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# Taxonomy and phylogeny of the Japanese species of the genus *Dasycerus* Brongniart (Coleoptera: Staphylinidae: Dasycerinae) with description of a new species and notes on *D. poseidon* Hu & Liang

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# Abstract

*Dasycerus occultus* Hashizume & Maruyama, **sp. nov.** is described and illustrated based on specimens from Japan (Honshu and Kyushu). The holotype of *D. japonicus* Nakane, 1963 was revisited. The "*D. japonicus*" illustrated by Löbl & Calame (1996) was found not to be *D. japonicus* but rather to be *D. occultus* **sp. nov.** The discussion also includes *D. poseidon* Hu & Liang, 2021 from Taiwan. The phylogenetic relationships of this genus from Japan based on mitochondrial DNA sequences are discussed.

Key words: East Asia, Palaearctic region, redescription, rove beetle

# Introduction

Dasycerinae is a small subfamily of Staphylinidae, which includes 18 extant species in a single genus, *Dasycerus* Brongniart, 1800, and three extinct genera (†*Protodasycerus* Yamamoto, 2016, †*Vetudasycerus* Cai, Thayer, Newton, Yin & Huang, 2018, †*Cedasyrus* Yin & Cai, 2020) from Burmese amber (Yamamoto 2016; Cai *et al.* 2018; Yin *et al.* 2020). Only one species, *D. japonicus* Nakane, 1963, is known from Japan, while another East Asian species, *D. poseidon* Hu & Liang, 2021, was recently described from Taiwan (Hu & Liang 2021).

The present study describes a new species of *Dasycerus* from Japan (Honshu and Kyushu); it is the second *Dasycerus* species from Japan and the third from East Asia. The female genital chamber, which has not been used in *Dasycerus* taxonomy, was recognized as a useful character.

The mitochondrial DNA of several species of the genus *Dasycerus* has been sequenced. DNA analyses by Caterino & Langton-Myers (2019) and Hu & Liang (2021) suggest that intra- and interspecific genetic distances are large within *Dasycerus*. We conducted molecular phylogenetic analyses to estimate the intra- and interspecific phylogenetic relationships among Japanese *Dasycerus* species.

# Materials and methods

Specimens studied in this paper are deposited in the Kyushu University Museum, Fukuoka (KUM), the Laboratory of Systematic Entomology, Hokkaido University, Sapporo (SEHU), Ehime University Museum, Matsuyama (EUM), the Natural History Museum and Institute, Chiba (Zoology, Insecta) (CBM-ZI), Hiwa Museum of Natural Science, Shôbara (HIWA), Shinji Sugimoto's private collection, Kawanishi (pcSS), and Tateo Ito's private collection, Yawata (pcTI). The holotype of the new species is deposited in CBM-ZI. Some specimens are preserved in absolute ethanol. The label data of the holotypes are quoted verbatim. Label data are verbatim cited into double quotation marks ("") for the holotype; a slash (/) was used to separate lines on the same label, and a double slash (//) was used to separate different labels on the same pin.

Dissected parts were soaked in a 10% KOH solution and then warmed in hot water until the muscles and other tissues were dissolved and suitable for observation. Later, they were sealed in Euparal and preserved on a glass plate, following Maruyama (2004). Female copulatory organs were stained with Chlorazol black E staining solution for observation.

The morphological observations were conducted using Olympus SZ40, Olympus SZX10, and Nikon ECLIPSE Ci-L microscopes.

The habitus photos were taken by a Canon MP-E65 mm  $1-5 \times$ macro lens mounted on a Sony  $\alpha$  7R IV digital camera. The photos of the detailed parts were taken by a Canon EOS KissX8i camera attached to an Olympus BX50 microscope. These photos ware combined by the Zerene Stacker (Zerene System LLC) software. Line drawings were made using a Nikon ECLIPSE Ci-L microscope fitted with a Nikon Y-IDT drawing tube and the Inkscape 1.1 software. Figures were edited using the GIMP 2. 8. 22 software. The specimens were also examined with a scanning electron microscope (SEM: HITACHI SU3500) at the Center for Advanced Instrumental and Educational Supports, Faculty of Agriculture, Kyushu University. The specimens for scanning electron microscope were sputter-coated with gold. The morphological terminology mainly follows Hu & Liang (2021).

The following abbreviations were applied: BL—apex of frontoclypeus to end of elytron; HL—apex of frontoclypeus to nuchal ridge; HW—maximum width of head; EL—maximum length of eye; PL—maximum length of pronotum; PW—maximum width of pronotum. All measurements are in millimeters and are reported in the format "mean (minimum-maximum)".

**DNA analysis.** Thirteen individuals of *Dasycerus* collected from Japan were used for DNA extraction. DNA was extracted from the whole body of each specimen using the DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's protocol. We amplified a region of the mitochondrial COI gene using the primer set C1-J-2183 (Jerry) + L2-N-3014 (Pat) (Simon *et al.* 1994) with the following PCR protocol: 98 °C for 3 mins,  $35 \times (98 °C$  for 10 secs, 48 °C for 5 secs, 68 °C for 5 secs), 68 °C for 3 mins. The sequences of the outgroup, *D. angulicollis* Horn, 1882 (Genbank accession number: MK834425), *D. bicolor* Wheeler & McHugh, 1994 (Genbank accession number: MK834419), *D. carolinensis* Horn, 1882 (Genbank accession number: MK834384) (Caterino & Langton-Myers 2019), were obtained from GenBank and added to our data. The alignment of the sequences was carried out with MAFFT v7.222 (Katoh & Sandley 2013) using the accurate alignment method L-INS-i. Pairwise sequence distances were calculated using MEGA-X 10.2.6 (Kumar *et al.* 2018) with the Kimura 2-parameter model (K2P). We carried out a maximum likelihood (ML) analysis, and model selection was conducted based on the Bayesian Information Criterion (BIC) using Kakusan 4 (Tanabe 2011). Maximum likelihood trees were created using RAxML 8.2.12 (Stamatakis 2014), and bootstrap values were calculated with 1000 replicates. The sequences were registered in GenBank.

# Results

# Taxonomy

Dasycerus occultus Hashizume & Maruyama sp. nov.

(Fig. 1) [Japanese name: Yotsumon-itohige-nisemakimushi]

Dasycerus japonicus: Löbl & Calame, 1996: 278 (in part).

**Specimen examined. Type series.** Holotype: male (CBM-ZI), JAPAN: Honshu: "Honzawa Rindo / Sakamoto / Kamogawa-shi / Chiba Pref., 18.VI.2020 / Akiko Saito leg. // CBM-ZI / 224407 // HOLOTYPE / *Dasycerus / occultus* sp. n / det. Hashizume & Maruyama 2022" (recorded as *Dasycerus japonicus* in Saitô & Murakawa (2020)). Paratypes: **Honshu**: Chiba-ken: 8 exs., same data as holotype. (CBM-ZI: 224405–224406, 224408–224413) (recorded as *D. japonicus* in Saitô & Murakawa (2020)); Aichi-ken: 1 ex., Mennoki-tôge, Toyota-shi, 2 V 1989, N. Kanie leg. (KUM); 1 ex., alt. 930 m, Dandouradani, Tamine, Shitara-chô, 7 VIII 2020, F. Nakano leg. (KUM); Tottori-ken: 1 ex., Dai-sen, 6 VII 2008, I. Tanaka leg. (KUM); **Kyushu**: Fukuoka-ken: 2 exs., Shaka-dake, Yabemura, Yame-shi, 23 VI 2017, S. Imasaka leg. (KUM); 1 ex., same data, but 26 VII 2017 (KUM); Saga-ken: 7 exs., Hiroseyama - Kô, Arita-chô, 29 V 2021, T. Hashizume leg. (KUM); 2 exs., Kurokami-yama, Takeo-shi, 21

IX 2016, M. Nishida leg. (KUM); 1 ex., Kurokami-yama, Arita-chô, 5 V 2016, M. Nishida leg. (KUM); 2 exs., Kurokami-yama, Arita-chô, 29 V 2021, Y. Hisasue leg. (KUM);1 ex., Tôsen-zan, Ureshino-shi, 26 V 2016, M. Nishida leg. (KUM); 2 exs., same data, but 13 VII 2017 (KUM); Nagasaki-ken: 2 exs., Unzen-dake, 24 X 1978, S. Imasaka leg. (KUM); 1 ex., Gokahara-dake, Tara-dake, 11 VII 1978, S. Imasaka leg. (KUM); 2 exs., Ônobaru-kôgen, Higashisonogi-chô, 17 XI 2002, M. Nishida leg. (KUM); 1 ex., same data, but 7 XII 2002 (KUM); Ôita-ken: 4 exs., Shaka-dake, Maetsue, Hita-shi, 23 VI 2017, S. Imasaka leg. (KUM); 2 exs., same data, but 14 VII 2017 (KUM); 2 exs., same data, but 2 VIII 2017 (KUM); 3 exs., same data, but 23 VIII 2017 (KUM); 2 exs., same data, but 14 VII 2017 (KUM); 1 ex., same data, but 10 VII 2018 (KUM); 1 ex., same data, but 21 VII 2018 (KUM); 1 ex., same data, but 11 VIII 2018 (KUM); 1 ex., same data, but 11 VIII 2018 (KUM); 1 ex., same data, but 11 VIII 2018 (KUM); 1 ex., same data, but 10 VII 2018 (KUM); 1 ex., same data, but 21 VII 2015, T. Miyake leg. (KUM); Miyazaki-ken: 6 exs., alt. 385 m, Miike, Natsuo-chô, Miyakonojô-shi, 17 VIII 2019, F. Nakano leg. (KUM); 1 ex., Gokasho, Takachiho-chô, 25 VII 2020, T. Hashizume leg. (KUM); Kagoshima-ken: 2 exs., Maruo Scenic Nature Path, Makizono, Kirishima-shi, 9–10 X 2021, N. Tsuji & T. Nozaki leg. (KUM); 1 ex., Izashiki, Sata, Minamiôsumi-chô, 22 VI 2021, S. Inoue leg. (KUM); 1 ex., Teuchi, Shimokoshiki-shima, Satsumasendai-shi, 22 VII 2020, R. Ito leg. (KUM); 1 ex., Shimokoshiki-shima, Satsumasendai-shi, 25 VII 2020, R. Ito leg. (KUM);

**Diagnosis.** This species is similar to *D. fasciatus* Löbl, 1977 from India. However, this species can be distinguished from *D. fasciatus* by its larger body, and by the shape of the median lobe of the aedeagus. The number of rows of punctures between first and second internal discal costae is also different (*D. occultus* **sp. nov.** with two rows of punctures; *D. fasciatus* with two rows of punctures and additional short row). In contrast to another Japanese species, *D. japonicus*, *D. occultus* **sp. nov.** has two pairs of dark brown spots on their elytra, and the female genital chamber of *D. occultus* **sp. nov.** (Fig. 1H) is weakly sclerotized and has a number of fine spines on its surface. The median groove of the pronotum is relatively long (*D. occultus* **sp. nov.**: 0.52–0.54 times as long as pronotum; *D. japonicus*: 0.42–0.43 times as long as pronotum) (Fig. 1B). The punctures of elytron are relatively large and circular (Fig. 1F).

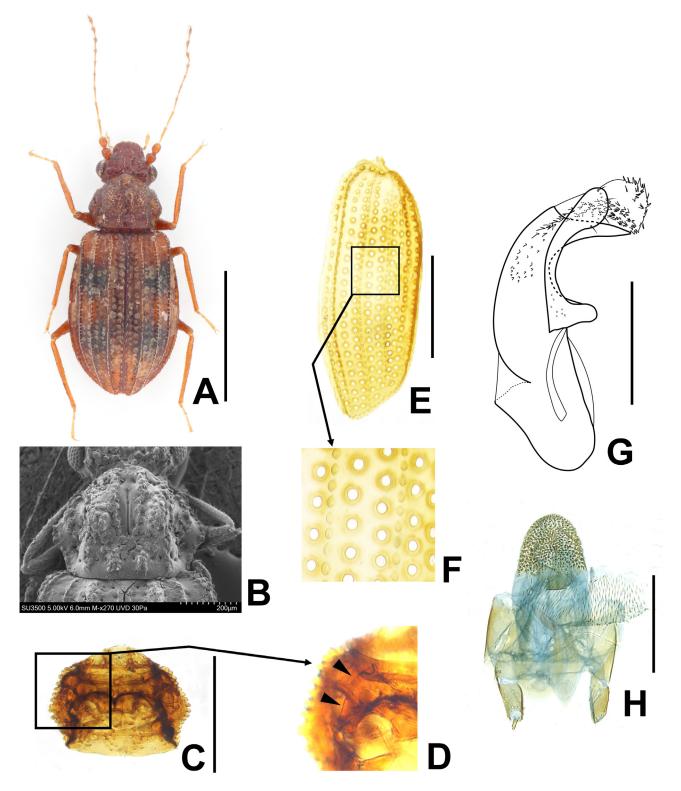
**Description.** Measurements. (n=8): BL: 1.82 (1.72–1.92); HL: 0.34 (0.33–0.36); HW: 0.46 (0.45–0.48); EL: 0.14 (0.13–0.14); PL: 0.42 (0.41–0.44); PW: 0.56 (0.54–0.58).

Coloration. Body, legs, and antennae reddish brown, with two pairs of dark brown spots on elytra.

Head. Apex of frontoclypeus arcuate; vertexal grooves indistinct; pair of rows of tubercles present on mesal vertex extending to frontoclypeus, each row with 8–9 tubercles each with one microseta on apex; group of tubercles present on external margin of frontoclypeus beside the mesal vertex row of tubercles on each side. Antenna 11-segmented, inserted above anterior part of eye; long and slender, sparsely setose on antennomeres III–VII, densely setose on antennomeres I–II and VIII–XI; antennomere I and II globular, enlarged, with dorsal setiferous tubercles; antennomere II slightly smaller than I; antennomeres III–VII extremely slender, filiform, slightly dilated at the apex; antennomeres VIII–XI globular; antennomere XI wider than all other antennomeres. Eyes large; eye pedestal present.

Thorax. Pronotum hexagonal (Fig. 1B), with rows of tubercles on the lateral margin and disc, each tubercle with one microseta on apex. Apicolateral angle distinct, not prominent. Disc with a pair of swellings in front of antebasal transverse groove. Median groove distinct, 0.52-0.54 times as long as length of pronotum, extending from antebasal transverse groove. Oblique tubercle row absent. Lateral tubercle row parallel to margin. Middle of antebasal transverse groove strongly arcuate; basal area with five groups of irregular foveae separated by tubercles. Hypomeron with anterior transverse groove. Protergosternal keel entire (Fig. 1D). Keel of procoxal process weekly arcuate; some prosternal foveae on prosternum of each side. Elytra rounded laterally and posterolaterally, widest near middle, covering whole abdomen; rows of microsetae along sutural margin and costae; elytra humeral area rounded and raised. Elytral disc with three costae on each elytron, two internal discal costae extending from base to apex of elytron; one external discal costa shorter than internal discal costae, extending from base to 4/5 point of elytron; posterior-lateral margin of elytron with few tubercles which are similar to those on costae. Each elytron with ten rows of circular punctures (Fig. 1E): two rows between sutural margin and first internal discal costa; two rows between first and second internal discal costae; two rows between second and external discal costae; three rows between external discal costa and the edge of elytron (punctures strongly reduced on humeral area, the three rows gradually fused to one toward apex), and one row between marginal costa and margin of elytron. Each discal row with 20–28 punctures; rows 1–4 each with about 26 punctures, rows 5–10 with fewer. Hind wings well developed. Scutellum glossy, oblique. Mesoventral median keel extending from anterior margin of prepectus to apex of internal process. Prepectus as long as distance from its posterior margin to procoxae. Posterior margin of mesovaxal cavity with a distinct projection on each side.

Abdomen gradually narrowed apically, not visible in dorsal view. Abdominal tergites V–VIII sclerotized, IV– VI with median furrows. Sternite III with three pairs of coxal foveae and five pairs of microsetae on basal margin; intercoxal process depressed at anterior end.



**FIGURE 1.** *Dasycerus occultus* **sp. nov.** (A) Habitus in dorsal view. (B) SEM image of pronotum in dorsal view. (C–D) Prothorax in ventral view (black triangles indicate the protergosternal keel). (E–F) Right elytron in dorsolateral view. (G) Aedeagus in lateral view. (H) Female genital chamber in ventral view. Scale bars: 1.0 mm for A; 0.5 mm for C & E; 0.2 mm for G–H.

Male. Aedeagus (Fig. 1G) symmetrical. Median lobe with basal bulb moderately large, about as long as apical portion. Apical portion strongly arcuate. Paramere weakly arcuate, narrow in middle, widened at apex; base of paramere triangular; four setae on apex of apex of each paramere.

Female. Female genital chamber (Fig. 1H) weakly sclerotized and has a number of fine spines on its surface. Distal gonocoxite has about 10 preapical setae. Gonostylus has one seta slightly shorter than gonostylus at the apex and shorter preapical setae.

**Bionomics.** They appeared to be feed on fruiting bodies of basidiomcetous fungi that arose on the surfaces of dead trees.

Distribution. Japan (Honshu, Kyushu (incl. Shimo-Koshiki-shima)).

**Etymology.** The epithet of this new species is derived from the Latin adjective "*occultus*", which means "hidden", because this species was previously confused with *D. japonicus*.

**Remarks.** Löbl & Calame (1996) redescribed "*D. japonicus*" based on the paratype and additional specimens in the revision of *Dasycerus* but illustrated the male genitalia of this species. Because it was initially believed that there was only one species of *D. japonicus* in Japan, all previous records of *D. japonicus* should be reviewed. This species has been collected from lowland laurel forest to the montane zone at elevations of up to 1,200 m.

# Dasycerus japonicus Nakane, 1963

(Figs 2–3) [Japanese name: Itohige-nisemakimushi]

Dasycerus japonicus Nakane, 1963 (original description; type locality: Sasayama, Hyogo): 22; Löbl, 1977: 103 (key); Löbl & Calame, 1996: 278 (in part); Hu & Liang, 2021: 251 (key).

# **Specimen examined.** Type specimen. Holotype: male, "Sasayama / Hyogo Pref. / 28. IV. 1952 / T. Nakane // HOLOTYPE // *Dasycerus / japonicus* Nak. / Det. T. Nakane // NAKANE Coll. / SEHU JAPAN / 1999 // 0000005404 / Sys. Ent / Hokkaido Univ. / Japan [SEHU]"

Additional specimens. Hokkaido: 1 ex., alt. 175 m, Atsuta, Yakumo-chô, 24 VIII 2017, H. Kamezawa leg. (KUM); 1 ex., Toyama, Minami-ku, Sapporo-shi, 18 VII 2021, Y. Tasaku leg. (KUM); Honshu: Fukushima-ken: 1 ex., Near Toriki-bashi, Suketsune-rindô, Minamisôma-shi, 23 V 1999, K. Haga leg. (KUM); 1 ex., Ôtakine-yama-Sendaihira, Tamura-shi, 13 VI 2004, K. Haga leg. (KUM); Saitama-ken: 1 ex., Yamatomizu, Fûppu, Kamafuseyama, Yorii-machi, 6 VI 2009, K. & S. Arai leg. (KUM) (recorded in Arai (2009)); 3 exs., same data, but 20 VI 2009 (KUM) (recorded in Arai (2009)); Tôkyô-to: 2 exs., alt. 340 m, Mahikizawa-tôge, Ôguno, Hinode-machi, 27 V 2017, H. Kamezawa leg. (KUM); Kanagawa-ken: 1 ex., Uenomaru, Tanzawa-sanchi, 6 VII 1980, M. Nishikawa leg. (KUM); Niigata-ken: 6 exs., Bijinbayashi, Matsunoyama, Tôkamachi-shi, 21 VII 2014, J. Itô leg. (KUM);1 ex., alt. 300 m, Aoneba-keikoku, Sado-ga-shima, Sado-shi, 22 IX 2020, Y. Senda leg. (HIWA); Yamanashi-ken: 1 ex., alt. 1380 m, Sakubadaira, Ichinose-gawa, Hontani, Kôshû-shi, 13–19 X 1999, R. B. Kuranishi leg. (CBM-ZI: 180201); Nagano-ken: 1 ex., Nagawa-Kawaura, Matsumoto-shi, 15 VIII 2020, T. Hashizume leg. (KUM); 5 exs., same data, but 30 VI 2021 (KUM); 2 exs., Agematsu, Agematsu-machi, 18 VII 2016, F. Nakano leg. (KUM); 1 ex., Shirabisokôgen, Iida-shi, 25 VIII 2019, N. Kanie leg. (KUM); Gifu-ken: 2 exs., alt. 850 m, North side of Daihachigagawa, Öjima-machi, Takayama-shi, 1 VIII 2003, H. Kamezawa leg. (KUM); 1 ex., alt. 1530 m, Sengendaru-zawa, Hiwada, Takane-machi, Takayama-shi, 24 VII 2016, F. Nakano leg. (KUM); 1 ex., Sengendaru-zawa, Hiwada, Takane-machi, Takayama-shi, 15 VII 2018, F. Nakano leg. (KUM); 1 ex., Hagiwara, Inatsu-chô, Mizunami-shi, 16 VII 2016, F. Nakano leg. (KUM); 4 exs., same data, but 20 VII 2016 (KUM); 8 exs., same data, but 24 VII 2016, (KUM); 22 exs., same data, but 29 VII 2016 (KUM); 7 exs., Washimi, Takasu-chô, Gujô-shi, 29 IX 2019, F. Nakano leg. (KUM); 1 ex., Hirono, Shirakawa-chô, 10 X 2016, Y. Takai leg. (KUM); Aichi-ken: 1 ex., alt. 590 m, Rokushosan, Asahi-yama, Sakaue-chô, Toyota-shi, 5 V 2018, R. Wakimura leg. (KUM); 1 ex., alt. 610 m, Rokusho-san, Sakaue-chô, Toyota-shi, 27 V 2017, F. Nakano leg. (KUM); 3 exs., Iyama, Inabuchô, Toyota-shi, 26 VIII 2020, T. Ôno leg. (KUM); 2 exs., Tamine, Shitara-chô, 16-17 VIII 2019, T. Ôno leg. (KUM); 4 exs., Ishiharachô, Okazakishi, 27 X 2019, T. Ôno leg. (KUM); Mie-ken: 1 ex., Tonaio-rindô, Fujiwara-chô, Inabe-shi, 24 V 2009, N. Tsuji leg. (KUM); 18 exs., Sakura-tôge, Marubashira, Iga-shi, 10 VI 2017, N. Narukawa leg. (KUM); Kyôto-fu: 1 ex., Tennô-zan, Ôyamazaki-chô, 21 X 2011, I. Tanaka leg. (KUM); Ôsaka-fu: 1 ex., Mi-yama, Tennô, Nose-chô, 14 IX 2008, I. Tanaka leg. (KUM); 2 exs., Mi-yama, Tennô, Nose-chô, 30 XI 2008, I. Tanaka leg. (KUM); Satsuki-yama,

Higashiyama-chô, Ikeda-shi, 16 IX 2019, T. Saito leg. (KUM); Hyôgo-ken: 4 exs., Ôya-san, Inagawa-chô, 30 VIII 2018, S. Sugimoto leg. (pcSS); 1 ex., Iwane-yama, Sashikumi, Inagawa-chô, 31 X 2018, T. Saito leg. (KUM); 2 exs., Iwane-san, Sashikumi, Inagawa-chô, 21 XI 2018, T. Saito leg. (KUM); 1 ex., Iwane-yama, Akamatsu, Kawanishishi, 22 XI 2018, T. Saito leg. (KUM); 2 exs., Iwane-yama, Kawanishi-shi, 21 XI 2018, T. Ito leg. (pcTI); 2 exs., 890 m, Ôsasa, Muraoka-ku, Kami-chô, 22 VIII 2017, R. Wakimura leg. (KUM); Nara-ken: 1 ex., Ôdaigahara-yama, Kamikitayama-mura, 15 VII 2018, N. Kanie leg. (KUM); 16 exs., Yumitehara, Nosegawa-mura, 19 IX 2021, F. Nakano leg. (KUM); Okayama-ken: 4 exs., Sangajô, Kamisaibara, Kagamino-chô, 27 VII 2014, O. Yamaji leg. (KUM); Hiroshima-ken: 2 exs., Chichikino, Jinsekikôgen-chô, 1 XI 2019, Y. Akiyama leg. (HIWA) (recorded in Akiyama (2020)); Shikoku: Tokushima-ken: 1 ex., Tsurugi-san, 3 V 1969, Y. Nameta leg. (KUM); 11 exs., alt. 1800 m, Tsurugi-san, Tsurugi-chô, 22 VII 2007, M. Sakai leg. (EUM); Kagawa-ken: 1 ex., alt. 600 m, Kosen-zan, Miki-chô, 25 IX 2021, H. Fujimoto leg. (KUM); 1 ex., alt. 960 m, Daisen-zan, Mannô-chô, 19 IX 2021, H. Fujimoto leg. (KUM); 1 ex., same data, but 3 X 2021 (KUM); Ehime-ken: 4 exs., Yoshinogawa, Oda-chô, 10 IX 1993, M. Kawanabe leg. (EUM); 2 exs., Odamiyama, Uchiko-chô, 31 VII 2009, E. Yamamoto leg. (EUM); 5 exs., same data, but 4 VIII 2009 (EUM); 9 exs., same data, but 17 VIII 2009 (EUM); Kyushu: Fukuoka-ken: 1 ex., Shaka-dake, Yabemura, Yame-shi, 22 VI 2018, S. Imasaka leg. (KUM); 1 ex., Hôman-zan–Sangun-san, 27 VI 2014, N. Tsuji leg. (KUM); 6 exs., Hiko-san, 6 VI 2021, S. Inoue leg. (KUM); Saga-ken: 1 ex., Haramaki, Sefuri-machi, Kanzaki-shi, 19 VII 2019, T. Hashizume leg. (KUM); Kumamoto-ken: 5 exs., Momigi, Izumi-machi, Yatsushiro-shi, 15 V 2021, T. Hashizume leg. (KUM); 11 exs., alt. 1230 m, Shiratori-yama, Momigi, Izumi-machi, Yatsushiro-shi, 29 V 2021, S. Kakizoe & S. Inoue leg. (KUM); Ôita-ken: 1 ex., Senomoto, Kokonoe-machi, 7 V 2015, T. Miyake leg. (KUM); 3 exs., Kawakami-keikoku, Obira, Ogata-machi, Bungoôno-shi, 27 V 2015, T. Miyake leg. (KUM); 2 exs., Shônaichô-Asono, Yufu-shi, 7 VII 2019, T. Hashizume leg. (KUM); 4 exs., same data, but 20 VI 2021 (KUM); 1 ex., Oike (foot of Kuro-dake), Shônai, Yufu-shi, 11 IX 2021, N. Tsuji leg. (KUM); Miyazaki-ken: 1 ex., Ômoridake-rindô, Aya-chô, 2 V 2019, Y. Sasaoka leg. (KUM).

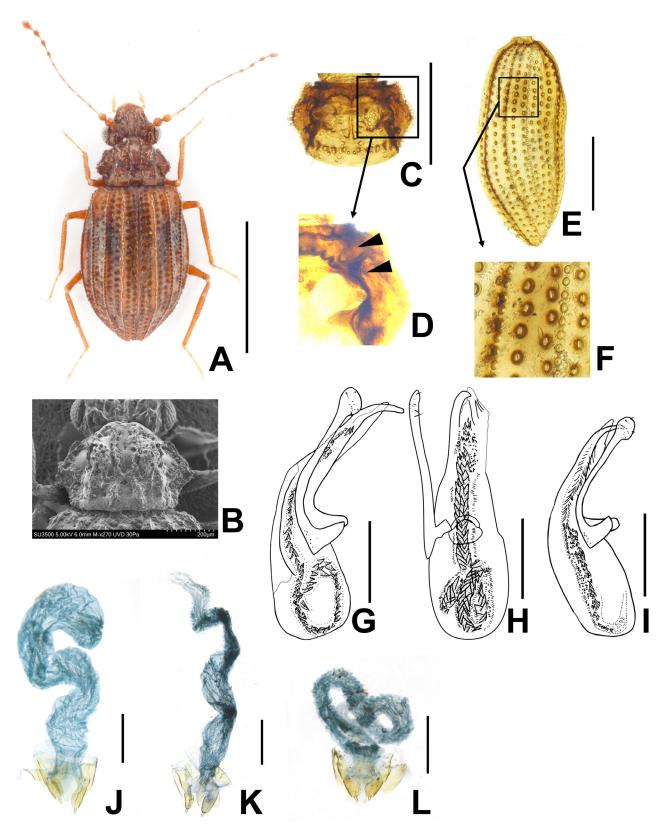
**Diagnosis.** This species is closely related to *D. poseidon* Hu & Liang, 2021 from Taiwan. However, this species can be easily distinguished from *D. poseidon* by its larger body, curved median lobe of aedeagus and more dilated apical portion of paramere. In contrast to *D. occultus* **sp. nov.**, *D. japonicus* has a pair of indistinct dark brown spots on their elytra, and the female genital chamber of *D. japonicus* (Figs 2J–L) is not sclerotized and does not have fine spines on its surface. The punctures of the elytron are relatively small and roughly ovoid (Fig. 2F). The median groove of the pronotum of this species is longer than that of *D. poseidon* and shorter than that of *D. occultus* **sp. nov.** (*D. japonicus*: 0.42–0.43 times as long as pronotum; *D. occultus* **sp. nov.**: 0.52–0.54 times as long as pronotum; *D. poseidon*: 0.36–0.40 times as long as pronotum) (Fig. 2B).

**Redescription.** Measurements (n=9): BL: 1.87 (1.52–2.08); HL: 0.33 (0.30–0.37); HW: 0.48 (0.43–0.51); EL: 0.14 (0.12–0.16); PL: 0.41 (0.38–0.46); PW: 0.60 (0.51–0.65).

Coloration. Body, legs, and antennae yellowish brown, with a pair of indistinct dark brown spots on elytra.

Head. Apex of frontoclypeus arcuate; vertexal grooves indistinct; pair of rows of tubercles present on mesal vertex extending to frontoclypeus, each row with 8–9 tubercles each with one microseta on apex; group of tubercles present on external margin of frontoclypeus beside the mesal vertex row of tubercles on each side. Antenna 11-segmented, inserted above anterior part of eye; long and slender, sparsely setose on antennomeres III–VII, densely setose on antennomeres I–II and VIII–XI; antennomere I and II globular, enlarged, with dorsal setiferous tubercles; antennomere II slightly smaller than I; antennomeres III–VII extremely slender, filiform, slightly dilated at the apex; antennomeres VIII–XI globular; antennomere XI wider than all other antennomeres. Eyes large; eye pedestal present.

Thorax. Pronotum hexagonal (Fig. 2B), with rows of tubercles on the lateral margin and disc, each tubercle with one microseta on apex. Apicolateral angle distinct, not prominent. Disc with a pair of swellings in front of antebasal transverse groove. Median groove distinct, 0.42–0.43 times as long as length of pronotum, extending from antebasal transverse groove. Oblique tubercle row absent. Lateral tubercle row parallel to margin. Middle of antebasal transverse groove strongly arcuate; basal area with five groups of irregular foveae separated by tubercles. Hypomeron with anterior transverse groove. Protergosternal keel entire (Fig. 2D). Keel of procoxal process weekly arcuate; some prosternal foveae on prosternum of each side. Elytra rounded laterally and posterolaterally, widest near middle, covering whole abdomen; rows of microsetae along sutural margin and costae; elytra humeral area rounded and raised. Elytral disc with three costae on each elytron, two internal discal costae extending from base to 4/5 point of elytron; one external discal costa shorter than internal discal costae, extending from base to 4/5 point of elytron;



**FIGURE 2.** *Dasycerus japonicus*. (A) Habitus in dorsal view. (B) SEM image of pronotum in dorsal view. (C–D) Prothorax in ventral view (black triangles indicate the protergosternal keel). (E–F) Right elytron in dorsolateral view. (G) Aedeagus of *D. japonicus* from Nagano-ken in lateral view. (H) Ditto in ventral view (paramere omitted on one side). (I) Aedeagus of *D. japonicus* from Saga-ken in lateral view. (J) Unraveled female genital chamber of *D. japonicus* from Gifu-ken in ventral view. (K) Unraveled female genital chamber of *D. japonicus* from Kumamoto-ken in ventral view. (L) Not unraveled female genital chamber of *D. japonicus* from Fukuoka-ken in dorsal view. Scale bars: 1.0 mm for A; 0.5 mm for C & E; 0.2 mm for G–L.

posterior-lateral margin of elytron with few tubercles which are similar to those on costae. Each elytron with ten rows of roughly ovoid punctures (Fig. 2E): two rows between sutural margin and first internal discal costa; two rows between first and second internal discal costae; two rows between second and external discal costae; three rows between external discal costa and the edge of elytron (punctures strongly reduced on humeral area, the three rows gradually fused to one toward apex), and one row between marginal costa and margin of elytron. Each discal row with 21–35 punctures; rows 1–4 each with about 30 punctures, rows 5–10 with fewer. Hind wings well developed. Scutellum glossy, oblique. Mesoventral median keel extending from anterior margin of prepectus to apex of internal process. Prepectus somewhat longer than distance from its posterior margin to procoxae. Posterior margin of mesovaxal cavity with a distinct projection on each side.

Abdomen gradually narrowed apically, not visible in dorsal view. Abdominal tergites V–VIII sclerotized, IV– VI with median furrows. Sternite III with three pairs of coxal foveae and five pairs of microsetae on basal margin; intercoxal process depressed at anterior end.

Male. Aedeagus (Figs 2G–I) asymmetrical. Median lobe with basal bulb relatively small. Paramere arcuate, widened apically; base of paramere triangular; four setae on apex of each paramere.

Female. Female genital chamber (Figs 2J–L) membranous and long, without spines on surface. Distal gonocoxite has about 10 preapical setae. Gonostylus has one seta as long as gonostylus at the apex and shorter preapical setae. **Bionomics.** Many individuals were obtained from the surface of dead trees.

**Distribution.** Japan (Hokkaido, Honshu (incl. Sado-ga-shima), Shikoku, Kyushu).

**Remarks.** This species is collected at higher latitudes and elevations than those of *D. occultus* **sp. nov.** The number of punctures of each row of the elytron varies depending on the size of the individual. In large females, the apex of the elytron is slightly elongated.



FIGURE 3. Holotype and labels of *Dasycerus japonicus* (photographed by Y. Tasaku).

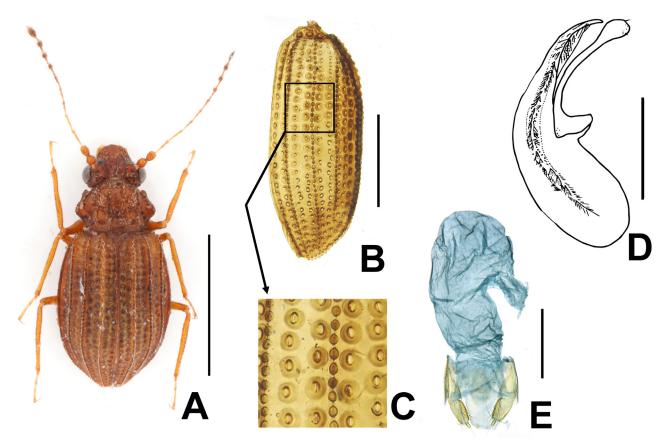
# Dasycerus sp.

(Fig. 4)

**Specimen examined.** Kyushu: Kagoshima-ken: 2 exs., Hetsuka, Sata, Minamiôsumi-chô, 29 V–5 VI 2021, R. Ito leg. (KUM); 1 ex., alt. 420 m, Hoyoshi-dake, Ushiroda, Kimotsuki-chô, 30 IV 2021, F. Nakano leg. (KUM); 3 exs., same data, but 16 VIII 2019 (KUM); 3 exs., same data, but 17 VIII 2019 (KUM); 2 exs., same data, but 30 IV 2021 (KUM); 2 exs., alt. 245 m, Hoyoshi-dake, Kitakata, Kimotsuki-chô, 30 IV 2021, F. Nakano leg. (KUM);1 ex., Inao-dake, 22 VI 2021, S. Inoue leg. (KUM).

Distribution. Japan (Kyushu: Ôsumi Peninsula).

**Remarks.** It is almost identical in appearance to *D. japonicus* but is smaller and lacks dark spots on the elytra. It also differs in the shape of the female genital chamber (Fig. 4E). As described below, we have not yet determined the name of this population. This population was found only on the Ôsumi Peninsula and was collected at a relatively low elevation compared with *D. japonicus*.



**FIGURE 4.** *Dasycerus* sp. from Ôsumi Peninsula, Kagoshima-ken. (A) Habitus in dorsal view. (B–C) Right elytron in dorsolateral view. (D) Aedeagus in lateral view. (E) Female genital chamber in ventral view. Scale bars: 1.0 mm for A; 0.5 mm for B; 0.2 mm for D–E.

# Dasycerus species from Taiwan

# *Dasycerus poseidon* Hu & Liang, 2021 (Fig. 5)

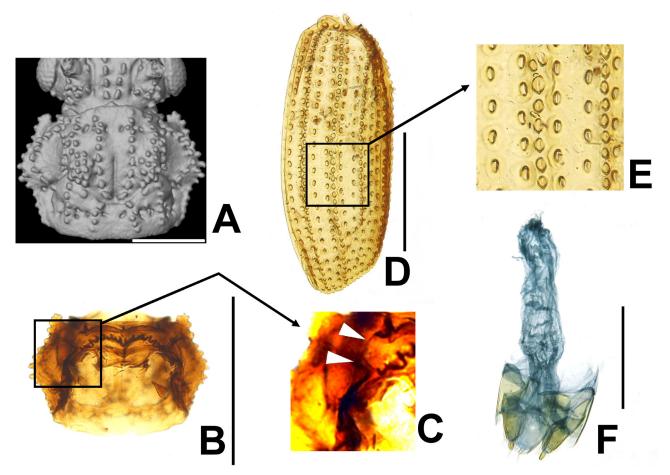
Dasycerus poseidon Hu & Liang, 2021: 244 (original description; type locality: Taiwan, Nantou County, Guando Mt. (關刀山), Puli To., 24.0217, 121.0103, ca. 1582 m,).

**Specimen examined.** Taiwan: Nantou County: 5 exs., Guando Mt., 8 VII 2021, Y.-H. Ho leg. (KUM). 4+ exs., alt. 1800 m, Nandongyan Shan, 13 X 2015, M. Tanaka leg. (KUM).

Additional description. Female genital chamber (Fig. 5F) membranous and short, without spines on surface. Distal gonocoxite has about 10 preapical setae. Gonostylus has one seta as long as gonostylus at the apex and shorter preapical setae.

# Distribution. Taiwan.

**Remarks.** In the original description, this species was described as lacking a protergosternal keel (Hu & Liang, 2021), but a specimen identified as this species based on its morphological characters, including its aedeagus, had a keel visible in transmitted light (Fig. 5C). The female genital chamber (Fig. 5E) is membranous and shorter than that of *D. japonicus*. Median groove of pronotum is relatively short (0.36–0.40 times as long as pronotum) [Fig. 5A (modified from Hu & Liang (2021))]. Punctures of the elytron are relatively small and roughly ovoid (Fig. 5E).



**FIGURE 5.** *Dasycerus poseidon.* (A) Pronotum in dorsal view (modified from Hu & Liang (2021)). (B–C) Prothorax in ventral view (white triangles indicate the protergosternal keel). (D–E) Right elytron in dorsolateral view. (F) Female genital chamber in ventral view. Scale bars: 0.2 mm for A & F; 0.5 mm for B & D.

# Phylogeny

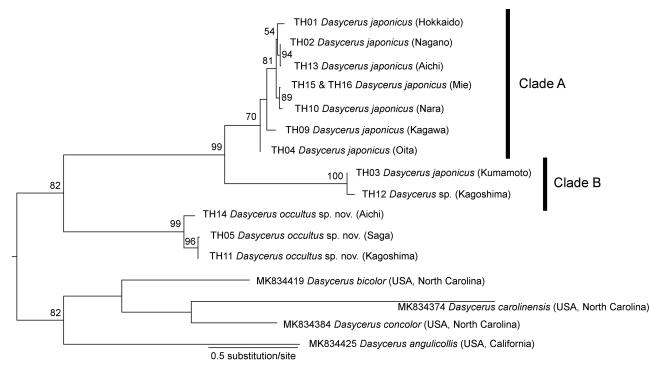
The maximum likelihood phylogenetic tree confirmed the monophyly of the two species with high bootstrap values (Fig. 6).

The genetic distance between the clade including *D. japonicus* and *D. occultus* **sp. nov.** was 12.3–14.7% (Table 1). Two major clades were identified in the clade including *D. japonicus*: a clade consisting of individuals from the Ôsumi Peninsula (TH12) and Kumamoto Prefecture (TH03) (Clade B) and one consisting of other individuals (Clade A). The clades from the Ôsumi Peninsula and Kumamoto were 9.2–9.9% and 9.4–10.3% apart, respectively, from those in Clade A (Table 1). However, the morphology of the Kumamoto specimens differed from that of the Ôsumi Peninsula specimens and was similar to that of the Clade A specimens. The genetic distance between the two specimens in Clade B was small (1.8%) despite the great difference in morphology.

Two *D. japonicus* samples collected at the same location (TH15 and TH16) were sequenced and showed 0% difference in nucleotide sequence.

IAB	<b>IABLE 1.</b> Intraspecific and interspecific pairwise KZP distances in	se NZP ai	stances 1	n the Jei	the Jerry-Pat CUI DINA region		v region.									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	TH01 Dasycerus japonicus (Hokkaido)															
2	TH02 Dasycerus japonicus (Nagano)	0.021														
3	TH13 Dasycerus japonicus (Aichi)	0.023	0.003													
4	TH10 Dasycerus japonicus (Nara)	0.026	0.028	0.028												
5	TH15 & TH16 Dasycerus japonicus (Mie)	0.025	0.021	0.021	0.010											
9	TH09 Dasycerus japonicus (Kagawa)	0.041	0.036	0.036	0.041	0.039										
7	TH04 Dasycerus japonicus (Ôita)	0.045	0.040	0.040	0.041	0.039	0.031									
8	TH03 Dasycerus japonicus (Kumamoto)	0.099	0.098	0.100	0.103	0.102	0.094	0.100								
6	TH12 Dasycerus sp. (Kagoshima)	0.095	0.092	0.094	0.099	0.097	0.095	0.095	0.018							
10	TH14 Dasycerus occultus sp. nov. (Aichi)	0.123	0.125	0.128	0.126	0.126	0.130	0.138	0.136	0.136						
11	TH05 Dasycerus occultus sp. nov. (Saga)	0.133	0.135	0.138	0.136	0.133	0.140	0.140	0.144	0.142	0.033					
12	TH11 Dasycerus occultus sp. nov.	0.133	0.135	0.138	0.136	0.133	0.140	0.140	0.147	0.146	0.032	0.004				
	(Kagoshima)															
13	MK834419 Dasycerus bicolor (USA, North Carolina)	0.153	0.152	0.154	0.147	0.141	0.139	0.156	0.144	0.141	0.143	0.143	0.143			
14	MK 834384 Dasycerus conclor (USA, North Carolina)	0.176	0.172	0.172	0.171	0.166	0.162	0.175	0.168	0.171	0.133	0.146	0.148	0.166		
15	MK834374 Dasycerus carolinensis (USA, North Carolina)	0.157	0.162	0.164	0.152	0.156	0.161	0.168	0.176	0.173	0.149	0.156	0.156	0.153	0.174	
16	MK834425 Dasycerus angulicollis (USA, California)	0.157	0.156	0.157	0.159	0.156	0.161	0.159	0.155	0.149	0.126	0.129	0.129	0.115	0.150	0.136

TABLE 1. Intraspecific and interspecific pairwise K2P distances in the Jerry–Pat COI DNA region.



**FIGURE 6.** Maximum likelihood tree based on the COI sequences. Branch lengths are proportional to maximum likelihood estimated genetic distances. Numbers associated with branches indicate bootstrap values higher than 50%. Within sample names, species names and collecting site are followed by each sample ID.

# Discussion

Two Japanese *Dasycerus* species, *D. japonicus* and *D. occultus* **sp. nov.**, were identified, and unidentified individuals were found. Löbl & Calame (1996) stated that specimens of this genus have been obtained from the Kuril Islands, but it is unclear to which species these specimens belong. *D. japonicus*, *D. poseidon*, and *D. occultus* **sp. nov.** are relatively closely related in that the hind wings are well developed, the 5<sup>th</sup> to 8<sup>th</sup> tergites are sclerotized, and the 4<sup>th</sup> to 6<sup>th</sup> tergites have a median groove. *D. japonicus* and *D. poseidon* share many features, such as the morphology of the male aedeagus and relatively small longitudinal punctures in the elytra, and are considered to be closely related.

*Dasycerus* species with developed hind wings (*D. fasciatus* Löbl, 1977; *D. inexspectatus* Löbl, 1986; *D. japonicus*; *D. monticola* Löbl, 1988; *D. poseidon*; *D. suthepensis* Löbl, 1988; and *D. occultus* **sp. nov.**) are all found in Asia (Löbl & Calame, 1996; Hu & Liang 2021). Additionally, these species may be closely related based on morphological information (Yin *et al.* 2020). These species may have similar ecologies.

We also observed differences in the morphology of the female copulatory organs, which were not previously used for the classification of *Dasycerus*. In *D. occultus* **sp. nov.**, the female genital chamber was weakly sclerotized and had numerous fine spines, whereas in *D. japonicus* and *D. poseidon*, they were membranous and had no spines. The details of the use of the female genital chamber are unknown, but the morphology of female genital chamber may be related to the morphology of the aedeagus. The female genital morphology, which has not been used for taxonomy in this genus, may be important for taxonomic study. It would be interesting to observe the female genital chamber in other species.

In *D. japonicus*, variations in the amount and size of the spines on the inner sac of the aedeagus were observed. For example, individuals from Sefuri-san, Saga Prefecture have fine spines (Fig. 2I); individuals from some areas have large spines throughout the entire inner sac, while individuals from other areas have large spines that disappear in the middle of the inner sac. Such intraspecific variation in the inner sac has also been observed in other staphylinid beetles (Herman 1975), and it is appropriate to consider this difference as intraspecific variation in this species as well. Regional variation in the aedeagus is also known in *D. carolinensis* Horn, 1882, which occurs in the United States (Wheeler 1984), but there was no information on the differences. The female genital chamber is very long

in *D. japonicus* but clearly short in individuals closely related to *D. japonicus* from the Ôsumi Peninsula. The Ôsumi Peninsula specimens could hardly be distinguished from *D. japonicus*, except in terms of the female genital chamber.

Molecular phylogenetic analysis suggested that *D. occultus* **sp. nov.** is monophyletic, and the genetic distance between *D. japonicus* and *D. occultus* **sp. nov.** is 12.3–14.7%. Japanese *Dasycerus* excluding *D. occultus* **sp. nov.** is divided into clades A and B. Clade B includes individuals from Kumamoto Prefecture and the Ôsumi Peninsula, which differ from each other by only 1.8% in genetic distance, but differ significantly in the morphology of their female genital chambers. The Kumamoto specimens have female genital chambers (Fig. 2K) that are elongate and bend several times in the middle like individuals in clade A, whereas all females from the Ôsumi Peninsula that we examined had female genital chambers that were short and bent only once. The Kumamoto specimen also has dark spots on the elytra, as do the Clade A specimens. Considering the morphology, specimens from Kumamoto are considered to be *D. japonicus*. There may be a discrepancy between the morphological and molecular information. This may be explained by the fact that we analyzed mitochondrial DNA, which is affected by hybridization. The Ôsumi population differs from *D. japonicus*, excluding specimens from Kumamoto, in morphology and COI sequences, so this population is considered a different species, but there is no evidence of hybridization. This problem has not been resolved, and we have not described this population as a new species at this time. Molecular phylogenetic analysis using nuclear genes is needed to investigate phylogenetic relationships within the clade containing *D. japonicus*.

Analysis using the primer set HCO + LCO (Folmer *et al.* 1994) suggests that *D. japonicus* and *D. poseidon* are closely related (Hashizume unpublished). In the future, sequencing of *D. poseidon* using the primer set C1-J-2183 (Jerry) + L2-N-3014 (Pat) (Simon *et al.* 1994) will allow us to investigate the interspecific relationships of Japanese *Dasycerus* in more detail.

# Conclusion

Two species of Japanese *Dasycerus*, *D. occultus* **sp. nov.** and *D. japonicus*, were described or redescribed. A group very closely related to *D. japonicus* was found on the Ôsumi Peninsula. *D. poseidon* distributed in Taiwan is considered to be closely related to *D. japonicus* based on its morphology.

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#### References

Akiyama, Y. (2020) Coleoptera species in Jinseki-gun (19). *Hiroshima Mushi-no-Kai Kaiho*, 59, 31–33. [in Japanese] Arai, K. (2009) Newly recorded beetles from Saitama Prefecture (16). *Yosegaki*, 134, 1–7. [in Japanese]

Cai, C., Thayer, M.K., Newton, A.F., Yin, Z. & Huang, D. (2018) A new genus of dasycerine rove beetles from Upper Cretaceous Burmese amber and its phylogenetic implications (Coleoptera, Staphylinidae). *Cretaceous Research*, 84, 431–436. https://doi.org/10.1016/j.cretres.2017.12.004

- Caterino, M.S. & Langton-Myers, S.S. (2019) Intraspecific diversity and phylogeography in Southern Appalachian *Dasycerus* carolinensis (Coleoptera: Staphylinidae: Dasycerinae). *Insect Systematics and Diversity*, 3 (6), 8, 1–12. https://doi.org/10.1093/isd/ixz022
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3 (5), 294–299.
- Herman, L.H. (1975) Revision and phylogeny of the monogeneric subfamily Pseudopsinae for the World (Staphylinidae, Coleoptera). *Bulletin of the American Museum of Natural History*, 155 (3), 242–317.
- Hu, F.-S. & Liang, W.-R. (2021) The first record of the subfamily Dasycerinae in Taiwan, with description of a new species (Coleoptera: Staphylinidae). *Zootaxa*, 4903 (2), 242–254. https://doi.org/10.11646/zootaxa.4903.2.4
- Katoh, K. & Standley, D.M. (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution*, 30 (4), 772–780. https://doi.org/10.1093/molbev/mst010
- Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35, 1547–1549. https://doi.org/10.1093/molbev/msy096
- Löbl, I. (1977) Beitrag zur Kenntnis der Gattung *Dasycerus* Brongniart (Coleoptera, Dasyceridae). *Mitteilungen der* Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse, 50, 95–106.
- Löbl, I. & Calame, F.G. (1996) Taxonomy and phylogeny of the Dasycerinae (Coleoptera: Staphylinidae). *Journal of Natural History*, 30, 247–291.

https://doi.org/10.1080/00222939600771151

Maruyama, M. (2004) A permanent slide pinned under a specimen. Elytra, 32 (2), 276.

- Nakane, T. (1963) New or little-known Coleoptera from Japan and its adjacent regions. XVII. *Fragmenta Coleopterologica*, 5, 21–22.
- Saito, A. & Murakawa, I. (2020) Additions and Corrections to "Insect Fauna of the University of Tokyo Chiba Forest" No. 5. *Boso no Konchu*, 67, 82–83. [in Japanese]
- Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87, 651–701. https://doi.org/10.1093/aesa/87.6.651
- Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30 (9), 1312–1313.

https://doi.org/10.1093/bioinformatics/btu033

Tanabe, A.S. (2011) Kakusan4 and Aminosan: two programs for comparing nonpartitioned, proportional, and separate models for combined molecular phylogenetic analyses of multilocus sequence data. *Molecular Ecology Resources*, 11 (5), 914– 921.

https://doi.org/10.1111/j.1755-0998.2011.03021.x

- Wheeler, Q. (1984) Notes on host association and habitats of Dasyceridae (Coleoptera) in the southern Appalachian Mountains. *The Coleopterists Bulletin*, 38, 227–231.
- Yamamoto, S. (2016) The first fossil of dasycerine rove beetle (Coleoptera: Staphylinidae) from Upper Cretaceous Burmese amber: Phylogenetic implications for the omaliine group subfamilies. *Cretaceous Research*, 58, 63–68. https://doi.org/10.1016/j.cretres.2015.09.022
- Yin, Z.-W., Lü, L., Yamamoto, S., Thayer, M.K., Newton, A.F. & Cai, C.-Y. (2020) Dasycerinae rove beetles: Cretaceous diversification, phylogeny and historical biogeography (Coleoptera: Staphylinidae: Dasycerinae). *Cladistics*, 37 (2), 185– 210.

https://doi.org/10.1111/cla.12430