



## A taxonomic review of *Sueus* Murayama, 1951 ambrosia beetles (Coleoptera: Curculionidae: Scolytinae: Hyorrhynchini) aided by molecular phylogenetic analyses

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### Abstract

Four *Sueus* Murayama, 1951 species occur in Southeast Asia and Oceania. They all likely have a female-biased haplodiploid inbreeding mating system and feed on symbiotic ambrosia fungi. These life history traits increase the potential of adventive events. Indeed, *Sueus* has been recently discovered on the Caribbean island of Martinique. Morphological variation has been observed among some populations of *Sueus niisimai* (Eggers, 1926), which questioned species boundaries. Given the beetle's potential economic importance, we provide a molecular phylogeny as a foundation for systematic study and review the status of the known species. We sequenced a total of 1117 nucleotides from mitochondrial COI and nuclear CAD genes for 25 specimens. Parsimony and Bayesian phylogenies were similar in topology and demonstrated the sister placement of *S. granulatus* (Eggers, 1936) to the other *Sueus* species, reciprocal monophyly of *S. niisimai* and *S. pilosus* (Eggers, 1936) **status restored**, the monophyly of *S. obesus* Browne, 1977 and elevated levels of nucleotide divergence (interspecific = 16–22%). *Sueus chatterjeei* Smith & Cognato **sp. nov.** (India) and *Sueus insulanus* Schiffer, Smith & Cognato **sp. nov.** (Papua New Guinea) are described. *Hyorrhynchus granulatus* Eggers, 1936 is removed from synonymy with *Hyorrhynchus lewisi* Blandford, 1894 and reinstated as a valid species, *Sueus granulatus* (Eggers, 1936) **status restored, comb. nov.** A key to the eight recognized species is given. In addition, the identity of the Martinique species is revised as *S. pilosus*. Geographic distribution of species and the potential existence of cryptic species are discussed.

**Key words:** Oriental region, molecular systematics, mitochondrial, nuclear DNA

### Introduction

*Sueus* Murayama, 1951, (Curculionidae: Scolytinae: Hyorrhynchini), comprises four species, *S. obesus* (Browne, 1977), *S. niisimai* (Eggers, 1926), *S. borneensis* Bright, 1994 and *S. striatulus* (Schedl, 1954). An antennal club that is slightly longer than wide and a five or six-segmented funicle distinguishes these species from other Hyorrhynchini. They exhibit a female-biased sex ratio, an inbreeding mating system, and haplodiploid genetics, where males are haploid, and females are diploid. Sexual dimorphism is evident; females have additional funicular segment and are larger than males. The species are distributed from Japan and South Korea across Southeast Asia and Oceania (Beaver & Gebhardt 2005). *Sueus niisimai* exhibits the broadest geographic distribution and has recently been discovered on the Caribbean island of Martinique (Smith *et al.* 2022). Although knowledge of their ecology is mainly limited to *S. niisimai*, all species are believed to create brood galleries in the sapwood of various tree species, where they cultivate and consume symbiotic ambrosia fungi (Beaver 1984; Li *et al.* 2020). Specifically, the pathogenic fungus *Diatrypella japonica* has been identified as the symbiont associated with *S. niisimai*, although a mycangium was not found (Li *et al.* 2020). The decline of specific tree species has not been associated with *S.*

*niisimai* and this fungus. However, *Sueus* species have similar habits to Xyleborini ambrosia beetles which raises concerns as to their potential as pests in agriculture and forestry, particularly due to their association with pathogenic fungi, transportability, and mating systems (Rabaglia *et al.* 2019).

The phylogenetic relationships among *Sueus* species remain unexplored. A phylogeny would provide an evolutionary context to *Sueus* taxonomy, ecology, and behavior and contribute to understanding this beetle's potential impact on forest health and pest management. In this study, we reconstructed a phylogeny using DNA sequences and used the phylogeny, in part, to justify the description of a new species and other taxonomic changes.

## Materials and methods

### Specimens and Imaging

Specimens, including types, were sourced from entomological collections (see below) and recent collecting events by the authors (Table 1, Fig. 1). Species descriptions of all Hyorrhynchini species were studied to ensure correct generic placement. The study was based on female specimens, as males are infrequently encountered in the field and rare in collections. Museum specimens were used for morphological examination while the recently collected specimens were used for the molecular phylogenetic study (Table 1). These specimens represented all described *Sueus* species, including two suspect new species and *Hyorrhynchus ebianensis* Huang & Yin as an outgroup species (GenBank #KY805901). Specimens were directly compared to type material for identification. Specimens were examined using a Leica (Wetzlar, Germany) MZ6 and MZ16 stereomicroscopes and illuminated with an Ikea Jansjö LED work lamp (Delft, Netherlands) for diagnostic characters used in previous studies (e.g. Beaver & Gebhardt 2005). Specimens were photographed with a Visionary Digital Passport II system (Dun Inc., Palmyra, VA) using a Canon EOS 5D Mark II, 65.0 mm Canon Macro photo lens, and two Elinchrom (Elinchrom LTD, Renens, Switzerland) ELC 500 dual studio monolights and a Stack Shot (Cognisys, Inc, Traverse City, MI). Montage images were assembled using Zerene Stacker 1.04 and improved in Adobe Photoshop 2023 v. 24.6 (San Jose, CA). Total length was measured from apex of the pronotum to the apex of the elytra, and width was measured at the widest point of the specimen. The pedicel is excluded from the count of number of funicle segments. New distribution records are denoted with an asterisk.

### Specimens were sourced from or deposited in the following collections

BPBM Bernice P. Bishop Museum, Honolulu, USA;  
CNCI Canadian National Collection of Insects, Ottawa, Canada;  
MSUC Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, USA;  
NHMUK The Natural History Museum, London, United Kingdom;  
NMB Natural History Museum Basel, Switzerland;  
NMNH National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA;  
MNHN Muséum national d'Histoire naturelle, Paris, France;  
RABC Roger A. Beaver, private collection, Chiang Mai, Thailand;  
UFFE University of Florida, Forest Entomology Laboratory, Gainesville, USA.

### DNA extraction, PCR, and sequencing

For the molecular phylogenetic analysis, 25 specimens representing *S. granulatus*, *S. niisimai*, *S. obesus*, a new suspect species, and *Hyorrhynchus* Blandford (outgroup) were available. DNA was extracted from each specimen's uncrushed head and pronotum separately, using a Qiagen Tissue DNA extraction kit following the manufacturer's protocols. After this process, the head, pronotum, and the remaining body were glued to a paper point, pinned, labeled, and vouchered at MSUC. The purified DNA extracts were used to amplify portions of cytochrome oxidase I (COI) and (CAD) via PCR using the following primer pairs: COI—1495b

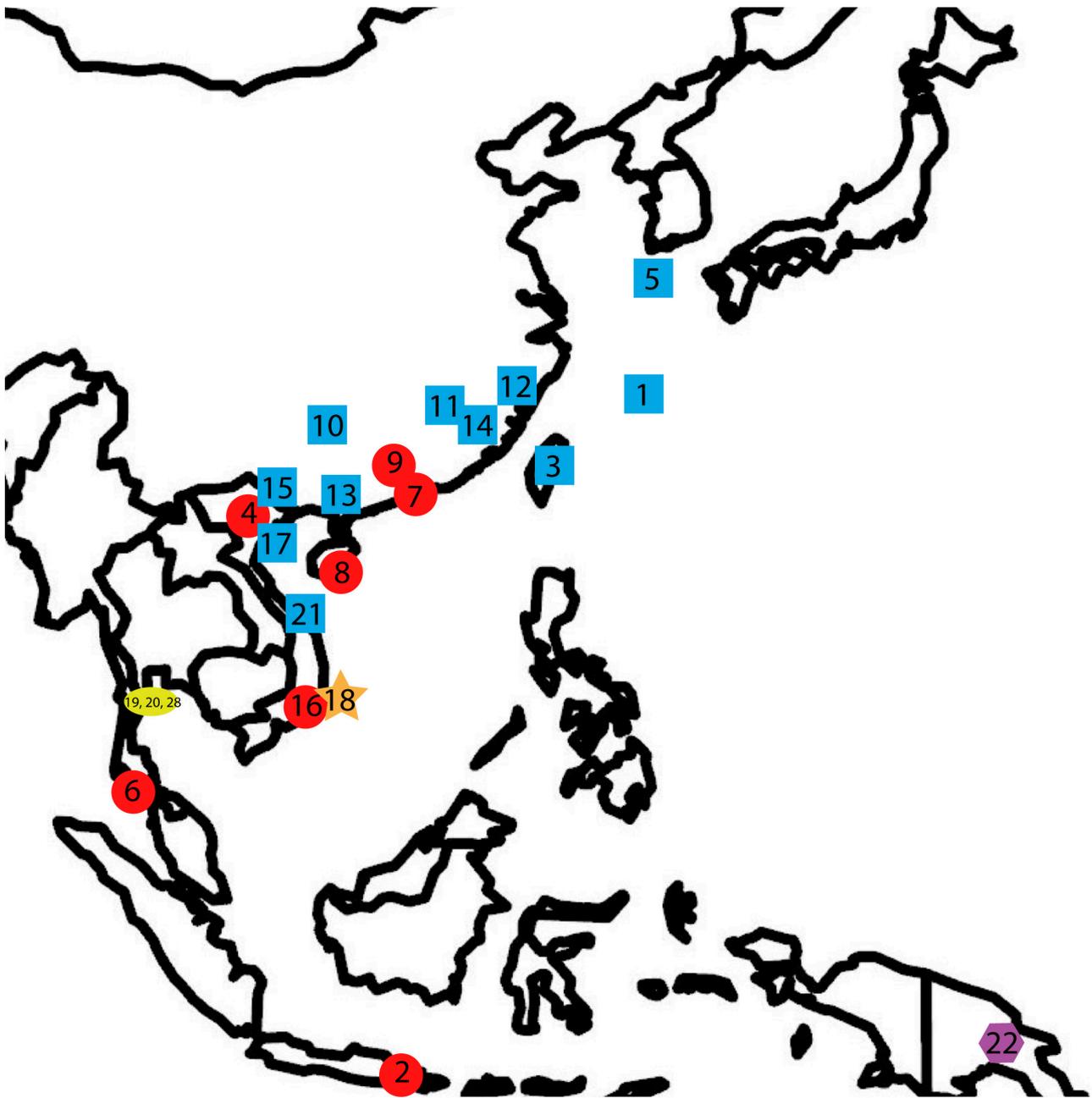
**TABLE 1.** *Strueus* species, voucher label, locality, host and GenBank numbers. N/A= not available.

Species	DNA voucher	Country/Territory	State/Province	Locality	Collected from	Coordinates	Date	Collector(s)	COI GenBank #	CAD GenBank #
<i>S. granulatatus</i>	SMS418	Vietnam	Dong Nai	Cat Tien National Park	N/A	11.42232, 107.42834	22ii2017	A.I. Cognato, T.A. Hoang	PP592646	PP589656
<i>S. insulanus</i>	SMS422	Papua New Guinea	N/A	Mt Wilhelm, 700m	Flight Intercept Trap	-5.732514, 145.2568,	1-3xi2012	Keltim, Uma, Novotny, Leponce	PP592650	N/A
<i>S. niisimai</i>	SMS401	Japan	Okinawa	Kunigami District, Yona Experimental Forest	N/A	N26.763, E128.216	xi2010	J. Hulcr	PP592629	PP589639
<i>S. niisimai</i>	SMS403	Taiwan	Nantou	nearby mountain	<i>Machilus</i>	N/A	6x2015	A. Black	PP592631	PP589641
<i>S. niisimai</i>	SMS405	South Korea	Jeju	Jeju Island	<i>Machilus thunbergii</i>	N/A	N/A	C. Bateman	PP592633	PP589643
<i>S. niisimai</i>	SMS410	China	Guizhou	Guiyang, Huaxi	<i>Ligustrum</i>	N/A	10i2015	You Li	PP592638	PP589648
<i>S. niisimai</i>	SMS411	China	Jiangxi	Xunwu, Xiangshan	N/A	N/A	6ix2018	You Li	PP592639	PP589649
<i>S. niisimai</i>	SMS412	China	Zhejiang	Linan, Zhejiang Agriculture and Forestry University campus	N/A	N30.26, E119.72	26xii2019	You Li	PP592640	PP589650
<i>S. niisimai</i>	SMS413	China	Guangxi	Shangsi, Shiwandashan	N/A	N22.15, E107.98	27iii2018	You Li	PP592641	PP589651
<i>S. niisimai</i>	SMS414	China	Fujian	Fuzhou, Guling	N/A	N26.09, E119.36	30vii2019	You Li	PP592642	PP589652
<i>S. niisimai</i>	SMS415	Vietnam	Cao Bang	Phia Oca	N/A	22°36.454'N 105°52.033'E	15iv2014	A.I. Cognato, S.M. Smith, T.H. Pham	PP592643	PP589653
<i>S. niisimai</i>	SMS417	Vietnam	Ninh Binh	Cuc Phuong National Park	N/A	20.34932, 105.59669	3iii2018	A.I. Cognato, S.M. Smith	PP592645	PP589655
<i>S. niisimai</i>	SMS421	Vietnam	Thua Thien Hue	Bach Ma National Park	N/A	16.22994, 107.85007	16iii2023	A.I. Cognato, P. Gorring	PP592649	PP589659
<i>S. obesus</i>	SMS419	Thailand	Petchaburi 1	Kaeng Krachan N.P., 348m elevation	N/A	12.80344N, 99.44015E	11iv23	S. Smith, W. Sittichaya	PP592647	PP589657
<i>S. obesus</i>	SMS420	Thailand	Petchaburi 2	Kaeng Krachan N.P., 348m elevation	<i>Lithocarpus</i>	12.80344N, 99.44015E	11iv23	S. Smith, W. Sittichaya	PP592648	PP589658
<i>S. obesus</i>	SMS428	Thailand	Petchaburi 3	Kaeng Krachan N.P., 348m elevation	N/A	12.80344N, 99.44015E	11iv23	S. Smith, W. Sittichaya	PP592651	N/A
<i>S. pilosus</i>	SMS402	Indonesia	East Java	Jombang: Bangunrejo	N/A	N/A	18viii2014	A.J. Johnson	PP592630	PP589640

.....continued on the next page

TABLE 1. (Continued)

Species	DNA voucher	Country/Territory	State/Province	Locality	Collected from	Coordinates	Date	Collector(s)	COI GenBank #	CAD GenBank #
<i>S. pilosus</i>	SMS404	Vietnam	Vinh Phuc	Tam Dao National Park	N/A	N/A	N/A	M. Jusino	PP592632	PP589642
<i>S. pilosus</i>	SMS406	Thailand	Trang	Khao Bentad Wildlife Sanctuary	Bombacaceae	N/A	7v2015	S. Steininger	PP592634	PP589644
<i>S. pilosus</i>	SMS407	China	Hong Kong	Tai Po Kau	N/A	N/A	vi2017	J. Skelton	PP592635	PP589645
<i>S. pilosus</i>	SMS408	China	Hainan	Jinping: Qiongzong	<i>Lisea glutinosa</i>	N/A	24x2016	You Li	PP592636	PP589646
<i>S. pilosus</i>	SMS409	China	Guangdong	Guangzhou, South China Agricultural University	N/A	N/A	28v2017	You Li	PP592637	PP589647
<i>S. pilosus</i>	SMS416	Vietnam	Dong Nai	Cat Tien National Park	N/A	11.4605, 107.37375	22ii2017	A.I. Cognato, T.A. Hoang	PP592644	PP589654
<i>S. pilosus</i>	SMS429	Martinique	Morne-Rouge	320 m. elevation	N/A	14.75818°N, 61.1242°W	16-30v12021	F. Deknuydt	PP592652	PP589660



**FIGURE 1.** Approximate collection localities of *Sueus* specimens used in the phylogenetic analysis. Numbers refer to last digits of DNA vouchers in Table 1. Blue square = *Sueus niisimai*, red circle = *Sueus pilosus*, yellow oval = *Sueus obesus*, purple polygon = *Sueus insulanus*, and orange star = *Sueus granulatus*.

AACAAATCATAAAGATATTGGRAC + rev750 GAAATTATNCCAATTCCTGG

and CAD—apCADfor4 TGGAARGARGTBGARTACGARGTGGTYCG + apCADrev1mod

GCCATYRCYTCBCCYACRCTYTTTCAT (Danforth *et al.* 2006; Smith & Cognato, 2014). PCR reactions

contained 0.3 $\mu$ M each forward and reverse primers, 1x buffer, 1.75 mM magnesium chloride, 200 $\mu$ M dNTPs, 1.25 units hot star Taq (Qiagen), and ~20 ng of DNA template. Each reaction cocktail was subjected to 15 min denaturation (95°C) and 38 cycles of 30 s denaturation (95°C), 30 s annealing (50°C for COI, 55°C for CAD), and 5 min extension (72°C). PCR success was confirmed by gel electrophoresis with a 1.5% agarose gel stained with ethidium bromide. PCR reactions were prepared for DNA sequencing with ExoSAP-IT enzymatic reagent (Thermo Fisher Scientific, Waltham, MA) and Sanger sequencing was performed at the Michigan State University Research Technology Support Facility using Bigdye terminator 1.1 chemistry (Applied Biosystems, Waltham, MA). The

resulting forward and reverse sequences were assembled into a consensus sequence using Sequencer software (Ann Arbor, MI). The sequences were examined for anomalies such as pseudogenes and DNA other than *Sueus*. Verified consensus sequences were deposited in GenBank (Table 1).

## Phylogenetic analyses

The verified consensus sequences were compiled into a NEXUS file for phylogenetic analysis using PAUP\* 4.0a build 167 (Swofford 2002) and Mr. Bayes (Ronquist *et al.*, 2012). In PAUP\*, a heuristic search, using all data, for the most parsimonious trees consisted of 100 random stepwise addition via bisection/reconnection. Gaps were treated as missing, and each character was unordered and equally weighted. A bootstrap analysis of 500 pseudoreplications was also conducted using heuristic searches with simple stepwise addition. In Mr. Bayes, both genes were partitioned by codon position and a model of general time reversal + gamma + proportion of invariable sites was applied to each partition (unlinked parameters). Four Metropolis-Coupled Markov Chain Monte Carlo chains (one cold, three heated) were run in two simultaneous analyses for 3 million generations and sampled every 100<sup>th</sup> generation. All parameters reached stability and the split distribution between analyses achieved a mean standard deviation of 0.0066. Bayesian posterior probabilities were calculated as a majority-rule consensus tree after a 25% burn-in of saved trees (45,002 total trees). The average estimated sample size for run parameters was greater than 100. Percent pairwise DNA difference was calculated as p-distance in PAUP\*.

## Species concept

Given that *Sueus* exhibits similar traits such as, female-biased sex ratios, an inbreeding mating system, and haplodiploid genetics, with xyleborine ambrosia beetles, we adopt the same species concept (Cognato *et al.* 2020; Smith & Cognato 2022). Species are hypotheses of evolutionary lineages (Hey 2006; Yeates *et al.* 2011) that are delimited by monophyly, exhibit molecular differences beyond a threshold indicative of species limits for the taxon, and are diagnosable. In the case of xyleborines, DNA sequence difference >10% for COI and >2% for CAD were associated with monophyletic individuals that exhibit diagnostic morphological characters. These thresholds are applied to *Sueus*.

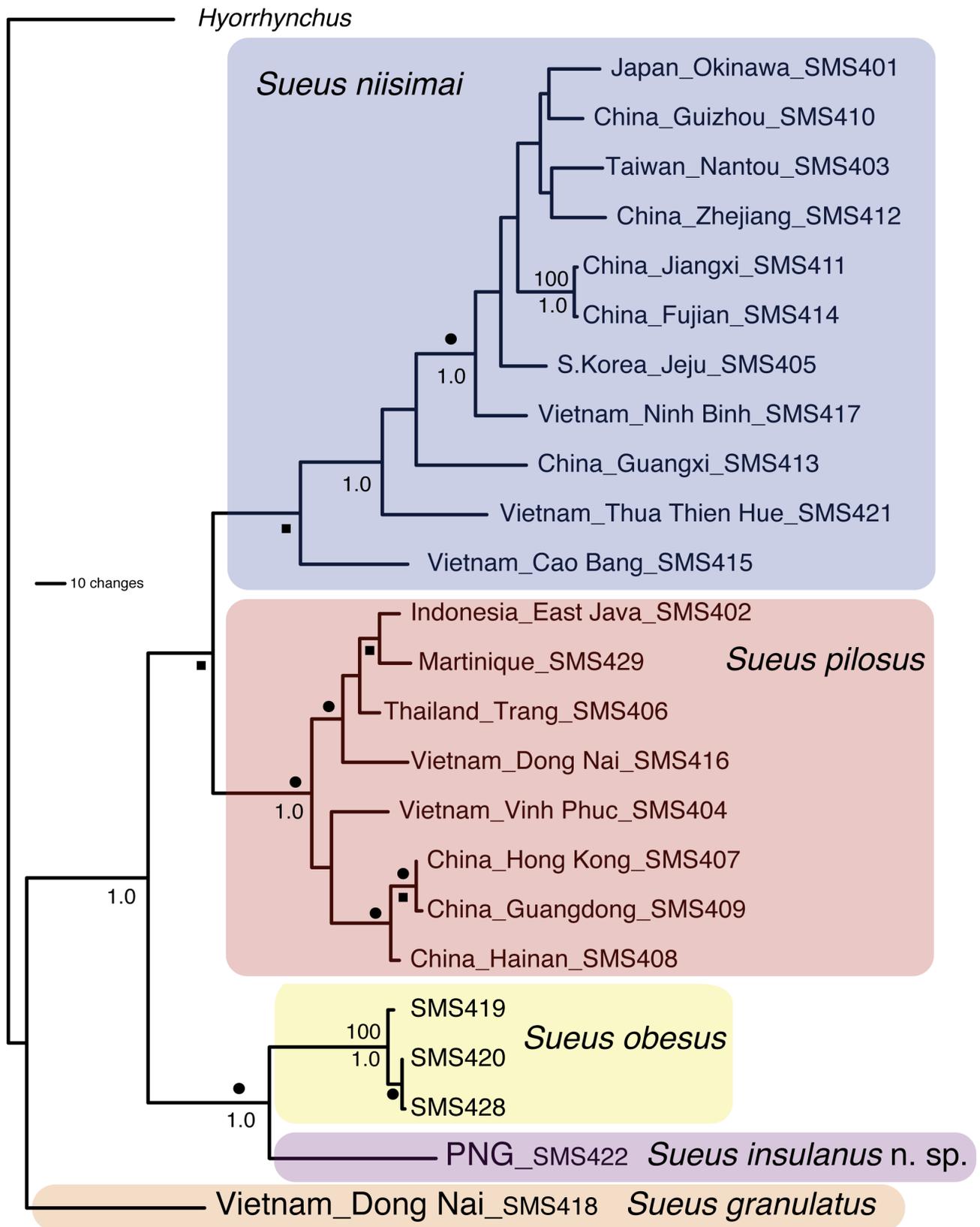
## Results

A single parsimonious phylogenetic tree (length = 875) that was completely resolved was found (Fig. 2). *Sueus niisimai* was monophyletic but the bootstrap was < 50%. It consisted of two clades that associated with approximately northern (bootstrap = 71%) and southern populations (bootstrap = 99%) (map figure). Morphological differences associated with these clades and the individuals in the southern clade was identified as the synonymized *S. pilosus*. A specimen from Martinique grouped in the southern clade. *Sueus obesus* was monophyletic and had a bootstrap value of 100%. *Sueus granulatus* was sister to the remaining specimens and a specimen from Papua New Guinea (new species) was sister to *S. obesus*. Both species exhibited DNA differences comparable to the other species. The topology of the phylogeny resulting from the Bayesian analysis was similar to the results of the parsimony analysis (Fig. 2). It differed in intraspecific resolution and arrangement of individuals within *S. niisimai* and *S. pilosus*. The posterior probabilities were 1.0 for all species and 0.99 for the clade *S. niisimai* + *S. pilosus*.

The genetic divergence among conspecifics displayed an average range of approximately 0.00 to 0.02 for the CAD gene and 0.00 to 0.15 for the COI gene. The interspecific comparisons among the *Sueus* species, encompassed a range of 0.01 to 0.07 for CAD and 0.14 to 0.22 for COI, respectively.

## Key to *Sueus* species (females only)

- 1 Elytral declivity acutely tapered to the apex, apex 1/4 width of the declivity base (Fig. 4) ..... *S. chatterjeei* Smith & Cognato sp. nov.
- Elytral declivity broad to the apex, apex at least 1/2 width of the declivity base (Fig. 3) ..... 2



**FIGURE 2.** Phylogeny of *Sueus* species resulting from the parsimony analysis inferred from COI and CAD DNA sequences. Numbers above branch are bootstrap values, numbers below are posterior probabilities, circles are bootstrap values 90–99%, and squares are posterior probabilities 0.9–0.99.

2	Declivital interstriae bearing rows of large and prominent denticles or granules, clearly visible above setae in lateral profile (Fig. 5)... 3	
-	Declivital interstriae bearing minute granules, obscured by setae in lateral profile .....	4
3	Declivital interstriae and the apical margin bearing widely separated prominent denticles with sharply hooked apices (Fig. 10) .....	<i>S. striatulus</i> (Schedl)
-	Declivital interstriae but not the apical margin bearing narrowly separated rows of large and prominent granules with rounded apices .....	<i>S. granulatus</i> (Eggers)
4	First fifth of elytral disc at base rugose (Fig. 8) .....	5
-	First fifth of elytral disc at base granulate (Fig. 7) .....	6
5	Elytral striae strongly impressed on the elytral disc .....	<i>S. obesus</i> (Browne)
-	Elytral striae weakly impressed on the elytral disc .....	<i>S. borneensis</i> Bright
6	Elytral interstitial setae appressed; body size larger, 2.0–2.7 mm and stouter 1.92–2.08 × as long as wide (Fig. 6) .....	<i>S. insulanus</i> Schiffer, Smith & Cognato sp. nov.
-	Elytral interstitial setae erect; body size smaller, 1.6–1.95 mm and more elongate, 2.1–2.4 × as long as wide (Fig. 7) .....	7
7	Main elytral interstitial setae and ground vestiture similar sizes; ground vestiture longer than width of an interstria .....	<i>S. pilosus</i> (Eggers)
-	Main elytral interstitial setae longer than ground vestiture; ground vestiture shorter than width of an interstria .....	<i>S. niisimai</i> (Eggers)

## Taxonomic treatment

### *Sueus* Murayama, 1951

*Sueus* Murayama, 1951: 1. Type species *Sueus sphaerotrypoides* Murayama, 1951 = *Hyorrhynchus niisimai* Eggers, 1926, original designation.

**Diagnosis.** Length 1.6–3.0 mm, 1.82–2.5 × longer than wide, body black. *Sueus* is distinguished by the following combination of characters: eyes completely divided without a separating carina in either sex; antennal club less than 1.5 × longer than wide, forming a slightly flattened cone; female antennal funicle five or six segmented; protibia outer apical angle produced into one conspicuous spine; procoxae widely separated; and dwarf males. *Sueus* can be further distinguished from the other Hyorrhynchini genera *Hyorrhynchus* and *Pseudohyorrhynchus* which have eyes completely divided and separated, in part, by a carina (males); antennal club that is 1.5–2.0 × longer than wide and flattened; antennal funicle six segmented; and males that are comparable to females in size.

### *Sueus borneensis* Bright, 1994

Fig. 3

*Sueus borneensis* Bright, 1994: 271.

**Type material.** Holotype, female, Borneo: Sabah, Mt. Kinabalu N.P., Poring Hot Spgs., 850m, V-11-1987, small cut sampling, D.E. Bright Collector, CNC1589602 (CNCI) (photographs examined).

**Diagnosis.** Length 2.5–2.8 mm, about 2.0 × longer than wide (Bright 1994); declivital interstriae bearing minute granules; first fifth of elytral base rugose; striae weakly impressed on the elytral disc.

**Distribution.** Indonesia (Sulawesi), East Malaysia (Sabah) (Beaver & Gebhardt 2005).

**Hosts.** The type series was collected from a small cut sapling and a large fallen branch (Bright 1994). Presumably mycetophagous.

### *Sueus chatterjeei* Smith & Cognato, sp. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:D3454C2D-C0FD-4F69-9F95-992C67D42493>

Fig. 4

**Type material.** Holotype, female, India: [West] Bengal, Jalpaiguri, Gazalduba [=Gajoldoba], 16-X-1933, N.C. Chatterjee, S.L. Wood Collection, USNMENT01595085 (NMNH).



**FIGURE 3.** *Sueus borneensis*, female (Indonesia, Sulawesi Utara, RABC) 2.25 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

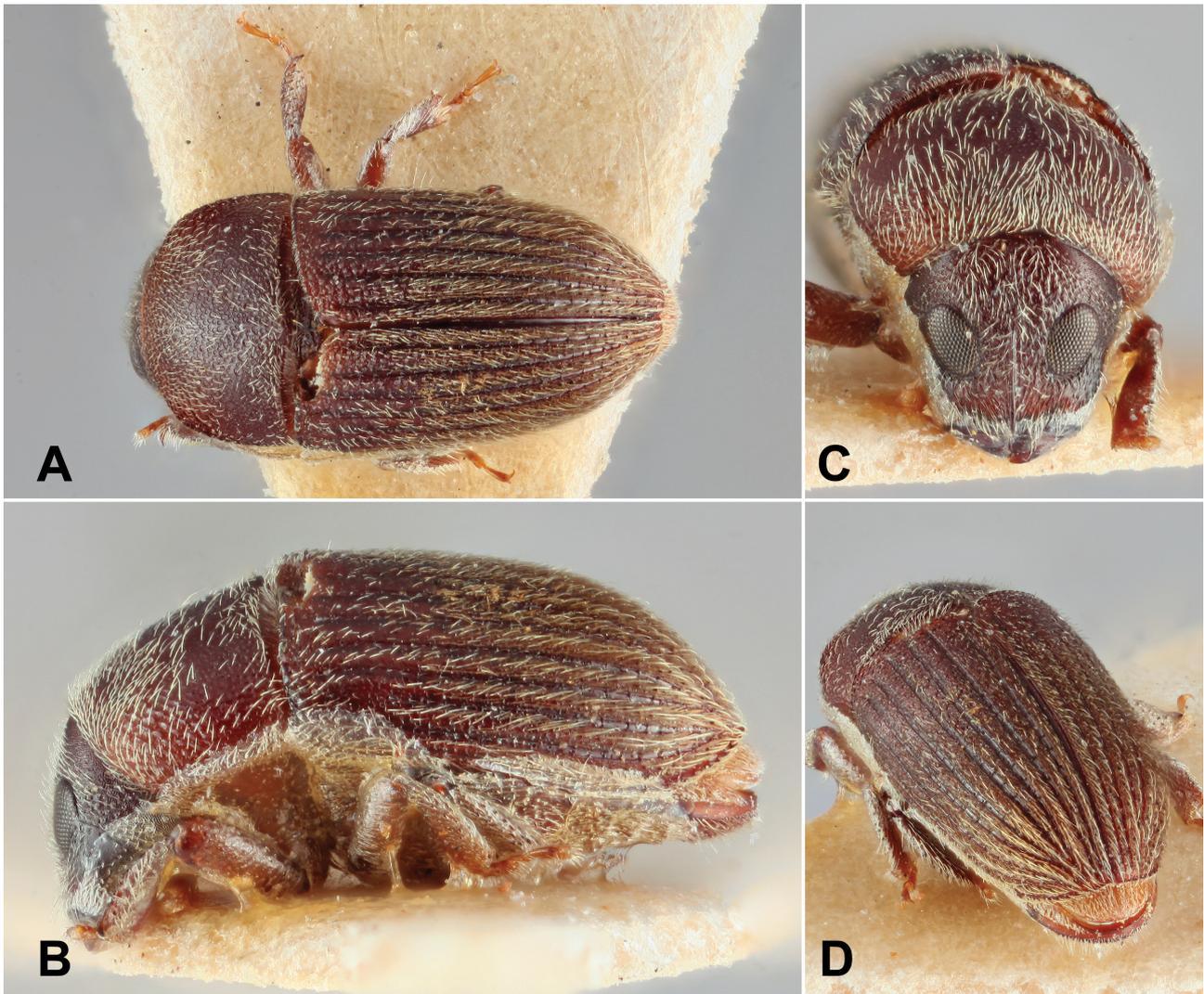
**Diagnosis.** Length 2.4 mm,  $2.09 \times$  longer than wide; elytral declivity acutely tapered to the apex, apex  $1/4$  width of the declivity base.

**Description.** Female: Length 2.4 mm,  $2.09 \times$  longer than wide. Frons weakly convex, with a distinct, sharply elevated, longitudinal carina extending from epistomal margin to upper level of eyes; surface dull, densely and finely punctate-granulate, with fine, brown setae. Antennal funicle and club not observable. Pronotum  $1.77 \times$  wider than long, widest slightly behind middle; lateral margin evenly arcuate, more strongly converging on anterior half; surface densely, moderately punctate, with scattered, long, golden-brown setae. Elytra  $1.52 \times$  longer than wide,  $2.69 \times$  longer than pronotum; sides weakly arcuate, declivity tapered to narrowly rounded apex; discal striae very narrow, shining, lightly impressed, more strongly impressed toward declivity, striae punctures fine, shallow; discal interstriae much wider ( $2-3 \times$ ) than striae, granulate, with three or four rows of long, fine, semi-erect, golden-brown setae. Declivity convex; surface as on disc except striae distinctly more deeply impressed, interstriae slightly narrower, fewer granules. Third tarsal segment entire.

**Etymology.** Named in honor of the collector of the holotype, Nibaran Chandra Chatterjee (1890-1942) and his contribution to forest entomology in India ([https://insaindia.res.in/old\\_website/detail.php?id=N42-0153](https://insaindia.res.in/old_website/detail.php?id=N42-0153)).

**Distribution.** India (West Bengal).

**Hosts.** Unknown. Presumably mycetophagous.



**FIGURE 4.** *Sueus chatterjeei* sp. nov. female holotype (USNMENT01595085), 2.4 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

***Sueus granulatus* (Eggers, 1936), stat. res., new combination**

Fig. 5

*Hyorrhynchus granulatus* Eggers, 1936: 80.

**Type material.** Holotype, female, [Indonesia] Java, Buitenzorg, II.1924, 250m, L.G.E. Kalshoven (NHMW) (photographs examined).

**New records.** China: Guangxi, Shangsi, Shiwandashan, N22.15, E107.98, 27iii2018, You Li (1, UFFE). Vietnam: Dong Nai Prov., Cat Tien NP, 11.42232, 107.42834, 128 m. 25.iii.2017, AI Cognato, TA Hong, ex 1–3 cm dia. branch (3, MSUC).

**Diagnosis.** Length 2.5–3.0 mm (2.9–3.4mm when including tergite 8), 2.43–2.5 × longer than wide; declivital interstriae bearing rows of nearly contiguous large rounded granules, clearly visible above setae in lateral profile.

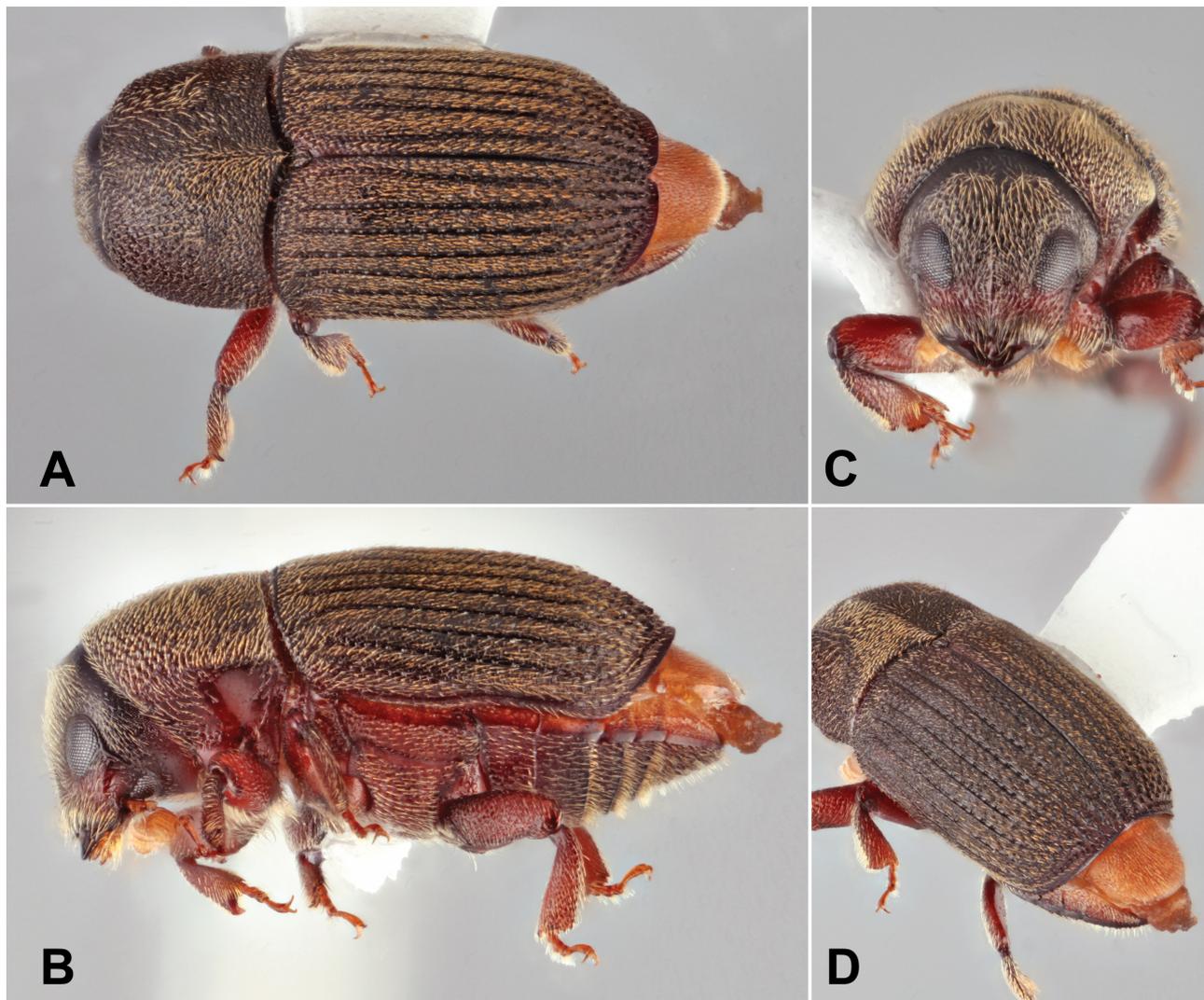
**Distribution.** China\* (Guangxi), Indonesia (Java), Vietnam\* (Dong Nai).

**Hosts.** Unknown. Presumably mycetophagous.

**Remarks.** Eggers' (1936) original description states that the type was deposited in the Kalshoven collection, however it is part of the Schedl collection in NHMW.

Wood & Bright (1992) attributed the synonymy of *H. granulatus* and *H. drescheri* Eggers with *H. lewisi*

Blandford, to Schedl (1962). However, this was a misinterpretation of Schedl's (1962) generic grouping of these species. Inspection of images of type specimens revealed that the granulate elytral declivity is only diagnostic for *H. granulatus*. As with Beaver & Liu (2010) and M. Knižek (in Beaver & Liu 2010), we recognize this dissimilarity and we remove *H. granulatus* from synonymy with *H. lewisi*. Furthermore, generic level diagnostic characters, especially the shape of the antennal club, are consistent with those of *Sueus*.



**FIGURE 5.** *Sueus granulatus* female (MSUC\_ARC\_320283), 2.43 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

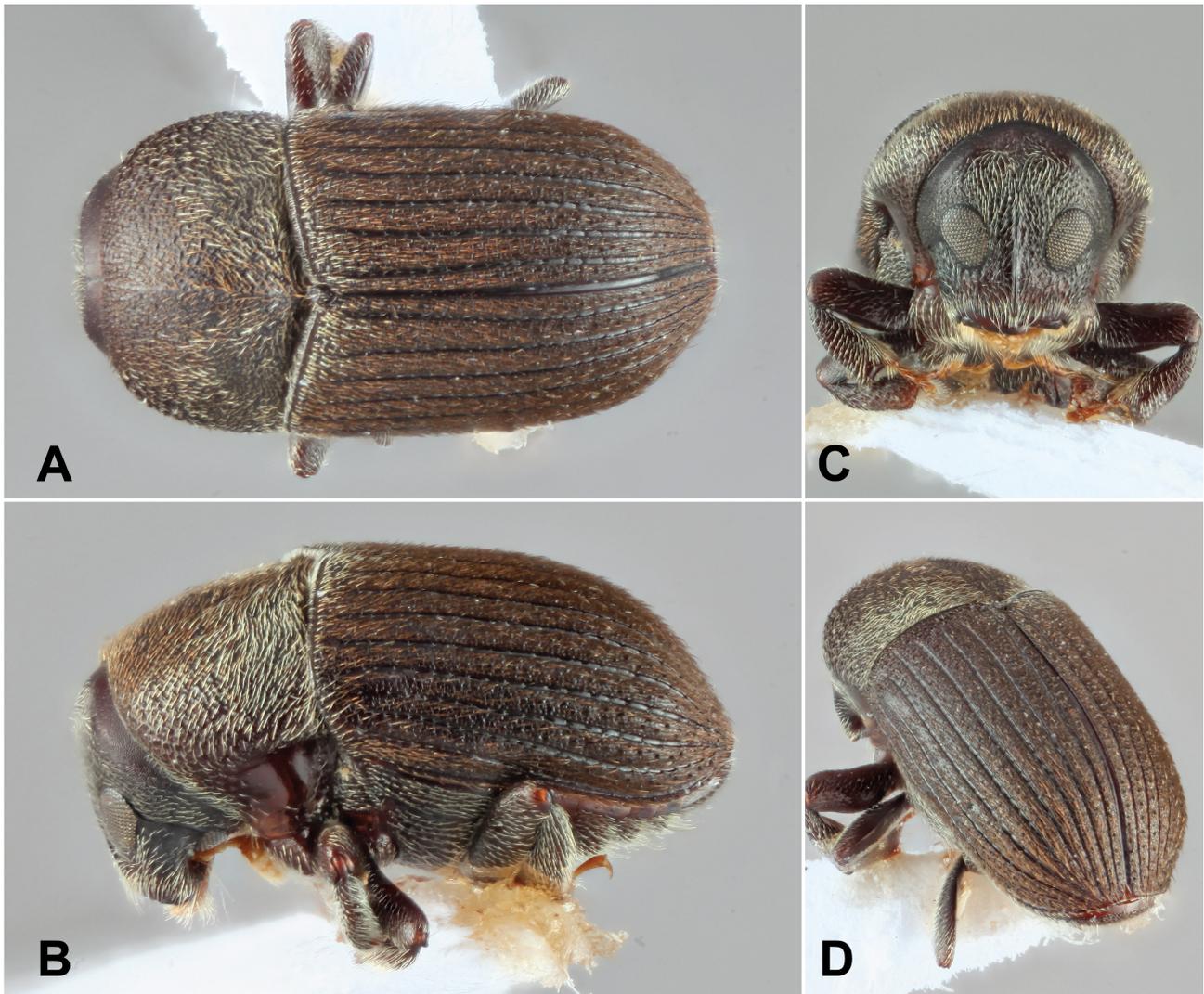
***Sueus insulanus* Schiffer, Smith & Cognato, sp. nov.**

<http://zoobank.org/urn:lsid:zoobank.org:act:E9458BE8-3FD7-4FA9-86ED-D0C1C8D71BBA>

Fig. 6

**Type material.** Holotype, female, Papua New Guinea: Mt Wilhelm, -5.732514, 145.2568, 700m, Coll. by Keltim, Uma, Novotny, Leponce; P1117 Plot 3, FIT-MW700-C-4/8-d07, 31/10/20]12-2/11/[20]12 (MNHN). Paratypes, females, Papua New Guinea: Mt Wilhelm, -5.731961, 145.2522, 700m, Coll. by Keltim, Uma, Novotny, Leponce; P1237 Plot 18, FIT-MW700-R-4/8-d08, 1/11/[20]12 -3/11/[20]12; DNA Voucher SMS422 (MSUC). Papua New Guinea: Mt Wilhelm, -5.739897, 145.3297, 200m, Coll. by Dilu, Ray, Novotny, Leponce; P0802 Plot 12, FIT-MW200-L-7/8-d14, 7/11/[20]12 -9/11/[20]12 (MNHN). Each specimen includes the label, “Our Planet Reviewed –MNHN/PNI/IRD 2012”.

**Diagnosis.** Length 2.0–2.6 mm, 1.82–2.08 × longer than wide; declivital interstriae bearing minute granules; interstitial setae of the elytral declivity appressed.



**FIGURE 6.** *Sueus insulanus* sp. nov. female holotype, 2.0 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

**Description. Female:** length 2.0–2.6 mm, 1.82–2.08× longer than wide. Frons weakly convex, with a distinct, sharply elevated, longitudinal carina extending from epistomal margin to upper level of eyes; surface dull, densely, and finely punctate-granulate, with fine, golden-brown setae. Antennal funicle 5-segmented; club conical slightly flattened, with three transverse sutures. Pronotum 1.2–1.44× wider than long, widest slightly behind middle; lateral margin evenly arcuate, more strongly converging on anterior half; surface densely, finely granulate and weakly punctate, with scattered, long, golden-brown setae. Elytra 1.18–1.38× longer than wide; sides weakly arcuate, apex narrowly rounded; discal striae very narrow, shining, lightly impressed, more strongly impressed toward declivity, striae punctures fine, shallow; discal interstriae much wider (2–4×) than striae, granulate, with 3 or 4 rows of long, fine, appressed, golden-brown setae. Declivity convex; surface as on disc except striae distinctly more deeply impressed, interstriae slightly narrower, fewer granules. Third tarsal segment entire.

**Male.** Unknown.

**Etymology.** L.= islander, a noun in apposition.

**Distribution.** Papua New Guinea.

**Hosts.** Unknown. Presumably mycetophagous.

***Sueus niisimai* (Eggers, 1926)**

Fig. 7

*Hyorrhynchus niisimai* Eggers, 1926: 133.

*Neohyorrhynchus niisimai* (Eggers): Schedl 1962: 202.

*Sueus niisimai* (Eggers): Wood 1983: 650.

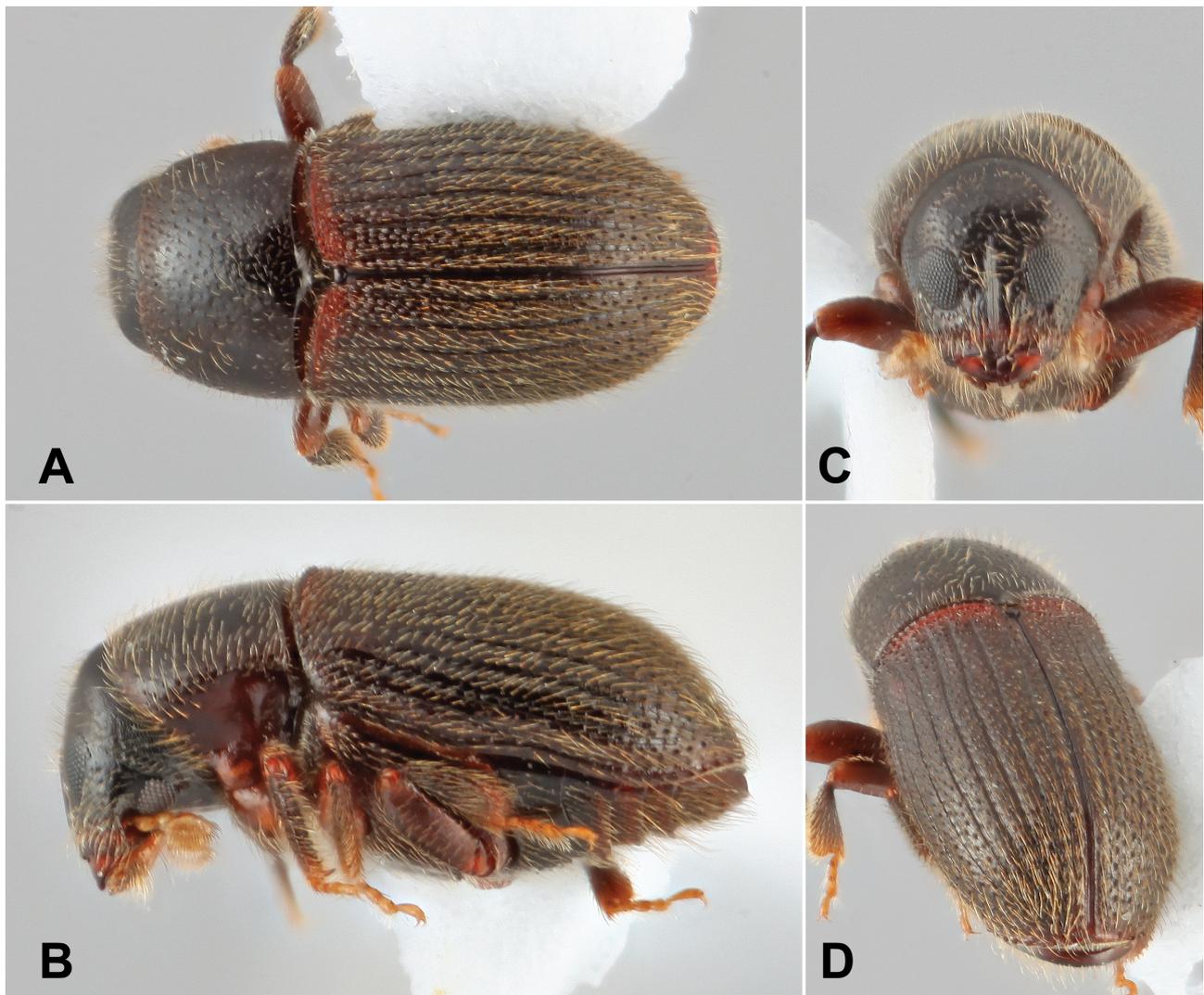
*Sphaerotrypes controversae* Murayama 1950: 62. Synonymy: Wood 1992: 85.

*Sueus sphaerotrypoides* Murayama 1951: 2. Synonymy: Wood 1983: 650.

**Type material.** *Hyorrhynchus niisimai* holotype, female, Japan, Urakawa (Hakodate), USNMENT01547084 (examined). *Sphaerotrypes controversae* lectotype, female, Japan, Kochi Pref., Daidominamiyama, Shikikiu (examined). *Sueus sphaerotrypoides* holotype, female, Japan, Wakayama Pref., Nishimuro County, Ohshima Vill, Sue (NMNH) (examined).

**Other specimens examined.** Vietnam: Ninh Binh Prov., Cuc Phuong NP, 20.34932, 105.59669, 431m, 7.iii.2018, VN134, SM Smith, AI Cognato, ex standing dead laurel; base of bole, 5 cm (MSUC\_ARC\_320284). Additional records in Table 1.

**Diagnosis.** Length 1.7–2.0 mm, 2.11–2.25 × longer than wide; declivital interstriae bearing minute granules; first fifth of elytral base granulate; main elytral interstitial setae longer than ground vestiture (> width of interstria); ground vestiture shorter than width of an interstria.



**FIGURE 7.** *Sueus niisimai* female (MSUC\_ARC\_320284) 1.7 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

**Distribution.** Found throughout eastern Asia including China (Fujian, Guangxi, Guizhou, Jiangxi, Zhejiang), Japan (Kochi, Okinawa, Wakayama), South Korea (Jeju), Taiwan (Nantou), and northern Vietnam\* (Cao Bang, Ninh Binh, Thua Thien Hue). It may have a more northerly distribution than *S. pilosus*. There are records from Australia, Fiji (introduced), Malaysia, Sri Lanka, and Papua New Guinea (Beaver 1984; Beaver & Gebhardt 2005; Li *et al.* 2020) which need verification given potential misidentification with the more southerly distributed *S. pilosus*.

**Host.** *Cornus controversa* (Cornaceae) (Murayama 1950), *Machilus* (Lauraceae), *Ligustrum* (Oleaceae). Mycetophagous and presumably polyphagous.

***Sueus obesus* (Browne, 1977)**

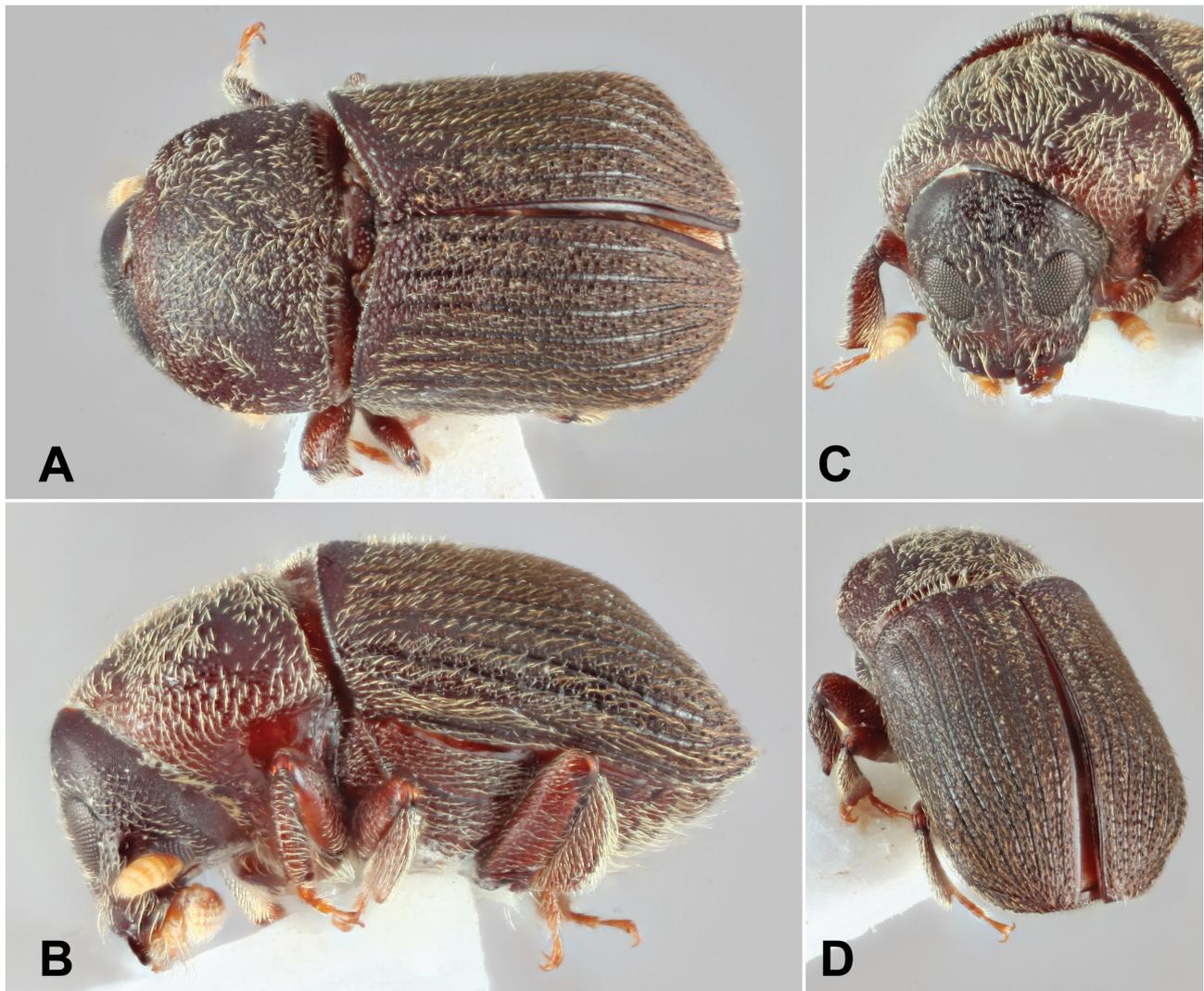
Fig. 8

*Hyorrhynchus obesus* Browne, 1977: 369.

*Sueus obesus* (Browne): Beaver & Gebhardt 2005: 96.

**Type material.** Holotype, female, Malaysia, Penang, Telok Bahang, 22.iv.1975, NHMUK014591790 (NHMUK), examined.

**Other specimens examined.** Thailand: (S): [Nakon Si Thammarat Prov.]: Chawang [District] nr. Nabon, Banna, 70m, Sept. 6, 1958, J.L Gressitt collector (1, BPBM); Suratthani, Khao Sok N.P. 23.ii.2012, R.A. Beaver, ex cut liane c. 3 cm diam., 30288 (1, RABC). Additional records in Table 1.



**FIGURE 8.** *Sueus obesus* female (Thailand, Suratthani) 2.5 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

**Diagnosis.** Length 2.3–2.7 mm, 2.0–2.3 × longer than wide; declivital interstriae bearing minute granules; first fifth of elytral base rugose; striae strongly impressed on the elytral disc.

**Distribution.** Thailand (Nakon Si Thammarat\*, Phetchaburi\*, Surat Thani, Trang), West Malaysia (Penang), East Malaysia (Sabah) (Beaver *et al.* 2014; Bright 2021).

**Hosts.** Reported only from *Lithocarpus* (Fagaceae). Presumably polyphagous and mycetophagous.

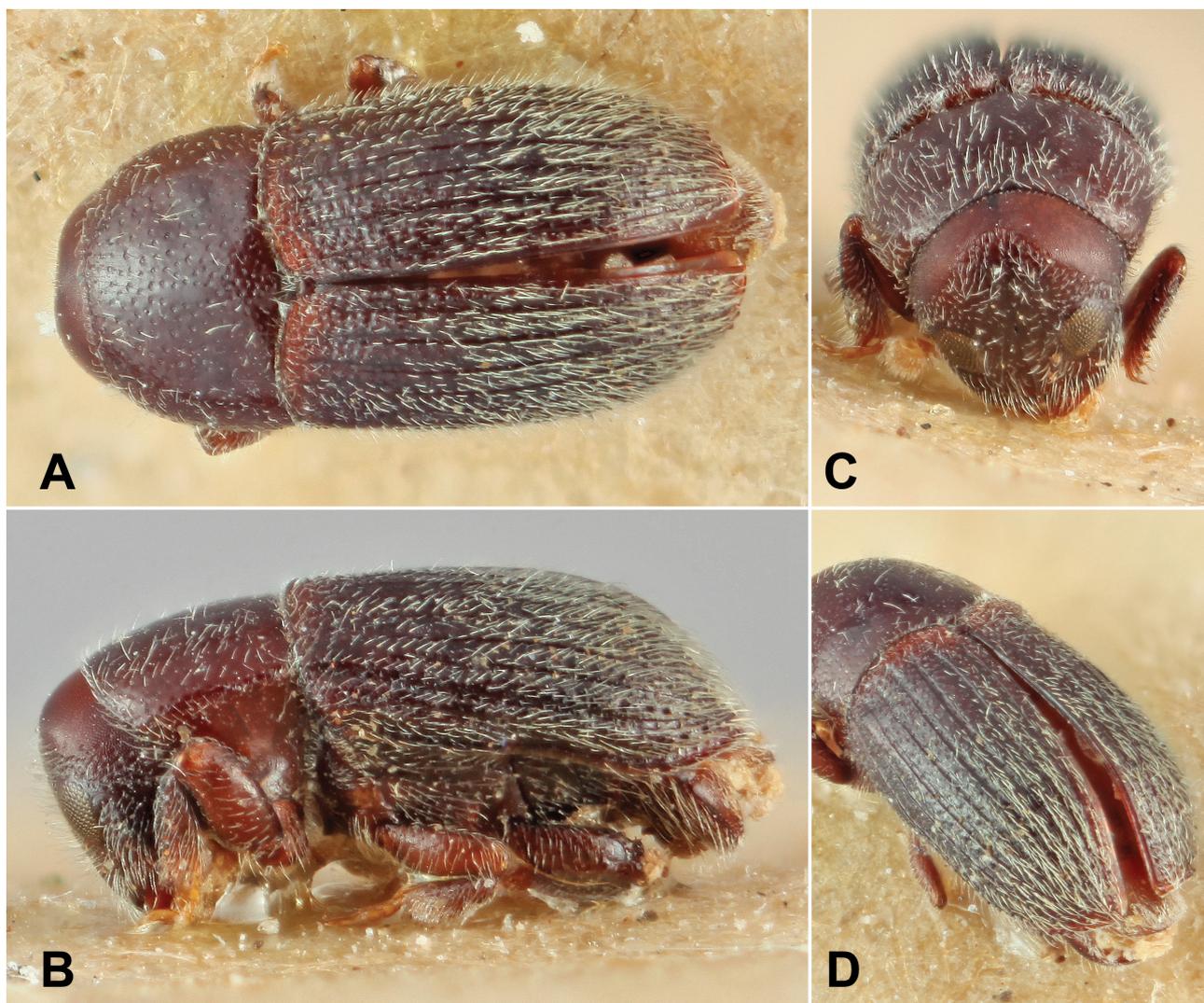
*Sueus pilosus* (Eggers, 1936), *stat. res.*

Fig. 9

*Hyorrhynchus pilosus* Eggers, 1936: 81.

**Type material.** Paratype, female, [Indonesia] Java, Salatiga, 600 m, 10.XI.1922, L.G.E. Kalshoven, USNMENT\_01595294 (NMNH), examined.

**Other specimens examined.** [Indonesia]: Sumatra, G. Sinngalang, S of Bukittinggi. 14-16ii1991, 1300m. Bocák & Bocáková lgt. (1, NMB). Laos: Bolikhamxai Prov. 18°21'N, 105°08'E, Nape (8 km NE), ~600m, Vit Kubán leg. (1, NMB); Hua Phan Prov. 20°12'N, 104°01'E, Phu Phan Mt., ~1750m, 17v-3vi2007, Vit Kubán leg. (1, NMB); Phongsaly Prov., 21°41'N, 102°6'E, Phongsaly env., 6-17v2004, ~1500m, Vit Kubán leg (1, NMB). Additional records in Table 1.



**FIGURE 9.** *Sueus pilosus* female paratype (USNMENT01595294), 1.6 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

**Diagnosis.** Length 1.6–1.95 mm, 2.13–2.4 × longer than wide (n = 5); declivital interstriae bearing minute granules; first fifth of elytral base granulate; main elytral interstitial setae and ground vestiture subequal (> width of interstria); ground vestiture longer than width of an interstria.

**Distribution.** Occurring in southern China\* (Guangdong, Hainan, Hong Kong), Laos\* (Bolikhambxai, Hua Pha, Phongsaly), Thailand\* (Trang), southern Vietnam\* (Vinh Phuc) and Indonesia (Java, Sumatra\*). Possibly with a more southerly distribution than *S. niisimai*. Introduced to Martinique.

**Hosts.** Reported from Bombacaceae, *Litsea glutinosa* (Lauraceae). Presumably mycetophagous.

**Remarks.** Schedl (1962: 202) placed *S. pilosus* in synonymy with *S. niisimai* without an explicit reason. Reciprocal monophyly, greater than 10% COI nucleotide difference, and morphological diagnostic characters support the restored status of *S. pilosus*.

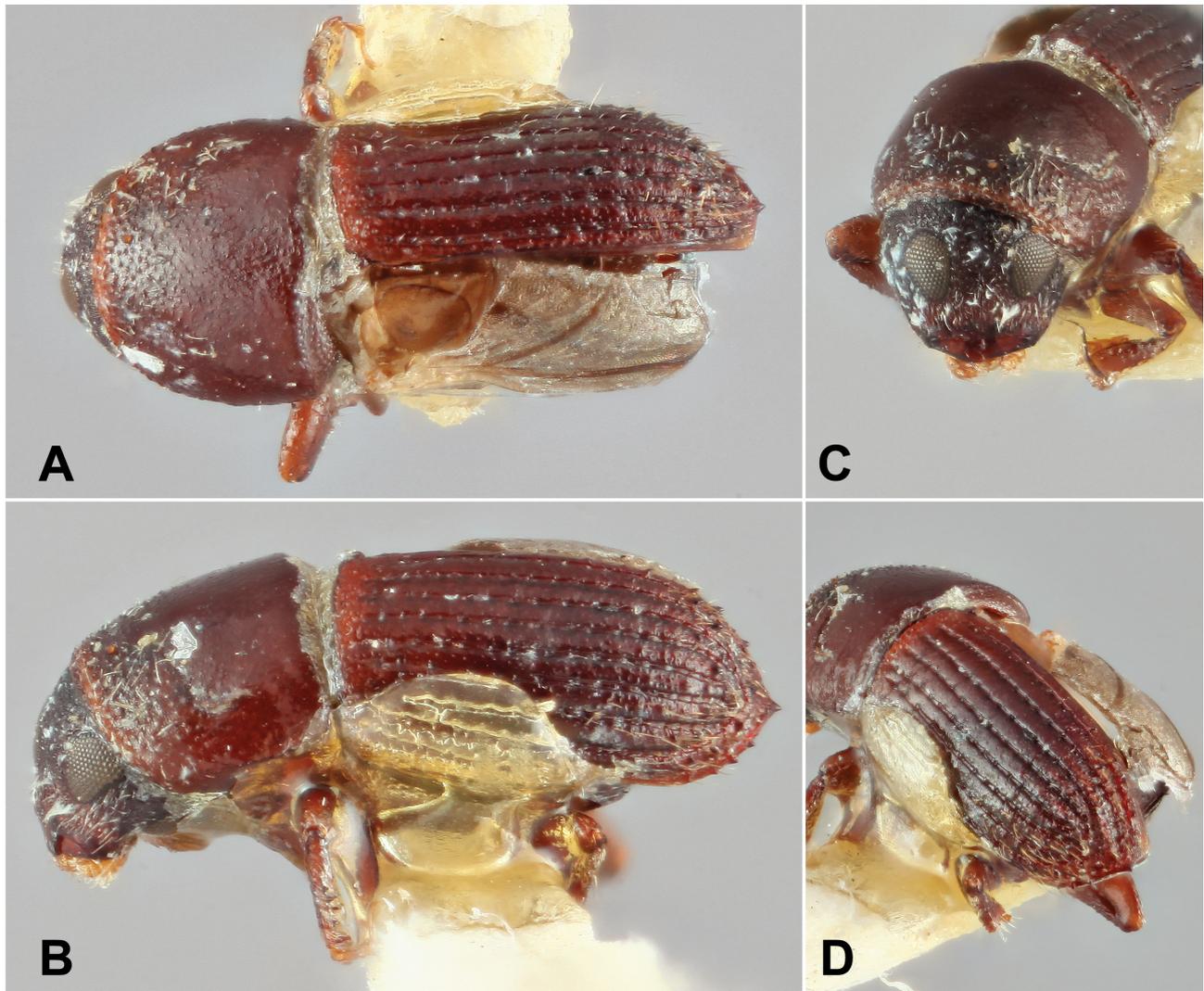
### *Sueus striatulus* (Schedl, 1954)

Fig. 10

*Hyorrhynchus striatulus* Schedl, 1954: 145.

*Neohyorrhynchus striatulus* (Schedl): Schedl 1962: 202.

*Sueus striatulus* (Schedl): Wood 1983: 650.



**FIGURE 10.** *Sueus striatulus* female holotype (NHMW), 1.75 mm A) dorsal view; B) lateral view; C) frons; D) posterolateral view.

**Type Material.** Holotype, female, [presumably Java] (NHMW), examined.

**Diagnosis.** Length 1.75 mm, 2.5 × longer than wide; declivital interstriae bearing rows of large and prominent acute denticles widely separated, clearly visible above setae in lateral profile.

**Hosts.** Unknown. Presumably mycetophagous.

**Distribution.** Likely Java, Indonesia (Schedl 1954).

## Discussion

The phylogenetic analyses allowed for the reassessment of *Sueus* species relationships. The general concordance of the parsimony and Bayesian phylogenies provided insight to diagnostic characters used for the recognition of a new species and taxonomic revision of others. Characters of the elytra including granules, setae, and striae are most useful for distinguishing species boundaries as observed with other scolytines (e.g., Smith *et al.* 2020; Smith & Cognato 2022). Although DNA data was unavailable for *Sueus chatterjeei*, new species, its tapered elytra are unique to the Hyorrhynchini and thus we hypothesize that it is an evolutionary lineage. *Sueus insulanus*, new species, exhibited morphological differences consistent with the differences observed in other species, such as, the state of the elytral declivital setae and corresponding long branch lengths in the phylogenies. The DNA divergence of *S. insulanus* was comparable to other species. Its placement sister to *S. obesus* in the phylogenies was well supported but given the long branch lengths, an alternative sister species relationship may be possible (Fig. 2). As for the other species, the sister position of *S. granulatus* to all other *Sueus* species gives credence to its previous generic placement in *Hyorrhynchus*; however, the morphological diagnostic character of the antennal club is clearly of *Sueus*. An expanded phylogenetic analysis including more *Hyorrhynchus* species will test the generic placement of *S. granulatus*.

Most illuminating was the discovery of phylogenetic structure among individuals of the widespread *S. niisimai*. Assumed to occur throughout eastern Asia, Indonesia and Oceania, we demonstrated that *S. niisimai* comprised two main clades separated by a mean of 17% COI DNA divergence. These clades associate with diagnostic morphology—short ground vestiture versus long ground vestiture. Also, the clades roughly correspond to geographic location: *S. niisimai* in the north and *S. pilosus* in the south (Fig. 1). The intraspecific COI divergence of some *S. niisimai* individuals ranged beyond the 10% approximated for species boundaries as with other inbred scolytines with female biased sex ratios; however, the intraspecific CAD divergence remained below 2% within hypothetical species boundaries (Cognato *et al.* 2020). The lineages represented by individuals SMS413, SMS415, and SMS421 may represent cryptic or pseudocryptic species given that obvious morphological differences were not observed (Smith & Cognato 2022).

In addition, we demonstrated that the *S. niisimai* discovered in the Caribbean is *S. pilosus* (Smith *et al.* 2022). It is unknown if the presence of *S. pilosus* in Martinique is due to prehistoric dispersal and/or contemporary human mediated dispersal as observed with other ambrosia beetles (Gohli *et al.* 2016; Rabaglia *et al.* 2019). The DNA-based phylogeny suggests that the *S. pilosus* from Martinique is closely related to *S. pilosus* from East Java. An Asian/Neotropical relationship between populations of widespread ambrosia beetles has been observed (Gohli *et al.* 2016; Urvois *et al.* 2023). Given that the similarity of the Martinique and East Java COI DNA sequences are not near zero (COI divergence = 2.6%), there is the potential that the Martinique specimen was sourced from another location in southeast Asia. Additional sampling of *S. pilosus* throughout Indonesia and southeast Asia is needed to confidently determine the origins of the Martinique *S. pilosus*.

This study provides a foundation for future phylogenetic investigation of Hyorrhynchini species. Additional taxa, specimens from diverse locations, and DNA data will be needed to robustly test taxonomic, ecological, biogeographical hypotheses. Coupled with a more extensive phylogenetic analysis much attention is needed to fill the knowledge gaps in the beetle's ecology and biology so to understand the evolution of *Sueus* and its allies.

## Acknowledgements

We thank the following curators and collection managers for facilitating specimen loans: Jeremy Frank (BPBM), Matthias Borer and Isabelle Zürcher (NHB), Maxwell Barclay, Michael Geiser (NHMUK), Harry Schilhammer (NHMW), Lourdes Chamorro (NMNH) and Roger Beaver (RABC). We thank our colleagues for sharing specimens

(especially Jiri Hulcr (University of Florida) and Wisut Sittichaya (Prince of Songkla University), and Thai Pham (Mientrung Institute for Scientific Research and Vietnam National Museum of Nature) for facilitating the collection of specimens for DNA extraction. We thank Michail Mandelshtam for sharing *Hyorrhynchus* type images and Bjarte Jordal (University of Bergen) for review of the identification key. We appreciate the anonymous reviews which helped to improve this paper. In addition, specimens of *S. insulanus* were collected in the framework of “Our Planet Reviewed Papua-New-Guinea 2012-2013” set up by Pro-Natura International, the National Museum of Natural History (MNHN, France), the Institut de Recherche pour le Développement (IRD, France) in partnership with the Royal Belgian Institute of Natural Sciences, the New Guinea Binatang Research Center, the University of Papua New Guinea, and the Divine Word University of Madang and with core funding of Prince Albert II of Monaco Foundation, the Stavros Niarchos Foundation, the Total Foundation, the Fondation d’entreprise EDF, the Fonds Pacifique, Spiecapag, Entrepose Contracting, the New Caledonia Government, the Reef Foundation, FNRS (Belgium) and the Belgian National Lottery. The IBISCA expert network, the patron for this project, Prof. R.L. Kitching, and all other participants in this collective effort are thanked for their contribution. This study was supported, in part, by a Cooperative Agreement from USDA Forest Service (16-CA-11420004-072 [to A.I.C.]).

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