Dtsch. Entomol. Z. 70 (1) 2023, 143–157 | DOI 10.3897/dez.70.96994

PENSOFT

für Natur MUSEUM FÜR NATURKUNDE BERLIN

The genus *Anacaena* Thomson from the Ryukyu Archipelago of Japan (Coleoptera, Hydrophilidae)

Yûsuke N. Minoshima[1], Yuuki Kamite[2], Martin Fikáček[3,4]

1 *Natural History Division, Kitakyushu Museum of Natural History and Human History, 2-4-1 Higashida, Yahatahigashi-ku, Kitakyushu-shi, Fukuoka 805-0071, Japan*

2 *Nagoya City Public Health Research Institute, 4-207 Sakurazaka, Moriyama-ku, Nagoya-shi, Aichi 463-8585, Japan*

3 *Department of Biological Sciences, National Sun Yat-sen University, No.70 Lien-hai Rd., Kaohsiung City 80424, Taiwan*

4 *National Museum, Department of Entomology, Cirkusová 1740, CZ-19300 Prague 9, Czech Republic*

https://zoobank.org/12B52C90-3F09-4093-9DDF-2A89DB92255C

Corresponding author: Yûsuke N. Minoshima (minoshima@kmnh.jp)

Academic editor: Matthias Seidel ♦ **Received** 8 November 2022 ♦ **Accepted** 7 March 2023 ♦ **Published** 24 March 2023

Abstract

We review the genus *Anacaena* Thomson, 1859 from the Ryukyu Archipelago, southern Japan. Three aquatic species are recognised: *A. torikaii* **sp. nov.** from Amami-ôshima Island, *A. okinawana* **sp. nov.** from Okinawa-jima Island and Kerama Islands, and *A. kumejimana* **sp. nov.** from Kumejima Island. All three species are very similar, with the morphology of the aedeagus being essential for a reliable identification. Dorsal colouration is also useful as a diagnostic character, despite some variation within species. We observe a possible geography-based variation between *A. okinawana* from Okinawa-jima I. and the neighbouring Kerama Is., but we treat both populations as conspecific based on genital morphology. *Anacaena kumejimana* and *A. okinawana* share many morphological characters possibly indicating their close relationship. We compare the endemism of aquatic Hydrophilidae in the Ryukyu Archipelago to that in other groups of aquatic beetles: the proportion of endemic species is higher in aquatic Hydrophilidae than in Dytiscidae, but much lower than in stream-inhabiting Hydraenidae and Elmidae. A list of Japanese species of *Anacaena* and a key to the Japanese species of the genus are provided.

Key Words

Amami Islands, Anacaenini, aquatic beetles, Chaetarthriinae, new species, Okinawa Islands, water scavenger beetles

Introduction

The Ryukyu Archipelago, also called Nansei-shotô, is an island arc of more than 900 islands in south-west Japan spanning about 1,200 km between Kyushu Island and Taiwan (Government of Japan 2019). The archipelago is in a transition area between the Palaearctic and Oriental regions, with a subtropical climate and high precipitation. Almost all islands are of continental origin. They formed on the eastern margin of the Asian continent in the past and underwent a complex geological history in the last two million years (Ota 1998; Osozawa et al. 2012; Government of Japan 2019), resulting in complex biogeography of lineages inhabiting the islands (e.g., Ota 1998; Kato and Yagi 2004; Kaito and Toda 2016; Hirano et al. 2019). The combination of all these aspects, i.e., the position of the islands, their climate, and their recent repeated connections and isolations from the continent and neighbouring islands, is the primary reason for the unique fauna and flora inhabiting the Ryukyu Archipelago.

The fauna of the Ryukyu Archipelago has attracted the interest of professional and amateur entomologists for a long time. This is also the case for aquatic beetles that were considered as a rather well studied group (e.g., Matsui 1988, 1990a, b, 1991; Satô 1998; Sasaki et al. 2002; Hayashi 2007; Hayashi and Fujiwara 2008; Ohmomo et al. 2008; Hayashi et al. 2009). Yet, unexpected findings concerning aquatic beetles have still been reported

even in recent years (e.g., Biström and Watanabe 2017; Kamite and Nakajima 2017; Kamite et al. 2017; Inahata and Minoshima 2019; Kitano et al. 2019; Minoshima and Inahata 2019; Watanabe and Minoshima 2020). These facts indicate that our knowledge about the biodiversity of aquatic insects on the archipelago is still limited and additional inventories, field work, and taxonomic studies are necessary to understand the biodiversity of the area.

Anacaena Thomson, 1859 is a widespread genus of the hydrophilid subfamily Chaetarthriinae comprising about 130 species worldwide (Short and Fikáček 2011; Komarek 2013; Short and Fikáček 2013; Komarek 2014; Komarek and Freitag 2014; Komarek 2021a, b; Sanchez et al. 2022). They are small-sized (2–3 mm long) beetles inhabiting various aquatic and semi-aquatic habitats, and are rarely also found in forest leaf litter (Komarek 2012). Although not previously recorded from the Ryukyu Archipelago, recent investigations have yielded many unidentified *Anacaena* individuals, confirming the occurrence of the genus in the islands (Kamite and Aoyagi 2018; Kamite et al. 2019). In the areas neighbouring to the Ryukyus, one species is recorded from central and northern Honshû and Hokkaidô islands in Japan (*A. asahinai* Satô, 1982; Komarek 2006; Fikáček et al. 2015; Nakajima et al. 2020), two endemic species are known from Taiwan (Komarek 2011), 15 mostly endemic species from China (Komarek 2012, 2014), and at least 17 endemic species from the Philippines (Komarek and Freitag 2014; Sanchez et al. 2022).

The identity of the *Anacaena* specimens from the Ryukyus remained ambiguous. We examined their morphology in detail and found out that they represented undescribed species. In this paper, we review *Anacaena* on the Ryukyu Archipelago, to provide a better understanding of the unique fauna of aquatic beetles on the archipelago.

Materials and methods

Observations and dissections were carried out using Leica MZ16 (Leica Microsystems GmbH) and Olympus BX50 (Olympus Corp.) microscopes. Dissected parts were cleaned using warm 10% KOH solution or proteinase K solution (20 µl proteinase K solution and 180 µl Buffer ATL; Qiagen). They were rinsed in 70% ethanol and dehydrated in 99.5% ethanol, after that, they were mounted in a drop of Euparal solution (Waldeck GmbH & Co. KG) on a small glass slide attached under the specimen (Maruyama 2004) or glued on a paper card with the specimen. Some body parts were stained in warm lactic acid containing acid fuchsine. Specimens were mounted on a paper card using isinglass or polyvinyl acetate resin. Some parts were examined in temporary slides in lactic acid, then rinsed and mounted according to the above-mentioned protocol.

Photographs were taken with Olympus OM-D E-M5 Mark II or E-M1 Mark II digital cameras with Laowa 25 mm f/2.8 2.5-5X Ultra Macro lens (Anhui Changgeng Optics Technology Co., Ltd.) or these cameras attached to a BX50 microscope. Photographs were edited using Adobe Lightroom Classic CC and Photoshop CC (Adobe Inc.) when necessary. Composite images were created using the focus stacking software Helicon Focus (Helicon Soft Ltd.). Line drawings were prepared using the software Clip Studio Paint (CELSYS, Inc.) and Photoshop.

Morphological terminology largely follows Komarek (2004). The definition of the Ryukyu Archipelago follows Tôyama (2014), Ryukyu Archipelago is same as Nansei-shotô Islands.

Label data of the holotype were cited verbatim, which were enclosed in double quotes (“”); a slash (/) indicates separate lines and double slash (//) indicates separate labels.

Examined specimens will be deposited in the following collections: JNC: Private collection of Jun Nakajima, Dazaifu-shi, Japan; YKC: Private collection of Yuuki Kamite, Nagoya-shi, Japan; KMNH: Kitakyushu Museum of Natural History and Human History, Kitakyushu-shi, Japan (Y. Minoshima).

Results

Genus *Anacaena* Thomson, 1859

Anacæna Thomson, 1859: 18 [Type species: *Hydrophilus globulus* Paykull, 1798 by original designation.]. For detail synonymy, see Hansen (1999).

Differential diagnosis. Within the hydrophilid species on the Ryukyu Archipelago, *Anacaena* is the most similar to *Chaetarthria* Stephens, 1835 (Chaetarthriini, Chaetarthriinae) and *Paracymus* Thomson, 1867 (Laccobiini, Hydrophilinae) by the small-sized, oval, and convex body. *Chaetarthria* has a fringe of setae on the first abdominal ventrite, whereas *Anacaena* does not have the fringe; in addition, the known distributions of both genera do not overlap: *Chaetarthria* is known from Sakishima Islands in the Southern Ryukyus (Inahata and Minoshima 2019; Watanabe 2019), *Anacaena* from Amami Islands and Okinawa Islands in the Central Ryukyus. *Paracymus* has a longitudinal median carina on the prosternum, whereas *Anacaena* does not have a carina (Matsui and Nakane 1985; Short and Fikáček 2013). Moreover, *Paracymus* differs considerably from *Anacaena*, e.g., by the shape of eyes, labrum, maxilla, mentum, mesoventrite, and metafemur (Komarek and Beutel 2007).

Ryukyu species of *Anacaena* are easily distinguishable from the other Japanese *Anacaena*, *A. asahinai* Satô, 1982 by the shape of the pubescent area of the metafemur: Ryukyu species have a horizontal hairline (Fig. 3J–M) on the metafemoral area, whereas an oblique hairline is present in *A. asahinai*.

Characters of taxonomic importance. *Anacaena* species of the Ryukyu Archipelago are morphological-

ly similar to each other as well as to the species from adjacent areas. As in other species of *Anacaena*, the morphology of the aedeagus is the most reliable character set to delimit species; the shape of all structures of aedeagus is useful for identification, but the apparent shape of this part can be affected by preparation when the manubrium is curved dorsally. Shape and colour or maxillary palpomeres are used as diagnostic characters; apical infuscation is easily recognisable but may vary within species (Fig. 3A–D). Colouration of the pronotum and elytra, i.e., the width of yellowish margin of the pronotum, and the ground colour of elytra, are useful despite their slight intraspecific variation. Pubescence on the metafemur (Fig. 3J–M) cannot separate the species on the Ryukyu Archipelago, but it is a significant character to delimit Ryukyu species from other similar species distributed in Southeast Asia.

Anacaena kumejimana sp. nov.

https://zoobank.org/F4E63981-8151-4E0B-8951-4552EC89AD32

Figs 1A–C, 3A, F, J, 4A, 5H, I, 6A, B

Type locality. Japan, Okinawa-ken (Prefecture), Kumejima I., Suhara.

Type series. ***Holotype*:** Japan • male; "KUMEJIMA JPN" / "Suhara" / "Kumejima-chô" // "19. V. 2007" / "Y. Kamite leg." // "spec.#" / "20-138" // "HOLOTYPE" / "ANACAENA" / "kumejimana" / "des. YN Minoshima 2021"; KMNH. ***Paratypes*:** Japan – **Okinawa Pref., Kumejima I.** • 1 male, 2 females, 2 exs; same collection data as holotype; KMNH, YKC • 1 ex.; Daruma-yama; 21 May 2007; Y. Kamite leg.; YKC • 1 ex.; Nakandakari; 20 May 2007; Y. Kamite leg.; YKC • 1 ex.; Shirase-gawa-jôryû (upstream of Shirase-gawa R.); 19 May 2007; Y. Kamite leg.; YKC.

Diagnosis. Pronotum dark brown to black, with broad yellowish lateral margin. Antenna with eight antennomeres; antennomere 3 narrow. Maxillary palpus yellowish with very slightly infuscate apex. Pronotum with very fine and sparsely distributed ground punctation consisting of uniformly-sized punctures. Elytra with yellowish spot around scutellar shield. Metafemoral pubescence with horizontal hairline. Median lobe wide, elongate triangular with narrow basal apophyses. Gonopore large, situated at apex. Parameres widest in basal half, then slightly attenuated apically, rounded apically with weak inner angle. Lateral margin of paramere weakly sinuate in dorsal view. Phallobase as long as or slightly shorter than paramere, nearly parallel-sided in basal half, then narrowing to somewhat narrow and short manubrium.

Differential diagnosis. This species is similar to *A. okinawana* and *A. torikaii* in size and external features. Based on the observation of specimens available in this study, dorsal colouration of pronotum and elytra (Fig. 1C) and aedeagus morphology (Fig. 4A) separate these species.

Anacaena kumejimana has a light yellow spot on the proximal medial portion of each elytron (Fig. 1C), whereas *A. okinawana* does not have such distinct spot (the proximal areas may be only indistinctly paler) and *A. kumejimana* has a broader yellowish margin of the pronotum than *A. okinawana* (Fig. 1A, C). Lateral face of parameres is convex in the basal third in *A. kumejimana* (Fig. 4A), whereas convexity is restricted to the more basal portion in *A. okinawana* (Fig. 4C–F). This results in a different lateral margin of the lateral face of the paramere in dorsal view. Wide median lobe separate *A. kumejimana* (Fig. 4A) and *A. okinawana* (Fig. 4C–F) from *A. torikaii* (Fig. 4B). The median lobe is nearly as long as parameres in *A. kumejimana* (Fig. 4A), whereas slightly longer than the parameres in *A. okinawana* (Fig. 4C–F); the apex of the median lobe is reaching close to the parameral apices in *A. okinawana*.

Anacaena yunnanensis Orchymont, 1942 (the *A. yunnanensis*-group sensu Komarek 2012) known from China and *A. zamboangana* Komarek & Freitag, 2014 from Mindanao I., the Philippines, seem to be similar to *A. kumejimana* (Komarek 2012; Komarek and Freitag 2014), but the extent of the metafemoral pubescence separate the Ryukyu species: it has a horizontal borderline (Fig. 3J), compared to rounded borderline in the Chinese and Philippine species (e.g., fig. 99 in Komarek 2012, 72 in Komarek and Freitag 2014).

Description. ***Body*** 2.1–2.3 mm in length, oval, slightly attenuated posteriad (Fig. 1C). ***Colour*** (Fig. 1A–C). Head black, lateral part of clypeus yellowish. Pronotum and elytra dark brown; margins of pronotum broadly yellowish; elytra with yellowish patch at anteromesal part around scutellar shield. Ventral face dark brown, legs slightly paler. Maxillary palpus yellowish with very slightly infuscate apex.

Head. Labrum with a fringe of long erect setae. Ground puncture of clypeus and frons fine, densely arranged; interspace between punctures ca. 2–4 times the width of a puncture. Presence of fine setae on clypeus ambiguous (possibly already broken when collected or during preparation). Frontoclypeal sulcus indistinct. Systematic punctures on clypeus and frons slightly larger than ground punctures, each bearing a fine seta. Systematic punctures of clypeus sparsely distributed. Systematic punctures of frons on anterolateral and posterolateral parts close to compound eye and frontoclypeal sulcus.

Antenna with eight antennomeres. Scape stout, moderately long. Antennomere 2 stout, somewhat conical, ca. as long as antennomeres 3 and 4 combined; antennomere 3 narrow; antennomere 4 wider than 3; antennal club longer than antennomeres 2–5 combined. Maxillary palpus short (Fig. 3A); palpomere 2 stout, longer than palpomere 3; palpomere 3 short, about half as long as palpomere 4; palpomere 4 longest, shorter than palpomeres 2 and 3 combined. Labial palpus short, shorter than width of mentum. Mentum ca. 1.7 times wider than long, subtrapezoidal, rounded anteriorly with median depression;

Figure 1. A–C. *Anacaena kumejimana*, holotype; **D–F.** *A. torikaii*, holotype (**D, E**) and paratype (**F**).

lateral margin with lateral angle but generally indistinct (this character was observed without dissection of head appendages, thus not very accurate) (Fig. 3F). Ground punctation on mentum fine, rather sparsely distributed. Lateral margin of mentum with fringe of fine setae.

Thorax. Pronotum with very fine and sparsely distributed ground punctation consisting of uniformly sized punctures. Systematic punctures on pronotum arranged as irregular transverse row along anterolateral and posterolateral areas. Prosternum weakly and evenly convex.

Ground punctation on elytra coarser than that of head and pronotum; punctures rather densely distributed; interspaces between punctures ca. 1–3 times the width of a puncture. Mesoventrite with median process

pointed apically; process as subtrigonal pyramid with posterior transverse and anterior median longitudinal carinas. Metaventrite with inverted triangular elevated portion medially, with small, oval, postero-medial glabrous area.

Metafemora pubescent in anterior half of basal portion (Fig. 3J), excluding apical area; hairline indistinct along basal part.

***Abdomen*.** Aedeagus (Fig. 4A; see also Fig. 5H, I): Median lobe wide, elongate triangular with narrow basal apophyses, ca. 2.2 times longer than its greatest width, dully pointed apically, as long as parameres. Basal apophysis weakly incurved apically. Gonopore large, situated at apex of median lobe. Parameres widest in basal half, then slightly attenuated apically, rounded apically with weak inner angle; apical third of dorsal parameres membranous. In dorsal view, lateral margin of paramere weakly sinuated. Lateral face of paramere convex at basal third. Dorsal inner margin of parameres sinuated. Phallobase as long as or slightly shorter than paramere, nearly parallel-sided in basal half, then narrowing to somewhat narrow and short manubrium; borderline between membrane and sclerite (unpigmented and pigmented area) of ventral face of phallobase very indistinct.

Distribution. Kumejima I.

Habitat. Aquatic species. Examined specimens were collected in a shallow small pool at the side of a stream (Fig. 6A). The specimen from Nakandakari was collected from a pond (Fig. 6B).

Etymology. Named after the type locality: Kumejima I., Japan.

Anacaena okinawana sp. nov.

https://zoobank.org/28410C22-C8A5-4EDD-A41A-5DEC6A4FE8E7

Figs 2, 3B–D, G, H, K, L, 4C–F, G, 5A–G, 6C–E

Anacaena sp.: Kamite and Aoyagi 2018: 26.

Paracymus orientalis: Kamite et al. 2019: 23 [misidentification, see Kamite 2020: 42].

Type locality. Japan, Okinawa-ken (Prefecture), Okinawa-jima I., Kunigami-son, Benoki, tributary of Benoki Dam.

Type series. ***Holotype*:** Japan • male, "JAPAN: Okinawa Pref.," / "Okinawa-jima I.," / "Kunigami-son, Benoki," / "tributary of Benoki Dam;" / "26.VII.2015; Y. Kamite leg." // "spec.#" / "20-47" // "HOLOTYPE" / "ANACAENA" / "okinawana" / "des. YN Minoshima 2021"; KMNH. ***Paratypes*:** Japan – **Okinawa Pref., Okinawa-jima I.** • 1 male, 4 females, 3 exs; same data as holotype; KMNH, YKC • 2 males, 3 females, 1 ex.; Benoki, Kunigami-son; 16 Oct. 2020; M. Moriguchi leg.; KMNH • 1 male, 1 female; Nishime-dake, Uka, Kunigami-son; 3 Oct. 2020; M. Katô leg.; KMNH • 2 exs; same locality; 27 Oct. 2020; J. Nakajima leg.; JNC. – **Aka-jima I. (Kerama Is.)** • 3 males, 1 female, 2 exs; Aka; 15 Mar. 2019; Y. Kamite leg.; small stream; KMNH, YKC • 2 males; Aka; 16 Mar. 2019; Y. Kamite leg.; small stream; KMNH, YKC • 1 female; Aka; 17 Mar. 2019; Y. & N. Kamite leg.; marsh, slow water flow; YKC. – **Geruma-jima I. (Kerama Is.)** • 1 male; Geruma; 15 Mar. 2019; Y. Kamite leg.; YKC. – **Zamami-jima I. (Kerama Is.)** • 1 male, 2 exs; upstream of Zamami Dam; 16 Mar. 2018; Y. Kamite leg.; KMNH, YKC • 1 ex.; Ama; 17 Mar. 2018; Y. Kamite leg.; KMNH • 2 males, 1 female, 1 ex.; Zamami; 17 Mar. 2018; Y. Kamite leg.; KMNH, YKC • 1 male; same locality; 19 Mar. 2018.; YKC.

Diagnosis. Pronotum and elytra variable in colour, black to light yellowish brown. Pronotum with yellowish lateral margin. Antenna with eight antennomeres; antennomere 3 narrow. Maxillary palpus uniformly yellowish or with infuscate apex. Pronotum with very fine and sparsely distributed ground punctation consisting of uniformly-sized punctures. Metafemoral pubescence with horizontal hairline. Median lobe wide, elongate triangular with narrow basal apophyses. Gonopore large, situated at apex. Parameres slightly attenuated apically, rounded apically with weak inner angle; lateral margin of paramere weakly sinuate in dorsal view. Phallobase longer to slightly longer than parameres, almost parallel-sided in basal half, then narrowing to narrow and short manubrium.

Differential diagnosis. The species is most similar to *A. kumejimana*. Dorsal colouration and the morphology of the aedeagus separate this species from *A. torikaii* and *A. kumejimana*.

Light brown individuals (Fig. 2A) are not known in *A. torikaii* and *A. kumejimana* so far. In dark coloured specimens, yellowish margin on pronotum is narrower in *A. okinawana* than in *A. torikaii* (Fig. 3F). The median lobe (Fig. 4C–F) is wider in *A. okinawana* than in *A. torikaii* (Fig. 4B). Lateral face of the paramere is weakly convex at base in *A. okinawana*, the convexity ends more apically (at basal third) in *A. kumejimana* (Fig. 4A). This results in a different lateral sinuation of the lateral margin of the paramere in dorsal view. The median lobe is slightly longer in *A. okinawana* than in *A. kumejimana*, in which the apex of the median lobe does not reach close to the parameral apices (Fig. 4A).

The pale specimens of *A. okinawana* resemble *A. maculata* Pu, 1964 distributed in southeast Asia and China: *A. maculata* has distinctly speckled elytra (with very small blackish spots) and a different morphology of the aedeagus (fig. 12 in Komarek 2012). For other similar species in Asia, see Differential diagnosis of *A. kumejimana*.

Description. ***Body*** (Fig. 2) 1.9–2.6 mm in length, oval, slightly attenuated posteriad (Fig. 2). ***Colour*** (Fig. 2). Head black, lateral part of clypeus yellowish. Pronotum and elytra light yellowish brown to black; margins of pronotum yellowish in dark-coloured specimens. Ventral face dark brown, legs slightly paler. Antenna yellow with infuscate antennal club. Maxillary and labial palpi uniformly yellowish or with infuscate apex.

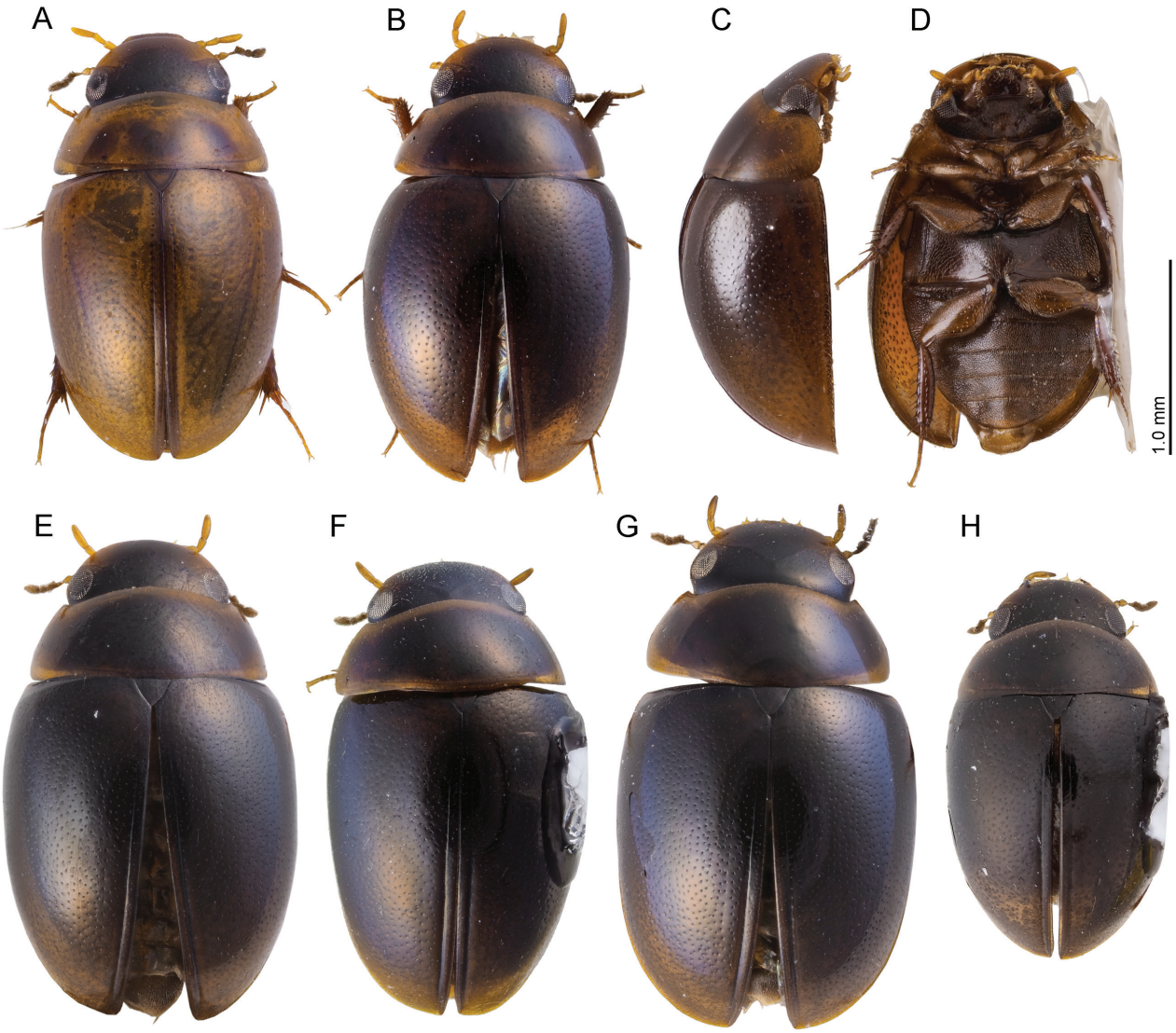

Figure 2. *Anacaena okinawana*, holotype (**C, D**) and paratypes (**A, B, E–H**). **A–D.** From Okinawa-jima I.; **E–H.** From Kerama Is. (**E, F.** Aka-jima I., **G, H.** Zamami-jima I.).

Head. Labrum with a fringe of long erect setae. Clypeus and frons bearing densely arranged fine setae but very often setae missing (possibly already broken when collected or during preparation). Ground punctures of clypeus and frons fine, densely arranged; interspace between punctures ca. 2–4 times the width of a puncture. Frontoclypeal sulcus indistinct. Systematic punctures on clypeus and frons slightly larger than ground punctures, each bearing a fine seta. Systematic punctures of clypeus sparsely distributed, especially on anterior part. Systematic punctures of frons on anterolateral and posterolateral parts close to compound eye and frontoclypeal sulcus.

Antenna with eight antennomeres. Scape stout, moderately long. Antennomere 2 stout, somewhat conical, ca. as long as antennomeres 3 and 4 combined; antennomere 3 narrow; antennomere 4 wider than 3; antennal club longer than antennomeres 2–5 combined. Maxillary palpus short (Fig. 3B–D); palpomere 2 stout, longer than palpomere 3; palpomere 3 short, about half or slightly shorter than palpomere 4; palpomere 4 longest, shorter than palpomeres 2 and 3 combined. Labial palpus short, shorter than width of mentum. Mentum (Fig. 3G, H) ca. 1.7 times wider than long, subtrapezoidal, rounded anteriorly with median depression; lateral margin with lateral angle but generally indistinct (this character was observed without dissection of head appendages, thus not very accurate). Ground punctation on mentum fine, rather sparsely distributed. Lateral margin of mentum with fringe of fine setae.

Thorax. Pronotum with very fine and sparsely distributed ground punctation consisting of uniformly-sized punctures. Systematic punctures on pronotum arranged as irregular transverse row along anterolateral and posterolateral areas. Prosternum weakly and evenly convex.

Ground punctation on elytra coarser than that of head and pronotum; punctures rather densely distributed; interspaces between punctures ca. 1–3 times the width of a puncture. Mesoventrite with median process pointed

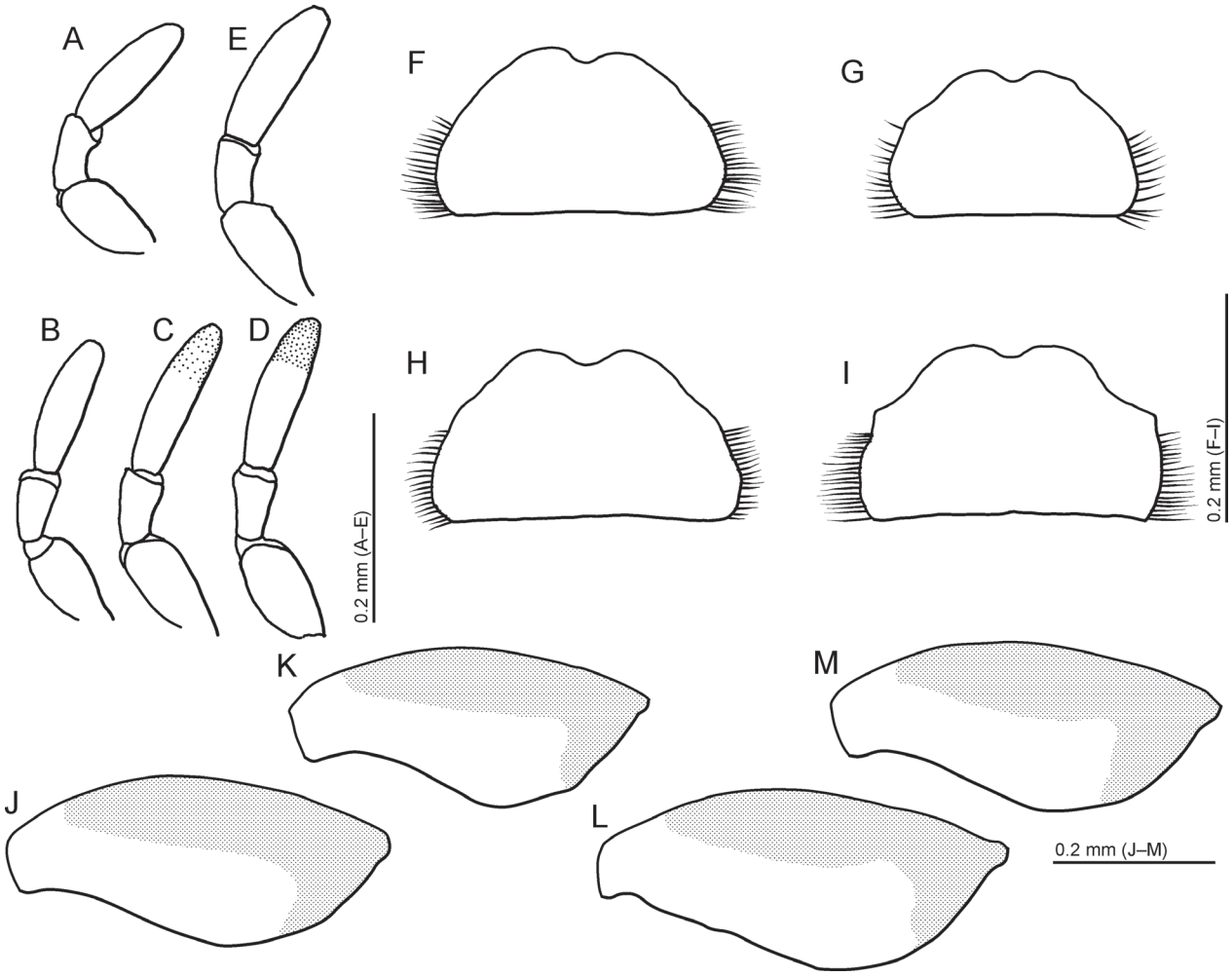

Figure 3. A–E. Maxillary palpus; **A.** *Anacaena kumejimana*, paratype; **B–D.** *A. okinawana*, paratypes; **B.** from Okinawa-jima I., **C, D.** from Aka-jima I. (Kerama Is.); **E.** *A. torikaii*, holotype; **F–I.** Mentum; **F.** *A. kumejimana*, paratype; **G, H.** *A. okinawana*, paratypes; **G.** from Okinawa-jima I.; **H.** from Aka-jima I. (Kerama Is.); **I.** *A. torikaii*, holotype; **J–M.** Hind femora, indicating femoral pubescence but borderline of pubescence often not clear at base; **J.** *A. kumejimana*, paratype; **K, L.** *A. okinawana*, paratypes; **K.** from Okinawa-jima I.; **L.** from Aka-jima I. (Kerama I.); **M.** *A. torikaii*, holotype.

apically; process as subtrigonal pyramid with posterior transverse and anterior median longitudinal carinas. Metaventrite with inverted triangular portion medially elevated, with small, oval, glabrous area. Metafemora (Fig. 3K, L) pubescent along basal area and anterior half excluding apical area, with horizontal hairline; hairline indistinct along basal part.

***Abdomen*.** Aedeagus (Fig. 4C–F; see also Fig. 5A–G): Median lobe wide, elongate triangular with narrow basal apophyses, ca. 2.5 times longer than its greatest width, dully pointed apically, longer than parameres. Basal apophysis weakly incurved in proximal part. Gonopore large, situated at apex. Parameres rather variable, slightly attenuated apically, rounded apically with weak inner angle; apical third of dorsal face of paramere membranous or very weakly sclerotised. In dorsal view, lateral margin of paramere weakly convex to slightly sinuate in specimens from Okinawa-jima I. (Figs 4C, D; 5A–C), slightly sinuate from Kerama Is. (Figs 4E, F, 5D–G). Lateral face of parameres convex basally; dorsal inner margin of parameres sinuated. Phallobase longer to slightly longer than paramere, almost parallel-sided in basal half, then narrowing to narrow and short manubrium; borderline between membrane and sclerite (unpigmented and pigmented area) of ventral face of phallobase generally indistinct, incision of anterior margin moderately deep.

Distribution. Okinawa Is.: Okinawa-jima I. and Kerama Is. (Aka-jima I., Geruma-jima I., Zamami-jima I.).

Habitat. Aquatic species. Examined specimens were collected from a small stream (Fig. 6C, D) and from a marsh with a slow water flow. The specimen from Geruma-jima I. was collected from small pool on a concrete drainage (Fig. 6E) (Kamite and Aoyagi 2018; Kamite et al. 2019).

Etymology. Named after the type locality: Okinawa Is., Japan.

Variation. This species shows morphological variations partly correlated with geography (Fig. 5), indicating

that the populations from Okinawa I. and Kerama Is. may be isolated from each other (see Discussion).

1. Colouration of pronotum and elytra. Dorsal colouration is highly variable, yellowish brown (Fig. 2A) to black (Fig. 2B, C, E–H). We examined two yellow individuals collected from Okinawa-jima I.; although they are females, we consider them conspecific with dark specimens from the same population based on external characters. The range of variation seems to be smaller in specimens from Kerama Is. (mostly black specimens) than in those from Okinawa-jima I. (yellowish to black).
2. Maxillary palpus. Two types of colourations of maxillary palpus were observed (Fig. 3B–D): uniformly yellowish palpus and infuscate at apex. This variation seems not to be affected by geography.
3. Aedeagus of the species vary both within and between islands. Specimens of Okinawa-jima I. (Figs 4C, D; 5A–C) have slightly smaller aedeagus with not or weakly sinuate lateral face of parameres and slightly narrower median lobe in dorsal view. Aedeagus of the specimens from Kerama Islands (specimens from Aka-jima I., Geruma-jima I., and Zamami-jima I. were examined) is slightly larger, with weakly sinuate lateral face of parameres and slightly wider median lobe (Figs 4E, F, 5D–G).

Anacaena torikaii sp. nov.

https://zoobank.org/53816B36-A6B2-4762-BD69-F6A7D5DF3BE9

Figs 1D–F, 3E, I, M, 4B, 6F

Type locality. Japan, Kagoshima-ken (Prefecture), Amami-ôshima I., Amami-shi, Naze, Kinsakubaru.

Type series. ***Holotype*:** Japan • male; "AMAMI JPN" / "Kinsakubaru" / "Naze" // "Amami-shi" / "17. VII. 2006" / "Y. Kamite leg." // "JAPAN: Amami Is.," / "Amamiôshima I.," / "Amami-shi, Naze," / "Kinsakubaru;" / "17.VII.2006; Y. Kamite" // "spec#" / "20-66" // "HOLOTYPE" / "ANACAENA" / "torikaii" / "des YN Minoshima 2021"; KMNH. ***Paratypes*:** Japan •1 male, 1 female; same collection data as holotype; KMNH, YKC.

Diagnosis. Pronotum dark brown with broad yellowish lateral margin; elytra brown, weakly speckled, slightly paler at base. Antenna with eight antennomeres; antennomere 3 narrow. Maxillary palpus uniformly yellowish. Pronotum with very fine and sparsely distributed ground punctation consisting of uniformly sized punctures. Metafemoral pubescence with horizontal hairline. Median lobe elongate, tapering apically. Gonopore large, situated at apex. Parameres widest in basal third, rounded apically with inner angle. Lateral margin of paramere weakly sinuate in dorsal view. Phallobase as long as paramere, nearly parallel-sided in basal half, then narrowing to short and wide manubrium.

Differential diagnosis. This species can be distinguished from other Ryukyu species by the slender, ca 3 times longer than wide, median lobe (Fig. 4B). In addition, examined specimens have broader yellowish margins on pronotum (Fig. 1D, F) than in dark-coloured specimens of *A. okinawana* (Fig. 2); examination of additional specimens is, however, needed to understand the variation of dorsal colouration of *A. torikaii*. *Anacaena kumejimana* has a yellowish patch on the base of elytra (Fig. 1C), whereas the area is only slightly paler in *A. torikaii* (Fig. 1F).

Outside of the Ryukyus, *Anacaena jiafenglongi* Komarek, 2012 known from China and *A. hajeki* Komarek, 2013 from Laos are similar to *A. torikaii* based on the morphology of the aedeagus. The maxillary palpomere 4 of *A. jiafenglongi* is stout (fig. 29 in Komarek 2012), whereas it is slender in *A. torikaii*. The basal piece is distinctly longer than the parameres of *A. hajeki* (fig. 5 in Komarek 2013) and separates the species from *A. torikaii*.

Description. ***Body*** (Fig. 1F) 2.1–2.5 mm in length, oval, slightly attenuated posteriad. ***Colour*** (Fig. 1D–F). Head black, lateral part of clypeus yellowish. Pronotum dark brown with broad yellowish margins. Elytra brown, weakly speckled, slightly paler at base. Ventral face dark brown. Maxillary palpus uniformly yellowish.

Head. Labrum with a fringe of long erect setae. Ground punctures of clypeus and frons fine, densely arranged; interspace between punctures ca. 2–4 times the width of a puncture. Presence of fine setae on clypeus ambiguous (possibly already broken when collected or during preparation). Frontoclypeal sulcus indistinct. Systematic punctures on clypeus and frons slightly larger than ground punctures, each bearing a fine seta. Systematic punctures of clypeus sparsely distributed, especially on anterior part. Systematic punctures of frons on anterolateral and posterolateral parts close to compound eye and frontoclypeal sulcus.

Antenna with eight antennomeres. Scape stout, moderately long. Antennomere 2 stout, somewhat conical, ca. as long as antennomeres 3 and 4 combined; antennomere 3 narrow; antennomere 4 wider than 3; antennal club longer than antennomeres 2–5 combined. Maxillary palpus short (Fig. 3E); palpomere 2 stout, longer than palpomere 3; palpomere 3 short, slightly shorter than palpomere 4; palpomere 4 longest, shorter than palpomeres 2 and 3 combined. Labial palpus short, shorter than width of mentum. Mentum (Fig. 3I) ca. 1.7 times wider than long, subtrapezoidal, rounded anteriorly with median depression, with indistinct lateral angle (this character was observed without dissection of head appendages, thus not very accurate). Ground punctation on mentum fine, rather sparsely distributed. Lateral margin of mentum with fringe of fine setae.

Thorax. Pronotum with very fine and sparsely distributed ground punctation consisting of uniformly

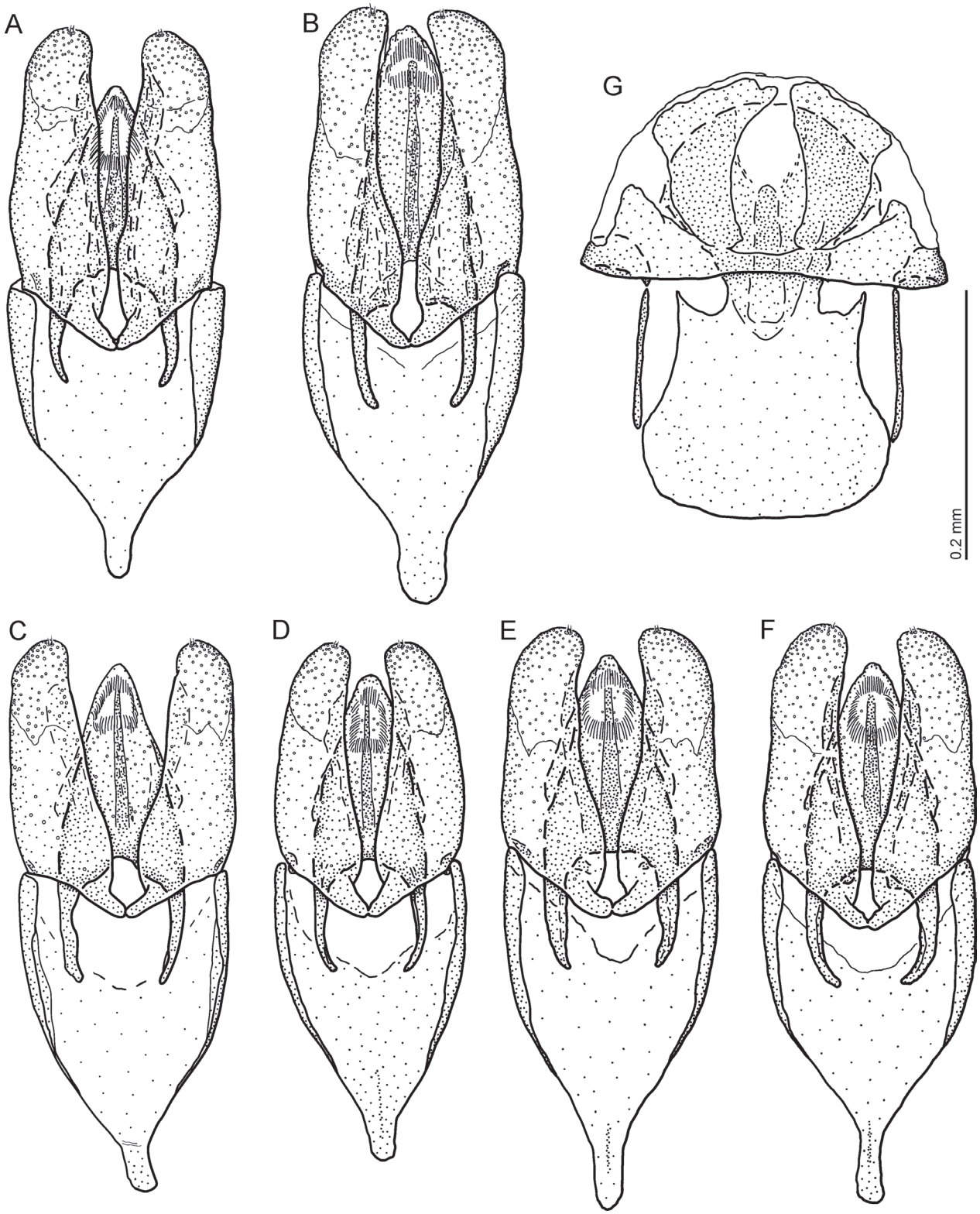

Figure 4. A–F. Aedeagus (**A–F**) and abdominal segment 9 (**G**), dorsal view. **A.** *Anacaena kumejimana*, holotype; **B.** *A. torikaii*, holotype; **C–G.** *A. okinawana*, holotype (**C**) and paratypes (**D–G**); **C, D, G.** from Okinawa-jima I.; **E, F.** from Kerama Is. (**E.** Aka-jima I.; **F.** Zamami-jima I.).

sized punctures. Systematic punctures on pronotum arranged as irregular transverse row along anterolateral and posterolateral parts. Prosternum weakly and evenly convex.

Ground punctation on elytra coarser than that of head and pronotum; punctures rather densely distributed; interspaces between punctures ca. 1–3 times the width of a puncture. Mesoventrite with median process pointed

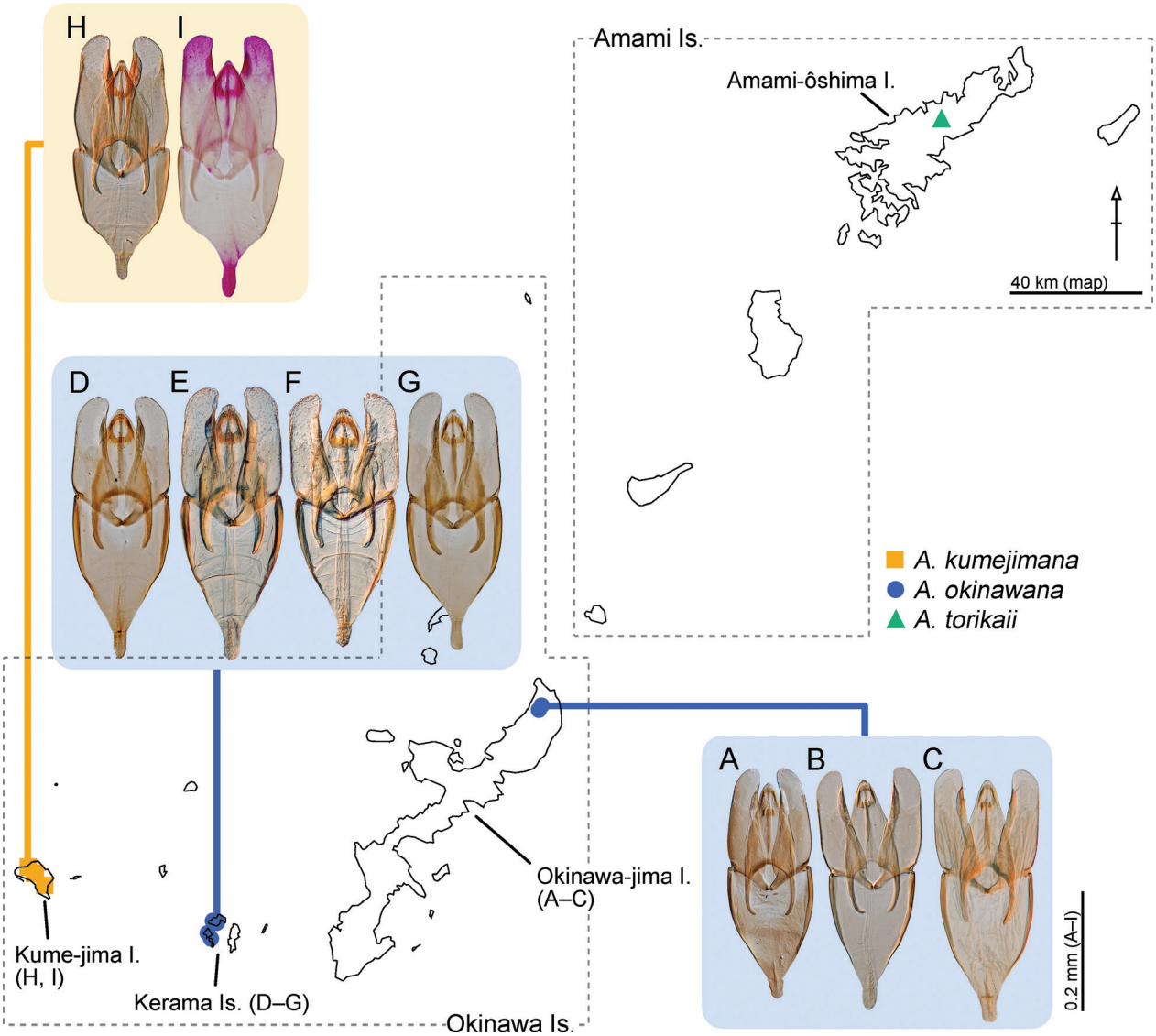

Figure 5. Map of the Central Ryukyus (Amami Is. to Okinawa Is.) and aedeagus of *Anacaena* species. **A–G.** *Anacaena okinawana*; **A–C.** from Okinawa-jima I., **D–G.** from Kerama Is. (**D, E.** Aka-jima I.; **F.** Geruma-jima I.; **G.** Zamami-jima I.); **H, I.** *A. kumejimana*.

apically; process as subtrigonal pyramid with posterior transverse and anterior median longitudinal carinas. Metaventrite with inverted triangular medially elevated portion with small oval glabrous area. Metafemora (Fig. 3M) pubescent in basal part and anterior half excluding apical area with horizontal hairline; hairline indistinct along basal part.

***Abdomen*.** Aedeagus (Fig. 4B): Median lobe elongate tapering apically, ca. 3 times longer than its greatest width, dully pointed or nearly rounded apically. Basal apophyses narrow, weakly incurved apically. Gonopore large, situated at apex. Parameres widest at basal third, membranous in apical half dorsally, rounded apically with inner angle, attenuated apically at midlength of parameres; apical half of lateral margin and inner margin almost parallel-sided in dorsal view. In dorsal view, lateral margin of paramere weakly sinuated. Phallobase as long as paramere, nearly parallel-sided in basal half, then narrowing to wide and short manubrium; borderline between membrane and sclerite (unpigmented and pigmented area) of ventral face of phallobase very indistinct, incision of anterior margin possibly shallow.

Distribution. Amami-ôshima I. Only known from the type locality.

Habitat. Aquatic species. Examined specimens were collected in a small stream in a forest (Fig. 6F).

Etymology. Named after Mr. Hisahiro Torikai (Amami-shi), who kindly assisted with Y. Kamite's field work on Amami-ôshima Island.

Checklist of the *Anacaena* species of Japan

1. *Anacaena asahinai* Satô, 1982 Hokkaidô, Honshû; Russia
2. *Anacaena kumejimana* sp. nov. Kumejima Island
3. *Anacaena okinawana* sp. nov. Okinawa Islands (Okinawa-jima Island, Kerama Islands)
4. *Anacaena torikaii* sp. nov. Amami-ôshima Island

Key to the species of *Anacaena* of Japan

The key is based on the selection of most reliable characters only and follows our understanding of the intraspecific variation based on material examined in this study (updates may be needed for coloration characters after additional specimens are collected). Additional quantitative characters may help with the identification, see the differential diagnoses of the respective species.

1 Metafemoral pubescence with horizontal hairline (Fig. 3J–M). Endemic to Ryukyu Archipelago 2
– Metafemoral pubescence extended with oblique hairline, covering basal two-thirds to three-quarters of femur. Honshû and Hokkaidô islands ..... *A. asahinai*
2 Median lobe of aedeagus slender, ca. 3 times longer than wide, attenuated towards apex with nearly straight lateral margins (Fig. 4B). Amami-ôshima Island ..... *A. torikaii*
– Median lobe of aedeagus wide, ca. 2.2–2.5 times longer than wide, triangular and attenuated towards apex in apical part, nearly parallel-sided in basal part (Fig. 4A, C–F). Okinawa Islands (Okinawa-jima I., Kerama Is., and Kumejima I.)..... 3
3 Colouration of elytra dark, with yellowish spot anteromesally around scutellar shield (Fig. 1C). Lateral face of paramere convex at basal third (Fig. 4A). Kumejima Island ..... *A. kumejimana*
– Colouration of elytra variable, yellowish to black but elytra without yellowish spot anteromesally around scutellar shield (Fig. 2). Lateral face of paramere convex at base (Fig. 4C–F). Okinawa-jima Island and Kerama Islands ..... *A. okinawana*

Discussion

Anacaena species on the Ryukyu Archipelago

In this study we described three aquatic species of *Anacaena* distributed in the Ryukyu Archipelago, representing the only *Anacaena* species known in the area at present. The Ryukyu Archipelago is composed mostly of continental islands, with the exception of Daitô Islands which consists of a few oceanic islands far from the island arc. The archipelago excluding Daitô Islands is subdivided into tree biogeographical regions, namely the Northern, Central and Southern Ryukyus (Motokawa 2000; Komaki and Ebach 2021); *Anacaena* species are found only in the Central Ryukyus, with the Tokara Strait (Watase line) and the Kerama Gap as the boundaries. However, the presence of *Anacaena* in the Southern Ryukyus, which is located close to Taiwan and China, cannot be ruled out so far.

Species of *Anacaena* of the Ryukyus are morphologically distinguishable from the species in other regions of Asia, and their distributions seem to be restricted to single islands or a group of neighbouring islands. This pattern of endemism is very similar to the situation reported for *Anacaena* in previous studies: *Anacaena* species distributed in Taiwan (Komarek 2011), Philippines (Komarek and Freitag 2014; Sanchez et al. 2022), Indonesia (Komarek 2010), New Guinea (Komarek 2009) and Madagascar (Komarek 2004, 2021a) are endemic, most of them restricted to a single island. This stands in contrast to continental Asian species, many of which have a wide distributional range (Komarek 2012, 2013). *Anacaena asahinai* is an exceptional case; the species is distributed in Honshu and Hokkaidô islands of Japan and Far East Russia (Fikáček et al. 2015).

Ryukyu species of *Anacaena* are morphologically similar but can be divided into the species on Okinawa Islands (*A. kumejimana* and *A. okinawana*) and Amami-ôshima Island (*A. torikaii*) based on their morphology. *Anacaena kumejimana* and *A. okinawana* share many morphological characters possibly indicating their close relationship. *Anacaena okinawana* shows a slight geography-based variation of local populations (Okinawa-jima Island and Kerama Islands, ca. 30 km of distance) in colour and aedeagal morphology (see the section 'Variation' in *A. okinawana*). The morphological differences correlated with geography rule out the possibility of the recent human-mediated origin of both populations. Variation of colouration and aedeagal morphology in *Anacaena* was also observed in Chinese species; in particular, a remarkable morphological variation of the aedeagus was observed in *A. yunnanensis* Orchymont, 1942 (Komarek 2012). The variation between populations of *A. okinawana* is rather small in contrast to most species of *Anacaena* and partly overlaps, and we hence considered both populations as conspecific. The distribution pattern and the structure of local single-island populations of *A. okinawana* are similar to a Ryukyus endemic frog *Babina holsti* (Boulenger, 1892). The frog is distributed to the northern area of Okinawa-jima Island and Tokashiki-jima Island of Kerama Islands, and their genetic data show clear separation of populations on Okinawa-jima Island and Tokashiki-jima Island (Tominaga et al. 2014).

Comparing the species of *Anacaena* on the Ryukyus with those of other Asian areas, some similar species can be found based on genital morphology. The characters of the aedeagus (triangular median lobe and wide paramere in *A. kumejimana* and *A. okinawana*) are not rare in Asian species, these are similar to the species in Taiwan and continental Asia (e.g., *A. yunnanensis* group; Komarek 2012). The slender median lobe and shape of parameres in *A. torikaii* is also similar to Asian species such as the Chinese *A. jiafenglongi* and the Laotian *A. hajeki* (Komarek 2011, 2012, 2013). Hence, we cannot rule out that the Okinawa Islands species *A. kumejimana* and *A. okinawana* are not closely related to the Amami Islands species *A. torikaii*.

Figure 6. Collecting localities of the species of *Anacaena* on the Ryukyu Archipelago. **A–B.** *Anacaena kumejimana*; **A.** Daruma-yama, Kumejima I., 21 May 2007; **B.** Nakandakari, Kumejima I., 20 May 2007; **C–E.** *A. okinawana*; **C.** tributary of Benoki Dam, Kunigami-son, Okinawa-jima I., 26 Jul. 2015; **D.** Aka, Aka-jima I., 15 Mar. 2019; **E.** Geruma, Geruma-jima I., 15 Mar. 2019, after Kamite et al. (2019); **F.** *A. torikaii*; F, Kinsakubaru, Amami-ôshima I., 17 Jul. 2006.

Ryukyu *Anacaena* clearly represent newly discovered species easily distinguishable from known Asian species; however, their origin is still unclear. To understand better the age and origin of the species as well as to clarify the status of the Okinawa and Kerama populations, it is desirable to examine the status of all populations studied here by DNA markers, and to confirm the presence or absence of the genus in the other areas of the Ryukyu Archipelago.

Endemism of aquatic Hydrophilidae on the Ryukyu Archipelago

About two-thirds of the species of the family Hydrophilidae are aquatic (Short and Fikáček 2011). Aquatic hydrophilids are present in all lineages across the family – some of them represent ancestrally aquatic groups, others are highly derived terrestrial groups with some lineages which returned to water (Short and Fikáček 2013; Song et

al. 2014). Despite being an ecological rather than a natural (monophyletic) group, we use the term "aquatic Hydrophilidae" for convenience, in the same way as aquatic Coleoptera or aquatic insects. In Japan, aquatic Hydrophilidae contains representatives of the subfamilies Hydrophilinae, Chaetarthriinae, Enochrinae, and Acidocerinae, plus the genus *Coelostoma* Brullé, 1835 of the subfamily Sphaeridiinae. Aquatic representatives of other largely terrestrial lineages (e.g., Cylominae) do not occur in Japan.

A total of 49 aquatic hydrophilid species in 19 genera is recorded from the Ryukyu Archipelago, representing about 60% of species and 95% of genera in Japan. Twelve species (24% of the fauna) are endemic to the archipelago (Nakajima 2022, this study). When compared to other groups of aquatic beetles based on the data provided by Nakajima et al. (2020) and Hayashi et al. (2020), the proportion of endemics is higher in aquatic Hydrophilidae (24%) than in Dytiscidae (four endemic species: 8%). In contrast, Hydraenidae (10 endemic species: 71%) and Elmidae (17 endemic species: 74%) show much higher endemism than Hydrophilidae and Dytiscidae. Other aquatic groups of beetles have six or less species in the archipelago and we do not consider them here.

Ribera and Vogler (2000) hypothesized that distributional ranges of aquatic Coleoptera correlate with their habitat preferences: ranges of species from running waters are generally smaller than those of species from standing waters. Sheth et al. (2020) and Mai et al. (2022) discussed species diversity of Indian and Chinese *Coelostoma* in a similar context. Members of Hydrophilidae and Dytiscidae inhabit a wide spectrum of aquatic habitats, whereas the majority of Hydraenidae and Elmidae are restricted to running waters (Jäch and Díaz 1999; Hayashi et al. 2020; Nakajima et al. 2020). Collecting data indicate that all three *Anacaena* species on the Ryukyus inhabit running waters or adjacent habitats, thus they can be considered as running water inhabiting species. Hence, all endemic species of aquatic Hydrophilidae except *Enochrus satomii* Nakane & Matsui, 1986 inhabit running waters or hygropetric habitats which may be considered as a special type of running waters. The same patterns are seen in the Dytiscidae: three of four endemic species inhabit running water or its surroundings. The distribution data of water beetles of Ryukyu Archipelago correspond well with the hypothesized relationship between habitat preferences and the size of distributional range.

Satô (1998) pointed to the possibility of a recent human-based dispersal in well-flying aquatic species or those inhabiting lowland standing waters. He suspected that the dispersal between islands has been facilitated by ship transportation. The aquatic Hydrophilidae are very often attracted to light and may hence be attracted to the lights in the harbours and on ships and transported to the islands. This way was also recently hypothesized to explain the discovery of a few South American water beetles in Saudi Arabia (Fikáček and Liu 2019; Fikáček et al. 2021). Although this type of dispersal on ship was not yet formally demonstrated for aquatic beetles, we suppose it is quite probable especially for species living in urban areas close to harbours, in paddy fields or in artificial ponds. If valid, this would further contribute to low local endemism of species inhabiting lowland standing waters and disturbed habitats. It should be noted, however, that areas with low local endemism are not necessarily of lower conservation priority.

Acknowledgements

We are grateful to Masaya Katô (Urasoe-shi), Mitsuru Moriguchi (Okinawa University, Naha-shi) and, Jun Nakajima (Fukuoka Institute of Health and Environmental Sciences, Dazaifu-shi) who allowed us to study their specimens. Masaru Aoyagi (Urasoe-shi), Nami Kamite (Gifu-shi), Tomonari Katô (Zamami-son), Itsurô Kawashima (Yokosuka-shi), Kôshin Miyahira (Zamami-son), Hajime Miyamura (Zamami-son), Noriko Moriuchi (Zamami-son), Yasuyuki Moriuchi (Zamami-son), and Hisahiro Torikai (Amami-shi) kindly helped YK's field work in various ways; Albrecht Komarek (Naturhistorisches Museum Wien, Wien) provided us valuable information on *Anacaena* taxonomy; Masako Izawa (KMNH) provided us useful information on the definition of the Ryukyu Archipelago. We would also like to thank Nanbu Regional Public Works Office, Okinawa Prefectural Government for permitting the YK's collecting in upstream of Zamami Dam. Article processing charge was generously supported by the Museum für Naturkunde, Berlin, Germany. Part of the work of MF was supported by the Ministry of Culture of the Czech Republic (DKRVO 2019–2023/5.I.d, National Museum, 00023272).

References

Biström O, Watanabe K (2017) A new species of the genus *Hydrovatus* (Coleoptera, Dytiscidae) from Iriomote Island, southwestern Japan, with a key to the Japanese species. Elytra. New Series 7(1): 5–13.

Boulenger GA (1892) Descriptions of new reptiles and batrachians from the Loo Choo Islands. Annals and Magazine of Natural History. Sixth Series 10(58): 302–304. https://doi.org/10.1080/00222939208677414

Fikáček M, Liu H-C (2019) A review of *Thysanarthria* with description of seven new species and comments on its relationship to *Chaetarthria* (Hydrophilidae: Chaetarthriini). Acta Entomologica Musei Nationalis Pragae 59(1): 229–252. https://doi.org/10.2478/aemnp-2019-0020

Fikáček M, Angus RB, Gentili E, Jia F-L, Minoshima YN, Prokin A, Przewoźny M, Ryndevich SK (2015) Family Hydrophilidae Latreille, 1802. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera Vol. 2, Revised and Updated Edition, Hydrophiloidea – Staphylinoidea. Brill, Leiden, 37–76.

Fikáček M, Matsumoto K, Perkins P, Prokin A, Sazhnev A, Litovkin S, Jäch MA (2021) The family Epimetopidae (Coleoptera: Hydrophiloidea): review of current knowledge, genus-level phylogeny, and taxonomic revision of *Eupotemus*. Acta Entomologica Musei Nationalis Pragae 61(1): 1–34. https://doi.org/10.37520/aemnp.2021.001

Government of Japan (2019) Nomination of Amami-Oshima Island, Tokunoshima Island, Northern Part of Okinawa Island, and Iriomote Island for Inscription on the World Heritage List. Government of Japan, Chiyoda-ku, [xxxiii+] 343 pp. https://kyushu.env.go.jp/okinawa/amami-okinawa/world-natural-heritage/plan/index-en.html

Hansen M (1999) World Catalogue of Insects 2: Hydrophiloidea (s. str.) (Coleoptera). Apollo Books, Amsterdam, 416 pp.

Hayashi M (2007) Records on aquatic Coleoptera from streams and rivers in Amami-Oshima, Kagoshima Prefecture, Japan. Coleopterists'. News 158: 9–12. [In Japanese]

Hayashi M, Fujiwara J (2008) Records on aquatic Coleoptera from streams and rivers in Amami-Oshima, Kagoshima Prefecture, Japan (Part 2). Coleopterists'. News 163: 1–5. [In Japanese]

Hayashi M, Fujiwara J, Kamite Y (2009) Lotic and riparian Coleoptera of Okinawa-jima, Ryukyu, Japan. Coleopterists'. News 167: 15–19. [In Japanese]

Hayashi M, Nakajima J, Ishida K, Kitano T, Yoshitomi H (2020) Species diversity of aquatic Hemiptera and Coleoptera in Japan. Japanese Journal of Systematic Entomology 26: 191–200.

Hirano T, Kameda Y, Saito T, Chiba S (2019) Divergence before and after the isolation of islands: Phylogeography of the *Bradybaena* land snails on the Ryukyu Islands of Japan. Journal of Biogeography 46(6): 1197–1213. https://doi.org/10.1111/jbi.13575

Inahata N, Minoshima YN (2019) Occurrence of the tribe Chaetarthriini in Japan (Coleoptera: Hydrophilidae). Japanese Journal of Systematic Entomology 25(1): 95–96.

Jäch MA, Díaz JA (1999) The genus *Hydraena* Kugelann, 1794 (Insecta: Coleoptera: Hydraenidae) in the Ryukyu Archipelago (Nansei-shoto), Japan. Annalen des Naturhistorischen Museums in Wien. Serie B, Fur Botanik und Zoologie 101: 201–215. https://www.jstor.org/stable/41767146

Kaito T, Toda M (2016) The biogeographical history of Asian keelback snakes of the genus *Hebius* (Squamata: Colubridae: Natricinae) in the Ryukyu Archipelago, Japan. Biological Journal of the Linnean Society. Linnean Society of London 118(2): 187–199. https://doi.org/10.1111/bij.12726

Kamite, Y (2020) [Corrigendum] Misidentification in Kamite et al. (2019) in Sayabane New Series, No. 36]. Sayabane New Series 38: 42. [In Japanese]

Kamite, Y, Aoyagi, M (2018) Records on aquatic Coleoptera of Zamami-jima, Okinawa Prefecture, Japan. Sayabane New Series 32: 26–31. [In Japanese]

Kamite Y, Nakajima J (2017) Notes on the *Stenelmis hisamatsui* species group in Japan, with description of a new species from Kume-jima, Ryukyu Islands (Coleoptera: Elmidae). Koleopterologische Rundschau 87: 253–273.

Kamite Y, Yoshitomi H, Hayashi M (2017) A remarkable new species of the genus *Leptelmis* Sharp from Amami-Ôshima, with redescription of the larva of *Leptelmis gracilis* Sharp (Coleoptera, Elmidae, Elminae). Elytra. New Series 7(2): 395–408.

Kamite, Y, Aoyagi, M, Kamite, N (2019) Records on aquatic Coleoptera of Aka-jima and Geruma-jima, Okinawa Prefecture, Japan Sayabane New Series, 36 pp. [In Japanese]

Kato Y, Yagi T (2004) Biogeography of the subspecies of *Parides* (*Byasa*) *alcinous* (Lepidoptera: Papilionidae) based on a phylogenetic analysis of mitochondrial ND5 sequences. Systematic Entomology 29(1): 1–9. https://doi.org/10.1111/j.1365-3113.2004.00238.x

Kitano T, Tahira Y, Kohno H (2019) Discovery of the family Spercheidae (Coleoptera, Hydrophiloidea) from Japan, with redescription of *Spercheus stangli* Schwarz et Barber, 1917. Elytra. New Series 9(2): 291–295.

Komaki S, Ebach M (2021) Widespread misperception about a major East Asian biogeographic boundary exposed through bibliographic survey and biogeographic meta-analysis. Journal of Biogeography 48(9): 2375–2386. https://doi.org/10.1111/jbi.14210

Komarek A (2004) Taxonomic revision of *Anacaena* Thomson, 1859 I. Afrotropical species (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 74: 303–349.

Komarek A (2006) Taxonomic revision of *Anacaena* Thomson, 1859 III. The Indian Subcontinent (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 76: 283–314.

Komarek A (2009) Taxonomic revision of *Anacaena* Thomson, 1859. V. New Guinea (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 79: 197–254.

Komarek A (2010) Taxonomic revision of *Anacaena* Thomson, 1859. VII. Indonesia except Papua (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 80: 113–128.

Komarek A (2011) Taxonomic revision of *Anacaena* Thomson, 1859 VIII. Taiwan (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 81: 229–236.

Komarek A (2012) Taxonomic revision of *Anacaena* Thomson, 1859 IX. The People's Republic of China (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 82: 235–284.

Komarek A (2013) A revision of *Anacaena* Thomson, 1859 X. Laos, Malaysia, Myanmar, Thailand, and Vietnam (Coleoptera: Hydrophilidae). Entomologica Basiliensia et Collectionis Frey 34: 137–177.

Komarek A (2014) Corrections and additions to the taxonomy of *Anacaena* Thomson, 1859 from the People's Republic of China. Koleopterologische Rundschau 84: 233–234.

Komarek A (2021a) A new species of *Anacaena* Thomson, 1859 from Madagascar (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 91: 125–130.

Komarek A (2021b) *Anacaena* Thomson, 1859 from New Caledonia: description of a new species, and corrections and additions concerning two previously described species (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 91: 323–326.

Komarek A, Beutel RG (2007) Phylogenetic analysis of Anacaenini (Coleoptera: Hydrophilidae: Hydrophilinae) based on morphological characters of adults. Systematic Entomology 32(2): 205–226. https://doi.org/10.1111/j.1365-3113.2006.00359.x

Komarek A, Freitag H (2014) Revision of *Anacaena* Thomson, 1859 XI. Republic of the Philippines (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 84: 235–276.

Mai Z, Hu J, Jia F (2022) Additional fauna of *Coelostoma* Brullé, 1835 from China, with re-establishment of *Coelostoma sulcatum* Pu, 1963 as a valid species (Coleoptera, Hydrophilidae, Sphaeridiinae). ZooKeys 1091: 15–51. https://doi.org/10.3897/zookeys.1091.79564

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

Matsui E (1988) [The aquatic Coleoptera collected on Amami Islands (1987–1988)]. Kita-Kyūshū no. Konchu (Tokyo) 35(2): 113–121. [In Japanese]

Matsui E (1990a) [Collecting records of aquatic Coleoptera from Ryukyu Archipelago (1)]. Kita-Kyūshū no Konchū 37(2): 69–76. [pls 9, 10] [In Japanese]

Matsui E (1990b) Collecting records of aquatic Coleoptera from Ryukyu Archipelago (2). Kita-Kyūshū no Konchū 37(3): 163–170. [pls 19, 20] [In Japanese]

Matsui E (1991) Collecting records of aquatic Coleoptera from Okinawa-hontô I., Ishigaki-jima I., and Iriomote-jima I. (continued). Coleopterists'. News 95: 11–12. [In Japanese]

Matsui E, Nakane T (1985) Notes on some species of Hydrophilidae in Japan (Insecta, Coleoptera). Reports of the Faculty of Science, Kagoshima University (Earth Sciences and Biology) 18: 89–95. https://hdl.handle.net/10232/5959

Minoshima YN, Inahata N (2019) First record of *Paracymus atomus* Orchymont (Coleoptera, Hydrophilidae) from Japan, with key to the Japanese species of Paracymus. Elytra. New Series 9(2): 285–288.

Motokawa M (2000) Biogeography of living mammals in the Ryukyu Islands. Tropics 10(1): 63–71. https://doi.org/10.3759/tropics.10.63

Nakajima J (2022) List of aquatic Coleoptera and Hemiptera of Japan. http://kuromushiya.com/mlist/mlist.html [Accessed Feb. 10 2022] [In Japanese]

Nakajima J, Hayashi M, Ishida K, Kitano T, Yoshitomi H (2020) Aquatic Coleoptera and Hemiptera of Japan. Bun-ichi Sôgô Shuppan, Tokyo, 351 pp. [In Japanese]

Nakane T, Matsui E (1986) A new species of the genus *Enochrus* Thomson from Japan, with a key to the species of the genus in Japan. The Journal of Law and Economics. Bulletin of Ohyodo Gakuen, Miyazaki 2(2): 78–84.

Ohmomo S, Takahashi K, Takai M (2008) List of Coleoptera collected on Amami-ôshima Island in 2007. Insect 58(2): 141–150. [In Japanese]

Orchymont A (1942) Contribution a l'étude de la tribu Hydrobiini Bedel, spécialement de sa sous-tribu Hydrobiae (Palpicornia-Hydrophilidae). Mémoires du Musée Royal d'Histoire Naturelle de Belgique 24(2): 1–68.

Osozawa S, Shinjo R, Armid A, Watanabe Y, Horiguchi T, Wakabayashi J (2012) Palaeogeographic reconstruction of the 1.55 Ma synchronous isolation of the Ryukyu Islands, Japan, and Taiwan and inflow of the Kuroshio warm current. International Geology Review 54(12): 1369–1388. https://doi.org/10.1080/00206814.2011.639954

Ota H (1998) Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Population Ecology 40(2): 189–204. https://doi.org/10.1007/BF02763404

Paykull G (1798) Fauna Svecica. Insecta. Tomus I. Joh. F. Edman, Upsaliæ, 358 pp.

Pu C (1964) The genus *Anacaena* Thomson of China (Coleoptera, Hydrophilidae). Acta. Entomologia Sinica 13: 396–400. [In Chinese]

Ribera I, Vogler AP (2000) Habitat type as a determinant of species range sizes: The example of lotic–lentic differences in aquatic Coleoptera. Biological Journal of the Linnean Society. Linnean Society of London 71(1): 33–52. https://doi.org/10.1111/j.1095-8312.2000.tb01240.x

Sanchez EGS, Delocado ED, Freitag H (2022) Two new species of *Anacaena* Thomson, 1859 (Coleoptera, Hydrophilidae) from Northern Luzon, Philippines. ZooKeys 1112: 11–25. https://doi.org/10.3897/zookeys.1112.85752

Sasaki T, Kimura M, Kawamura F (2002) Coleoptera. In: Yafuso M, Kinjo M, Hayashi M, Kohama T, Sasaki T, Kimura M, Kawamura F (Eds) Check List of the Insect of the Ryukyu Islands. Second Edition. The Biological Society of Okinawa, Nishihara-chô, Okinawa, 157–284. [In Japanese]

Satô M (1982) The Coleoptera of the Ozegahara moor. In: Hara H, Asahina S, Sakaguchi Y, Hogetsu K, Yamagata, N (Eds) Ozegahara: Scientific Researches of the Highmoor in Central Japan. Japan Society for the Promotion of Science, Tokyo, 379–408.

Satô M (1998) Aquatic Coleoptera of the Ryukyu Archipelago, III. Coleopterists'. News 121: 7–13. [In Japanese]

Sheth SD, Ghate HV, Fikáček M (2020) Review of *Coelostoma* of the Indian subcontinent (Coleoptera: Hydrophilidae) Part 1: *Coelostoma* s. str. and *Holocoelostoma*. European Journal of Taxonomy 690(690): 1–32. https://doi.org/10.5852/ejt.2020.690

Short AEZ, Fikáček M (2011) World catalogue of the Hydrophiloidea (Coleoptera): Additions and corrections II (2006–2010). Acta Entomologica Musei Nationalis Pragae 51(1): 83–122.

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38(4): 723–752. https://doi.org/10.1111/syen.12024

Song K-Q, Xue H-J, Beutel RG, Bai M, Bian D-J, Liu J, Ruan Y-Y, Li W-Z, Jia F-L, Yang X-K (2014) Habitat-dependent diversification and parallel molecular evolution: Water scavenger beetles as a case study. Current Zoology 60(5): 561–570. https://doi.org/10.1093/czoolo/60.5.561

Stephens JF (1835) Illustrations of British entomology; or, a Synopsis of Indigenous Insects: Containing Their Generic and Specific Distinctions. Mandibulata. Vol. V. Baldwin and Cradock, London. [Vol. 5 issued in 1832–1835; Hydrophiloidea (396–401, including Hydraenidae) is issued in 1835]

Thomson CG (1859) Skandinaviens Coleoptera, Synoptiskt Bearbetade. 1. Tom. Berlingska Boktryckeriet, Lund, [6 +] 290 pp. https://doi.org/10.5962/bhl.title.138677

Thomson CG (1867) Skandinaviens Coleoptera, Synoptiskt Bearbetade. Tom. IX. Berlingska Boktryckeriet, Lund, 407 pp. https://doi.org/10.5962/bhl.title.138677

Tominaga A, Matsui M, Nakata K (2014) Genetic diversity and differentiation of the Ryukyu endemic frog *Babina holsti* as revealed by mitochondrial DNA. Zoological Science 31(2): 64–70. https://doi.org/doi.org/10.2108/zsj.31.64

Tôyama M (2014) A note on the names of the Ryukyu Islands. Bulletin of the Historiographical Institute 37: 59–68. [In Japanese]

Watanabe K (2019) A new distributional record of *Chaetarthria saundersi* d'Orchymont, 1923 (Coleoptera, Hydrophilidae) from Yonaguni-jima Island, the Ryukyus, Japan. Elytra. New Series 9(2): 289–290.

Watanabe K, Minoshima YN (2020) First record of *Coelostoma bhutanicum* Jayaswal, 1972 (Coleoptera: Hydrophilidae) from Japan. Japanese Journal of Systematic Entomology 26(1): 151–152.