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# *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, a new subspecies of stag beetle (Coleoptera: Lucanidae) from northern Vietnam

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## Abstract

The stag beetle genus *Odontolabis* Hope, 1842 (Lucanidae: Odontolabini) contains approximately 60 species, predominantly restricted to the Oriental Region, with 6 named species from Vietnam. Here, we describe a new subspecies of *Odontolabis pareoxa* Bomans, Lacroix & Ratti, 1973 from Yên Bái Province in northern Vietnam: *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies**. This new subspecies is distinguishable from the nominotypical subspecies by cephalic and pronotal characteristics in males. The findings also indicate a partial similarity in the stag beetle fauna between northern Vietnam and adjacent areas of northern Myanmar.

Key words: Lucaninae, Odontolabini, Odontolabis pareoxa, Southeast Asia, Indochinese Peninsula, taxonomy

## Introduction

With about 60 species, *Odontolabis* Hope, 1842 (Lucanidae: Odontolabini) is a relatively species-rich genus of stag beetles (Fujita 2010; Maruyama 2024). The genus is widely distributed in Southeast Asia, China, India, and Sri Lanka, covering the entire Oriental Region (Mizunuma & Nagai 1994; Krajcik 2001, 2003; Fujita 2006, 2010; Dooseok 2023; Maruyama 2024). They are important commercially as members of this genus are popular among insect collectors and breeders because of their large size, vivid body colors, and attractive body parts, especially the mandibles in males (Matsumoto & Knell 2017; Wang *et al.* 2018; Ying *et al.* 2021). *Odontolabis* is also of considerable interest among researchers in evolutionary biology and behavior (*e.g.*, Rowland & Emlen 2009; Matsumoto & Knell 2017; Kawano 2020).

Many *Odontolabis* species are regionally endemic, with each island or region having its own unique fauna. *Odontolabis* has diversified markedly in Indonesia, especially on the large islands of Sulawesi, Borneo, and Sumatra (Fujita 2006 2010; Maruyama 2024). In contrast, several *Odontolabis* species occur in the Indochinese Peninsula. To date, six *Odontolabis* species, with three subspecies, have been known from Vietnam (Bartolozzi *et al.* 2016; Levet 2019; Maruyama 2024): *Odontolabis mouhoti paulei* Levet, 2019; *Odontolabis cuvera sinensis* (Westwood, 1848); *Odontolabis siva siva* (Westwood, 1845); *Odontolabis pareoxa* Bomans, Lacroix & Ratti, 1973; *Odontolabis platynota* (Westwood, 1845); and *Odontolabis macrocephala* Lacroix, 1984. Of these, the latter three species are morphologically similar to each other. These species can be readily distinguished from other *Odontolabis* by their small blackish bodies, mandible structure, and several other morphological features of the head and pronotum, although they exhibit a generally typical shape for *Odontolabis*.

*Odontolabis pareoxa* is distributed in northeastern India, northern Myanmar, and southwestern Yunnan in China (Bomans *et al.* 1973; Fujita 2010; Zhan *et al.* 2022; Maruyama 2024) but was recently recorded in Lào Cai Province, northern Vietnam, based on a prionodont form male (Bartolozzi & Bambi 2019). This paper describes a new

subspecies of *O. pareoxa* within the Vietnamese population, namely *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies**, based on 11 male specimens from Yên Bái Province, northern Vietnam.

## Materials and methods

All specimens examined in this study have been deposited at the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Hanoi, Vietnam. In addition, a dorsal habitus image of the holotype of O. pareoxa (O. pareoxa pareoxa), available through Flickr (https://www.flickr.com/photos/nhm beetle id/45288220744; accessed on September 19, 2024), was examined (Fig. 7A, B). The data label of the holotype is quoted verbatim, with the text in double quotation marks (""); a slash (/) was used to separate lines on the same label. To examine the male genitalia, the specimens were relaxed and softened in hot water for 2 hours, and then the abdominal terminalia were detached from the body. These were treated with an 8% aqueous solution of potassium hydroxide (KOH) for half a day and then transferred to distilled water to flush out the remaining KOH solution. The terminalia were dissected, observed, and photographed under 80% ethyl alcohol (EtOH) aqueous solution. After examination, the dissected body parts were preserved with glycerin in a small plastic (polyethylene) vial that was attached to the same pin as the main body for future studies. Observations were made using a Nikon SMZ1500 stereomicroscope. Habitus photographs were taken using a Canon macro photo lens EF-S 60 mm f/2.8 Macro USM on a Canon EOS 90D digital camera, with the aid of a Canon MT-24EX twin flash. Detailed photographs of the abdominal terminalia and genitalia were obtained using an EOS 90D with an MP-E 65 mm f/2.8  $1-5\times$  macro lens and an MT-24EX. Helicon Focus 8.2.0 was optimized for image stacking. Adobe Photoshop Elements 15 was used for post-processing the images and grouping them into figure plates.

The morphological terminology follows Holloway (2007) and Yamamoto & Qodri (2023). The generic and species concepts follow Maruyama (2024), rather than Dooseok (2023), who established the distinct genus *Wallacealucanus* Dooseok, 2023, comprising 15 small-sized species previously classified in *Odontolabis* from Sulawesi Island (Indonesia) and also recognized the resurrected genus *Odontotyranus* Séguy, 1955. All measurements are provided in millimeters (mm) and expressed as "minimum-maximum."

The following measurements were used:

**Body length with mandibles (BLM)**: length of the body measured between the apex of the mandible and elytral apex along the midline;

**Body length without mandibles (BL)**: length of the body measured between the apex of the clypeus (or anterior margin of the head if the clypeus is not visible dorsally) and the elytral apex along the midline;

Body width (BW): maximum width of the body (equivalent to the pronotal width in this paper);

Mandible length (ML): length of the right mandible from the apex to its base;

**Head length (HL)**: length of the head from the apex of the clypeus (or anterior margin of the head if the clypeus is not visible dorsally) to the posterior margin of the occiput in the midline;

Head width (HW): maximum width of the head (including ocular canthi);

Pronotal length (PL): maximum length of the pronotum at the midline;

Pronotal width (PW): maximum width of the pronotum;

Elytral length (EL): length of the elytra from the basal border to the apex of the elytra along the suture (midline).

#### Results

#### Odontolabis pareoxa vietnamensis Yamamoto & Pham, new subspecies

(Figs 1-6; 7C)

*Odontolabis pareoxa*: Bartolozzi & Bambi 2019: 266. *Odontolabis* sp.: Maruyama 2024: 31, 91.

Type locality. Vietnam, Yên Bái.

**Type material.**  $(11 \& \bigcirc)$ . **Holotype:**  $\bigcirc$  (telodont form), "N. Vietnam: / Yen Bai, / July 2023" (IEBR). **Paratypes** (n=10): 1  $\bigcirc$  (priodont form), Mù Cang Chải, Yên Bái, Vietnam, June 2020 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, September 2022 (IEBR); 1  $\bigcirc$  (amphidont form), same data, but June 2023 (IEBR); 1  $\bigcirc$  (amphidont form), Yên Bái, North Vietnam, June 2020 (IEBR); 1  $\bigcirc$  (telodont form), same data, but June 2020 (IEBR); 1  $\bigcirc$  (telodont form), same data, but June 2020 (IEBR); 1  $\bigcirc$  (telodont form), same data, but July 2020 (IEBR); 2  $\bigcirc \bigcirc$  (mesodont form), same data, but May 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but June 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but May 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR); 1  $\bigcirc$  (telodont form), same data, but August 2021 (IEBR).

**Diagnosis.** The new subspecies is closely allied to the nominotypical subspecies in general appearance but can be differentiated by the following combination of characters in the males:

1) Post-ocular margin less developed, only weakly to moderately produced laterally (Fig. 7C), rather than strongly projecting laterally (Fig. 7A, B);

2) Pronotal anterolateral margins, particularly in the telodont form, usually smooth and rounded (sometimes only weakly emarginate) (Fig. 7C), instead of apparently roundly emarginate (Fig. 7A, B);

3) Pronotal anterior angles more or less rounded (Figs 4A; 7C), whereas those being angulate in *O. pareoxa pareoxa* (Fig. 7A, B);

4) Pronotal posterolateral angles, especially in the telodont form, only weakly emarginate (Fig. 7C), rather than deeply and strongly emarginate (Fig. 7A, B).

**Description of holotype, telodont male.** Size small for the genus, BLM: 45.3 mm. Measurements of different body parts in millimetre (mm): BL, 33.5; BW, 16.4; ML, 12.2; HL, 6.1; HW, 13.1; PL, 8.5; PW, 16.4; EL, 19.1; EW, 15.7.

Body (Fig. 1A–C) rather narrowly elongate, about 2.8 times (with mandibles) longer than wide. Surface (Fig. 1A–C) generally glabrous; dorsal surface matte in forebody, but strongly glossy in elytra (Figs 1A; 3A). Color uniformly blackish-brown to black; tarsi ventrally with yellowish-reddish brown fine and dense setae.

Head (Figs 1A–C; 3A; 4A, C, D) comparatively small, rectangular, moderately transverse, about twice as wide as long, widest across post-ocular projection, maximum width narrower than that of pronotum or elytra; surface matte textured; anterior margin broadly emarginate, somewhat vertically, shield-like in frontal view (Fig. 4D); pre-ocular margin with canthus well developed, flattened, with broadly arcuate lateral margin (Fig. 4A); post-ocular margin or temple (Figs 1A; 4A) somewhat projecting laterally, very slightly beyond level of ocular canthus; frons and vertex with large and shallow depression forming inverted triangle. Eyes (Figs 1A–C; 3A; 4A, C) moderately large, each completely margined with developed canthus. Mandibles (Figs 1A–C; 3A; 4A, C) long, slender, L-shaped, strongly curved near basal 1/3, about 2.0 times as long as head, shorter than head capsule and pronotum combined; first (basal) inner teeth short, inconspicuous, weakly directed inwards; median inner teeth absent; subapical longest (2<sup>nd</sup>) inner teeth short, simply pointed inward, with serration consisted of two small teeth between 2<sup>nd</sup> inner teeth and apex of mandibles (Fig. 4A). Clypeus small, narrow, weakly produced anteriorly, not visible dorsally. Antennae (Fig. 4A, C) with three-segmented club. Mentum (Fig. 4C) strongly transverse, trapezoidal, about 2.7 times wider than long, with weakly bilobate anterior margin, lacking keel in middle.

Pronotum (Figs 1A; 3A; 4A) short and wide, about 1.9 times wider than long; anterior margin with median area only weakly produced apically; pronotal anterolateral margins smooth, arcuate (not roundly emarginate); pronotal anterior angles rounded, rather than angulate; lateral margins in apical 3/4 almost parallel (except apical narrowing), only very weakly narrowed apically; basolateral margins rather weakly emarginate, forming obtusely acute posterolateral angles; posterior margin moderately sinuate; disc leathery, uniformly finely granulate. Prosternal process between procoxae (Figs 1C; 4C, D) strongly produced, subparallel-sided, with rounded apex. Scutellum (Fig. 4A) subtriangular, slightly wider than long, uniformly black; surface leathery, finely granulate.

Elytra (Figs 1A; 3A) long, elongate-oval, about 1.2 times longer than wide, broadest in basal 1/4; shoulders obtusely angulate; lateral margins broadly curved; surface smooth, very strongly glossy, coarsely very finely punctate, without metallic sheen.

Legs (Figs 1A–C; 3A; 4A, C) short; protibiae somewhat thick, straight, gradually widened apically, with three noticeable and one inconspicuous teeth and apical bifurcate paired teeth along outer margins in apical half (Fig. 4A, C); protibial teeth short, moderately developed, somewhat wide but acutely projecting; mesotibiae straight, with row of yellowish dense microsetae along inner edges, outer margins without external spines, apices with large apical spines; metatibiae similar structure and size with mesotibiae (but with shorter apical outer spines), as long as metatarsi.



FIGURE 1. Male habitus of *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies**, telodont form. A–C, holotype; D–F, paratypes (different specimen each). Dorsal (A, D–F), lateral (C) and ventral (B) views. Body sizes including mandibles: 45.3 mm (A–C); 43.1 mm (D); 46.3 mm (E); 42.4 mm (F).



FIGURE 2. Male habitus of *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies**, mesodont–priodont forms (mesodont: **A**, **B**; amphidont: **C**; priodont: **D**–**F**). **A**–**F**, paratypes (**A**–**C**, different specimen each; **D**–**F**, same specimen). Dorsal (**A**–**D**), lateral (**F**) and ventral (**E**) views. Body sizes including mandibles: 38.6 mm (**A**); 37.0 mm (**B**); 35.1 mm (**C**); 30.8 mm (**D**–**F**).



FIGURE 3. Male habitus of *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies**, dorsolateral view. A, holotype; **B**–**D**, paratypes (different specimen each). A, telodont form; B, mesodont form; C, amphidont form; D, priodont form. Body sizes including mandibles: 45.3 mm (A); 37.0 mm (B); 35.1 mm (C); 30.8 mm (D).

Abdomen (Fig. 1B) short, broad, strongly tapering posteriorly; ventrite V about 1.3 times as long as ventrite IV, with feebly medially emarginate apex. Tergite VIII (Fig. 5A) crescent shape, with membranous band along basal (anterior) margin, with incised longitudinal membranous area along midline of basal half. Sternite VIII (Fig. 5B) very strongly transverse, with small emargination along basal margin medially. Pleurite IX (Fig. 5C) not conterminous dorsally, well separated by membranous area. Sternite IX (Fig. 5D) with posterior margin weakly sclerotized.

Aedeagus (Fig. 6A–D) elongate, about 2.9 times longer than wide; basal piece (Fig. 6B–D) slightly longer than parameres, moderately constricted in basal part, constriction somewhat narrowed in dorsal and ventral views (Fig. 6B, C) or nearly straight in lateral view (Fig. 6D); flagellum thick and very long, weakly expanded at apex; parameres simple, with apex curved outward, acutely pointed in lateral view (Fig. 6D).

**Variation.** Male paratypes (n=10). Large sized (*i.e.*, telodont form) males much more easily and frequently found than those of nominotypical subspecies (*cf.* BLM: 28.0–45.2 mm in *O. pareoxa pareoxa*; Maruyama 2024). Telodont form (Figs 1D–F): body shape and size (BLM: 42.4–46.3 mm (average 44.68±1.79 mm, n=5)) generally similar to the holotype without evident morphological variations, but one specimen (Fig. 1E) with protibial teeth seemingly more developed. Mesodont and amphidont forms (Figs 2A, B; 3B, C; 4B): body size (BLM: 35.1–38.6 mm) smaller, with mandibles similar to those of mesodote and amphidont forms in *O. pareoxa pareoxa* and *O. platynota*; head with anterior margin not shield-like in frontal view (Fig. 4E; protibiae and other features generally matched with the holotype). Priodont form (Figs 2D–F; 3D; 4E): body size (BLM: 30.8 mm) much smaller, with short and entirely serrate mandibles; head with anterior margin not shield-like in frontal view (Fig. 4E), post-ocular projection slightly but more produced (Fig. 2D); protibiae and other features generally matched with the holotype. Measurements of the paratypes (n=10) in millimetres: BLM, 30.8–46.3; BL, 26.2–34.5; BW, 12.9–16.4; ML, 4.6–13.1; HL, 4.1–6.9; HW, 9.2–13.4; PL, 6.8–8.7; PW, 12.9–16.4; EL, 16.1–20.2; EW, 12.4–16.1.



FIGURE 4. Male forebody and head of *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies.** A, C, D, holotype; B, E, paratypes (different specimen each). A, forebody, telodont form, dorsal view; B, forebody, mesodont form, dorsal view; C, forebody, telodont form, ventral view; D, head, telodont form, frontal view; E, head, priodont form, frontal view.



**FIGURE 5.** Male abdominal terminalia of *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies**, holotype. **A**, tergite VIII, dorsal view; **B**, sternite VIII, ventral view; **C**, abdominal segment IX, dorsal view; **D**, abdominal segment IX, ventral view.

Female. Unknown.

Etymology. This new subspecies is named after the country of origin, Vietnam.

Distribution. Vietnam (Yên Bái, but also in Lào Cai based on Bartolozzi & Bambi 2019).

**Bionomics.** The detailed lifestyle has not been known yet, although the specimens were collected from early to late summer (May–September).



**FIGURE 6.** Male genitalia of *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies**. **A–D**, holotype; **E–H**, paratype (telodont form). **A**, **E**, aedeagus with flagellum, ventral view; **B**, **F**, aedeagus without flagellum, ventral view; **C**, **G**, aedeagus without flagellum, dorsal view; **D**, **H**, aedeagus without flagellum, lateral view.



FIGURE 7. Comparisons of mesodont males of *Odontolabis pareoxa pareoxa* Bomans, Lacroix & Ratti, 1973 (holotype: A, B) and *Odontolabis pareoxa vietnamensis* Yamamoto & Pham, **new subspecies (C).** A, general habitus, dorsal view; B, head and pronotum, dorsal view; C, ditto. Photo credits (A, B): photo by Keita Matsumoto, © 2018 Natural History Museum, London, both modified, licensed under the Creative Commons Attribution 2.0 Generic Deed license (CC BY 2.0, https://www.flickr. com/photos/nhm\_beetle\_id/45288220744), derived from Flickr.

## Discussion

Recently, Bartolozzi & Bambi (2019) recorded "Odontolabis pareoxa" in Vietnam for the first time, but this was based on a single small male specimen. Here, we examined additional specimens from this country, revealing a wide range of forms and sizes. Our study of these new materials identified several notable morphological differences between the Vietnamese population of "O. pareoxa" and populations from the type locality (Naga Hills, Nagaland, northeastern India) and surrounding areas, as shown in Table 1. Notably, a substantial geographical gap exists between these populations, spanning northern Laos and Thailand. Therefore, it is reasonable to differentiate these two populations as distinct subspecies: Odontolabis pareoxa pareoxa Bomans, Lacroix & Ratti, 1973, and O. pareoxa vietnamensis Yamamoto & Pham, new subspecies. The new subspecies has been found exclusively in northern Vietnam, whereas the nominotypical subspecies occurs in a geographically distant region: India, northern Myanmar, and southwestern China (Dehong Dai and Jingpo Autonomous Prefecture, southwestern Yunnan, near the border of Kachin, northern Myanmar; Zhan et al. 2022). Recent discoveries of stag beetles from northern Vietnam, including Lucanus ludivinae flavipes Xin, He, Zhong & Qi, 2024 (Xin et al. 2024) and Hemisodorcus branaungi ssp. (Dooseok 2023) as well as the present example, suggest a partial similarity in faunal elements between northern Vietnam and the surrounding areas of northern Myanmar. Further investigation into the relationship between these two subspecies is necessary, particularly through the study of specimens from additional localities, especially in the areas between them. Given the higher elevation of the known locality (*i.e.*, Mù Cang Chải, Yên Bái) of O. pareoxa vietnamensis Yamamoto & Pham, new subspecies, it is unlikely to be distributed in Cambodia (Maguart et al. 2023), where much of the country is at a lower elevation. Additional biodiversity surveys are needed to identify overlooked lucanid taxa in the Indochinese Peninsula (e.g., Maquart et al. 2023; Yamamoto & Sengsay 2023).

Characters	<i>O. pareoxa</i> <i>vietnamensis</i> , new subspecies	O. pareoxa pareoxa	O. platynota	O. macrocephala
Mandible forms in telodont males	strongly curved, L- shaped (Figs 1A, B, D–F; 4A, C)	strongly curved, L- shaped (Fujita 2010: fig. 383-1; Maruyama 2024: fig. 41-1)	moderately arcuate (Fujita 2010: fig. 381- 4; Maruyama 2024: fig. 40-4)	weakly broadly arcuate, nearly straight (Fujita 2010: fig. 382- 1; Maruyama 2024: fig. 43-6)
Post-ocular margin of head in telodont males	weakly to moderately but rather sharply projecting laterally (Fig. 1A, B, D–F)	strongly sharply projecting laterally (Fig. 7B; Fujita 2010: fig. 383-1; Maruyama 2024: fig. 41-1)	broadly rounded or somewhat triangularly rounded (Fujita 2010: fig. 381-4; Maruyama 2024: fig. 40-4)	very broadly rounded (Fujita 2010: fig. 382- 1; Maruyama 2024: fig. 43-6)
Pronotal apicolateral margins	rounded (sometimes weakly emarginate) (Figs 1A, D–F; 2A– D; 4A, B; 7C)	evidently roundly emarginate (Fig. 7B; Fujita 2010: fig. 383-1, 383-2, 383-3; Maruyama 2024: fig. 41-1, 41-2)	rounded (Fujita 2010: fig. 381-1, 381-4, 381- 5, 381-6; Maruyama 2024: fig. 40-1, 40-4, 40-6)	rounded (Fujita 2010: fig. 382-1, 382-2; Maruyama 2024: fig. 43-6)
Pronotal anterior corners	rounded to generally rounded (Figs 1A, D–F; 2A–D; 4A, B; 7C)	angulate (Fig. 7B; Fujita 2010: fig. 383-1, 383-2, 383-3; Maruyama 2024: fig. 41-1, 41-2)	rounded (Fujita 2010: fig. 381-1, 381-4, 381- 5, 381-6; Maruyama 2024: fig. 40-1, 40-4, 40-6)	rounded (Fujita 2010: fig. 382-1, 382-2; Maruyama 2024: fig. 43-6)
Pronotal posterolateral corners	weakly shallowly emarginate (Figs 1A, D–F; 2A–D; 4A, B; 7C)	strongly deeply emarginate (Fig. 7B; Fujita 2010: fig. 383-1, 383-2, 383-3; Maruyama 2024: fig. 41-1, 41-2)	very weakly emarginate (Fujita 2010: fig. 381-1, 381-4, 381-5, 381-6; Maruyama 2024: fig. 40-1, 40-4, 40-6)	weakly emarginate (Fujita 2010: fig. 382- 1, 382-2; Maruyama 2024: fig. 43-6)
Surface of elytra	strongly glossy (Figs 1A, D–F; 2A–D; 3)	strongly glossy (Fujita 2010: fig. 383-1, 383-2, 383-3; Maruyama 2024: fig. 41-1, 41-2)	matte (Fujita 2010: fig. 381-1, 381-2, 381-4, 381-5, 381-6; Maruyama 2024: fig. 40-1, 40-2, 40-4, 40-6)	matte (Fujita 2010: fig. 382-1, 382-2; Maruyama 2024: fig. 43-6)
Protibial teeth along outer edges	usually short, more or less wide, sparsely distributed (Figs 1A, B, D, F; 2A–E; 4A– C), but occasionally somewhat longer and narrower (Fig. 1E)	short to moderate length, rather narrow, sharply pointed, sparsely distributed (Fujita 2010: fig. 383-1, 383-2, 383-3; Maruyama 2024: fig. 41-1, 41-2)	inconspicuous to somewhat long, dull to sharply pointed, densely distributed (Fujita 2010: fig. 381- 1, 381-2, 381-4, 381-5, 381-6; Maruyama 2024: fig. 40-1, 40-2, 40-4, 40-6)	very long, slender, extremely sharply pointed, densely distributed (Fujita 2010: fig. 382-1, 382- 2; Maruyama 2024: fig. 43-6)
Distribution	Vietnam (Yên Bái, but also in Lào Cai based on Bartolozzi & Bambi 2019)	China (southwestern Yunnan), northeastern India, northern Myanmar (Maruyama 2024)	China, Laos, Myanmar, Thailand (?), and Vietnam (Maruyama 2024)	China (?), Laos, Myanmar, Thailand, and Vietnam (?) (Maruyama 2024)

TABLE 1. Differential diagnosis and distributions of the new subspecies and related species.

#### **Data Availability**

The higher-resolution figures are available through the Zenodo repository (https://doi.org/10.5281/ zenodo.14062659).

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