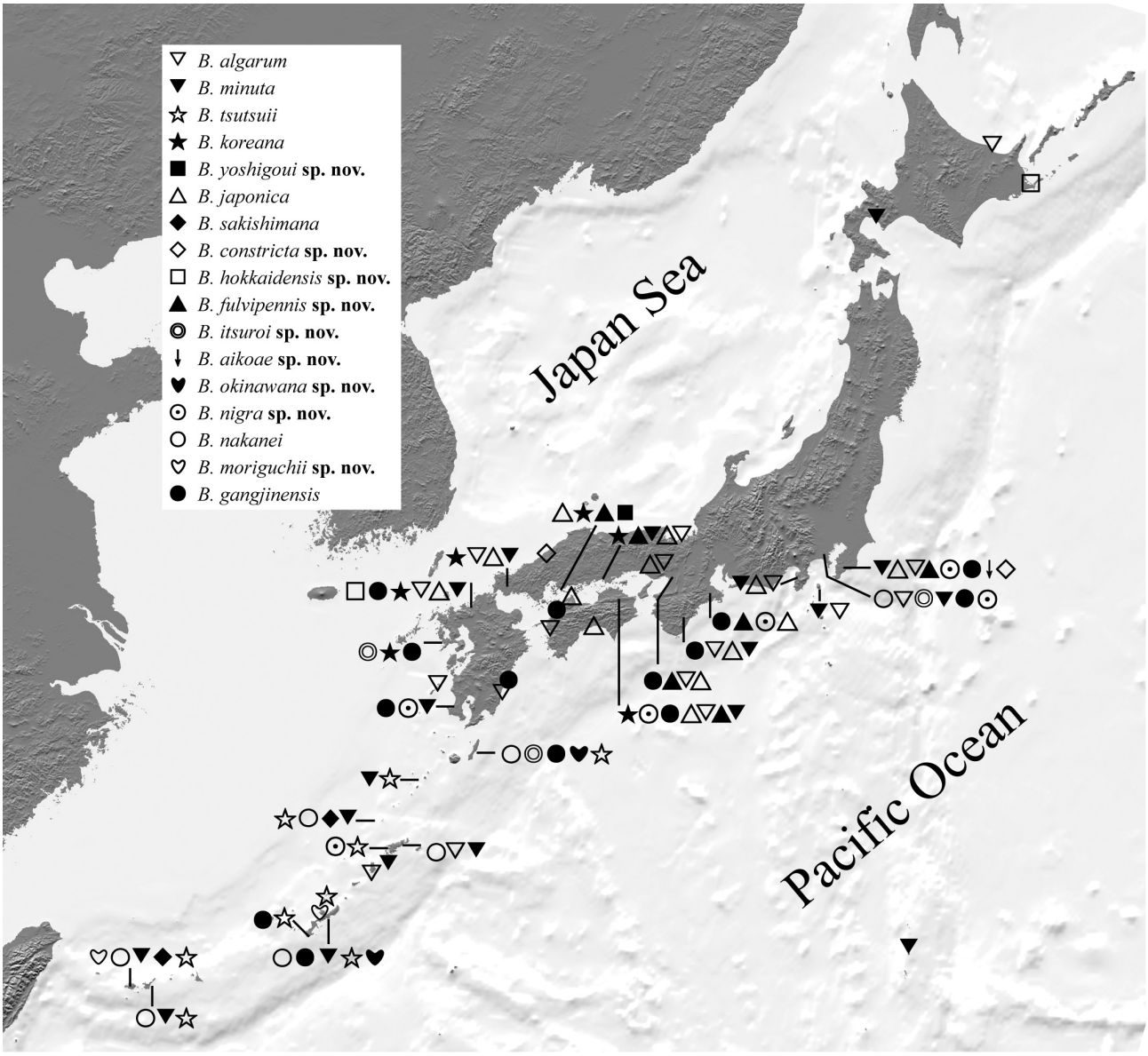

Fig. 22. Map of examined specimens of *Bryothinusa* spp. from Japan: white inverted triangle – *B. algarum* Sawada, 1971; black inverted triangle – *B. minuta* (Sawada, 1955); white star – *B. tsutsuii* (Sawada, 1955); black star – *B. koreana* Ahn & Jeon, 2004; black square – *B. yoshigoui* sp. nov.; white triangle – *B. japonica* Liu, Ono & Maruyama, 2020; black diamond – *B. sakishimana* Sawada, 1991; white diamond – *B. constricta* sp. nov.; white square – *B. hokkaidensis* sp. nov.; black triangle – *B. fulvipennis* sp. nov.; double circle – *B. itsuroi* sp. nov.; arrow – *B. aikoae* sp. nov.; black hart – *B. okinawana* sp. nov.; circled dot – *B. nigra* sp. nov.; white circle – *B. nakanei* (Sawada, 1955); white hart – *B. moriguchii* sp. nov.; black circle – *B. gangjinensis* Ahn & Jeon, 2004.

nakanei at sandy-rocky beach at Haemida of Iriomote-jima in Nansei-shotô (Fig. 20F) and also at mouth of Nakama-gawa at Haiminaka of Iriomote-jima (Fig. 20G).

The specimens of *B. koreana* were collected together with *B. itsuroi* sp. nov. at a small river mouth at Kakise of Nagasaki-ken in Kyûshû (Fig. 20H). *Bryothinusa koreana* and *B. japonica* were collected together at an estuary of Shima-Nogita of Fukuoka-ken in Kyûshû (Fig. 21A).

An extensive mud flat at Kuroto of Chiba-ken in Honshû, called Banzu-higata (Fig. 21B), has a rich and valuable fauna of intertidal staphylinids, where especially *B. japonica* and *B. nigra* sp. nov. were commonly found, and some *B. aikoae* sp. nov. and *B. fulvipennis* sp. nov. were collected together under stones.

Bryothinusa hokkaidensis sp. nov. was collected under stones on a mad flat at the brackish lake Shunkunitai in Hokkaidô (Fig. 21C).

In Kuruwa-kaigan of Yokosuka-shi, Kanagawa-ken in Honshû, *B. itsuroi* sp. nov. was found deep in sandy substrate around concrete blocks on the beach (the same habitat as in *Halorhadinus kawashimai* Ono & Maruyama, 2014).

Bryothinusa nigra sp. nov. and *B. tsutsuii* were collected together at a sandy beach of Edateku-jima in Amami-Ôshima, Kagoshima-ken, Nansei-shotô (Fig. 21D).

Bryothinusa nakanei was found at a coral rock beach near mangrove forest of Nagura-anparu in Ishigaki-jima, Okinawa-ken in Nansei-shotô (Fig. 21E).

Bryothinusa gangjinensis was collected with a net in the grass growing on the beach, at Iki-no-matsubara of Fukuoka-ken in Kyûshû (Fig. 21F). The individual was probably caught during its dispersal flight.

Behaviour. *Bryothinusa* beetles are generally found hiding under stones at high tide and roaming surfaces of the sandy beaches and mudflats in search of food at low tide. However, even at low tide they sometimes not emerge from under the stones, suggesting that conditions for activity on the surface of the substrate may be limited.

Some individuals of *B. constricta* sp. nov. at Futtsu-misaki in Chiba-ken of Honshû, *B. minuta*, *B. sakishimana* and *B. nakanei* at Ôgomori sandy beach in Takara-jima of Nansei-shotô were collected wandering on the surface of sandy shores at night.

At Sunosaki of Fukuoka in Kyûshû (Fig. 21G) some individuals of *B. algarum*, *B. minuta* and *B. japonica* followed the ebb of the tide and gradually move towards the sea while keeping a distance of about 3 to 4 meters from the shoreline. Also, at Ôgomori sandy beach at Takara-jima, same behaviour was observed for *B. minuta, B. sakishimana* and *B. nakanei*.

Wong & Chan (1977) reported that they *Bryothinusa* feeds on dead microorganisms in Hong Kong. Unfortunately, we have not been able to observe any feeding behavior in the field. In captivity, *B. japonica* and *B. koreana* ate a food used for feeding small fish (Liu, personal observation).

Distribution and dispersal ability

As listed in Table 1, three species are distributed in Hokkaidô, 11 species in Honshû, seven species in Shikoku, eight species in Kyûshû, 10 species in Nansei-shotô and one species distributed in Ogasawara-shotô. Most of the specimens examined were collected from Kantô-chihô (central Honshû, around Tôkyô) to Nansei-shotô (southwestern islands of Japan), while no specimens came from Tôhoku-chihô (northern Honshû). Many species are expected to be found in Tôhoku-chihô if field survey is conducted there.

Some species apparently have very wide distributional range. For example, *B. minuta* was found from Hokkaidô to Iriomote-jima of Nansei-shotô and the Ogasawara-shotô, covering almost the whole territory of Japan. *Bryothinusa algarum* also has very wide distributional range from Hokkaidô to Nansei-shotô. Interestingly, hind wings are completely absent in both these species.

Many researchers (e.g., Ikeda et al. 2012) suppose that flightless species have more or less narrower distribution than in the species with full flight capability. Some species are clearly under-surveyed due to their rarity (probably low population density at their localities), but the general trend observed in the species included in this study is that the distribution is often more restricted for species with hind wings (both fully developed and reduced ones) (Table 1).

We believe that the distributional range of individual *Bryothinusa* species is not correlated to the condition of their hind wings. We suppose that the dispersal of *Bryothinusa* species may happen more frequently due to sea currents than to flight. We have observed the behaviour of some flightless species, e.g., *B. minuta*, *B. algarum* and *B. japonica*, after lifting the stone at high tide: they float up, roll up their body and disappear somewhere in the current of the sea water. They are clearly adapted to floating on the water surface and are hence swept easily along by the water. On the other hand, the winged-but-reduced species, e.g., *B. hokkaidensis* sp. nov., and species with flight capability, e.g., *B. nigra* sp. nov. and *B. nakanei*, just floated with their legs spread, and those capable of flight take off directly from the water surface during warmer days (Maruyama & Ono, personal observation). We hence conclude that the potential ability of flightless species to disperse with the sea currents is quite higher than the dispersal ability of winged species.

Table 1. List of species used in this study of the genus of *Bryothinusa* with their hindwing condition and distributions.

Species	Flight ability (hindwing condition)	Distribution of species in Japan					
		Hokkaidô	Honshû	Shikoku	Kyûshû	Nansei-shotô	Ogasawara-shotô
B. algarum Sawada, 1971	No (absent)	●	●	●	●	●	
B. minuta (Sawada, 1955)	No (absent)	●	●	●	●	●	●
B. tsutsuii (Sawada, 1955)	No (absent)					●	
B. koreana Ahn & Jeon, 2004	No (absent)		●	●	●		
**B. yoshigoui* sp. nov.	No (absent)		●				
B. japonica Liu, Ono & Maruyama, 2020	No (absent)		●	●	●		
B. sakishimana Sawada, 1991	No (present but reduced)					●	
**B. constricta* sp. nov.	No (present but reduced)		●				
**B. hokkaidensis* sp. nov.	No (present but reduced)	●			●		
**B. fulvipennis* sp. nov.	No (present but reduced)		●	●			
B. itsuroi sp. nov.	No (present but reduced)		●		●	●	
**B. aikoae* sp. nov.	Yes (fully developed)		●				
B. okinawana sp. nov.	Yes (fully developed)					●	
B. nigra sp. nov.	Yes (fully developed)		●	●	●	●	
B. nakanei (Sawada, 1955)	Yes (fully developed)					●	
B. moriguchii sp. nov.	Yes (fully developed)					●	
B. gangjinensis Ahn & Jeon, 2004	Yes (fully developed)		●	●	●	●	

*) Species that are rare and under-surveyed: their true range is expected to be larger than indicated here.

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Appendix 1

Glossary of Japanese place names

In this paper, Japanese place names have been romanised as they are in Japanese. Japanese place names can also be anglicised. For example, "Fuji-san" is sometimes called "Mt. Fuji." However, due to the complexity of the Japanese language, it is difficult to do this kind of transliteration in a regular way, and it is also difficult to find the transliterated place names on maps. For example, "-yama", "-san", "-zan", "-sen", "-take" and "-dake" all mean mountain or hill, and if they are uniformly anglicised to "Mt. XX", the original place name is lost. Writing "Mt. Fuji-san" is also illogical, as it gives a double meaning to the mountain, such as "Mt. Mont Blanc." Also, of course, our sense of "yama" is different from the sense of "mountain" of people from other cultures. Place names often contain the meaning of environment, and it is possible to infer the environment to some extent from place names. In this section, we would like to list the words (suffixes) with the meaning of environment or administrative district contained in place names and explain their meanings.

-bana	cape
-bashi	bridge
-chô	township, town
-fu	prefecture
-gawa	river, creek
-gun	county
-hama	beach (usually sand or pebble)
-higata	mad flat
-jima	island
-kaigan	beach (various kind of substrate)
-kawa	river, creek
-ken	prefecture
-ko	lake, large pond
-ku	ward
-machi	township, town
-misaki	cape
-ôshima	island (meaning large island)
-ôura	small bay (meaning large "ura")
-rettô	archipelago
-saki	cape
-shi	city
-shima	island
-shotô	group of islands
-son	village (equal to "-mura")
-to	prefecture, metropolitan (only for Tôkyô)
-ura	small bay (also, lake connected to sea)
-wan	bay
-zaki	cape