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Little-Known Stag Beetles from Taiwan:
Notes on *Lucanus chengyuani* Wang & Ko, 2018
(Coleoptera: Lucanidae), with Taxonomic Remarks

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초록

대만 고유종의 소형 주행성 사슴벌레인 *Lucanus chengyuani* Wang & Ko, 2018는 기재 이후 생태와 분포에 관한 정보가 거의 알려져 있지 않았다. 본 연구에서는 야외에서의 서식 환경을 최초로 확인하고, 추가 표본을 확보하여 보고하였다. 형태 및 생태학적 근거를 바탕으로 *L. chengyuani*를 *Lucanus parryi* 종군에 잠정적으로 배치하였다. 또한 *L. chengyuani*와 동일한 기준산지(Alishan)를 공유하고 주행성이라는 공통된 생태적 특성을 고려하여, *Lucanus ritae* Lacroix, 1984의 명명학적 지위도 재검토하였다. 추정 완모식표본(MNHN, Paris; EC12557)을 조사한 결과, 표본 라벨의 불일치와 형태적 불일치가 확인되어 해당 표본의 담명모식표본으로서의 지위에 대한 신중한 재검토가 필요함을 시사하였다. 이 40여 년간 지속되어 온 분류학적 문제를 해결하기 위해 1) 모식산지 오기재, 2) 플라이스토세 빙하기 잔존집단, 3) 혼합 모식계열의 세 가지 검증 가능한 가설을 제시하고, 각각의 생물지리학적 및 계통학적 함의를 논의하였다. 아울러 *L. chengyuani*와 근연종의 수컷 생식기, 뒷날개 맥상 및 더듬이 형태에 대한 비교 자료를 함께 제시하였다. 본 연구는 대만산 소형 *Lucanus* 종들을 둘러싼 오랜 명명학적 불확실성을 해결하기 위한 기초적인 연구 틀을 제공하고자 한다.

Abstract

The Taiwanese endemic, small-sized, diurnal stag beetle *Lucanus chengyuani* Wang & Ko, 2018 has remained poorly known since its original description. This study confirms its wild habitat for the first time and documents additional specimens. Based on morphological and ecological evidence, *L. chengyuani* is provisionally assigned to the *Lucanus parryi* species group. Given their shared type locality (Alishan) and diurnal habits, the nomenclatural status of *Lucanus ritae* Lacroix, 1984 is also re-examined. Examination of the putative holotype

(MNHN, Paris; EC12557) reveals label inconsistencies and morphological discrepancies that invite careful consideration of its name-bearing status. Three testable hypotheses are proposed to address this four-decade-old taxonomic question: 1) mislabeled locality, 2) Pleistocene glacial relict, and 3) mixed type series, and their biogeographical and phylogenetic implications are discussed. Comparative data on male genitalia, hindwing venation, and antennal morphology of *L. chengyuani* and closely related congeners are also provided. This framework aims to provide a constructive foundation for resolving the long-standing nomenclatural uncertainty surrounding Taiwanese small-sized *Lucanus*.

Keywords: *Lucanus chengyuani*; *Lucanus ritae*; *Lucanus datunensis*; taxonomy; nomenclatural status; ICZN; type material; Alishan; Taiwan.

Introduction

Most species of the genus *Lucanus* Scopoli, 1763 (Coleoptera: Lucanidae: Lucanini) from Taiwan are nocturnal and predominantly medium- to large-bodied (Chang, 1993, 2006, 2024; Lin, 2025). Nevertheless, a highly specialized group of small-sized, diurnal species also occurs on the island (Lin et al., 2011; Wang & Ko, 2018; Lin, 2021). The taxonomic history of this diurnal group began when Kurosawa (1966) described *Lucanus miwai* Kurosawa, 1966 from the mountainous regions of central Taiwan, with one paratype recorded from Alishan. Hashimoto (1984) subsequently described *Lucanus datunensis* Hashimoto, 1984 from the wind-swept grasslands of Mount Datun in northern Taiwan. Later that same year, Lacroix (1984) described *Lucanus ritae* Lacroix, 1984 based on specimens whose type locality was recorded as Alishan in south-central Taiwan. Lacroix cautiously noted that a female paratype of *L. miwai* from Alishan shared the same locality as his new species and suggested that a thorough examination of that specimen might supplement knowledge of the female morphology of *L. ritae*. From the mid-1980s through the 1990s, several records of *L. datunensis* from central and southern Taiwan were published (Sakaino, 1985; Wang, 1990; Tanikado, 1992; Sakaino & Yu, 1994); however, no additional Alishan specimens were explicitly referred to *L. ritae* during this period. Araya (2000) subsequently concluded that *L. ritae* was morphologically identical to *L. datunensis* and treated the former as a junior synonym of the latter under the Principle of Priority treatment later adopted in Taiwanese checklists (Huang & Chen, 2010).

It was not until 2018 that Wang and Ko described *Lucanus chengyuani* Wang & Ko, 2018, an additional small-sized diurnal species from Alishan. Reports on its ecology and biology have remained entirely absent since its description, owing to the extreme scarcity of wild-collected specimens. The present author has recently confirmed its wild habitat and collected additional specimens, enabling a more thorough morphological examination. The rediscovery of *L. chengyuani* now warrants a reassessment of the nomenclatural relationships among *L. ritae*, *L. datunensis*, and *L. chengyuani*.

A critical review of the relevant literature reveals that Araya's (2000) synonymization was based primarily on two paratypes of *L. ritae* deposited in the Muséum d'histoire naturelle

de Genève (MHNG), rather than on the name-bearing holotype. Under the provisions of the ICZN, only the holotype serves as the ultimate nomenclatural standard for a nominal species; paratypes lack the authority to definitively fix a taxon's identity. The occasional incorporation of specimens from different taxa or localities into a paratype series has been documented in Taiwanese lucanid taxonomy (Huang & Chen, 2016), and any synonymic conclusion reached without examination of the holotype remains nomenclaturally insufficient. The present study therefore aims to provide a comprehensive re-evaluation of this four-decade-old controversy by utilizing freshly collected material, examining the holotype of *L. chengyuani*, and critically assessing the name-bearing status of the extant specimen catalogued as the holotype of *L. ritae* at the MNHN, Paris.

Materials & Methods

A total of 29 specimens were examined in this study. All specimens were collected in compliance with relevant ethical guidelines and local regulations governing entomological sampling. For specimens originating from protected areas, such as National Parks, selection was strictly restricted to historical specimens collected prior to the formal establishment of the respective national parks, thereby ensuring full regulatory compliance.

Taxonomic identification and terminology for external morphology followed primarily Huang & Chen (2010) and Wang & Ko (2018), supplemented by relevant regional literature.

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

External morphological characters, including mandible shape, clypeal structure, pronotal lateral margins, and body size, were examined under a stereomicroscope. All specimens were photographed using a digital camera equipped with a macro lens.

Specimens examined in this study are deposited in the following institutional or private collections:

JZLC	Private collection of Jing-Zhi Lin, Taipei, Taiwan
MHNG	Muséum d'histoire naturelle de Genève, Geneva, Switzerland
MNHN	Muséum national d'Histoire naturelle, Paris, France
NTUE	Department of Entomology, National Taiwan University, Taipei, Taiwan

Results

Family Lucanidae Latreille, 1804

Lucanini Latreille, 1804

Genus *Lucanus* Scopoli, 1763

Chinese name: 深山鋤形蟲屬

Lucanus chengyuani Wang & Ko, 2018

(Fig. 1B–C, Fig. 2A–I, Fig. 4A–C, Fig. 5A, E, Fig. 6A–B)

Chinese name: 承遠深山鋤形蟲

Lucanus chengyuani Wang & Ko, 2018: 257–263. Type locality: Alishan, Chiayi Co., Taiwan. (Original description, diagnosis, keys, figures of male holotype and paratypes); Wang et al., 2019: 3460–3462 (Complete mitochondrial genome, molecular data); Sato, 2020: 33 (Catalogue); Chang, 2024: 56–57 (Catalogue).

Type material examined. (Fig. 1B–C) *Lucanus chengyuani* Wang & Ko, 2018: Holotype ♂ (NTUE). Labels: (1) "TAIWAN: Chiayi Co. / Alishan - / 13.V.2018 / leg. C. Y. Wu" [printed]; (2) "HOLOTYPE / *Lucanus chengyuani* sp. nov. / Wang et Ko des. 2018" [printed, red label]; (3) "LCY001" [printed]; (4) "*Lucanus chengyuani* Wang & Ko, 2018 / Det. Lin Jing-Zhi, 2024" [printed, yellowish].

Additional material examined. (Fig. 2A–I) TAIWAN: Chiayi County (specimens from the type locality): 1♂, Alishan, V.2026, J.-Z. Lin leg.; 2♂♂, same locality, V.2023, J.-Z. Lin leg.; 1♂, same locality, V.2021, local collector leg.; 1♂, same locality, V.2021, local collector leg. All specimens are deposited in JZLC.

Variation. Body length (including mandibles): Male: 22.4–29.6 mm; Female: Unknown. In some specimens, yellowish markings are observed on the dorsal surface of the tibiae and the ventral surface of the femora.

Field observations. (Fig. 6A–B) This species is a typical diurnal species, primarily inhabiting the pristine forests of the mid-elevation Machilus–Castanopsis Forest zone. In addition, its distinct flight activity can be observed along the forest edges of bamboo forests (*Phyllostachys edulis* (Carrière) J. Houz.) and miscanthus secondary grasslands, with a characteristically slow and steady flight speed. Wang & Ko (2018) hypothesized that this daytime flight behavior is closely associated with males searching for females to mate. The active period of adults is concentrated in late spring to early summer. Based on the author's consecutive five-year field surveys from 2022 to 2026, no feeding behavior of adult beetles has been observed in the wild. Furthermore, they are neither attracted to tree sap (with no collection records obtained from fruit-baited traps) nor phototactic (with light traps failing to attract any individuals). To date, no female specimens have been recorded in the wild during this study; their precise ecological niche and cryptic life history remain to be clarified in future studies. However, the phenomenon where females are extremely difficult to observe or collect in the wild is a common attribute

among other diurnally specialized *Lucanus* species in Taiwan. For instance, the female of the congeneric *L. datunensis* was confirmed and described by science exactly 10 years after the description of the male (Sakaino & Yu, 1994).

The following specimens of the genus *Lucanus* were used for comparison:

Lucanus ritae Lacroix, 1984 (Fig. 1A, D–E): Holotype ♂ (MNHN, EC12557), labels: (1) "CENT. TAIWAN / Ali-Shan. FEB. / 2000m IV.1979 / R. IPSEN. Leg." [handwritten]; (2) "HOLOTYPE" [printed, red label]; (3) "PARATYPE: / *Lucanus* ♂ / *ritae* n. sp. / J.P. LACROIX det. 1981" [handwritten and printed on red-bordered label]; (4) "HOLOTYPE / *Lucanus* / *ritae* Lacroix, 1983" [printed]; (5) "MNHN, Paris / EC12557" [printed with QR code].

Lucanus swinhoi Parry, 1874 (Fig. 3G–I, Fig. 4D–F, Fig. 5B, F): TAIWAN: Hualien County: 4♂♂, Guangfu Township, VI.2018, local collector leg.; Hsinchu County: 2♂♂, Jianshi Township, VI.2025, J.-Z. Lin leg.; New Taipei City: 2♂♂, Wulai District, V.2023, J.-Z. Lin leg. All specimens are deposited in JZLC.

Lucanus parryi Boileau, 1899 (Fig. 3D–F, Fig. 4G–I, Fig. 5D, H): CHINA: Zhejiang Province: 1♂, 1♀, Mt. Tianmushan, Lin'an, VII.2019, H.-S. Xi leg.; 1♂, Mt. Longwangshan, VI.2022, local collector leg.; Fujian Province: 1♂, Mt. Baitashan, Jianyang District, Nanping City, 1200 m, VI.2022, local collector leg.; Sichuan Province: 3♂♂, 1♀, Mt. Daxiangling, Yingjing County, Ya'an City, 1400 m, VII.2017, local collector leg. All specimens are deposited in JZLC.

Lucanus gamunus Sawada & Watanabe, 1960 (Fig. 3A–C, Fig. 4J–L, Fig. 5C, G): JAPAN: Tokyo Metropolis: 3♂♂, 1♀, Mikura-jima Island, V.2007, local collector leg.; 2♂♂, Kozushima Island, V.2015, local collector leg. All specimens are deposited in JZLC.

Discussion

Biogeographical and Phylogenetic Implications

In the present study, *L. chengyuani* is provisionally assigned to the *L. parryi* species group based on the following male morphological characters: the dark blackish-brown body coloration, the presence of four small internal denticles along the inner margin of the mandibles, and the weakly developed mandibular apex with a slight apical-bifid condition. Its occurrence in the mid-elevation mountains of Taiwan fills a long-standing distributional gap between the *L. parryi* species group of mainland China and the insular endemic *L. gamunus* from the Izu Islands of Japan, thereby connecting these regions into a coherent East Asian island-arc pattern. This discovery bears relevance to two competing hypotheses regarding the origin of *L. gamunus*: the "palaeo-landbridge relict" hypothesis proposed by Kurosawa (1978) and the "Kuroshio Current

rafting" hypothesis advanced by Araya and Hosoya (2014).

The taxonomic discrepancy among previous studies can be attributed primarily to the limited number of specimens and the absence of female material at the time of the original description. Wang and Ko (2018) and Zhan and Young (2023) placed *L. chengyuani* in the *L. fortunei* group, whereas Sato (2020) assigned it to the *L. parryi* group. Female morphology remains the most reliable diagnostic criterion for species-group placement in *Lucanus* (Huang & Chen, 2010). Furthermore, *L. chengyuani* shares several notable ecological traits with *L. gamunus*, including strictly diurnal activity and a complete absence of phototaxis or attraction to tree sap (Sawada & Watanabe, 1960; Kurosawa, 1978; Fujita, 2014). Under the palaeo-landbridge framework, accumulating phylogeographical evidence indicates that Pleistocene glacial landbridges served as critical dispersal corridors for temperate biota across the region (Chiang & Schaal, 2006; Qiu et al., 2011; Shao et al., 2019), and that Taiwan's complex topography has repeatedly acted as a powerful driver of population isolation and local diversification in lucanid beetles (Huang & Lin, 2010; Tsai et al., 2014, 2021). It is therefore plausible that *L. chengyuani* represents a glacial relict lineage that retreated to the Alishan Range following post-glacial warming, potentially persisting with limited gene flow owing to the highly restricted nature of its microhabitat. Under the alternative Kuroshio Current hypothesis, Taiwan represents an essential stepping stone along the northward dispersal route toward Japan. Under either scenario, *L. chengyuani* bridges a previously unresolved distributional gap between the two regions.

Nevertheless, these biogeographical inferences must currently be regarded as tentative. Recent phylogenetic analyses indicate that *L. chengyuani* is molecularly sister to *Lucanus swinhoei* Parry, 1874 (H. C. Wu, pers. comm., unpublished data, 2026). If corroborated by peer-reviewed analysis, this result would be incongruent with the *L. parryi* group affinity inferred from external morphology. Such incongruence between morphological and molecular signals is not without precedent in lucanid beetles. The large and complex mandibular morphology that serves as a key diagnostic character has been demonstrated to be highly susceptible to convergent evolution driven by shared ecological selection pressures, particularly among small-sized, diurnal lineages occupying similar montane microhabitats (Huang & Lin, 2010; Tsai & Yeh, 2016). It is therefore conceivable that the *L. parryi*-like morphology of *L. chengyuani* represents an instance of convergent evolution or phenotypic parallelism, rather than reflecting true phylogenetic affinity with the mainland *L. parryi* group. Alternatively, incomplete lineage sorting among recently diverged Taiwanese *Lucanus* lineages could produce discordance between morphological and molecular phylogenetic signals (Wan et al., 2025). Resolving this incongruence will require a comprehensive molecular phylogenetic assessment incorporating *L. chengyuani*, *L. gamunus*, *L. parryi*, *L. swinhoei*, and representative members of both the *L. parryi* and *L. fortunei* species groups, together with the discovery of female specimens of *L. chengyuani* to enable definitive species-group diagnosis.

Taxonomic Identity and Nomenclatural Status of *Lucanus ritae*

Independently of the phylogenetic implications discussed above, the rediscovery of *L.*

chengyuani in Alishan necessitates a careful re-examination of its nomenclatural relationship with *L. ritae*, a taxon that shares the same type locality. The synonymization of *L. ritae* with *L. datunensis* by Araya (2000) was based primarily on the examination of two paratypes deposited in the Muséum d'histoire naturelle de Genève (MHNG), rather than on the primary name-bearing holotype. Under the provisions of the International Code of Zoological Nomenclature (ICZN), paratypes do not possess the name-bearing authority required to definitively fix the identity of a nominal taxon. Moreover, the inadvertent incorporation of heterogeneous specimens from disparate localities or distinct taxa into a paratypic series is a documented phenomenon in Taiwanese lucanid taxonomy (Huang & Chen, 2016). From a biogeographical perspective, *L. datunensis* is strictly restricted to the wind-swept montane grasslands of the Datun Volcano Group in northern Taiwan (Sakaino, 1985; Chang, 1993, 2006, 2024). A synonymy that binds an Alishan taxon to a geographically isolated northern population is highly anomalous, which suggests that Araya's (2000) conclusion, reached without examination of the primary type, may benefit from further procedural and biological clarification.

To address this four-decade-old ambiguity, the present study proposes three testable hypotheses.

Hypothesis 1: The Mislabeling Hypothesis

The original "Alishan" locality label may have resulted from commercial mislabeling, a practice occasionally employed by historical collectors to protect cryptic collecting sites. Under this scenario, the entire type series would have actually originated from the *L. datunensis* population of the Datun Mountains. If correct, Araya's (2000) synonymy would be substantially upheld, and *L. ritae* would remain a junior subjective synonym of *L. datunensis*.

Hypothesis 2: The Pleistocene Relict Hypothesis

In alignment with the discussion of *L. chengyuani* as a potential glacial relict in the Alishan Range, this scenario considers the possibility that a common ancestral lineage of *L. datunensis* and *L. ritae* was more widely distributed during Pleistocene glacial maxima. Following post-glacial warming, the majority of this lineage may have retreated northward into the Datun Volcano Group, while a highly isolated, low-density relict population persisted within the mid-elevation microclimates of Alishan, subsequently undergoing allopatric divergence. Although the probability of such a lineage remaining uncollected for four decades is extremely low, this evolutionary perspective offers an account of the Alishan locality that does not require invoking labeling or sorting errors.

Hypothesis 3: The Mixed Series Hypothesis

This alternative represents the primary emphasis of the present study. It is hypothesized that the primary name-bearing holotype designated by Lacroix (1984) was genuinely collected from Alishan and belongs to the same montane population as *L. chengyuani*, whereas specimens of *L. datunensis* were inadvertently intermixed only within the paratypic series. Because Araya

(2000) based his historical synonymy strictly on the examination of two paratypes deposited in the MHNG without inspecting the primary holotype, his conclusion may have been influenced by these heterogeneous elements. If verified, *L. ritae* would constitute the senior available name for the Alishan population, thereby posing a direct nomenclatural challenge to the validity of *L. chengyuani*.

Regarding nomenclatural procedure, Lacroix (1984) designated a male specimen collected from Alishan in 1979 as the holotype, deposited in the Muséum national d'Histoire naturelle (MNHN), Paris. Although specimen EC12557 matches the published collecting data, a significant label conflict was identified during examination. The specimen bears a curator-affixed red "HOLOTYPE" label; however, the original label directly above it, handwritten by Lacroix himself, explicitly states "PARATYPE: *Lucanus* ♂ *ritae* n. sp." Of additional nomenclatural significance, the locality label on EC12557 records R. IPSEN as the collector. This is the same individual listed in the original description as the holder of one male paratype ("1 ♂ in coll. R. IPSEN, R.F.A."; Lacroix, 1984). (Fig. 1E) These data collectively identify EC12557 as the paratype formerly held in R. IPSEN's collection and subsequently transferred to the MNHN, rather than as the designated holotype. The explicit paratype designation by the original author directly calls into question its name-bearing status.

Morphological discrepancies further support this interpretation. The original description states that the clypeus of *L. ritae* is "convex in its middle (convexe en son milieu)," a condition congruent with historical plates and with the holotype of *L. chengyuani* (Fig. 1A–B). Direct examination of EC12557 (Fig. 1D), however, confirmed that its clypeus is nearly flat, with additional differences observed in the head-to-pronotum ratio and mandibular dentition. The contradiction among the textual diagnosis, the historical illustrations, and the physical attributes of EC12557 raises further questions regarding its legitimacy as the nominal holotype.

While the possibility of a labeling error by Lacroix has been suggested (M. Zilioli, personal communication, 2021), it is equally plausible that the primary type specimen serving as the basis for the original description is not the individual currently housed in the MNHN. Lacroix has since passed away, and his private collection remains in the possession of his family. The MNHN currently maintains no communication channels with the heirs, rendering examination of any type series specimens retained within this private collection unfeasible at present (S. Boucher, personal communication, 2026). If the true holotype remains sequestered therein, the nomenclatural status of *L. chengyuani* would remain inherently vulnerable to historical uncertainty and potential synonymization. As emphasized by Meyer et al. (2026), the description of new taxa prior to resolving compromised historical type series constitutes a primary catalyst for nomenclatural instability.

In light of these unresolved questions, the present study conservatively maintains *L. chengyuani* as a valid species pending future resolution. Definitive taxonomic and nomenclatural conclusions must await further clarification through access to the primary type material. A

conclusive resolution will require a thorough audit of European institutional and private repositories. Should the primary type be confirmed lost, a neotype would need to be designated under Article 75 of the ICZN, or a petition submitted to the Commission under Article 81. Ultimately, the integration of historical archival investigations with high-throughput molecular analyses will provide the empirical foundation necessary to resolve this forty-year-old taxonomic question.

Key to males of the *Lucanus parryi* species group (male)

1. Mandibles elongate and relatively long; cephalic auricular projections well-developed, prominently expanded laterally; body length 26.0–59.4 mm; distribution: mainland China (Sichuan, Yunnan, Chongqing, Hubei, Henan, Guizhou, Shaanxi, Zhejiang, Jiangxi, Fujian, and Anhui Provinces/Municipalities)..... *L. parryi* Boileau, 1899
 – Mandibles markedly shorter and evenly arcuate; cephalic auricular projections weakly developed; body compact and small, 21.8–36.0 mm; distribution: insular or isolated montane environments (Taiwan or Japan)2
2. Mandibles robust, with a single enlarged, prominent inner tooth located near the apical one-third; distribution: Japan (Izu Islands: Mikurajima and Kozushima)..... *L. gamunus* Sawada & Watanabe, 1960
 – Mandibles relatively slender and flattened, with three to four small inner teeth of subequal size distributed along the inner margin; mandibular apex weakly developed and slightly apical-bifid; clypeus distinctly convex medially; distribution: Taiwan (Alishan Range)
*L. chengyuani* Wang & Ko, 2018

Competing Interests

The authors declared that no competing interest exists in the preparation of the manuscript.

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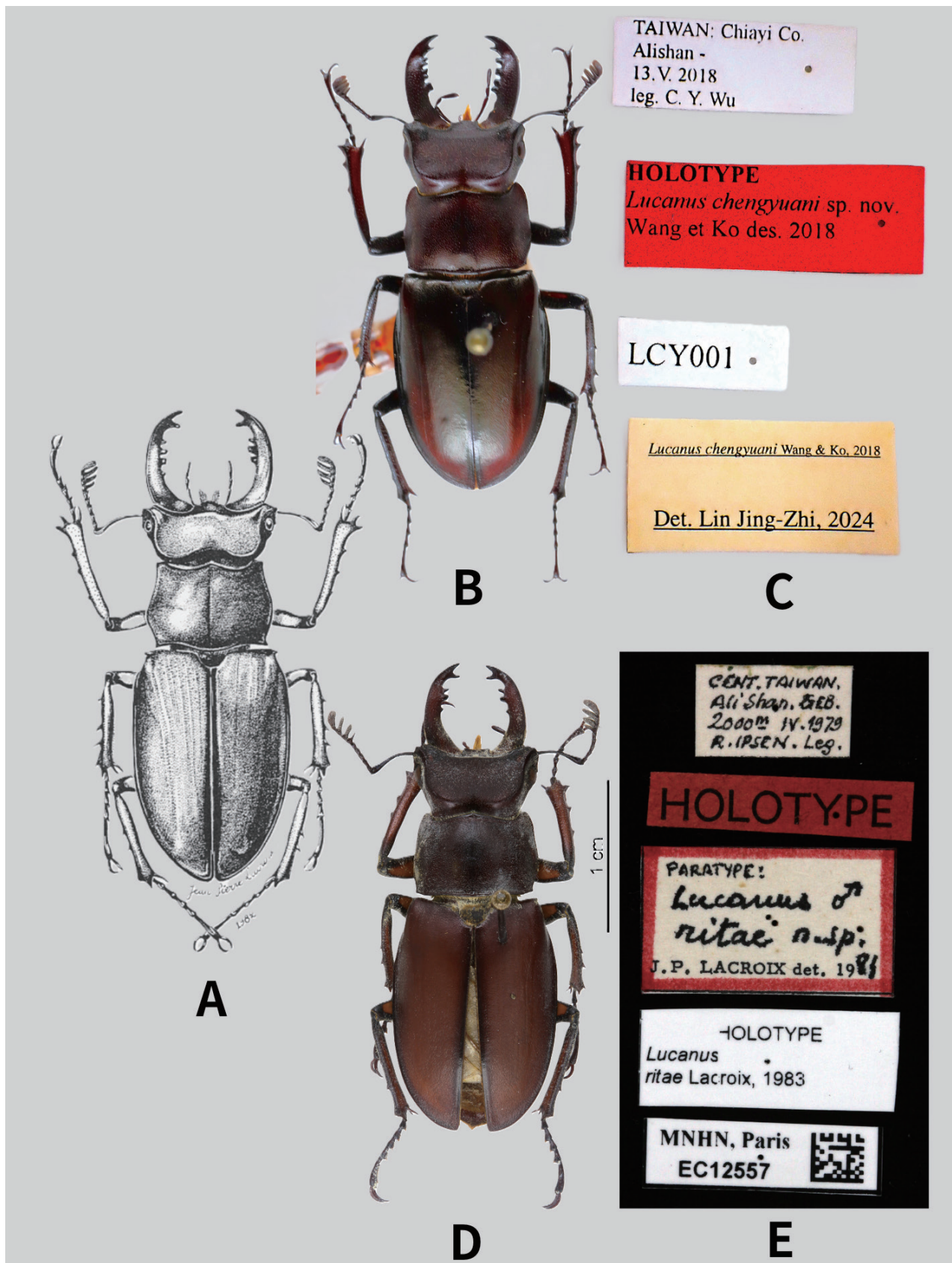


Figure 1. Type specimens and identification labels of *Lucanus* species. (A) Original line drawing of the holotype of *Lucanus ritae* Lacroix, 1984 in dorsal view (after Lacroix, 1984); (B) Holotype of *Lucanus chengyuani* Wang & Ko, 2018 in dorsal view; (C) Identification and collection labels of *L. chengyuani*; (D) Holotype of *L. ritae* in dorsal view; (E) Identification and collection labels of *L. ritae*. Photos D–E by Christophe Rivier, © MNHN, Paris. All images not to scale.

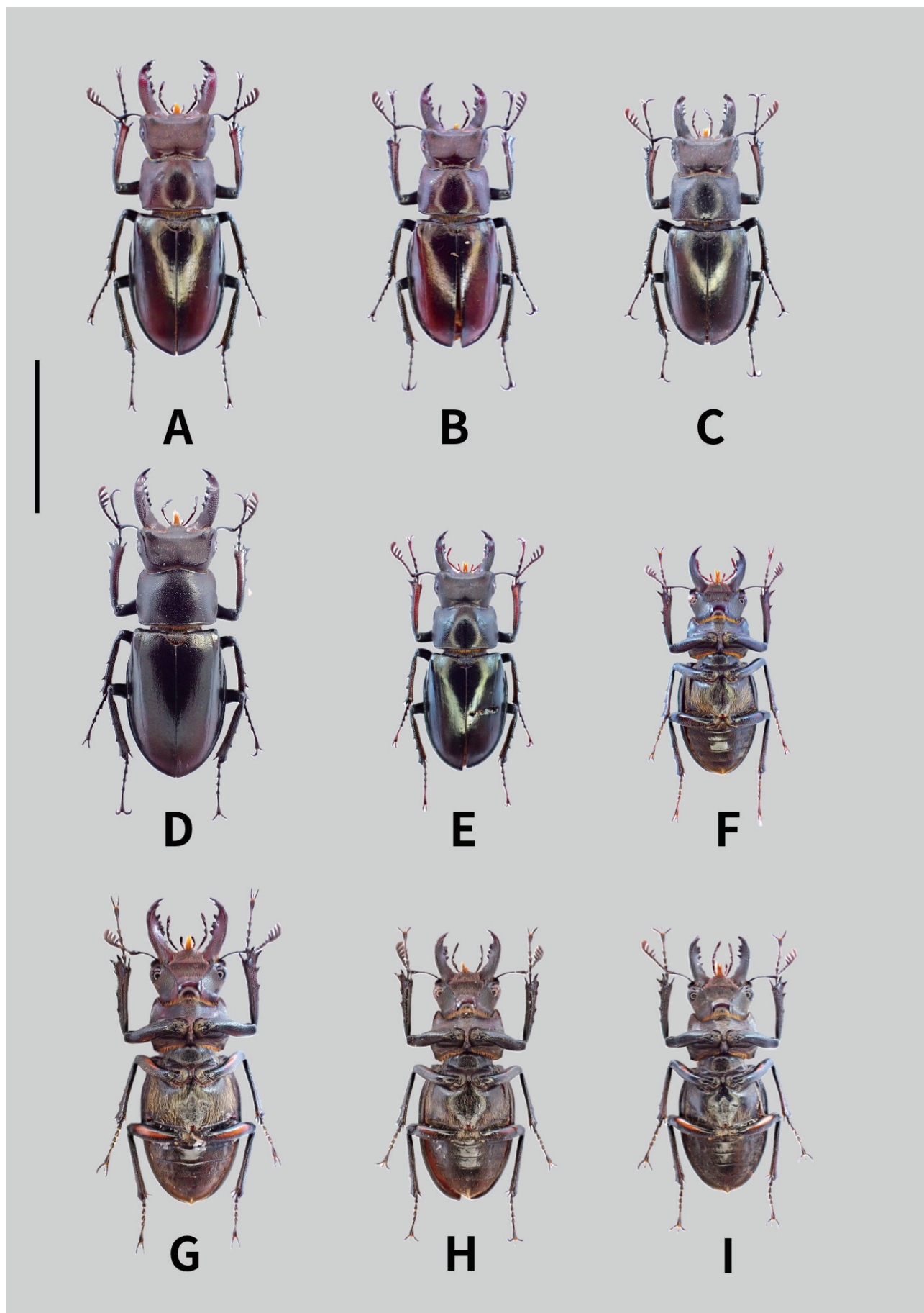


Figure 2. Intraspecific morphological variability in males of *Lucanus chengyuani* Wang & Ko, 2018. (A–E) Dorsal views; (F–I) Ventral views. Scale bar = 20.0 mm.

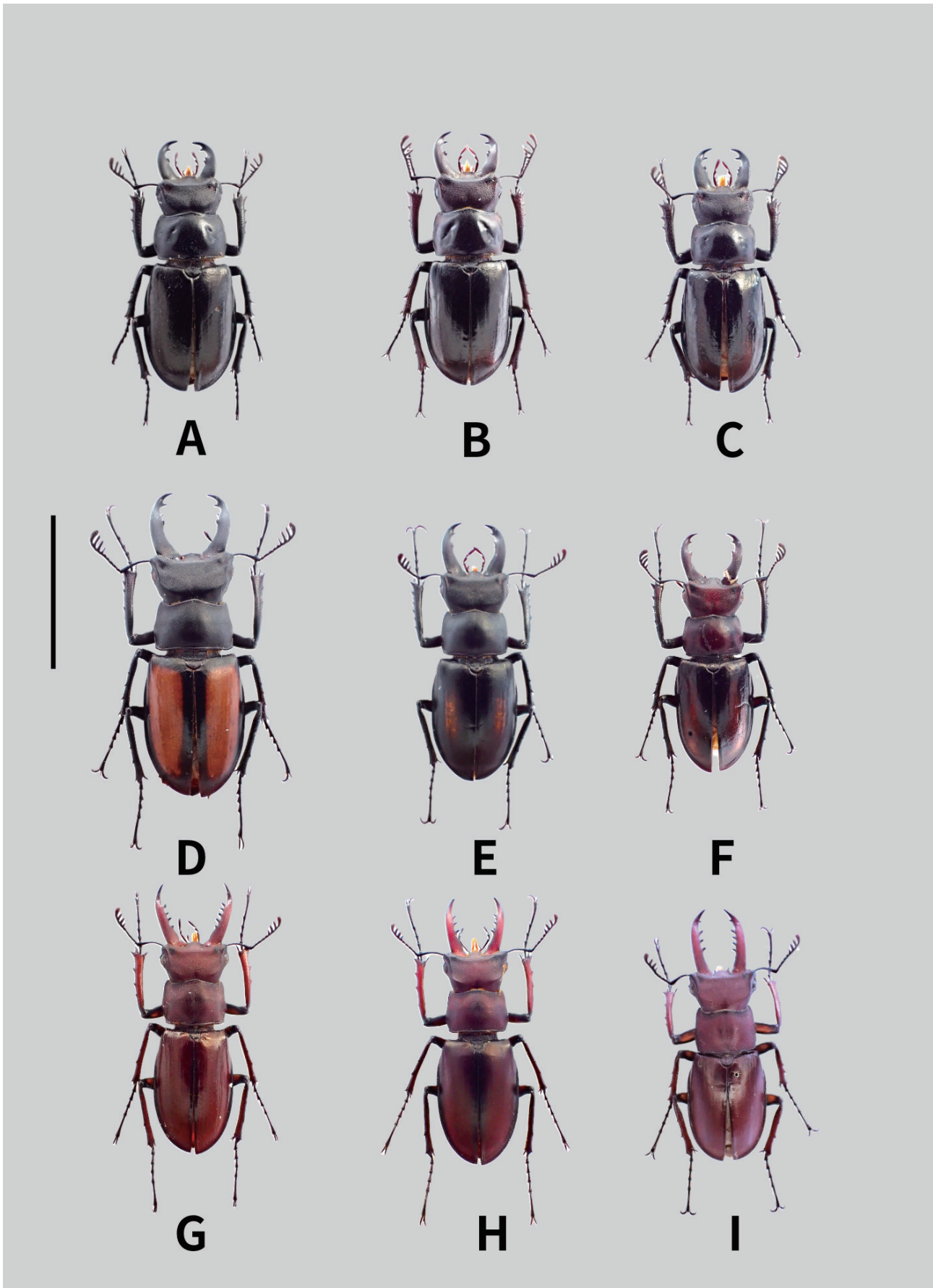


Figure 3. Morphological comparison of allied *Lucanus* species in dorsal and ventral views. (A–C) *Lucanus gamunus* Sawada & Watanabe, 1960; (D–F) *Lucanus parryi* Boileau, 1899; (G–I) *Lucanus swinhoei* Parry, 1874. Scale bar = 20.0 mm.



Figure 4. Comparative morphology of the male aedeagus in dorsal, ventral, views, and abdominal segment IX, within the *Lucanus parryi* species group and allied species. (A–C) *L. chengyuani*; (D–F) *L. swinhoei*; (G–I) *L. parryi*; (J–L) *L. gamunus*. Scale bar = 2.0 mm.

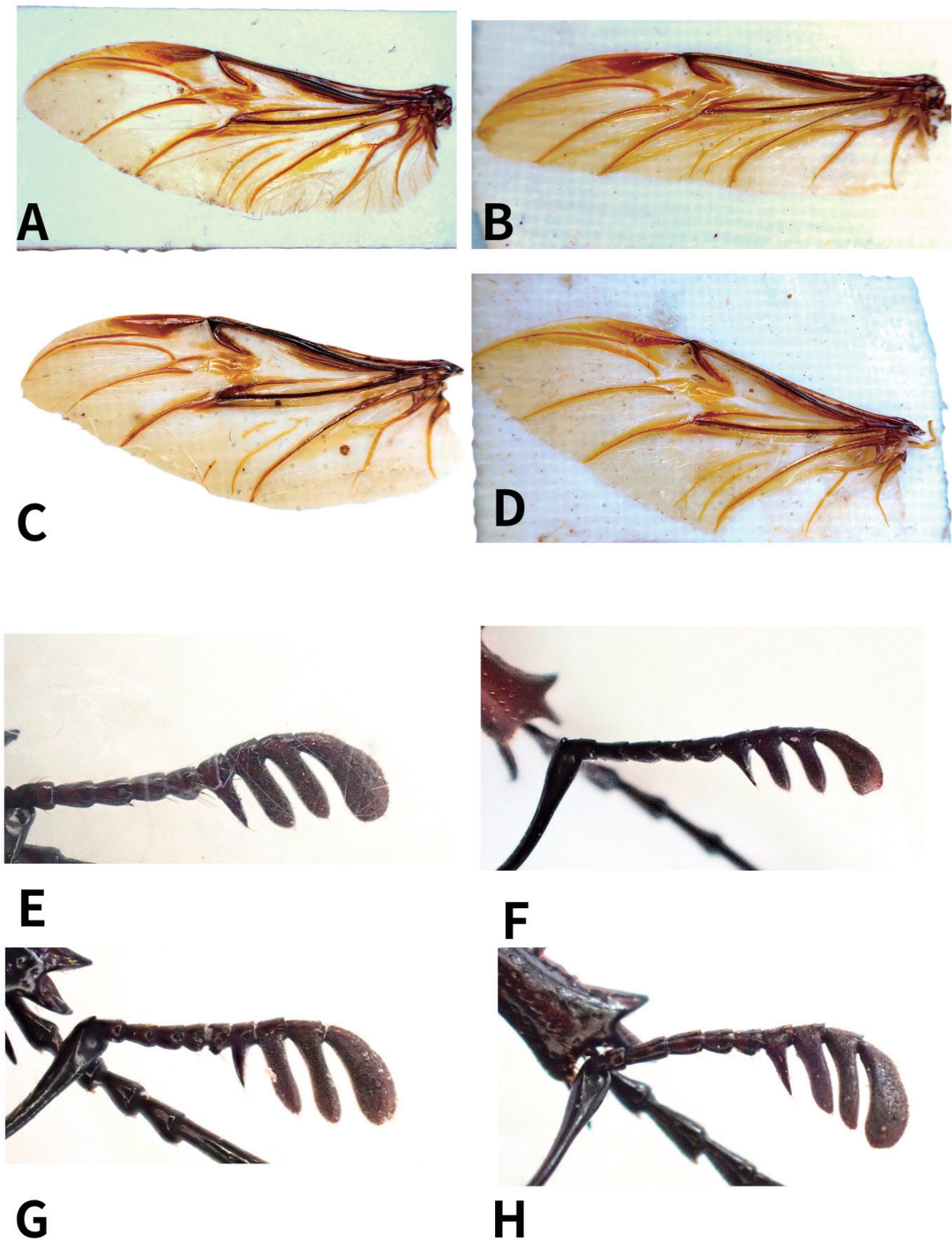


Figure 5. Male antennal flabellate lamellae and hindwing morphology of *Lucanus* species. (A, E) *L. chengyuani*; (B, F) *L. swinhoei*; (C, G) *L. gamunus*; (D, H) *L. parryi*. All images not to scale.



Figure 6. Field observations of *Lucanus chengyuani* Wang & Ko, 2018 males in their natural habitat. (A) Large-sized morph; (B) Medium-sized morph.



Figure 7. Alishan region, Chiayi County, Taiwan. (A) Mid-elevation broad-leaved evergreen forest (Machilus–Castanopsis forest zone); (B) Landscape of the Alishan region.