A new species of the East Asian endemic subgenus *Sadonebria* Ledoux et Roux (Coleoptera: Carabidae: *Nebria*) ground beetles from Japan

Новый вид жужелиц эндемичного восточно-азиатского подрода Sadonebria Ledoux et Roux (Coleoptera: Carabidae: Nebria) из Японии

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KEY WORDS: biogeography, comparative morphology, cryptic species, endophallus, male genitalia, new species, phylogeny, taxonomy.

КЛЮЧЕВЫЕ СЛОВА: биогеография, сравнительная морфология, скрытые виды, эндофаллус, гениталии самца, новый вид, филогения, таксономия.

ABSTRACT. Ground beetles in the East Asian endemic subgenus *Sadonebria* (Coleoptera: Carabidae: *Nebria*) show marked differentiation in the Japanese Archipelago, but their diversity has not been fully elucidated. Based on specimens from localities in western Chubu district, Honshu, Japan, *Nebria hakusana* Sasakawa, **sp.n.** is described. Comparison of male genital structures with the known consubgeners, and previously reported morphological and molecular phylogenies of this subgenus, suggest that *N. hakusana* Sasakawa, **sp.n.** is the most ancestral of the known Japanese endemic *Sadonebria*.

РЕЗЮМЕ. Жужелицы восточноазиатского эндемичного подрода Sadonebria (Coleoptera: Carabidae: Nebria) демонстрируют заметную дифференциацию на Японском архипелаге, но их разнообразие пока не выяснено в полном объёме. По экземплярам из западного округа Тюбу, Хонсю, Япония, описан новый вид, Nebria hakusana Sasakawa, sp.n. Сравнение строения мужских гениталий с известными близкими родами, а также ранее опубликованные морфологические и молекулярные филогении этого подрода позволяют предположить, что N. hakusana Sasakawa, sp.n. является наиболее плезиоморфным из известных эндемичных для Японии видов Sadonebria.

Introduction

Sadonebria Ledoux et Roux, 2005 is an endemic East Asian subgenus of the genus Nebria Latreille, 1802 (Coleoptera: Carabidae) and contains 17 species-group

taxa [Sasakawa, 2016]. Of these, Nebria chinensis Bates, 1872 has developed hind wings and is widely distributed in China, Korea, and Japan [Huber, 2017]. The remaining 16 taxa have atrophied hind wings and low dispersal ability, and are endemic to mountainous areas of Taiwan (Nebria niitakana Kano, 1930) and Japan (the remaining 15 taxa). Of the Japanese endemic taxa, 10 had previously been confused with Nebria sadona Bates, 1883 and have recently been recognized as distinct species [Sasakawa, Kubota, 2006; Sasakawa, 2008, 2009, 2010, 2016; Sasakawa, Toki, 2011]. These are typical cryptic species, which are similar to each other externally and distinguished by the shape of the endophallus, a membranous inner sac that is everted from the aedeagus of the male genitalia and had not been previously examined in these species [Habu, 1962; Uéno, 1985]. Sympatric occurrence was confirmed for one species pair [Sasakawa, Kubota, 2006], indicating that they are not subspecies of a single species (i.e., geographical races), but are distinct species that are reproductively isolated. Thus, the Japanese Archipelago is the center of diversification for the subgenus Sadonebria.

One of the unresolved issues in Japanese Sadonebria is that specimens have not been examined from many localities. In particular, specimens from western Chubu and eastern Kinki districts, which are the center of the distribution of Sadonebria in the archipelago (Fig. 1), have not yet been examined. Examination of specimens from localities from this region may elucidate the distributions of the known species and additional cryptic species, which are important for understanding the diversity of this subgenus. Here, a new species is

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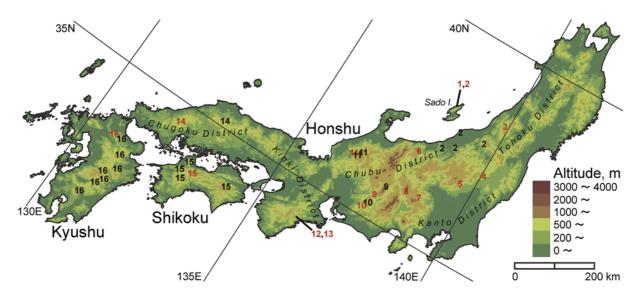


Fig. 1. Distribution of *Nebria (Sadonebria)* spp. in the Japanese Archipelago, compiled from Sasakawa [2016] and Sasakawa and Itô [2019]; *N. chinensis* Bates, which is distantly related to the remaining taxa, and samples that are not identified by genital morphology are not included. The numbers indicate: 1-N. sadona Bates; 2-N. saeviens Bates; 3-N. sasakawa; 4-N. nasuensis Sasakawa; 5-N. leechi Bates; 6-N. quinquelobata Sasakawa; 7-N. chichibuensis Sasakawa; 8-N. yatsugatakensis Sasakawa, 9-N. kiso Sasakawa; 10-N. mikawa Sasakawa; 11-N. hakusana Sasakawa **sp.n.**; 12-N. ohdaiensis Nakane, 13; N- tenuicaulis Sasakawa and Kubota; 14-N. jakuchisana Sasakawa; 15-N. shikokuensis Sasakawa; 16-N. trifida Sasakawa. Red letters denote the type localities of each species.

Рис. 1. Распространение видов Nebria (Sadonebria) на Японском архипелаге, по данным из Sasakawa [2016] и Sasakawa, Itô [2019]; находки N. chinensis Bates, который слабо связан с остальными таксонами, и экземпляры, которые не идентифицируются по морфологии гениталий, не показаны. Цифры соотвествуют: 1-N. sadona Bates; 2-N. saeviens Bates; 3-N. asahina Sasakawa; 4-N. nasuensis Sasakawa; 5-N. leechi Bates; 6-N. quinquelobata Sasakawa; 7-N. chichibuensis Sasakawa; 8-N. yatsugatakensis Sasakawa, 9-N. kiso Sasakawa; 10-N. mikawa Sasakawa; 11-N. hakusana Sasakawa sp.n.; 12-N. ohdaiensis Nakane, 13; N- tenuicaulis Sasakawa and Kubota; 14-N. jakuchisana Sasakawa; 15-N. shikokuensis Sasakawa; 16-N. trifida Sasakawa. Красные цифры обозначают типовые местонахождения для каждого вида.

described based on specimens obtained from the Fukui, Ishikawa, and Gifu Prefectures in the western part of Chubu district.

Materials and methods

Information on related species was obtained from Sasakawa [2008, 2009, 2010, 2016], Sasakawa and Kubota [2006], and Sasakawa and Toki [2011], who described key characters of the species, such as the male endophallus, based on their type specimens (species other than Nebria saeviens Bates, 1883) or specimens from the type locality (*N. saeviens*). Photographs of the holotypes of N. kiso Sasakawa, 2009 and N. mikawa Sasakawa, 2009, which were taken during my previous study [Sasakawa, 2009], were also used for comparisons. Two taxa, leechi Bates, 1889 and ohdaiensis Nakane, 1963, are treated as distinct species, not as subspecies of *N. sadona*, based on their non-monophyletic relationship in morphological phylogeny [Sasakawa, Kubota, 2006]. The endophallus was everted by injecting toothpaste from the basal end of the aedeagus [Berlov, 1992]. The terminology of endophallus structures follows Sasakawa [2016]. The following abbreviations are used for the collections to which specimens are deposited and for morphological characters: EUM — Ehime University Museum, Matsuyama, Japan; and KS — the K. Sasakawa collection deposited in the Laboratory of Zoology, Department of Science Education, Faculty of Education, Chiba University, Chiba, Japan; PL — pronotum length along the median line; PW — pronotum width at the widest part; PAW — width of the anterior margin of the pronotum; PPW — width of the posterior margin of the pronotum; EL — elytral length from the level of the shoulder tip to the apices; EW — elytral width at the widest part.

Taxonomy

Nebria (Sadonebria) hakusana Sasakawa, **sp.n.** Figs 2–7.

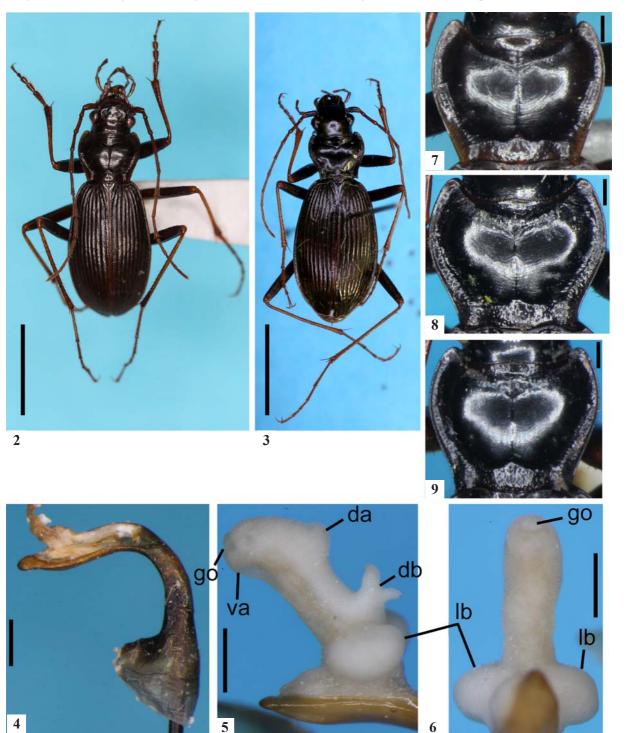
TYPE MATERIALS: Holotype, \circlearrowleft (KS), Shinmata Pass, Nomuki, Katsuyama, Fukui Prefecture, Japan, 1.vi.2020, S. Inoue leg.; paratypes, $1 \circlearrowleft$ (KS), Mt. Sanpôkuzure, ca 1,200 m, Shirakawa City, Gifu Prefecture, Japan, 23–24.vi.2005, H. Ikeda leg.; $1 \circlearrowleft$ 22 \looparrowright (EUM), "KAGA-Hakusan Nakahanba \sim Bettonozoki (1,500 \sim 1,750 m) 1 VIII. 1973 M. Miyatake" [Nakahanba (1,500 m) \sim Bettonozoki (1,500 m), Mt. Hakusan, Shiramine, Hakusan, Ishikawa Prefecture, Japan].

DESCRIPTION. External characters (Figs 2–3). Body length (including mandibles): \$\tilde{\sigma}\$, 12.5–13.6 mm; \$\varphi\$, 12.6–12.8 mm. PL/PW: 0.73–0.76; PAW/PW: 0.73–0.76; PPW/PW: 0.64–0.68. EL/EW: 1.59–1.71. Habitus slender. Hind wings atrophied. Dorsal surface shiny and almost black; head with a dark-brown patch between eyes; pronotal and elytral margins dark-brown; mouth appendages and antennae red-

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dish to dark brown; legs dark brown except for femora, which are blackish brown. Pronotum cordate and convex; lateral margins reflexed throughout; hind angle acute; laterobasal impression large and deep; median line distinct in the middle, absent near the anterior margin, rudimentary near the posterior margin; surface of central part and near the anterior

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Figs 2–9. *Nebria (Sadonebria)* spp.: 2–7 — *N. hakusana* sp.n.; 8 — *N. kiso*; 9 — *N. mikawa*; 2–3 — habitus; 4 — aedeagus; 5–6 — endophallus; 7–9 — pronotum; 2–3, 7–9 — dorsal view; 4–5 — right lateral view; 6 — ventral view; 2, 5–9 — holotype, male; 3 — paratype, female; 4 — paratype, male from Mt. Sanpôkuzure. Abbreviations: da — dorsoapical lobe; db — dorsobasal lobe; go — gonopore; lb — laterobasal lobe; va — ventroapical lobe. Scales: 5.0 mm for 2–3; and 0.5 mm for 4–9.

Рис. 2–9. *Nebria (Sadonebria)* spp.: 2–7 — *N. hakusana* **sp.n.**; 8 — *N. kiso*; 9 — *N. mikawa*; 2–3 — габитус; 4 — эдеагус; 5–6 — эндофаллус; 7–9 — переднеспинка; 2–3, 7–9 —сверху; 4–5 — справа; 6 — снизу; 2, 5–9 — голотип, самец; 3 — паратип, самка; 4 — паратип, самец с горы Санпокудзуре. Сокращения: da — дорсоапикальная доля; db — дорсобазальная доля; go — гонопор; lb — латеробазальная доля; va — вентропапикальная доля. Масштаб: 5,0 мм для рис. 2–3; 0,5 мм для рис. 4–9.

margin almost smooth; surface near the posterior margins very sparsely punctate; surface of the lateral margins very sparsely punctate and/or shallowly, transversely wrinkled; two marginal setae on each lateral side, anterior setae near the widest pronotal point, and posterior setae near hind angles. Elytra oblong, widest behind the middle; 7–10 setigerous pores on interval 3. Abdominal sterna 4–7 usually with a pair of setae, but in the male from Mt. Sanpôkuzure, additional setae on left side of sternum 4 and on both sides of sternum 7.

Male genitalia (Figs 4–6). Aedeagus slender and strongly bent at apical 2/5; ventral contour of subapical part from lateral view arcuate ventrally; apex simple and widely rounded. Endophallus straight, elongate, directed posterodorsally; laterobasal lobes large, hemispherical; lateroapical lobes absent; dorsobasal lobe bifid from lateral view, with the subapex of basal one smaller than that of apical one; dorsoapical lobe widely swollen, and smaller than the laterobasal and dorsobasal lobes; ventroapical lobe barely swollen. Both right and left parameres spatulate, with the former larger than the latter.

DIAGNOSIS. Distinguished from *N. quinquelobata* Sasakawa, 2016, *N. kiso*, and *N. mikawa*, which are relatively closely distributed (Fig. 1), by the following characters: from *N. quinquelobata* by dark brown legs [versus yellowish brown legs in *N. quinquelobata*; Sasakawa, 2016], and from *N. kiso* and *N. mikawa* by less cordate and less punctate pronotum (Figs 7–9).

ETYMOLOGY. Named after the Hakusan Mountains, where the type materials were collected.

Discussion

The new species is currently known only from the Hakusan Mountains, on the border of the Fukui, Ishikawa and Gifu Prefectures (Fig. 1). Specimens of *Sadonebria* from the Hakusan Mountains have been repeatedly recorded as *N. sadona* [Hiramatsu, Usio, 2018 and references therein], and these specimens are also most likely *N. hakusana*.

A comparative morphology revealed that *N. hakusana* shares most of the endophallus character states with the widely distributed *N. chinensis* and Taiwanese endemic *N. niitakana* (Table 1), which split from the Japanese endemic taxa at the basal node(s) within *Sadonebria* phylogeny [Sasakawa, Kubota, 2006; Kavanaugh et al., 2021]. This suggests that *N. hakusana* is the most ancestral of the known Japanese endemic *Sadonebria*. This result is not surprising, because *N. ohdaiensis*, which is distributed relatively close to *N. hakusana* (Fig. 1), also has endophallus with many presumed ancestral character states (Table 1). These patterns suggest that the initial differentiation of the flightless *Sadonebria* from Japan occurred around the known localities of *N. hakusana* and *N. ohdaiensis*.

Table 1. Character states of the endophallus structures of Nebria (Sadonebria) spp.Таблица 1. Признаки структур эндофаллуса Nebria (Sadonebria) spp.LateroapicalDorsobasalDorsoapicalEndophalluslobe sizelobe shapelobe sizelength

Taxa	Lateroapical	Dorsobasal	Dorsoapical	Endophallus
	lobe size	lobe shape	lobe size	length
N. chinensis*	absent	bifid	small	> 1.5 mm
N. niitakana*	absent	slightly bifid	small	> 1.5 mm
N. asahina	large	simple	small	< 1.5 mm
N. chichibuensis	absent	simple	large	< 1.5 mm
N. hakusana	absent	bifid	small	> 1.5 mm
N. jakuchisana	absent	simple	small	< 1.5 mm
N. kiso	small	simple	large	< 1.5 mm
N. mikawa	small	simple	large	< 1.5 mm
N. nasuensis	large	simple	small	< 1.5 mm
N. quinquelobata	large	simple	large	< 1.5 mm
N. leechi	absent	simple	large	< 1.5 mm
N. ohdaiensis	small	hook-shaped	small	> 1.5 mm
N. saeviens	large	simple	large	< 1.5 mm
N. shikokuensis	absent	simple	large	< 1.5 mm
N. tenuicaulis	absent	simple	small	< 1.5 mm
N. trifida	absent	simple	large	< 1.5 mm
N. yatsugatakensis	small	simple	large	< 1.5 mm

NOTE. Except for *N. sadona*, for which no specimens other than the lectotype have been obtained since its original description. Two species, *N. chinensis* and *N. niitakana*, which were determined to be placed in the basal lineages in both morphological [Sasakawa, Kubota, 2006] and molecular [Kavanaugh et al., 2021] phylogenies, are marked with asterisk. The sizes of the lateroapical and dorsoapical lobes are compared against the laterobasal lobes: if the lobe is larger (smaller) than the laterobasal lobe, it is classified as "large" ("small"). The endophallus length is measured from base to gonopore. Boxes in black, grey, and white indicate presumed ancestral, intermediate, and derived character states, respectively.

ПРИМЕЧАНИЕ. Не включена *N. sadona*, для которой с момента первоописания не было найдено ни одного экземпляра, кроме лектотипа. Два вида, *N. chinensis* и *N. niitakana*, которые были отнесены к базальным линиям как в морфологической [Sasakawa, Kubota, 2006], так и в молекулярной [Kavanaugh et al., 2021] филогениях, отмечены звёздочкой. Размеры латероапикальной и дорсоапикальной долей сравнивают с латеробазальными долями: если доля крупнее (меньше) латеробазальной доли, её классифицируют как «большую» («маленькую»). Длина эндофаллуса измеряется от основания до гонопора. Ячейки чёрного, серого и белого цвета обозначают предполагаемые предковые, промежуточные и производные состояния признаков, соответственно.

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Interestingly, a similar result has been reported based on a comparative morphology for *N. reflexa* Bates, 1883 and its related species that belong to a different *Nebria* subgenus (*Falcinebria*), inhabit a similar environment, and have almost the same distribution in the archipelago. That is, the basal lineages of these species are also distributed in the western part of the Chubu District [Sasakawa, 2020]. This concordance may indicate that the ancestors of *Sadonebria* and *Falcinebria* colonized the Japanese Archipelago at the same time. These hypotheses regarding the region and timing of the initial differentiation could be tested by future molecular phylogenetic analyses of the two groups.

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