Contributions to the genus *Pseudorhaetus* Planet 1899 (Coleoptera: Lucanidae), with remarks on *Weinreichius* Lacroix 1978 and *Yumikoi* Arnaud & Miyashita 2006

Jing-Zhi Lin (林敬智)

Abstract - A comprehensive taxonomic revision of the stag beetle genus *Pseudorhaetus* Planet 1899 (Coleoptera: Lucanidae) is presented. The Taiwanese subspecies *Pseudorhaetus sinicus concolor* Benesh 1960 is to be considered morphologically conspecific with the mainland Chinese *P. sinicus sinicus* (Boileau 1899), leading to the new synonymy: *Pseudorhaetus sinicus* (Boileau 1899) = *P. sinicus concolor* Benesh 1960, **syn. nov**. Furthermore, comparative analysis supports the synonymy of the monotypic genus *Weinreichius* Lacroix 1978 and genus *Yumikoi* Arnaud & Miyashita 2006 with *Pseudorhaetus* (**syn. nov.**), resulting in the new combination *Pseudorhaetus perroti* (Lacroix 1978) (**comb. nov.**) and *Pseudorhaetus makii* (Arnaud & Miyashita 2006) (**comb. nov.**). An updated catalogue and identification key for *Pseudorhaetus* are also provided.

Key words: Lucanidae, *Pseudorhaetus*, synonyms, Taiwan, taxonomy, Vietnam, *Weinreichius*, *Yumikoi*.

Riassunto - Contributi alla conoscenza del genere *Pseudorhaetus* Planet 1899 (Coleoptera: Lucanidae), con osservazioni su *Weinreichius* Lacroix 1978 e *Yumikoi* Arnaud & Miyashita 2006.

Viene presentata una revisione tassonomica completa dei coleotteri lucanidi del genere *Pseudorhaetus* Planet 1899 (Coleoptera: Lucanidae). La sottospecie taiwanese *Pseudorhaetus sinicus concolor* Benesh 1960 è da considerarsi morfologicamente conspecifica con la sottospecie cinese continentale *P. sinicus sinicus* (Boileau 1899), determinando la seguente nuova sinonimia: *Pseudorhaetus sinicus* (Boileau 1899) = *P. sinicus concolor* Benesh 1960, **syn. nov.** Inoltre, l'analisi comparativa supporta la sinonimia del genere monotipico *Weinreichius* Lacroix 1978 e del genere *Yumikoi* Arnaud & Miyashita 2006 con *Pseudorhaetus* (**syn. nov.**), con conseguente istituzione delle nuove combinazioni *Pseudorhaetus perroti* (Lacroix 1978) (**comb. nov.**) e *Pseudorhaetus makii* (Arnaud & Miyashita 2006) (**comb. nov.**). Vengono inoltre forniti un catalogo aggiornato e una chiave dicotomica per l'identificazione delle specie di *Pseudorhaetus*.

Parole chiave: Lucanidae, *Pseudorhaetus*, sinonimi, Taiwan, tassonomia, Vietnam, *Weinreichius*, *Yumikoi*.

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INTRODUCTION

The genus *Pseudorhaetus* Planet 1899 (Coleoptera: Lucanidae: Lucaninae: Dorcini) is an Oriental group distributed in the montane forests of Taiwan, southern China, and Vietnam. Comprising 4 recognized taxa (including subspecies) globally, the genus has been traditionally considered closely allied to *Rhaetulus* Westwood 1871 and *Rhaetus* Parry 1864 based on external morphology (Mizunuma & Nagai, 1994; Fujita, 2010; Tsuchiya, 2024). The diagnosis of the genus, according to revisions by Fujita (2010) and the subsequent redefinition by Huang & Chen (2013), relies on several consistent morphological and genitalic characters: (1) a prominent, rounded postocular expansion situated behind the male compound eyes; (2) male mandibles that are characteristically slender and lack a distinct apical fork; (3) weak or absent sexual dimorphism in protibial morphology; (4) a head length-to-width ratio in major males of approximately 0.42-0.54; (5) a pronotum with finely crenulate lateral margins and no distinct anterior lateral angle; (6) male genitalia featuring a permanently everted, trifurcate internal sac (basal portion constituting 65%-85% of the total length) and a pair of symmetrical, expansible dorsal penial pouches; and (7) females characterized by an evenly punctate head without protuberances, a bifurcate protibial apex, a distinct notch on the last ventrite, and a tubular spermatheca that widens toward the apex.

Although *P. oberthuri* is the type species of the genus, *P. sinicus* has a more complex and controversial taxonomic history. Initially described by Boileau (1899) and tentatively placed in *Rhaetulus*, it was later transferred to *Pseudorhaetus*. A primary source of ambiguity concerns the status of the Taiwanese population. While Miwa (1931) misidentified Taiwanese specimens as *Rhaetulus sauteri*, Benesh (1960) subsequently described them as the subspecies *P. sinicus concolor*, mainly diagnosed by the entirely black femora. Huang & Chen (2013) later noted that the male genitalia of Taiwanese and mainland populations show no significant differences, effectively leaving femoral coloration as the unique distinguishing character for the subspecies. However, the stability of this diagnostic trait has been increasingly questioned. Observations of reddish-femora individuals in Taiwan and black-femora individuals in mainland China suggest

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potential phenotypic plasticity or geographic variability (Zhan & Yang, 2025). These inconsistencies challenge the reliability of the current subspecific classification and underscore the absence of a comprehensive study integrating detailed morphological and genitalic comparisons to rigorously re-evaluate the validity of *P. sinicus concolor*. Furthermore, the generic placement of the monotypic genus *Weinreichius* Lacroix 1978 (with *W. perroti Lacroix 1978 as type species*) remains controversial. While some researchers (e.g., Tsuchiya, 2024) argue for its independent status based on some distinct external traits (e.g., the variable postocular lobe and pronotal form), others (e.g., Fujita, 2010) have suggested its close affinity or possible synonymy with *Pseudorhaetus* based on overall habitus. A decisive evaluation, particularly through comparison of the male genitalic structures, is still lacking.

The taxonomic status of the monotypic genus *Yumikoi* Arnaud & Miyashita 2006, has remained contentious since its description. Originally described from only two male specimens without genitalic or phylogenetic evidence, the genus was separated from *Weinreichius* primarily by clypeal characters, which are often subject to allometric variation. Although Tsuchiya (2024) subsequently suggested that *Yumikoi* may be synonymous with *Weinreichius* based on external morphology, no formal taxonomic action was taken. The recent molecular evidence from Zheng *et al*. (2026) unequivocally places *Yumikoi*, *Weinreichius*, and *Pseudorhaetus* within a single clade. Motivated by these findings, the present study integrates molecular and detailed genitalic evidence to resolve the long-standing taxonomic confusion surrounding this lineage.

This study aims to resolve these aforementioned taxonomic issues by: (1) re-evaluating the subspecific status of *P. sinicus concolor* based on detailed morphological and genitalic examinations; (2) determining the generic position of *Weinreichius* by assessing the allometric nature of its diagnostic characters; and (3) determining the generic placement of *Yumikoi* through comparative analysis of its key morphological features and systematic affinities. Thereby establishing a more robust and monophyletic definition for the genus *Pseudorhaetus*.

MATERIAL AND METHODS

A total of 62 specimens were examined in this study. All specimens were legally collected and procured in compliance with relevant ethical guidelines and local regulations concerning entomological sampling and trade.

Taxonomic identification was primarily based on Fujita (2010), Tsuchiya (2024), and Zhan & Yang (2025), with subsequent classification and nomenclature following Huang & Chen (2013).

Male genitalia were dissected from selected dry specimens. The genitalia were cleared in a 10% Potassium Hydroxide (KOH) solution for approximately 24 hours (with the duration adjusted based on the degree of sclerotization), rinsed in distilled water, and stored in glycerin microvials pinned beneath the corresponding specimens.

External morphological characters, including the shape of the mandibles, clypeus, pronotal lateral margins, and body size were observed using a stereomicroscope. All specimens were photographed with a digital camera equipped with a macro lens.

The material examined is deposited in the following collections:

- **JZLC**: Jing-Zhi Lin Collection, Taipei, Taiwan.
- **FMNH**: Field Museum of Natural History, Chicago, Illinois, USA.

RESULTS

Family Lucanidae Latreille 1804
Tribe Dorcini Parry 1864 *sensu* Huang & Chen 2013
Genus *Pseudorhaetus* Planet 1899
= *Weinreichius* Lacroix 1978, **syn. nov.**
= *Yumikoi Arnaud & Miyashita 2006,* **syn. nov.**
Chinese name: 擬鹿角鍬形蟲屬

Pseudorhaetus oberthuri Planet 1899 (Figs 1C, 3B, F, J, 5I-J)

Chinese name: 紅背漆黑鹿角鍬形蟲/紅背擬鹿角鍬

Pseudorhaetus oberthuri Planet 1899: 174. Type locality: “Haut Tonkin, N.-O. du Bas-Laos” [= Ha Giang Province, northern Vietnam]; figures of male and female provided in the original description.; Benesh, 1960: 110; Fujita, 2010: 230, pl. 148, figs. 675-1–675-5; Huang & Chen, 2013: 194-195 habitus and genitalia; Tsuchiya, 2024: 22, 26, 95; Zhan & Yang, 2025: 421-423.

Material examined. VIETNAM: Lao Cai Province: 2♂♂, 1♀, Sa Pa, VII.2016, local collector (JZLC).

Distribution. VIETNAM: Ha Giang Province, Lao Cai Province. **CHINA**: Yunnan Province (records require further confirmation; see Remarks). Occurs at elevations between 1400-1600 m.

Variation. Body length. (including mandibles): Male: 29.4-60.0 mm; Female: 26.2-36.0 mm.

Remarks. This species is the nomenclatural type of the genus. According to field observations summarized by Tsuchiya (2024), it has been recorded in Ha Giang Province, northern Vietnam, with an active season spanning from May to July. Recent local observations (N. M. Tuan, pers. comm., 2026) indicate that its occurrence peaks in June, with a distribution strongly localized in some areas within Ha Giang. The species is notably diurnal, frequently observed gathering on the sap flows of Fagaceae trees at elevations of 1,400-1,600 m; furthermore, individuals do not appear to be attracted to artificial light. Although Huang & Chen (2013) listed records from Honghe and Yuxi in Yunnan, China (approximately 200-300 km northwest of Ha Giang), these records were not based on personally examined specimens. Given the significant geographical disjunction from the confirmed core range, these authors emphasized that the presence of *P. oberthuri* in China requires further field verification.

Pseudorhaetus sinicus (Boileau 1899) (Figs 1D-F, 2A-F, 3D, H, L, 4A-C, 5E-H)

Chinese name: 漆黑鹿角鍬形蟲/黑擬鹿角鍬

Rhaetulus (?) *sinicus* Boileau 1899: 111. Type locality: “Koua Toun, par M. de Latouche” [= Kuatun, Fujian Province, China, collected by Mr. de Latouche];

Pseudorhaetus sinicus: Benesh 1960: 110; *Pseudorhaetus sinicus sinicus*: Mizunuma & Nagai 1994: 259, pl. 86, figs 3541–3544; Fujita, 2010: 230, pl. 148, figs 6771–6773; Huang & Chen, 2013: 192-193 (habitus and genitalia); Tsuchiya, 2024: 20, 95; Zhan & Yang, 2025: 418-419.

= *Rhaetulus sauteri* (*Auctorum*, non Möllenkamp 1912): Miwa, 1931: 325, figs of ♂ & ♀ (homonym of *Rhaetulus sauteri* Möllenkamp 1912).

= *Pseudorhaetus concolor* Benesh 1960: 110. Replacement name for *Rhaetulus sauteri* Miwa 1931 (nec Möllenkamp 1912); Chang, 1993: 15,43.

= *Pseudorhaetus sinicus concolor*: Mizunuma & Nagai, 1994: 259, pl. 86, figs 3545–3549; Chang, 2006: 82-83; Chang, 2024: 84-85.; Fujita, 2010: 230, pl. 148, figs 6774–6777; Huang & Chen, 2013: 193-194 (habitus and genitalia); Tsuchiya, 2024: 21, 95; Zhan & Yang, 2025: 420-421. **New synonymy.**

Type material examined. (Figs. 4A-C)

Pseudorhaetus sinicus concolor Benesh 1960: Holotype ♂ (FMNH, #4518592). Labels: (1) "FORMOSA S. MINOWA" [printed]; (2) "Arisan / 17VIII1935" [handwritten]; (3) "Chicago Nat Hist Mus / B. Benesh Colln. / Lucanidae (Benesh / Access No. 4389)" [printed]; (4) "*Rhaetulus* / *sauteri* / Möll." [handwritten]; (5) "*Pseudorhaetus* / *concolor* / BB '56 Benesh" [handwritten]; (6) "Holotype / B. Benesh" [handwritten, red]; (7) "*Pseudorhae* / *tus* / *concolor*" [handwritten, red]; (8) "FMNHINS / 4518592 / FIELD MUSEUM / Pinned" [printed, QR code]; (9) "PHOTOGRAPHED / Jessica Wadleigh 2024 / CIL Request" [printed, light blue].

Additional material examined. CHINA: Fujian Province: Sanming City, 15.VII.2012, 2♂♂, 1♀, local collector.

TAIWAN: New Taipei City: Sanxia District, 21.VI.2018, 2♂♂, 3♀♀, local collector; **Taoyuan City:** Fuxing Township, Mt. Lala, 28.VI.2016, 4♂♂, 2♀♀, local collector; **Yilan County:** Datong Township, Mingchi (Northern Cross-Island Highway), 11.VII.2011, 4♂♂, 1♀, local collector; Datong Township, Nanshan, 21.VI.2024, 2♂♂, local collector; Nan'ao Township, Jinyang Village, 28.VI.2023, 3♂♂, 2♀♀, local collector; **Hsinchu County:** Jianshi Township, Mamei, 15.VII.2018, 2♂♂, 2♀♀, local collector; **Hsinchu County:** Jianshi Township, Mamei, 15.VII.2018, 3♂♂, 2♀♀, local collector; **Hualien County:** Guangfu Township, Guangfu Forest Road, 16.VII.2022, 2♂♂, 1♀, local collector; **Taitung County:** Beinan Township, Lijia Forest Road, 1.IX.2025, 1♂, local collector; **Pingtung County:** Chunri Township, Dahan Mountain Forest Road, 25.VII.2019, 1♂, local collector. All specimens are deposited in the JZLC collection.

Variability. Body length. Male: 18.0-70.0 mm (including mandibles); Female: 16.0-46.0 mm.

Distribution. TAIWAN: (New Taipei, Taoyuan, Hsinchu, Miaoli, Nantou, Chiayi, Yunlin, Pingtung, Taitung, Hualien, Yilan) all specimens recorded at elevation between 800-2000 m. **CHINA:** (Fujian, Zhejiang, Jiangxi, Guizhou, Guangxi, Hainan?) all specimens recorded at elevation between 1400-1600 m.

Taxonomic notes. Historically, the only character distinguishing the nominotypical subspecies *Pseudorhaetus sinicus sinicus* from the Taiwanese *P. sinicus* concolor has been femoral coloration: reddish-brown in the former and entirely black in the latter (Mizunuma & Nagai, 1994; Fujita, 2010; Huang & Chen, 2013; Tsuchiya, 2024). This study demonstrates that this character is taxonomically unreliable.

At the population level, individuals with reddish and black femora occur sympatrically in Taiwan. Notably, the reddish femoral morph occurs in substantial numbers in regions such as Hsinchu and Miaoli, indicating it represents a stable population characteristic within Taiwan, not a rare aberration. Controlled breeding trials further confirmed the phenotypic lability of this trait, as single female broods produced offspring with both color forms. These results show that the character is not a diagnostic subspecies feature. Examination of the holotype (FMNH #4518592) of *P. sinicus concolor* revealed distinct reddish markings on the femora, directly contradicting the original diagnosis (Benesh, 1960) of a uniformly black ("concolorous") specimen. Furthermore, the entirely black femoral phenotype is not exclusive to Taiwan, as it is also documented in mainland Chinese populations (Zhan & Yang, 2025: 419), demonstrating a lack of geographical specificity.

Comparative dissection of male genitalia showed no diagnostic differences between the Taiwanese and China mainland populations, consistently with prior observations (Huang & Chen, 2013). Given the instability and broad geographic overlap of femoral coloration, and the absence of supporting morphological or genitalic evidence, the Taiwanese subspecies should be considered as a junior synonym: *Pseudorhaetus sinicus* (Boileau 1899) = *P. sinicus concolor* Benesh 1960; **syn. nov.**

Pseudorhaetus perroti (Lacroix 1978), **comb. nov.**
(Figs 1A, 3A, E, I, 5A-B)
Chinese name: 南越擬鹿角鍬 / 佩洛帝鹿角鍬形蟲

Weinreichius perroti Lacroix 1978: 255-258, fig. 3. Type locality: "Vietnam: Dalat" [= Đà Lạt, Lâm Đồng Province, Vietnam]; photograph of male provided in the original description.; Mizunuma & Nagai, 1994: 259, pl. 86, fig. 3531; Tsuchiya, 2024: 23, 96.

Pseudorhaetus perroti (Lacroix 1978); Fujita, 2010: 230, pl. 148, figs 676-1–676-3.

Material examined. VIETNAM: Lam Dong Province: 2♂♂, Da Lat, VII.2021, local collector (JZLC).

Distribution. S VIETNAM: Lam Dong Province. Occurs at elevations between 1500-1700 m.

Variability. Body length. (including mandibles): Male: 31.6-83.0 mm; Female: 32.7-45.2 mm.

Taxonomic notes. The generic status of *Weinreichius* has long been unstable, having been treated either as a synonym of *Pseudorhaetus* or as a distinct genus. Fujita (2010) emphasized overall morphological similarity and considered the hypertrophied clypeus an insufficient diagnostic character for generic delimitation, thereby supporting the synonymization of the taxa. In contrast, Tsuchiya (2024) defended its generic validity based on external traits, particularly the development of the postocular lobe and the distinct pronotal shape. The present study addresses this conflict by analyzing male genitalia, a critical character system previously overlooked in this debate.

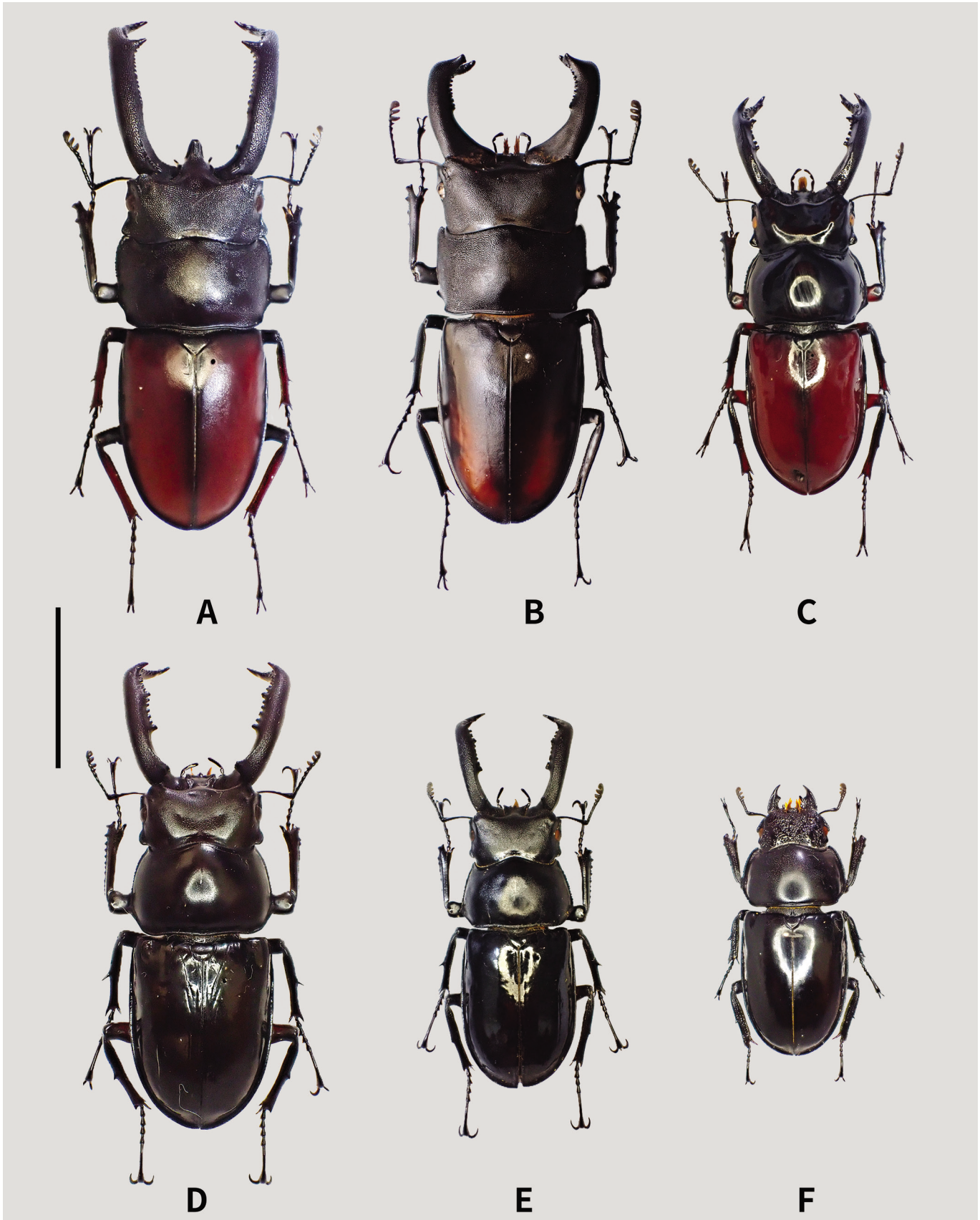


Fig. 1 - Morphological variability in *Pseudorhaetus*. Dorsal views of A) *P. perroti* male; B) *P. makii* male; C) *P. oberthuri* male; D) large male of P. *sinicus*; E) small male of P. *sinicus*; F) female of *P. sinicus*. / Variabillità morfologica in *Pseudorhaetus*. Viste dorsali di A) *P. perroti*, maschio; B) *P. makii*, maschio; C) *P. oberthuri*, maschio; D) grosso maschio di *P. sinicus*; E) piccolo maschio di *P.* sinicus; F) femmina di *P. sinicus*. Scale bar / Barra di scala: 20,0 mm.

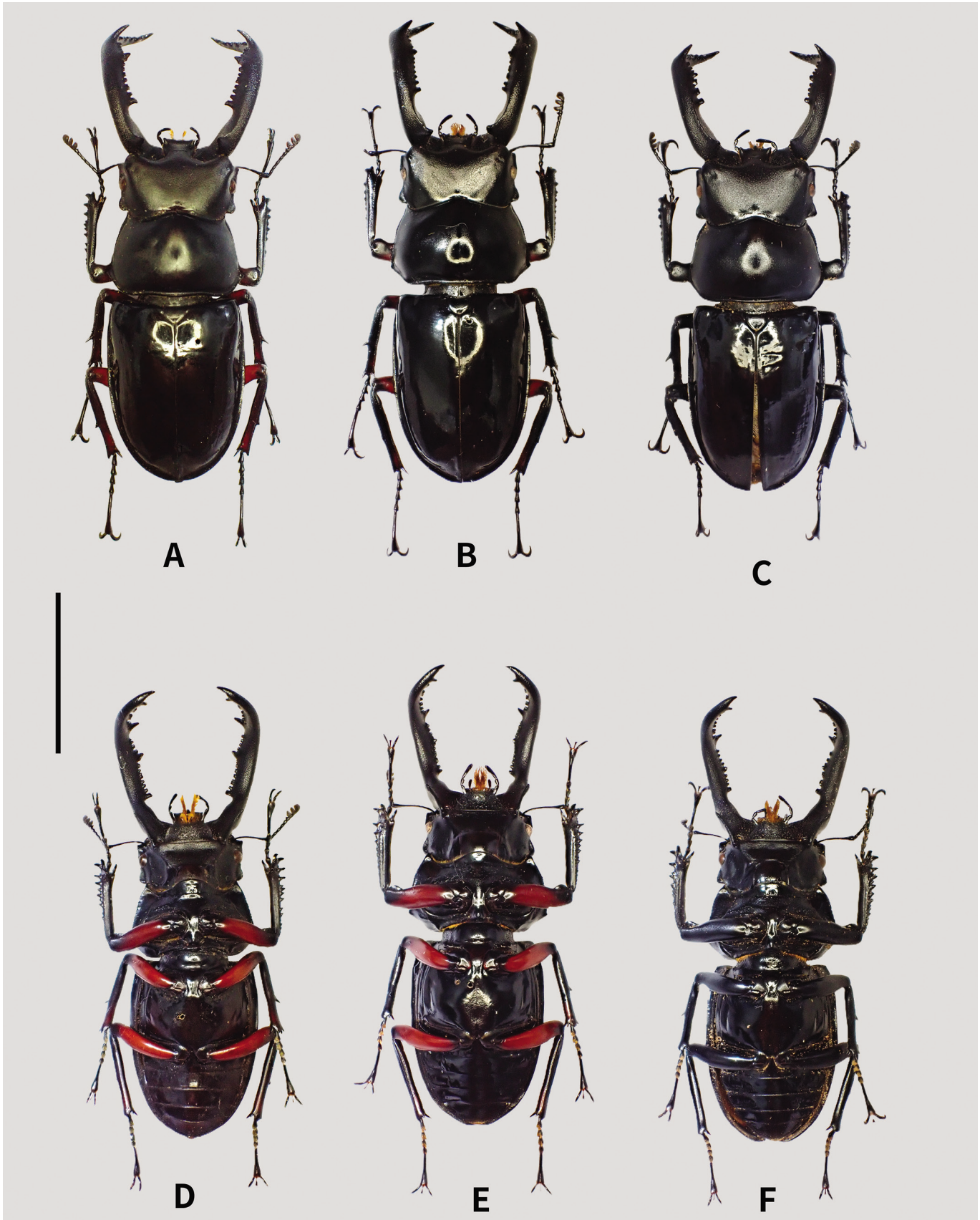


Fig. 2 - Geographical variability in *Pseudorhaetus sinicus*. Dorsal (A-C) and ventral (D-F) views of specimens from: A, D) Fujian Province, China; B, E) Sanxia, Taiwan; C, F) Taoyuan, Taiwan. / Variabilità geografica in *Pseudorhaetus sinicus*. Viste dorsali (A-C) e ventrali (D-F) di esemplari da: A, D) provincia di Fujian, Cina; B, E) Sanxia, Taiwan; C, F) Taoyuan, Taiwan. Scale bar / Barra di scala: 20,0 mm.

Dissection confirms that *Weinreichius perroti* exhibits the definitive synapomorphic characters that diagnose the genus *Pseudorhaetus* according to Huang & Chen (2013): a permanently everted internal sac with a trifurcate apex, and a basal portion constituting 65-85% of the total sac length. External morphology further supports this placement. The antennal club structure is consistent between *Weinreichius* and *Pseudorhaetus*. The postocular lobe, a key diagnostic feature of *Pseudorhaetus*, is also prominently developed in medium to large males of *Weinreichius*, fully consistent with the generic diagnosis. This lobe becomes less distinct only in minor males but is not absent, indicating that its expression follows an allometric pattern rather than representing a structural difference.

The combined evidence of genitalic synapomorphies (Huang & Chen, 2013) and consistent external morphology demonstrates that *Weinreichius* is nested within *Pseudorhaetus*. Consequently, this study synonymizes the genera and establishes the following taxonomic acts: *Weinreichius* Lacroix 1978, **syn. nov.** = *Pseudorhaetus* Planet 1899; *Pseudorhaetus perroti* (Lacroix 1978), **comb. nov.**

***Pseudorhaetus makii* (Arnaud & Miyashita 2006), comb. nov. (Figs 1B, 3C, G, K, 5C-D)**

Chinese name: 牧由美子鍬形蟲 / 牧氏擬鹿角鍬

Yumikoi makii Arnaud & Miyashita 2006: 2, figs. 1-4. Type locality: "South VietNam, Kontam" [= Kon Tum Province, Central Vietnam]; photograph of male provided in the original description.; Fujita, 2010: 225-226, pl. 145, figs. 669-1–669-3; Tsuchiya, 2024: 24, 27, 96.

Material examined. VIETNAM: Kon Tum Province: 4♂♂, 1♀, VII.2019, local collector (JZLC).

Distribution. VIETNAM: Nghe An Province, Quang Nam Province, Kon Tum Province. **LAOS**: Attapeu Province. Annamite Range, 800-1500 m.

Variation. Body length (including mandibles): Male: 42.7-73.8 mm; Female: 33.8-41.8 mm.

Taxonomic notes. This species was originally described as the sole member of a new monotypic genus, based on only two male specimens (Arnaud & Miyashita, 2006). Although the authors noted a remarkable similarity in thoracic characters between the new genus and *Weinreichius*, they maintained its generic status on the basis of clypeal morphology, without support from genitalic dissections or phylogenetic analyses. Given the difficulty of obtaining additional specimens from the type locality, its taxonomic status remained un resolved for many years. Subsequently Fujita (2010) provided a more detailed morphological account and the first description of the female. Fujita further suggested that *Yumikoi* appeared to represent a morphological mosaic of *Hexarthrius* Hope 1842, and *Rhaetulus* Westwood 1871. Later Tsuchiya (2024) noted that the thoracic morphology and female characters were highly consistent with those of *Weinreichius perroti*, suggesting a possible congeneric relationship. Nevertheless, these prior observations remained largely speculative due to the lack of supporting evidence from male genitalia or molecular phylogenetics.

In the present study, dissection of three male specimens revealed that the male genitalia exhibit the synapomorphic characters of the genus *Pseudorhaetus* as defined by Huang & Chen (2013). Furthermore, although the postocular expansion, one of the diagnostic character of *Pseudorhaetus*, had previously been considered absent in this species, detailed comparative examination showed that it is present albeit in a highly vestigial and inconspicuous state (Fig. 3C).

The most recent molecular phylogenetic study of *Hexarthrius* and its allied genera (Zheng *et al*., 2026) recovered *Weinreichius* and *Yumikoi* within the *Pseudorhaetus* lineage, together forming a well-supported monophyletic clade. Based on this combined morphological and molecular evidence presented herein, *Yumikoi* Arnaud & Miyashita 2006 is placed as a junior synonym of *Pseudorhaetus* Planet 1899 (**syn. nov.**). Consequently, the following new combination is established: *Pseudorhaetus makii* (Arnaud & Miyashita 2006) **comb. nov.**

Discussion. The present study does not consider the diagnostic characters used to establish *Weinreichius* Lacroix 1978 and *Yumikoi* Arnaud & Miyashita 2006 to be indicative of genuine intergeneric distinction. These characters, namely, clypeal morphology and the apparent absence of postocular expansion, are here regarded as homoplastic traits that reflect convergent modifications rather than reliable synapomorphies. Such external characters are susceptible to allometric variation, sexual selection, and habitat-driven plasticity, thus carrying limited phylogenetic weight at the generic level. Greater taxonomic weight should instead be placed on characters that are less susceptible to phenotypic plasticity. In Lucanidae, male genitalic and female structural morphology have proven to be informative sources of systematic evidence. Examination of the male genitalia revealed that both *P. makii* and *P. perroti* share the genitalic synapomorphies of *Pseudorhaetus* as defined by Huang & Chen (2013). Furthermore, re-examination of *P. makii* showed that the postocular expansion is present, although in a vestigial state, which aligns the species with the *Pseudorhaetus* ground plan.

These morphological findings are strongly corroborated by molecular evidence. Jing *et al*. (2018) recovered *Rhaetus* Parry 1864 as closely related to *Pseudorhaetus* based on mitogenomic data, suggesting a close phylogenetic relationship within this broader lineage. The comprehensive phylogeny of Zheng *et al*. (2026) further recovered a stable, well-supported monophyletic clade with the topology (*Pseudorhaetus* + (*Weinreichius* + *Yumikoi*)), sister to the (*Hexarthrius* + *Rhaetus*) lineage. The retention of *Weinreichius* and *Yumikoi* as separate genera would render *Pseudorhaetus* paraphyletic; their synonymisation is therefore a logical necessity for maintaining a monophyletic classification. Divergence time estimates from Zheng *et al*. (2026) further contextualise these relationships: the split between the *Pseudorhaetus* stem lineage and the (*Weinreichius* + *Yumikoi*) clade is dated to approximately 7.77 Ma (Late Miocene; 95% HPD: 0.72-19.22 Ma), while *Weinreichius* and *Yumikoi*

diverged considerably more recently, at approximately 1.05 Ma (Pleistocene; 95% HPD: 0.11-5.83 Ma). This comparatively recent divergence further suggests that the morphological differences historically invoked to justify generic separation are better interpreted as localized specializations rather than indicators of a deep evolutionary discontinuity.

Future research should aim to further clarify the systematic of *Pseudorhaetus* and related genera. Current divergence estimates exhibit wide confidence intervals, which underscores the need for expanded taxon sampling and increased locus coverage. The integration of genomic evidence with detailed morphological analyses, including intraspecific variation in mandibular morphology,

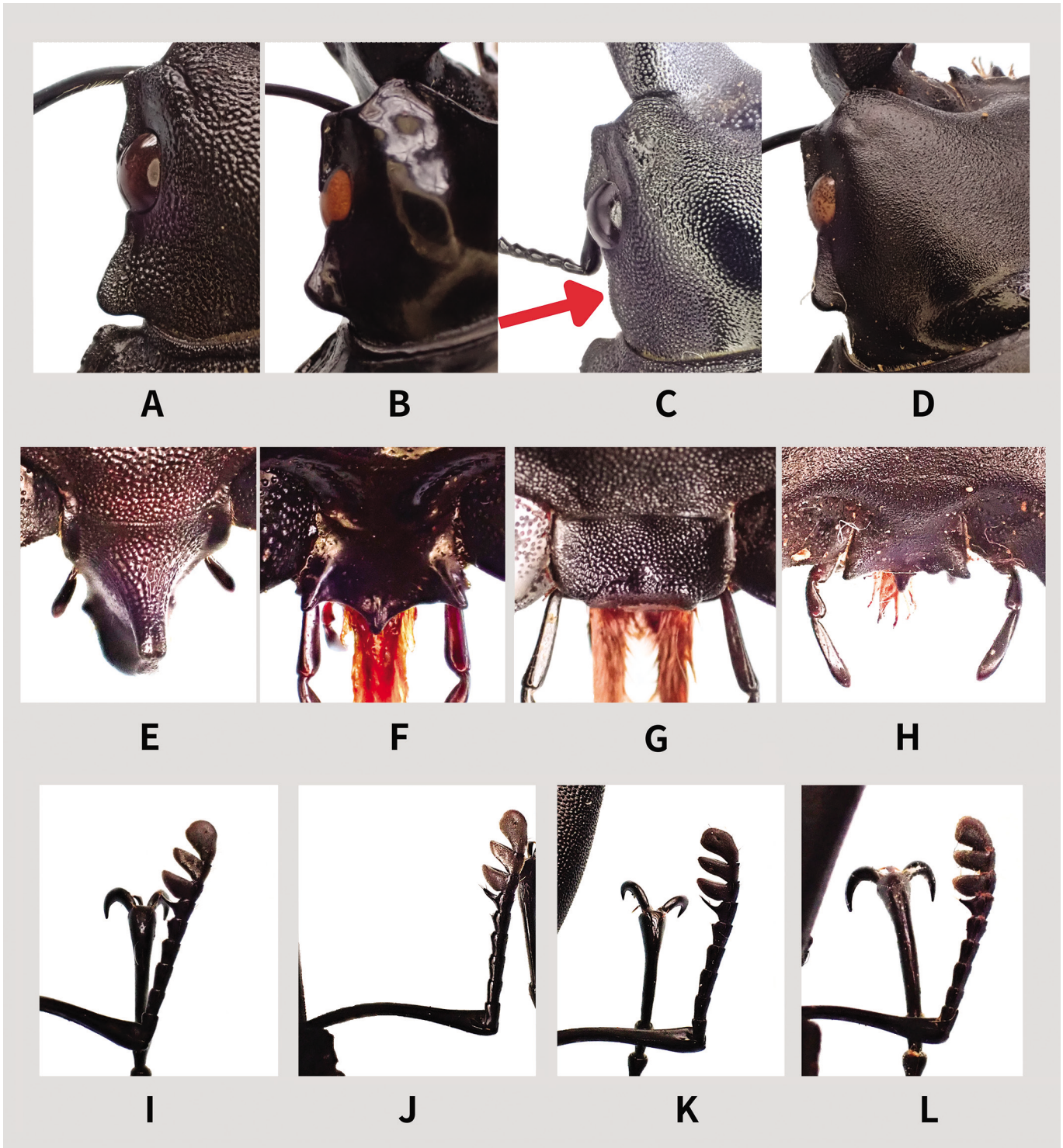


Fig. 3 - Comparative morphology of the postocular expansion, clypeus, and antennae in *Pseudorhaetus*. A, E, I) *P. perroti*; B, F, J) *P. oberthuri*; C, G, K) *P. makii*; D, H, L) *P. sinicus*. / Morfologia comparata dell'espansione postoculare, del clipeo e delle antenne in *Pseudorhaetus*. A, E, I) *P. perroti*; B, F, J) *P. oberthuri*; C, G, K) *P. makii*; D, H, L) *P. sinicus.* (Not to scale. / Non in scala.).

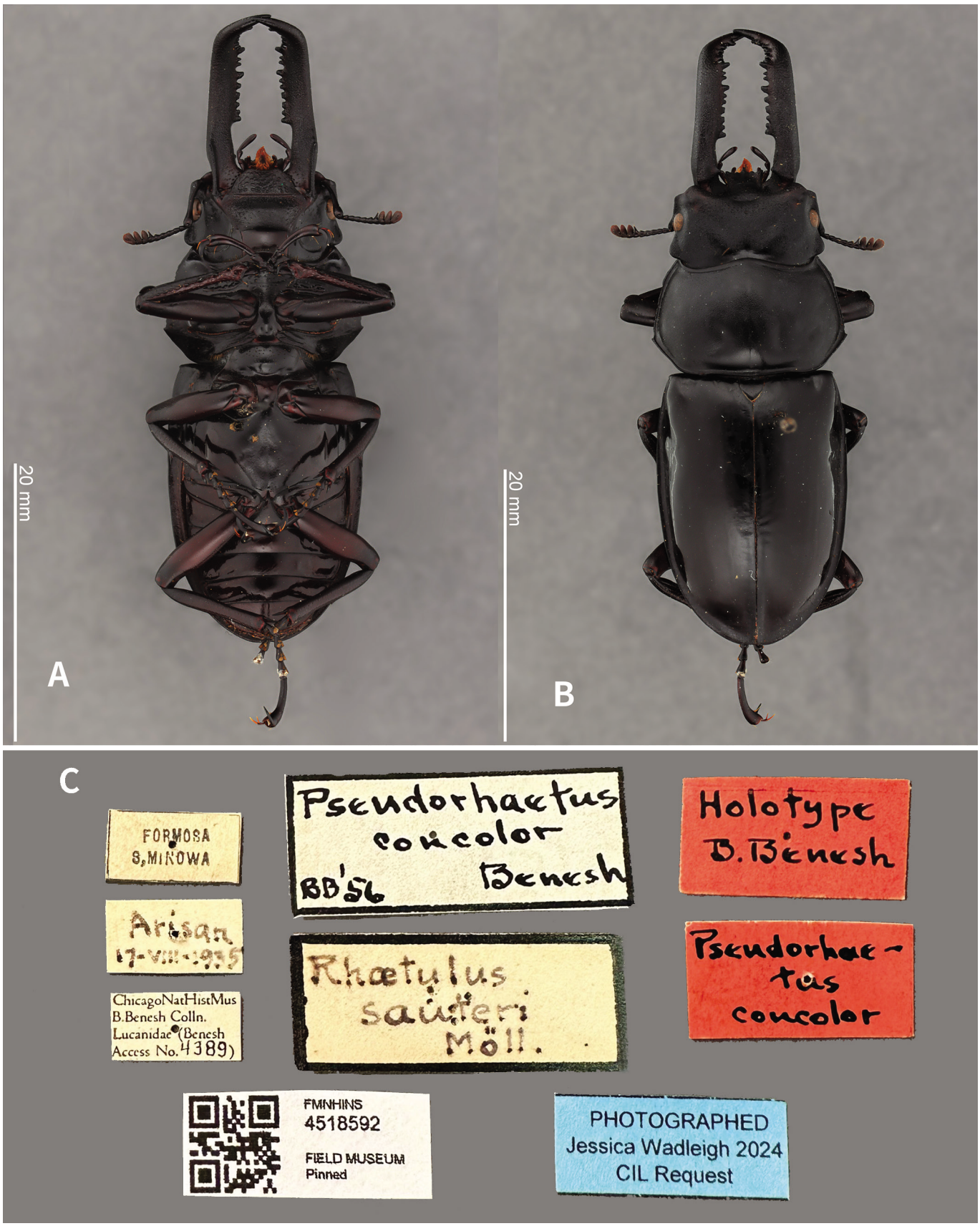


Fig. 4 - Holotype of *Pseudorhaetus sinicus concolor* Benesh 1960. A) ventral view; B) dorsal view; C) identification and collection labels. / Olotipo di *Pseudorhaetus sinicus concolor* Benesh 1960. A) vista ventral; B) vista dorsale; C) etichette di identificazione e di raccolta. (Photo credit / Crediti fotografici: Jessica Wadleigh @ The Field Museum of Natural History, Chicago, CIL). (Images not to scale. / Immagini non in scala).



Fig. 5 - Comparative morphology of the aedeagus and abdominal segment IX in *Pseudorhaetus*. A-B) *P. perroti*; C-D) *P. makii*; E-F) *P. sinicus* (mainland China); G-H) *P. sinicus* (Taiwan); I-J) *P. oberthuri*. / Morfologia comparata dell'edeago e del segmento addominale IX in in *Pseudorhaetus*. A-B) *P. perroti*; C-D) *P. makii*; E-F) *P. sinicus* (Cina continentale); G-H) *P. sinicu* (Taiwan). Scale bar / Barra di scala: 3.0 mm.

postocular structures, and genitalia will be critical for elucidating the lineage's diversification history and establishing a precise evolutionary framework for the genus.

Identification Key to the Males of the Genus *Pseudorhaetus* Planet, 1899

1. Mandibles without a basal dorsal tooth even in large males; clypeus mountain-shaped, slightly elevated but not elongated; posterior angles of pronotum with a distinct, sharp spine; elytra with yellowish-brown patches on the posterior half; distributed in central Vietnam and Laos …..... .... ***P. makii*** **(Arnaud & Miyashita 2006), comb. nov.**
– Mandibles with a prominent basal dorsal tooth (upturned or laterally directed) in large males; clypeus either extremely elongated or normal; posterior angles of pronotum contracted but without a sharp spine; elytra monochromatic (reddish-brown to black), without yellowish patches 2
2. Clypeus extremely elongated and strongly upturned; integument matt to semi-gloss with a dark reddish tinge; lateral margins of the pronotum posteriorly parallel, anteriorly not strongly convergent; distributed only in southern Vietnam .... ***P. perroti*** **(Lacroix 1978), comb. nov.**
– Clypeus normal, not elongated nor strongly upturned; lateral margins of the pronotum evenly arcuate or finely crenulate throughout. 3
3. Elytra reddish-brown to mahogany-red, with a strong, enamel-like glaze; male head more shining and more finely punctate, with middle part distinctly depressed; male pronotum with lateral margins more rounded; male mandibles relatively short; distribution restricted to northern Vietnam and southern China (Yunnan). ..... ***P. oberthuri*** **Planet 1899**
– Elytra dark brown to jet-black, luster distinctly weaker (never strongly glazed); male head less shining and more coarsely punctate, with middle part less deeply depressed; male pronotum with lateral margins less rounded; male mandibles relatively longer; femora variable from reddish to black; widespread in Taiwan, Hainan, and southeastern mainland China. ..... ***P. sinicus*** **(Boileau 1899)**

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