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A new adventive parthenogenetic *Nocticola* species (Blattodea: Nocticolidae) found in Florida, USA and Vienna, Austria

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Abstract

Nocticolidae cockroaches are primarily distributed in tropical Africa, South and Southeast Asia, and Australia. Three females of an unidentified nocticolid species were collected in Florida, USA, which is the first record of this family in the New World. Morphological and molecular data (COI and 16S) confirmed their identity as a *Nocticola* species which also occurs in the US pet trade and as a greenhouse population in Austria. Phylogenetic evidence supported its identification as an undescribed species that is a likely adventive from Southeast Asia. *Nocticola vagus* **sp. nov.** was described based on diagnostic morphology and DNA sequences. In addition, the new species is parthenogenetic which is the first record for Nocticolidae. This trait and human-mediated dispersal likely facilitated its establishment across the globe.

Key Words: cockroach, taxonomy, new species, parthenogenesis, introduced species, plant trade

Introduction

Nocticolid cockroaches include 39 species divided among ten genera that occur in tropical Africa, Southeast Asia, Papua-New Guinea, and Australia (Gupta & Chandra 2019; Lucañas & Maosheng 2023; Sendi *et al.* 2020). They are small with slender rather than flattened bodies and elongated - annulated antennae and legs (Roth 1988; Li & Huang 2020; Fujita *et al.* 2020). Most species are cavernicolous, with a few epigean or myrmecophilous exceptions (Roth 1988; Fujita *et al.* 2020). Knowledge of nocticolid biology is limited due to their cryptic nature, and current knowledge is inferred from laboratory colonies and the pet trade (Fujita *et al.* 2020). Parthenogenesis has not been previously recorded for Nocticolidae, but it is well documented for other cockroaches, as with *Pycnoscelus surinamensis* (Roth 1967). In Corydiidae for example, unmated females of *Polyphaga saussurei* (Dohrn, 1888) have been observed to form reproducing colonies (Roth & Willis 1956; Knebelsberger & Bohn 2003). Species level taxonomy is problematic because several species were described based on one sex, which also makes species diagnosis difficult especially when only males are available (Vidlicka 2017; Roth 2003; Roth 1999). Furthermore, the systematic position of Nocticolidae within Blattodea has been debated (Fujita *et al.* 2020) although Wang *et al.* (2017) demonstrated monophyly for Nocticolidae nested within Corydiidae, based on a well-supported DNA-based phylogeny (Wang *et al.* 2017; Fujita *et al.* 2020).

In June 2020, female specimens of a nocticolid species were collected for the first time in Florida, USA from a natural setting. The discovery raises questions about its identity and origin, given Nocticolidae's known absence from the wild in the New World. We compared mitochondrial cytochrome oxidase subunit I (CO1) and large ribosomal 16S DNA sequences from the Florida specimens, specimens from the pet trade's captive populations, and previously published cockroach DNA sequences in order to address the cockroaches' identity and origin.

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Materials and methods

Specimens

A total of three female specimens (various instars) were collected by the author, Alan Jeon, from University Park, Florida (25.7347°N, 80.3653°W) under rocks and wood boards in a moist, shaded environment beneath a large tree. They were reared in laboratory conditions at 25 ± 0.5 °C with moist coco-fiber substrate (Ecoearth, San Louis Obispo, California, USA) and fed a diet of dried dog food (Purina Dog Chow Complete, St. Louis, Missouri, USA). These females reproduce parthenogenetically and are currently maintained as a colony by Alan Jeon. Additional captive specimens of Nocticolidae were acquired from the pet trade (roachcrossing.com). These specimens originated from two different localities; Malaysia sold under the name *Nocticola* sp. "Malaysia", and from a greenhouse at the Schönbrunn Zoo, Vienna, Austria, which is unnamed. Specimens from these three collections were preserved in 100% ethanol and subsequently pinned as voucher specimens and deposited in the A.J. Cook Arthropod Research Collection, Michigan State University, East Lansing, MI.

The Florida specimens were identified as Nocticolidae based on descriptions provided in Roth (1988). These specimens are most likely *Nocticola* species given their similarity to described females of *Nocticola* species, which possess the following characters: small, apterous, simple eyes, very long antennae, and a parabolic pronotum (Bolivar 1892). The phylogenetic results of this study also support their placement in *Nocticola*.

DNA extraction, sequencing and phylogenetic analysis

DNA was extracted from two individuals from three different collections using a DNeasy tissue extraction kit (Qiagen, Hilden, Germany). Two sets of extractions were performed, the first set consisted of three specimens, one from each collection, where the entire head and thorax was used; and a second set consisted of three specimens, one from each collection, where the metathoracic leg of each specimen was used. The manufacturer's instructions were followed and DNA was eluted twice reusing 150µL of Qiagen buffer AE. For PCR using Qiagen Hotstar Taq, the 5'end of the CO1 gene (the barcoding region) was amplified using universal primers (Folmer *et al.* 1994) under the following conditions: initial denaturation at 94 °C for 15 min, followed by 5 cycles of 94 °C for 30 s, 45 °C for 90 s, and 72 °C for 90 s, 30 cycles of 94 °C for 30 s, 50 °C for 90 s, and 72 °C for 90 s, with a final extension at 72 °C for 5 min. A ~500 bp piece of the 16S gene was amplified with the PCR primers reported Cognato and Vogler (2001) under the following conditions: cycle 1, 95°C for 15 min, 45°C for 60 s, 72°C for 90 s; cycles 2–36, 95°C for 30 s, 45°C for 60 s, 72°C for 90 s; cycle 37, 95°C for 30 s, 45°C for 60 s, 72°C for 5 min. Sanger sequencing of cleaned PCR products was conducted at the Research Technology Support Facility at Michigan State University, East Lansing, MI, USA. Resulting chromatograms were processed using Sequencher software v.5.1 for assembly and comparison of consensus sequences. These sequences were deposited in GenBank (accession numbers: COI: PV655089 - PV655091; 16S: PV661489 - PV661491). Additional *Nocticola* and other cockroach families (outgroups) COI and 16S sequences were obtained from GenBank or Kovacs *et al.* (2024) and assembled in a Nexus file so to perform a phylogenetic analyses with PAUP* software (Swofford 2002). For the COI, the most parsimonious trees were derived through an exhaustive search of 10,395 possible trees. Branch support values were estimated with 200 bootstrap trees resulting from branch and bound searches. The 16S sequences were aligned using the default settings of Muscle software (Edgar 2004). A heuristic search using 200 random addition replicates was performed to find the most parsimonious tree. Gaps were treated as missing. A bootstrap analysis of 200 pseudoreplications was conducted using heuristic searches with simple stepwise addition. Uncorrected "p" nucleotide sequence difference was calculated in PAUP*.

Delimitation and Recognition of *Nocticola* species

We consider *Nocticola* species as hypotheses of evolutionarily independent lineages, where monophyly, in part, defines a species (Hey 2006; *e.g.*; Cognato & Smith 2024). The recognition of a species is based on the presence of diagnostic morphological and/or DNA characters consistent with other recognized species. A constant percent nucleotide difference may signify species boundaries but this measure has not been thoroughly examined for *Nocticola.* Kovacs *et al.* (2024) demonstrated that nocticolid species have high rates of mitochondrial nucleotide substitution (~ 3x other cockroaches). Thus, *Nocticola* species are expected to exhibit 8 - 9% pairwise nucleotide differences given that, in general, 2 - 3% pairwise mitochondrial nucleotide difference is observed for outbreeding animals (Hebert *et al.* 2003). We hypothesize that *Nocticola* species will be reciprocally monophyletic, have diagnostic morphological/ molecular characters, and conservatively demonstrate >10% pairwise mitochondrial proportional "p" distance between sister-species.

Results

The COI sequences from the two individuals from each population were identical. Given that the exact DNA sequences were produced for the cockroach's body and metathoracic leg, it is likely that these sequences represent roach DNA and not DNA from an associated organism, e.g., protozoans, nematodes, etc. The sequences from the wild Florida specimens were identical to captive pet trade "Malaysian" specimens and these four specimens differed by three base pairs compared to individuals from the Schönbrunn Zoo. Two most parsimonious trees were found with the COI data which was mostly resolved in the strict consensus of the two trees. The three specimens were monophyletic, had 100% bootstrap value, and grouped with Clade A *Nocticola* species found in Kovacs *et al.* (2024) (Fig. 1). Clade B had 100% bootstrap value but the remaining clades had lower values. The COI DNA sequence difference among the species was high (23–27%).

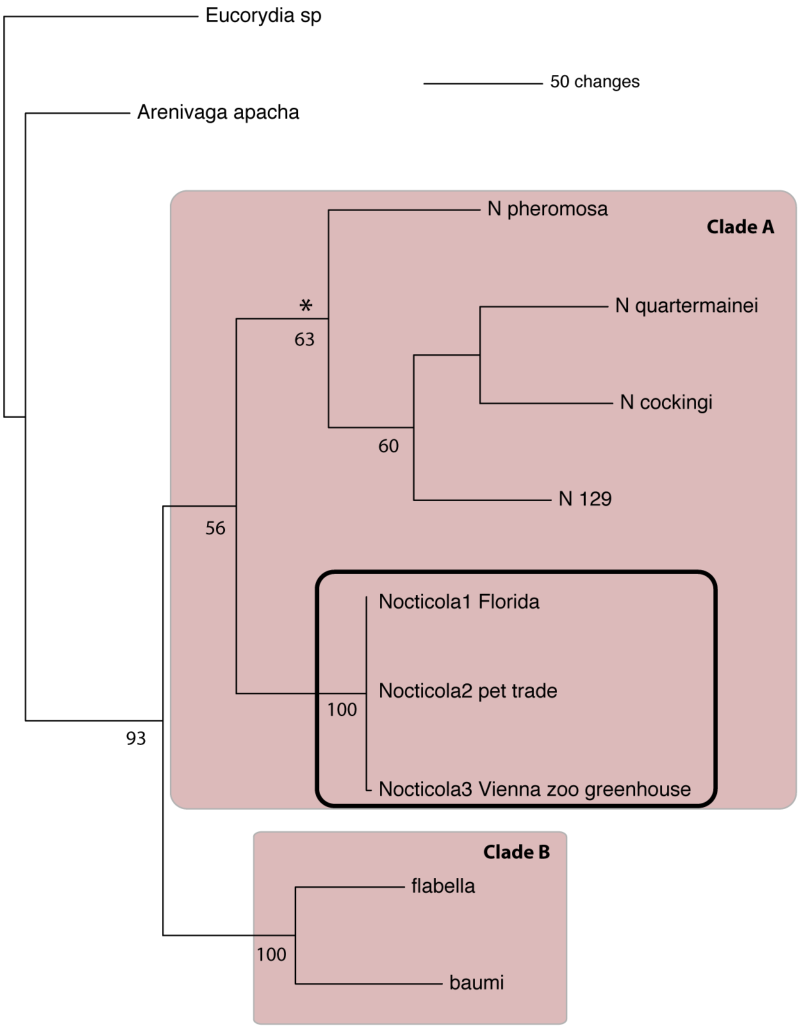

FIGURE 1. One of two most parsimonious trees found for *Nocticola* and outgroup species using COI DNA sequences. Numbers = bootstrap values, * = clade unresolved in the strict consensus of the two most parsimonious trees.

The 16S sequences from the wild Florida specimens were identical to captive "Malaysian" specimens and these four specimens differed by an insertion/deletion of one nucleotide compared to individuals from the Schönbrunn Zoo. Intraspecific sequence differences of other *Nocticola* species ranged 0 to 8%. Eighteen most parsimonious trees were found with the 16S data which was mostly resolved in the strict consensus of the 18 trees (Fig. 2). Clades with bootstrap values above 70% were few but the three *Nocticola* specimens were monophyletic with a 100% bootstrap value. This clade was sister to a specimen from Vietnam (76% bootstrap) and nested within *Nocticola* Clade A (Fig. 2) (Kovacs *et al.* 2024). The pairwise DNA sequence difference between the *Nocticola* Florida clade and Vietnam specimen was similar (17%) compared to other *Nocticola* species (11-17%). The remaining relationships of nocticolid specimens and the outgroups were mostly similar to a 16S maximum likelihood tree including more specimens (Kovacs *et al.* 2024, supplementary data).

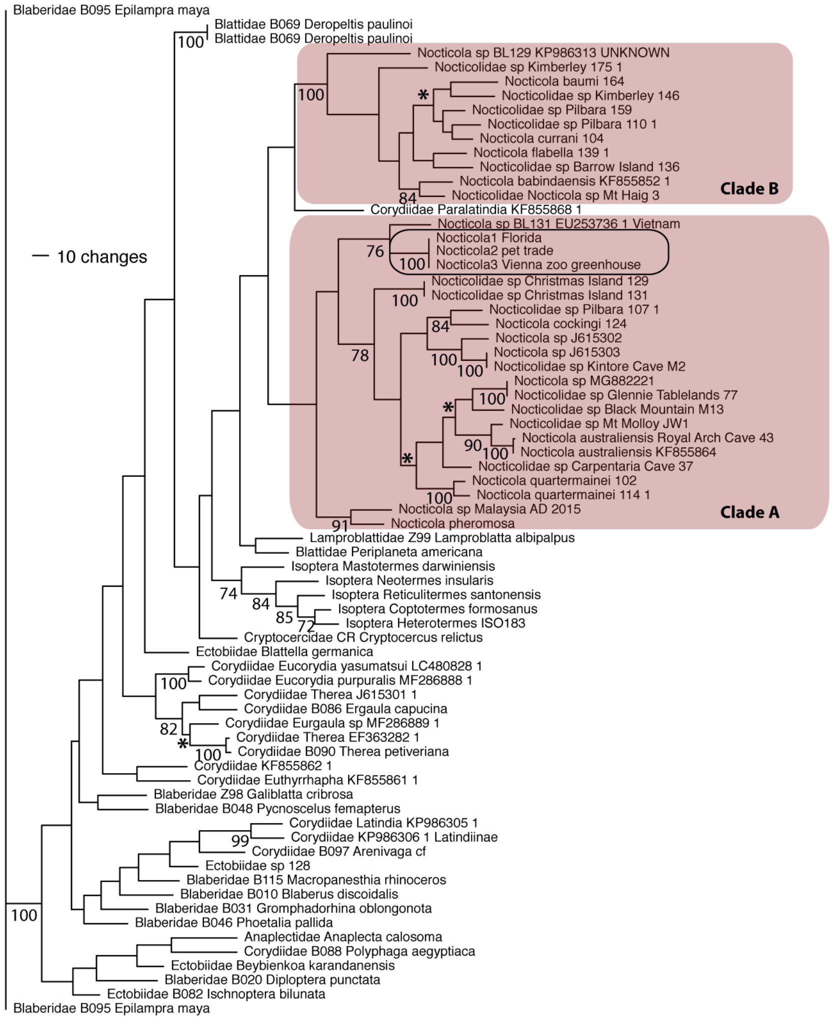

FIGURE 2. One of 18 most parsimonious trees found for *Nocticola* species and various cockroach families (outgroups) using 16S DNA sequences. Numbers = bootstrap values > 70%, * = clade unresolved in the strict consensus of the 18 most parsimonious trees.

Morphological similarity, monophyly, and scant nucleotide differences strongly suggest that the specimens from Florida, the pet trade, and the Schönbrunn Zoo are the same species. In addition, these specimens exhibit morphological differences, similar or higher pairwise nucleotide sequence divergence compared to other *Nocticola* species, and are parthenogenetic which distinguishes them from known *Nocticola* species. Very few females are described or known for *Nocticola* species thus assigning a known species name to the Florida population cannot be directly inferred. Eight of 25 described *Nocticola* species are present in Southeast and East Asia, *N. adebratti* Roth & McGavin, 1994 from Malaysia, *N. pheromosa* Lucanas & Maosheng, 2023 from Singapore, *N. sinensis* Silvestri, 1946 from Hong Kong, *N. termitophila* Silvestri, 1946 from Vietnam, and *N. uenoi* Asahina, 1974 from

Japan and *N. simoni* Bolívar, 1892, *N. caeca* Bolívar, 1892, *N. gonzalezi* Lucañas & Lit, 2016 from the Philippines (Lucanas & Maosheng 2023). Of these species, *N. pheromosa* and *N. adebratti* are epigean, *N. termitophila* and *N. sinensis* are termophilous, and the remaining species are cave restricted (Asahina 1974; Roth & McGavin 1994; Lucañas & Maosheng 2023; Bolívar 1892; Lucañas & Lit 2016; Silvestri 1946). Thus based on ecological similarity, the epigean Florida population could be *N. pheromosa* or *N. adebratti.* Based on the COI and 16S phylogenies, the Florida population and *N. pheromosa* occupy different clades indicating a distant relationship (Figs 1, 2). *Nocticola adebratti* is hypothesized as sister to *N. pheromosa* thus it is also excluded as a possible name for the Florida population. Given this deduction and the phylogenetic evidence, we hypothesize that the Florida clade is an unrecognized species and is described below.

Taxonomic treatment

Nocticola vagus Wang, Jeon, Cognato, sp. nov.

urn:lsid:zoobank.org:act:15693961-7A11-4131-9338-F5EC6FBCD598
Fig. 3

Type material. Holotype: female, USA. Florida, Miami-Dade Co., University Park, 25.7347°N, 80.3653°W, June 2020, A. Jeon Coll.; second label: DNA voucher 4; third label: MSUC_ARC_19917(MSUC).

Paratypes: 2 females, same locality as holotype (2 MSUC, one with second label "DNA voucher 1", all with MSUC_ARC_19916 & MSUC_ARC_19918 labels); (4) females, USA, pet trade, roachcrossing.com, *Nocticola* sp. "Malaysia" (4 MSUC, two with second label: DNA voucher 2 & 5, all with MSUC_ARC_19919 - 19922 labels). 1 female, USA, pet trade, roachcrossing.com, *Nocticola* sp. "Schönbrunn Zoo"; second label: DNA voucher 6; third label: MSUC_ARC_19923 label (1 MSUC).

Diagnosis: The eight ommatidia /eye and presence a subtrapezoidal supra-anal plate are diagnostic for *N. vagus* sp. nov. and it differs from females of the following species: *N. australiensis* has ten ommatidia; *N. baumi* is eyeless, has more elongated tibia and femur, and has a rounded supra-anal plate with weak medial notch; *N. flabella* is eyeless and has a supra-anal plate rounded; *N. remyi* has three ommatidia. Although female descriptions are lacking for other *Nocticola* species, phylogenetic placement using COI or 16S data will diagnose *N. vagus* sp. nov. That is, monophyly of unidentified specimens with the known *N. vagus* sp. nov. sequences and within 10% 16S sequence difference would suggest an identity as *N. vagus* sp. nov.

Description. Females: Completely apterous. Body small, partially pigmented, pale yellow to brown. Body with dense short sensilla chaetica. Head large, with long filiform antennae almost twice the length of the pronotum. Eyes largely reduced, each with 8 ommatidia, lateral ocelli not present. Maxillary palpi five segmented, nearly the length of the head. Pronotum parabolic, hairs along the margin pointing outwards. Front femur type C1. Fore tibiae almost spineless throughout the length with only two apical spines and one ventral preapical spine. Mid tibiae 6 spines and hind tibiae 8 spines. Tibiae cylindrical, slightly longer than compressed femora. First tarsomere elongated, longer than other tarsomeres combined. Last tarsomere with simple claws, lacking apical pads and arolium. Supra-anal plate subtrapezoidal, notched medially. Subgenital plate valvular. Cerci with three strong ventral spines on segment two and three.

Males: Unknown, not present in the discovered population or in the pet trade.

Ootheca: Approximately 1.2 mm length, 1.5 mm height, and 1.0 mm width. Eggs visible through the translucent oothecal wall in newly produced ootheca. Mature oothecal wall reddish. Small, denticulated keel along the dorsal median line. Flange poorly developed. Ootheca is formed of four eggs arranged in two rows, with eggs on one side offset by half an egg's width relative to those on the other side. Dorsoventral axis of ootheca corresponds to the anteroposterior axis of the contained eggs, dorsal side of each egg facing oothecal wall.

Distribution. Apparently adventive. Occurring wild in Florida, the USA pet trade, specimens originally sourced from Malaysia, and a greenhouse in Schönbrunn Zoo, Vienna, Austria. Native distribution unknown.

Biology. Unknown.

Etymology. *vagus* - Latin = wandering. This name signifies the occurrence of this species on three continents.

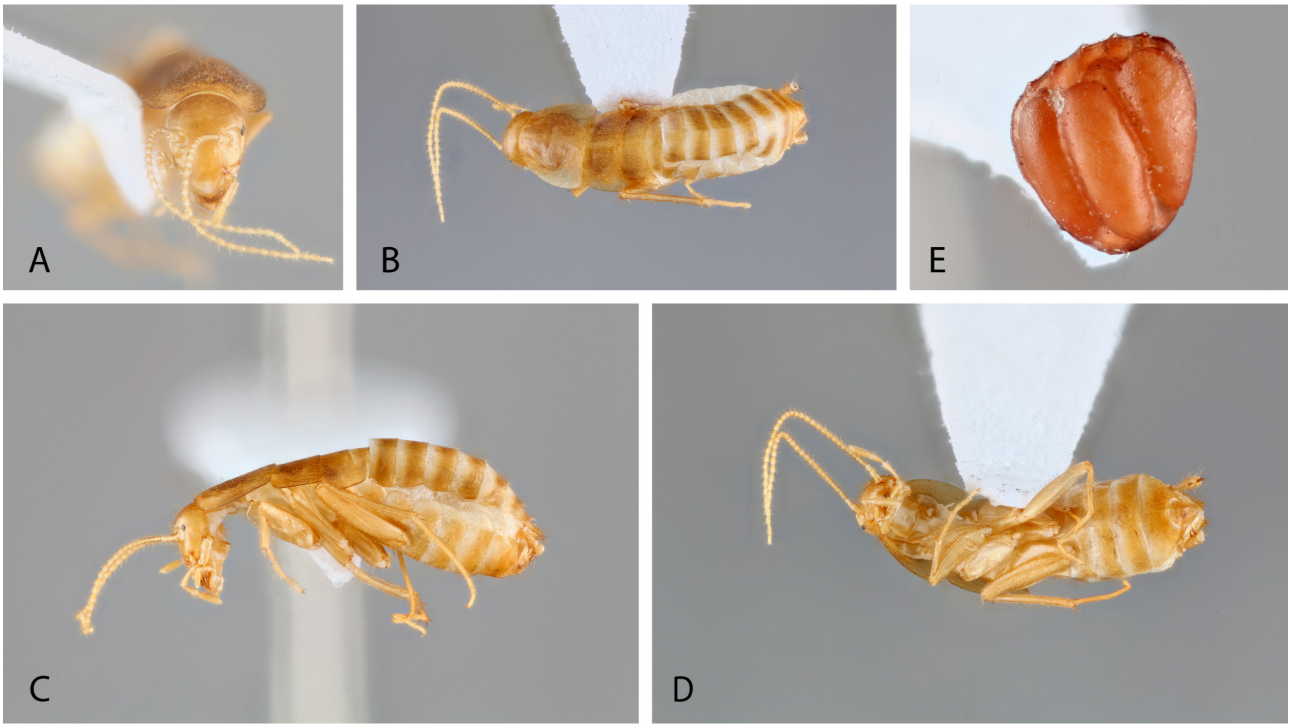

FIGURE 3. *Nocticola vagus* sp. nov. female holotype. Habitus A) frontal, B) dorsal, C) lateral, D) ventral view and ootheca E) lateral view.

Discussion

This study reports the first occurrence of a Nocticolidae species in the western hemisphere and adds to the cockroach diversity of the USA and Florida. It is not surprising that *N. vagus* sp. nov. was first described in this study because the diversity of Nocticolidae is poorly known and the number of pseudocryptic and cryptic species is likely substantial (Kovacs *et al.* 2024). Other highly diverse and adventive taxa have been described from a non-native range before they were discovered in their native range (e.g., Smith & Cognato 2022). *Nocticola vagus* sp. nov. is potentially native to southeast Asia given that its phylogenetic placement is sister to a specimen from Vietnam but peninsula Malaysia may be part of its native range given this area was the source of the US pet trade population. Details of the exact location and habitat of the source of the US pet trade population are unknown. Given that *N. vagus* sp. nov. also occurs in a greenhouse in Vienna, *N. vagus* sp. nov. is potentially established in other greenhouses and subtropical/tropical urban areas associated with potted plants. A parthenogenetic species, the Surinam cockroach (*Pycnoscelus surinamensis* (L.)), represents a similar situation; it is commonly found in worldwide greenhouses and is now abundant throughout the gulf coast of the USA and Florida (Hebard 1917, iNaturalist 2024). It is likely that *P. surinamensis* is spread in the soil of potted plants which we suggest as a mode of transport for *N. vagus* sp. nov.

In addition, this study suggests that *N. vagus* sp. nov. is parthenogenetic; a first occurrence for Nocticolidae. Parthenogenesis occurs as either facultative which is common among cockroaches including *Periplaneta americana*, or obligatory which is found in only a few cockroach taxa (Griffiths & Tauber 1942; Roth & Willis 1956; Tanaka & Daimon 2019). *Nocticola vagus* sp. nov. has been maintained as female-only colonies for 6 years; several cultures have been started from the original and males have never been observed (Alan Jeon pers. observ.). Potentially, *N. vagus* sp. nov. is facultatively parthenogenetic given that other females with known males are wingless and similar in morphology however, parthenogenetic populations are not known from the wild outside of Florida. The population of *N. vagus* sp. nov. in a Schönbrunn Zoo greenhouse differs from the North American populations by a few nucleotides in the COI and 16S genes. This indicates either different source populations or a substantial amount of time since the separation of North American and European populations and the ability of *N. vagus* sp. nov. to maintain parthenogenesis for generations. The diagnostic 16S DNA sequences observed among Nocticolidae (Kovacs *et al.* 2024) provides the means to discover potential males and/or additional populations of *N. vagus* sp. nov.

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