DIVERSIDADE NEOTROPICAL E FILOGENÔMICA GLOBAL DOS GORGULHOS-DAS-FLORES DA TRIBO EUGNOMINI (COLEOPTERA, CURCULIONIDAE, CURCULIONINAE)

por

ALINE DE OLIVEIRA LIRA

Sob Orientação do Professor Paschoal Coelho Grossi, UFRPE

RESUMO

Eugnomini compreende gorgulhos visitantes florais, alguns atuando como polinizadores de suas plantas hospedeiras. A tribo tem distribuição gondwânica, onde grande parte da sua diversidade se concentra na Austrálasia e ilhas oceânicas do Pacífico, enquanto quatro gêneros ocorrem na região Neotropical, dentre eles o gênero *Udeus* que possui especializada relação com suas plantas hospedeiras do gênero *Cecropia*. Apesar de sua importância como polinizadores e florívoros é notável a ausência de uma abordagem filogenética abrangente que permita compreender a história evolutiva e estabelecer uma delimitação taxonômica confiável de Eugnomini. Este estudo aborda esta lacuna, apresentando a primeira filogenia em nível de espécie de um táxon superior de gorgulho utilizando uma extensa amostragem da diversidade global de Eugnomini, empregando o método de Enriquecimento Híbrido Ancorado para avaliar a monofilia da tribo e elucidar sua história biogeográfica. Além da abordagem filogenômica, exploramos a diversidade neotropical de Eugnomini por meio da revisão taxonômica de *Udeus* investigando a íntima relação deste gênero com suas plantas hospedeiras. Nossas análises filogenômicas apoiaram a monofilia da subtribo Meriphina, ao mesmo tempo que revelaram a parafilia da subtribo Eugnomina e a polifilia da tribo Eugnomini conforme definida atualmente, indicando uma necessidade de reavaliação. Além disso,

nossa ampla amostragem taxonômica facilita o delineamento de gêneros monofiléticos e estimula uma reavaliação do diagnóstico tribal com base em características morfológicas à luz de nossas descobertas filogenéticas. Ao nos aprofundarmos nas relações internas de Eugnomini, exploramos brevemente sua biogeografia, sugerindo cenários tanto de vicariância quanto de dispersões para explicar a diversidade e distribuição atuais da tribo. A revisão de *Udeus* permitiu a reavaliação taxonômica das espécies válidas com o estabelecimento de novas sinonímias e a descrição de 22 espécies novas. Descobrimos que eugnomíneos não são apenas muito mais diversos do que se considerava anteriormente, mas também amplamente distribuídos por toda a região Neotropical.

PALAVRAS-CHAVE: Curculionoidea, enriquecimento híbrido ancorado, evolução, história natural, interação inseto-planta, polinização, taxonomia, visitantes florais

NEOTROPICAL DIVERSITY AND GLOBAL PHYLOGENOMICS OF FLOWER WEEVILS OF THE TRIBE EUGNOMINI (COLEOPTERA, CURCULIONIDAE, CURCULIONINAE)

por

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Sob Orientação do Professor Paschoal Coelho Grossi

ABSTRACT

The tribe Eugnomini comprises weevil flower visitors, some acting as pollinators of their host plants. The tribe has a Gondwanan distribution and the highest known diversity in Australasia and Pacific islands, while four genera occur in the Neotropics, including the genus *Udeus*, which has a specialized relationship with its host plant *Cecropia*. Despite their ecological significance, there has been a notable absence of a comprehensive phylogenetic framework that allows an understanding of their evolutionary history and establishes a reliable classification. This study addresses this gap by presenting the first species-level phylogeny of a higher weevil taxon utilizing an extensive sampling of the global diversity of Eugnomini, employing Anchored Hybrid Enrichment to assess the monophyly of the tribe and elucidate its biogeographic history. In addition to the phylogenomic approach, we explore the Neotropical diversity of Eugnomini through the taxonomic revision of *Udeus*, investigating the intimate relationship of this genus with its host plants. Our phylogenomic analyses robustly supported the monophyly of the subtribe Meriphina while revealing the paraphyly of Eugnomina and the polyphyly of the tribe as currently defined, indicating a need for reassessment. Moreover, our broad taxonomic sampling facilitates the delineation of monophyletic genera and prompts a reevaluation of tribal diagnosis based on

morphological traits in light of our phylogenetic findings. By delving into the internal relationships of Eugnomini, we briefly explored its biogeography, suggesting scenarios of both vicariance and dispersal to explain the current diversity and distribution of the tribe. The revision of *Udeus* allowed the taxonomic reassessment of valid species, establishing new synonymies and descriptions of 22 new species. We found that eugnomines are not only much more diverse than previously considered but also widely distributed throughout the entire Neotropical region.

KEY WORDS: Anchored Hybrid Enrichment, Curculionoidea, evolution, flower visitors, natural history, taxonomy

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INTRODUÇÃO

A superfamília Curculionoidea constitui um dos grupos mais diversos de animais, com cerca de 60 mil espécies descritas (Oberprieler 2014, McKenna et al. 2014). Seus integrantes são popularmente conhecidos como gorgulhos, curculionídeos ou bicudos. Essa enorme diversidade de espécies e modos de vida representa um imenso potencial para estudos evolutivos que não seriam possíveis em grupos menores, mas ao mesmo tempo um grande desafio. Embora já exista um arcabouço filogenético relativamente bem resolvido em nível de família (Shin et al. 2018), grande parte da diversidade do grupo nunca foi representada em uma filogenia. Uma das dificuldades para o desenvolvimento desses estudos é a escassez de especialistas e a falta de amostragem contemplando a grande diversidade distribuída ao redor do mundo, necessária para qualquer estudo nesse grupo hiper diverso.

Cerca de 80% das espécies de gorgulhos pertencem à grande radiação da família Curculionidae (Oberprieler 2014, McKenna et al. 2014). Assim como em número de espécies, Curculionidae tem grande diversidade de modos de vida, hábitos alimentares e associações ecológicas. A maior parte dos curculionídeos é herbívora, associados a angiospermas, muitos especializados em um determinado grupo botânico. Alimentam-se também de gimnospermas, pteridófitas, briófitas, líquens, algas e cianobactérias (Oberprieler 2014). Grande parte dos fitófagos se adaptou ao modo de vida endofítico, caracterizado pelo desenvolvimento das larvas no interior de praticamente todas as partes vivas e mortas da planta, comportamento considerado importante para a diversificação da família (Oberprieler et al. 2007). Além dos fitófagos, uma pequena porção

dos curculionídeos apresentam modos de vida particulares, atuando como coprófagos, mimercófilos ou predadores (Oberprieler 2014).

As últimas classificações propostas incluem dez subfamílias em Curculionidae (Oberprieler *et al.* 2007, Oberprieler *et al.* 2014), no entanto, muitas dessas subfamílias não formam grupos naturais e algumas não são bem caracterizadas mesmo morfologicamente (McKenna *et al*. 2009, Jordal *et al*. 2011, Oberprieler 2014). Curculioninae é um dos exemplos de táxons considerados problemáticos, pois mantém-se ainda sem clareza quanto sua delimitação e estabelecimento como um grupo monofilético (Caldara et al. 2014, Haran et al. 2023). As 34 tribos de Curculioninae não exibem caracteres consistentes e exclusivos que facilitem seu reconhecimento, sendo consideradas como um grande conglomerado de táxons de relacionamentos questionáveis, segundo Anderson (2002). Uma destas tribos é Eugnomini, um grupo relativamente pequeno, com cerca de 32 gêneros e 200 espécies conhecidas (Mazur 2017). Eugnomini é uma das duas tribos de Curculioninae que apresentam distribuição estritamente gondwânica (Caldara et al. 2014). A maior diversidade encontra-se na região Australasiana (Austrália, Nova Zelândia e Nova Caledônia), com poucos representantes no Novo Mundo (América do Sul, América Central e Caribe), e algumas espécies não descritas do sudoeste asiático e até o momento nenhum membro registrado para a Região Afrotropical (Cawthra 1966, Brown & Leschen 2018, Caldara et al. 2014). Na região Neotropical, são registrados quatro gêneros, *Rhopalomerus* Blanchard, *Omoides* Boheman, *Pedetinus* Faust e *Udeus* Champion (Mazur 2014, Mazur 2016, Brown & Leschen 2018, Bukejs & Legalov 2019), os dois últimos com ocorrência no Brasil (Wibmer & O'Brien 1986).

Grande parte dos gêneros da Região Australiana são endêmicos (Brown & Leschen 2018). *Rhopalomerus* é o único gênero com espécies presentes nas regiões Australiana (Nova Zelândia) e Neotropical (Argentina e Chile) (Cawthra 1966, Alonso-Zarazaga & Lyal 1999), uma das razões para a necessidade de delimitação da tribo, pois levanta questionamentos biogeográficos

condizentes com os limites taxonômicos questionáveis do grupo. Estes fatos, aliadas à distribuição gondwânica, ascendem indagações biogeográficas a respeito da dispersão da tribo, pontos ainda não explorados e que podem auxiliar na compreensão da história evolutiva de Eugnomini e da formação de biotas de insetos fitófagos de forma mais geral.

A composição taxonômica atual dos eugnomíneos deriva de Lacordaire (1863), que propôs *Eugnomides* como um dos cinco grupos oriundos da separação da tribo *Erirrhinides*. Inicialmente composto por oito gêneros, o grupo passou por diferentes arranjos taxonômicos, sempre posicionado como uma subdivisão de Erirrhininae, até o *Coleopterorum Catalogus* de Junk (Klima 1934). Voss (1937) estabeleceu Eugnominae como subfamília e logo depois Marshall (1937) fez uma nova proposta de classificação excluindo três gêneros de Eugnominae (*Meriphus* Erichson, *Myossita* Pascoe e *Orpha* Pascoe) e alocando-os em uma nova subfamília, Meriphinae. Cawthra (1966) retornou os gêneros removidos de Eugnominae, juntamente com os gêneros neotropicais *Udeus* e *Omoides* para a tribo Eugnomini, e propôs que a tribo Meriphini abrigasse os gêneros de mandíbulas exodonte *Meriphus*, *Myossita* e *Orpha*. Desde a publicação de Cawthra (1966), a classificação de Eugnomini se mantém com os gêneros agrupados nas subtribos Eugnomina e Meriphina.

As últimas contribuições para a composição taxonômica da tribo ocorreram na última década, sobretudo para a fauna da Região Australiana, com a descrição de seis novos gêneros, dois viventes e quatro fósseis, além de novas espécies em gêneros já conhecidos (Mazur 2012, 2014, 2016, 2019, Mazur & Jezuita 2015, Legalov 2016, Brown & Leschen 2018, Burkej & Legalov, 2019). Diversos outros gêneros e espécies australasianas permanecem depositados em coleções dessas regiões aguardando descrição (Pullen et al. 2014). Na região Neotropical as contribuições mais recentes se limitam a transferência de *Pedetinus* de Derelomini para Eugnomini (Franz 2006),

descrições de quatro espécies de *Udeus* (Rheinheimer 2018, 2019) e duas de *Pedetinus* (Rheinheimer 2018).

No estudo morfológico mais recente e completo para a tribo, Cawthra (1966) detalhou os caracteres diagnósticos e apresentou uma definição morfológica para Eugnomini, no entanto, ainda não foram identificados caracteres que permitam a distinção coerente de todos os gêneros da tribo (Caldara *et al*. 2014). Embora caracteres díspares sejam comuns para a fauna Australasiana e Neotropical, os eugnomíneos são identificados por combinações que incluem os seguintes caracteres: (a) rostro longo e robusto, (b) mandíbulas exodontes (capítulo 2, Fig. 12B) , (c) maxilas flexíveis com palpos longos (capítulo 2, Figs. 5D, E), (d) olhos grandes (capítulo 2, Fig. 4B), (e) cabeça alongada (capítulo 2, Fig. 12B), (f) procoxas cônicas e contíguas, (g) fêmures com dente interno, (h) tíbia mucronada (capítulo 3, Fig. 29), (i) garras tarsais livres (capítulo 3, Fig. 29)e (j) ventritos com margens posteriores fortemente retas (capítulo 2, Figs. 4G, H) (Cawthra 1966, Caldara et al 2014).

As informações conhecidas sobre biologia de Eugnomini da região australiana foram resumidas mais recentemente por Cawthra (1966) e May (1993). May (1993) descreveu os hábitos de vida de larvas de muitas espécies da Nova Zelândia. As larvas de diversos gêneros se desenvolvem em ramos e troncos mortos e em frutos de variadas espécies de plantas, enquanto os adultos são comuns em frutos e flores, se alimentando de néctar e pólen (Caldara et al. 2014). A associação comum dos eugnomíneos com flores de diversas plantas levanta a possibilidade de alguns gêneros atuarem como polinizadores. Alguns gêneros têm preferências em hospedeiros específicos. Na Nova Zelândia, o gênero *Gonoropterus* Broun se desenvolve em frutos de *Nestegis* Raf. (Oleaceae), *Nyxetes* Pascoe dentro de galhas em *Clematis* L. (Ranunculaceae), *Hoheria* A. Cunn. (Malvaceae) e *Nestegis* (May 1993). Na Austrália, *Myossita* se reproduz nas estruturas reprodutivas e frutos de *Banksia* L.fil. (Proteaceae) (Caldara et al. 2014). Na Nova Caledônia,

Pactola kuscheli Mazur, foi registrada recentemente causando danos em *Agathis montana* de Laub. (Araucariaceae), sendo a primeira praga confirmada para a planta, suspeita de ser responsável pelo declínio desta espécie de araucária, dominante em sua região de ocorrência e importante para a manutenção climática da região (Mazur et al. 2016).

Na América do Sul foram registrados *Omoides* associados a diversas famílias botânicas como Salicaceae, Quillajaceae, Rosaceae, Lauraceae, Rhamnaceae e Polygonaceae (Kuschel 1952), enquanto no Brasil, exemplares de *Pedetinus* foram coletados em *Leandra* spp. Raddi (Melastomataceae) (dados não publicados). O gênero Neotropical *Udeus* foi citado por Caldara et al. (2014) associado possivelmente a palmeiras, devido a identificação confusa com *Celetes* Schonherr (Derelomini), gênero especializado a este grupo botânico. No entanto, Bondar (1957) descreveu espécies de *Udeus* criadas em inflorescências de *Cecropia* Loefl. (Urticaceae). Além do registro inicial de Bondar (1957), um estudo não publicado de dissertação, apontou duas espécies de *Udeus* associadas a *Cecropia glaziovii* Snethl. (Mendonça 2014), neste último caso com o primeiro registro de *Udeus* em inflorescências femininas. Observações em campo do comportamento das espécies do gênero realizadas neste estudo, juntamente com dados da literatura (Bondar 1947, Mendonça 2014), confirmam a especificidade das espécies de *Udeus* com espécies de sua planta hospedeira *Cecropia* (Lira et al. no prelo).

Assim como para a maioria dos eugnomíneos, exemplares de *Udeus* são raros em coleções, e a alta especificidade com sua planta hospedeira indica que a diversidade do gênero é muito maior do que a conhecida atualmente, podendo se equiparar a diversidade de *Cecropia* (Bondar 1957), composta por 61 espécies (Berg & Franco-Rosselli 2005). O gênero *Cecropia*, composto por espécies popularmente conhecidas como embaúbas, são plantas pioneiras com forte interação com a fauna. Muito abundantes na região neotropical, são amplamente conhecidas pela associação mutualística com formigas do gênero *Azteca* Forel (Berg & Franco-Rosselli 2005, Dejean *et al.*

2012, Treiber *et al.* 2016), no entanto, quanto a polinização, tradicionalmente assume-se serem anemófilas (Berg & Franco-Rosselli 2005). A associação comum, porém, pouco conhecida de *Udeus* com seus hospedeiros tem se mostrado importante para entender a diversidade dos eugnomíneos neotropicais e com potencial para apoiar estudos sobre evolução das interações inseto-planta no contexto da polinização. A exploração da História Natural de *Udeus* é um exemplo de que a diversidade de Eugnomini pode compreender um número muito maior de espécies do que a documentada atualmente. Além disso, pode ser modelo para a investigação dos gêneros de Eugnomini australianos associados a flores, enfatizando a importância das informações biológicas para a compreensão da composição, origem e diversificação da tribo.

Diante da diversidade da tribo, ainda se sabe pouco sobre as relações ecológicas estabelecidas entre a maioria das espécies de Eugnomini e suas plantas hospedeiras. Este estudo abre caminho para a exploração dessas informações, que além de elucidar aspectos taxonômicos, poderá contribuir para dimensionar a importância ecológica do grupo, sobretudo a respeito dos serviços de polinização.

Dos 32 gêneros que compõem Eugnomini, cerca de 80% foram descritos antes dos anos 2000, a grande maioria ainda no século XIX. Desde as descrições originais, não foram propostas revisões ou foram descritas novas espécies para a maior parte destes gêneros. Nos últimos anos, as contribuições têm sido relevantes para a fauna da Nova Caledônia e algumas ilhas do Pacífico, no entanto, os demais Eugnomini do mundo, sobretudo os neotropicais, permanecem pouco estudados (Brown & Leschen 2018). Além da diversidade da tribo se concentrar na Região Australasiana, descrições de novos táxons e aspectos mais gerais do grupo como biologia, comentários biogeográficos e filogenéticos foram propostos por pesquisadores desta região. Na região Neotropical, o início das investigações a respeito da associação de *Udeus* com suas plantas hospedeiras revela uma diversidade subestimada, que pode ser extrapolada para os demais gêneros,

já que estudos com eugnomíneos neotropicais estão limitados unicamente às descrições taxonômicas. Este estudo revela-se como uma oportunidade para compreender a história evolutiva de Eugnomini, reunindo informações da fauna Australasiana e Neotropical para decifrar a diversidade da tribo no mundo e esclarecer sua real composição, lançando mão de atos taxonômicos necessários para a estabilidade da tribo.

Estudos filogenéticos com amostragem de Eugnomini são escassos. Apenas três estudos recentes incluíram Eugnomini como terminais (Gunter et al. 2016, Leschen *et al*. 2022, Haran *et al.* 2023), mas com amostragem aquém da diversidade conhecida e sem representatividade da distribuição geográfica atual do grupo. Apesar desses trabalhos terem indicado Eugnomini como um grupo natural, somente um estudo focado na diversidade da tribo poderá incluir mais representantes e formar uma base para melhores delimitações taxonômicas e estudos biogeográficos em escala global.

Este será o primeiro estudo em uma tribo de Curculionidae a incluir amostragem global e técnicas moleculares modernas, resultando em uma filogenia de alta resolução e suporte. Dessa forma, pretendemos testar a monofilia de Eugnomini, a fim de buscar delimitação taxonômica robusta para tribo e contribuir para o conhecimento da diversidade de eugnomíneos neotropicais por meio do estudo do gênero *Udeus*. Associado à investigação das relações de *Udeus* com suas plantas hospedeiras espera-se que os resultados obtidos abram novas possibilidades de estudo de polinizadores tropicais.

Os seguintes capítulos reúnem informações taxonômicas, biológicas e evolutivas da tribo Eugnomini levantadas durante o desenvolvimento desta tese de doutorado. Em uma sequência de três artigos, apresento inicialmente informações sobre a fauna da região Neotropical, com a descrição detalhada de imaturos e adultos de uma nova espécie de *Udeus*, do Cerrado brasileiro, com informações sobre sua história natural, a relação com sua planta hospedeira *Cecropia saxatilis*

(artigo publicado, https://doi.org/10.1111/aen.12691). Em seguida, apresento a revisão taxonômica do gênero *Udeus*, incluindo atualizações taxonômicas de espécies conhecidas, informações adicionais da biologia do gênero e a descrição de diversas espécies novas. Finalmente, os resultados preliminares da filogenia da tribo Eugnomini são apresentados no capítulo 4, com abordagem evolutiva e biogeográfica do grupo, envolvendo uma série de inferências a partir dos resultados filogenéticos obtidos, empregando análise filogenômica com uma ampla amostragem da tribo a nível global.

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CAPÍTULO 2

ADULTS AND IMMATURES OF *Udeus cerradensis* LIRA, DE MEDEIROS & GROSSI, SP. NOV. (COLEOPTERA: CURCULIONIDAE): A FLOWER VISITOR OF *Cecropia* LOEFL. (URTICACEAE) PREYED UPON BY PAPER WASPS (VESPIDAE) [1]

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Adults and immatures of *Udeus cerradensis* Lira, de Medeiros & Grossi, sp. nov. (Coleoptera: Curculionidae): a flower visitor of *Cecropia* Loefl. (Urticaceae) preyed upon by paper wasps (Hymenoptera: Vespidae)

Abstract

Udeus Champion, 1902 is a weevil genus in the tribe Eugnomini associated with the inflorescences of *Cecropia* Loefl. (Urticaceae), with eleven valid species distributed in the Neotropics. Species of *Udeus* are generally rare in collections and their biology is poorly known, despite a high abundance in nature. Here, we describe *Udeus cerradensis* Lira, de Medeiros & Grossi, sp. nov. from the Brazilian Cerrado, including the first descriptions of larvae and pupae for a Neotropical eugnomine. We assess their role as potential pollinators of their host plant *Cecropia saxatilis* Snethl. and find that adults do not visit pistillate flowers and therefore are unlikely to be pollinators. This contrasts with previous reports in a different pair of species in *Cecropia-Udeus*, suggesting that pollinator agents vary between species in this plant genus. Finally, we provide notes about the predation of larvae of *U. cerradensis* by social wasps *Synoeca surinama* (L.) and *Protopolybia* aff. *sedula* (Saussure), revealing that, in this instance, an endophytic larva does not prevent predation by a behaviourally flexible predator. This study is the first of a series on the natural history of *Udeus* and their specialized interactions with host plants.

Key words

Curculionoidea, host plant association, natural history, taxonomy, plant-insect interaction, weevil.

INTRODUCTION

Eugnomini is a small tribe of Curculioninae with about 32 genera and 200 known species (Mazur 2017). With a strictly Gondwanan distribution (Caldara *et al.* 2014), their greatest known diversity is found in the Australian region (Australia, New Zealand, and New Caledonia), with a few representatives in the Neotropical Region, some undescribed species from Mainland Southeast Asia, and none registered for the Afrotropical region (Cawthra 1966; Brown & Leschen 2018; Caldara *et al.* 2014). In the Neotropical region, there are four genera: *Rhopalomerus* Blanchard, *Omoides* Boheman, *Pedetinus* Faust, and *Udeus* Champion (Wibmer & O'Brien 1986; Caldara *et al.* 2014). No neotropical linage has ever been sampled in a phylogeny, but the Australian region clades sampled so far show evidence for monophyly of the tribe (Haran *et al*. 2023).

Udeus is the most diverse genus of Neotropical Eugnomini with eleven known species reported from Mexico (one species), Guadeloupe (one species), Martinique (one species), Panama (one species), French Guiana (three species), Bolivia (one species), Paraguay (one species), and Brazil (three species) (O'Brien & Wibmer 1982; Wibmer & O'Brien 1986; Rheinheimer 2018; Rheinheimer 2019). The three known species of *Udeus* from Brazil are distributed in the Atlantic Forest (Voss 1941; Bondar 1957). These weevils are recognized by a set of characters similar to other Eugnomini, such as large eyes, elongate head, exodont mandibles, flexible maxillae with long palps, contiguous procoxae, femora with an internal tooth, mucronate tibiae, and ventrites with straight posterior margins (Champion 1902; Cawthra 1966; Caldara *et al.* 2014). Nonetheless, the main diagnostic character of *Udeus* are the elongate tarsi with the last tarsomere longer than tarsomeres I–IV together (Champion 1902; Bondar 1957).

Like most Eugnomini, little is known about the ecological relations between *Udeus* species and their host plants. The first report on the biology of the genus registered *U. cecropiae* (Bondar) and

U. sergioi (Bondar) associated with inflorescences of two species of *Cecropia* Loefl. (Urticaceae) (Bondar 1957). More recently, Mendonça (2014) recorded the association of two *Udeus* species with the female and male inflorescences of *Cecropia glaziovii* Snethl., suggesting they may be pollinators of this species. Specimens of *Udeus* are rare in collections, each species usually represented by only a few individuals, and revisions on Eugnomini biology typically consider them as palm-associated due to the superficial similarity to palm-associated weevils in the Derelomini (Caldara *et al.* 2014). Considering the diversity of their known hosts, with 61 accepted species of *Cecropia* (Berg & Franco-Rosselli 2005), the number of *Udeus* species in the Neotropical region is likely to be much greater than the currently known diversity.

This study presents the first results of our investigation of the natural history of the genus *Udeus* and it begins to reveal the little-known diversity of these weevils. Here, we aim to describe a new species of *Udeus* associated with a species of *Cecropia* that is a dominant tree in the high-elevation grasslands part of the Cerrado biome in western Brazil. We also describe the immature stages of the new species, including remarks about the behaviour on its host plant, and the first report of predation of Eugnomini larvae by social wasps (Vespidae). This is the first species from the Brazilian Cerrado and the first description of immatures of Neotropical Eugnomini.

MATERIAL AND METHODS

Study area, collected material, and examined specimens

We performed the field observations in January 2022 in two urban areas in Barra do Garças, state of Mato Grosso, Brazil. The vegetation of the area is mostly composed of rock outcrop grasslands ("rupestrian Cerrado"), where *Cecropia saxatilis* Snethl. (Figure 2a) is widely distributed and abundant. Collections were carried out in two sites on the outskirts of the elevated part of "Parque

Estadual da Serra Azul" (PESA). The first observation point is in an urban area (15°54'24.8" S 52°18'39.7" W, 309 m a.s.l) distant about 6 kilometers West from the PESA, and the second observation point is in a periurban area at 2.5 kilometers West from the PESA (15°52'16''S 52°17'0.4" W, 379 m a.s.l) (Figure 1). The behaviour of *U. cerradensis* sp. nov. was observed directly in the field and recorded through photos and videos using a smartphone during the period from 10 am to 1 pm, in addition to occasional observations in the early morning and early evening. We manually collected adult weevils by bagging male (i. e. staminate) inflorescences (Figures 2b, e), and we collected immatures directly from the interior of the decaying inflorescences still connected to the plant. Collections were carried out from 2020 to 2022 in the summer (December to January). To test whether *U. cerradensis* is a possible pollinator, we used an entomological net to sample insects near female (i. e. pistillate) flowers, and 7cm×10cm yellow sticky traps (Figure 2f) maintained for seven days on male and female plants, installed near floral buds or newly opened inflorescences. We took the specimens collected to the "Laboratório de Taxonomia de Insetos, Universidade Federal Rural de Pernambuco" (LabTaxIn-UFRPE), where adults and immatures were examined under a stereomicroscope and optical microscope. Larvae and pupae were killed in hot water to maintain tissue integrity and preserved in 70% ethanol. Specimens of five wasp species were collected directly from *Cecropia* inflorescences. Adult weevils and wasps were pinned and initially deposited in the "Coleção Entomológica da Universidade Federal Rural de Pernambuco" (CERPE). Photographs of wasps in lateral, dorsal, and frontal views were taken and sent to Dr. Alexandre Somavilla from the National Institute of Amazonian Research (INPA) for identification. The *Cecropia* species identification (Figure 2a) was based on Berg & Franco-Rosselli (2005).

The holotype and 146 adult paratypes are deposited at CERPE and the Field Museum of Natural History (FMNH). Some of these paratypes will be sent to the following institutions (see material examined and supplementary table): American Museum of Natural History, USA (AMNH);

Australian National Insect Collection, Australia (ANIC); Canadian Museum of Nature, Canada (CMN); Coleção Entomológica do Instituto Oswaldo Cruz, Brazil (CEIOC); Seção de Entomologia, Coleção Zoológica, Universidade Federal de Mato Grosso, Brazil (CEMT); Coleção Entomológica da Universidade Federal de Pernambuco, Brazil (CEUPE); Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Brazil (DZUP); Field Museum of Natural History, USA (FMNH); Charles W. O'Brien Collection, Arizona State University, USA (ASUCOB); Museum of Comparative Zoology, Harvard University, USA (MCZ); Natural History Museum, London (BMNH); National Museum Bloemfontein, South Africa (NMB); National Museum of Natural History, USA (USNM); New Zealand Arthropod Collection, New Zealand (NZAC); Museum of Natural History, University of Wrocław, Poland (MNHW).

Host plant

Cecropia species, including *C. saxatilis*, are widespread and abundant pioneers in the Neotropics (Zalamea *et al.* 2012). These trees are characteristic of secondary vegetation in disturbed and urban areas, playing a crucial role in forest regeneration (Franco-Rosselli and Berg 1997; Treiber *et al.* 2016). *Cecropia saxatilis* (Urticaceae) is a dioecious species distributed in Central Brazil and eastern Bolivia, in Cerrado areas, particularly on sandstone or limestone rocks, and in grass savanna at high elevations in Bolivia (Berg and Franco-Rosselli 2005). These relatively small trees, reaching a height of 10 m, present 4–8 spikes per staminate (i. e. male) inflorescence (Figure 2b), and 4 spikes per pistillate (i. e. female) inflorescence (Figure 2c) (Berg and Franco-Rosselli 2005; Gaglioti and Aguiar 2022). Despite its ecological significance, information regarding the phenology of *C. saxatilis* has not been systematically documented. Berg and Rosseli (2005) provided insights based on examined specimens, noting fertile periods for male and female plants of *C. saxatilis* in

various regions. In the state of Bahia, the fertile period was registered in March, April, June, and November; in the more southwestern parts of the distribution (states of Goiás, Mato Grosso and Minas Gerais) it was observed between January and April. Our observations in Barra do Garças (on the border of Goiás and Mato Grosso) revealed flowering plants from November to February, though we did not track the phenology in the remaining months. According to Berg and Rosseli (2005) most *Cecropia* species exhibit intermittent flowering and fruiting throughout the year. However, the flowering patterns of some species are influenced by seasonal variations and water regimes.

Morphological analysis

Adult morphology was examined using pointed specimens under a stereomicroscope. Mouthparts, genitalia, and immatures were dissected, slide-mounted, and examined with an Olympus BX41 optical microscope. We obtained scanning electron micrographs with a TESCAN VEGA3 to examine the vestiture and ornamentation of the head, antennae, metasternum, elytra, legs, and ventrites. For dissections, adults were left for 15–30 minutes in soapy hot water, and then dissected with fine-tipped tweezers and micro pins. The mouthparts were removed directly from the apex of the rostrum. Female and male terminalia, after being removed from the abdomen, were incubated in warm 10% KOH for a few minutes to digest soft tissue. Mouthparts and female and male terminalia were mounted on permanent slides using “Downs’ gel” (polyvinyl lactophenol) (Downs 1943; Salmon 1947), a water-soluble mounting medium. Illustrations were prepared either based on images taken through an Olympus BX41 microscope with a Moticam Pro 285B camera and the Motic Images software, or a camera lucida attached to an Olympus SZX12. In both cases, illustrations were traced in the CorelDraw package. Habitus photos were taken using a Microptics

system composed by a Canon EOS 6D camera, P-51 Camlift Controller 2.8 and Canon Eos Utility software. The photos were stacked with Helicon Focus 6.5.2.0 and edited using Adobe Lightroom 5 and Adobe Photoshop CS 5. Measurements were taken directly from 5 male and 5 female pointed specimens using a Zeiss 508 DOC stereomicroscope with an eyepiece reticle, following measurements taken by de Medeiros & Vanin (2020). Terminology for adults follows Franz (2006); Ting (1936) for mouthparts; Wanat (2007) for male genitalia; Howden (1995), and Gíron & Franz (2010) for female genitalia. Terminology for immatures follows May (1993), Burke (1968), Vanin & Benà (2013), Oberprieler *et al.* (2014), but see also Lira *et al.* (2017).

RESULTS

Adult and larval behaviour

Initial observations of *U. cerradensis* sp. nov. were made in January 2021 when we retrieved a few adult weevils by bagging the staminate inflorescences of one individual of *C. saxatilis* around 4 pm, before sunset. The next day, using the same method, many adults were collected around dusk (7 pm), and it was possible to observe a cloud of *U. cerradensis* sp. nov. flying around the inflorescences. The sweet odour released from the staminate inflorescences (Figure 2b) is very noticeable at the end of the day, but remains throughout the anthesis, even after inflorescences are removed from the plant. In general, adults are abundant in staminate inflorescences, mainly in the late afternoon, evening, and early morning. When active, weevils move constantly around spikes and are covered in pollen. Pollen-covered weevils blend in the background. Upon noticing our approach, they quickly hide at the base of the spike or fly to take shelter in nearby inflorescences. They exhibit thanatosis behaviour when perturbed, falling off the inflorescences. We observed adults feeding on pollen and mating in staminate inflorescences. In the hottest hours of the day, adults aggregate between the spathe and spikes of inflorescences in anthesis (Figures 2b, d).

Sampling in staminate inflorescences resulted in more than 50 individuals captured per bagged active inflorescence (Figure 2e), and about 100 adults were collected in each sticky trap (Figure 2f). No adults were collected or observed on pistillate inflorescences (Figure 2c) or in sticky traps next to them.

We did not directly observe egg deposition either outside or inside the spikes of the inflorescences, but we collected larvae and pupae in the interior of the staminate spike directly from the plant. Spikes colonized by larvae initially have a dark colour, progressing to wrinkling and total browning due to the advanced consumption of internal tissue. Pupation occurs within galleries, and adults emerge from small holes. Attempts to rear the larvae in transparent plastic containers under ambient conditions were unsuccessful. Due to the high humidity, the larvae left the interior of the inflorescences and did not finish their development. Similarly to adults, no larvae or pupae were collected or observed in pistillate inflorescences.

In January 2022, on two occasions, between 11 am and 1 pm, we observed *Synoeca surinama* (L.) wasps foraging around staminate inflorescences of *C. saxatilis*. After landing on the inflorescences, these wasps began to chew on floral tissues. After 5–7 minutes, the holes were large enough (Figure 2g, 3b) so that wasps were able to insert their heads into the opening in the spike and capture a larva of *U. cerradensis* sp. nov., manipulating it in a circular motion with its anterior legs and mandibles until it was ingested. In addition to ingesting on site, wasps also held larvae in their mandibles, probably carrying them back to the nest (Figure 3 and video available on https://figshare.com/s/d2c8dc9975ab3b0a04c3). Wasps of species *Polybia* aff. *jurinei* Saussure, *P.* aff. *rejecta* (Fabricius), *P.* aff. *ruficeps* Schrottky, and *Protopolybia* aff. *sedula* (Saussure) were observed and collected on the examined inflorescences. One individual of P. *rejecta* was observed trying to perforate the inflorescences. Some individuals of *Pr.* aff. *sedula* were observed taking advantage of the openings made by *S. surinama*, capturing a larva of *U. cerradensis* sp. nov. and

carrying it in flight (see video on https://figshare.com/s/d2c8dc9975ab3b0a04c3). *Polybia* aff. *jurinei* and *P.* aff. *ruficeps* were not observed capturing larvae of *Udeus*.

Taxonomy

Eugnomini Lacordaire, 1863

Udeus Champion, 1902

(Figures 4–11)

Udeus Champion, 1902: 139 (type species: *Udeus eugnomoides* Champion, 1902, by monotypy)

Moracetribus Bondar, 1957: 257 (type species: *Moracetribus cecropiae* Bondar, 1957, by original designation); O'Brien & Wibmer 1982: 89 (synonym).

Udeus cerradensis Lira, de Medeiros & Grossi, sp. nov.

(Figures 4a–b)

https://zoobank.org/urn:lsid:zoobank.org:act:4514BB72-8322-4D67-AB6A-384A10E5C140

Material Examined

Holotype

♂ "BRASIL, MATO GROSSO, Barra do Garças, Nova Barra Sul, 10.i.2022, -15.906650 S, -52.3110009 W, em *Cecropia saxatilis* A.O. Lira leg.; code CERPE1017"; "Holotype: *Udeus cerradensis* Lira, de Medeiros & Grossi" (CERPE).

Paratypes

BRASIL, MATO GROSSO, same data as holotype, 1♀, 1♂ (AMNH); 1♀, 1♂ (ANIC); 1♀, 1♂ (CMN); 1♀, 1♂ (CEIOC); 1♀, 1♂ (CEMT); 1♀, 1♂ (CEUPE); 1♀, 1♂ (DZUP); 2♀, 1♂ (FMNH); 1♀, 1♂ (ASUCOB); 1♀, 1♂ (MCZ); 1♀ (BMNH); 1♀ (NMB); 1♀, 1♂ (USNM); 1♀, 1♂ (NZAC); 1♀ (MNHW); 15♀, 2♂ (CERPE). Barra do Garças, Av. Serra Azul, 21.i.2022, -15.871603 S, -52.288257 W, em *Cecropia saxatilis* A.O. Lira leg., 5♀, 18♂ (CERPE). Barra do Garças, Av. Serra Azul, 28.xii.2021, -15.87095 S, -52.28298 W, em *Cecropia saxatilis* A.O. Lira leg., 4♀, 5♂ (CERPE). Barra do Garças, Nova Barra, 06–13.ii.2021, 15º54'24.8" S, 52º18'39.7" W, em *Cecropia* sp., A.O. Lira leg., 32♀ 37♂ (CERPE).

Other material

BRASIL, MATO GROSSO, Barra do Garças, Nova Barra Sul, 10.i.2022, -15.906650 S, -52.3110009 W; 20 larvae (5 dissected), 7 pupae (2 dissected) (CERPE); 5 adults, code FMNHINS 4574449 (FMNH).

Diagnosis

Udeus cerradensis sp. nov. can be distinguished from *U. muticus* Hustache by the presence of a strong ventral tooth on the femora (Figure 4b). It differs from *U. bifasciatus* Rheinheimer and *U. martiniquensis* Rheinheimer by a row of elongate yellowish setae on each elytral interstria (Figure 4a–b), whereas the latter two species have a row of elongate setae just on odd-numbered elytral interstriae. *Udeus cerradensis* resembles *U. fonsecai* Voss by the median carina on the rostrum (Voss 1941), and *U. cecropiae* by the incomplete dark transverse band in the middle of the elytra.

It can be distinguished from both and also from other species of *Udeus* by the presence of whitish plumose setae on the elytral interstriae, pronotum, prosternum, and head (Figures 4a–b).

Description

Male (Figure 4a –b).

Body size: 2.2–2.9 mm.

Head. Rostrum 0.8–1.0 times as long as pronotum; as wide at apex as at base; with integument yellowish to dark brown, darkest near scrobes; with incomplete longitudinal carina from basal region to near apex; scrobe oblique, directed ventrally, almost reaching anterior eye margin; apex with elongate setae; elongate and decumbent setae arranged transversely from antennal insertion to base of the rostrum; with plumose setae concentrated at base; with small longitudinal sulcus near median carina. Eyes 0.8–1.1 times as high as wide; 1.0–1.3 times more separated anteriorly than posteriorly; with microsetae between ommatidia (Figure 4c). Head integument yellowish to dark brown; plumose setae concentrated from the base of rostrum to interorbital region; with few short setae between plumose setae; setae usually whitish, longer on interorbital region than base of head; with row of five or six elongate yellowish setae near internal margin of each eye. Antennal scape straight, widened at apex, extending to eye margin; funicle with seven antennomeres; antennomere I always longer than others, 1.8 times longer than antenomere II; antenomere II longer than antenomeres III–VII; antenomere V usually shortest; club 2.0–2.3 times longer than wide.

Mouthparts (Figures 5a–e). Mandibles exodont, symmetric, longer than wide, slightly curved outward, sinuous on internal margin, with short tooth at apex (Figure 5a–b); with one long seta close to external margin and several sensilla in dorsal view (Figure 5b). Maxillae (Figures 5d–e) elongate; palpiger rectangular, with two elongate setae; palpomere I with 3–4 apical setae; palpomere II cylindrical, slightly shorter than palpomere I, with three to four apical setae;

palpomere III with several short setae on apex. Apex of mala bilobate, not exceeding apex of palmopere I (Figure 5d); mala with several elongate setae distributed from base to apex; stipes merged with mala, slightly curved, with one seta on ventral view. Labium (Figure 5c) with prementum transverse, sclerotized on sides, with two long setae in apicolateral region; narrow submentum, with several tiny setae on center; palpomeres I and II with several elongate setae on apex, palpomere III shorter than I–II, with few short setae on apex; ligula not exceeding apex of palpomere I, with elongate setae throughout.

Thorax. Pronotum 1.1 times wider than long; lateral margins subparallel, with relatively deep transverse sulcus on median region; apically strongly constricted; integument yellowish to brown; entirely covered by three types of setae: very abundant whitish plumose setae, short whitish setae interspersed between plumose setae, and yellowish elongated setae sparsely distributed forming rows on sides, apex and center of pronotal disc, more abundant on center. Procoxae contiguous, more elevated than mesocoxae, both covered by plumose setae. Femora with well-defined ventral tooth, with set of elongate setae on ventral basal third. Profemora about 3.2 times as long as wide; about 2.5 times as wide as protibiae. Tibiae mucronate (Figure 4d)**.** Pro- and mesotibiae compressed antero-posteriorly, almost straight. Metatibiae with internal margin slightly curved, covered with elongate setae in apical third**.** Tarsus with last tarsomere 1.5 times longer than first tarsomere, and 1.3 times longer than tarsomeres II and III together; tarsomere III very short and bilobate. Scutellum triangular, as long as wide; integument dark brown; entirely covered with dense whitish scales. Elytra about 1.9 times longer than wide, 1.4 times wider than pronotum, 3.0 times longer than pronotum; humeri and incomplete band on middle of elytra darker than rest of elytra; humeri rounded; lateral margins subparallel; interstriae covered by whitish plumose setae, striae punctate with tiny yellowish setae inserted in each puncture, a row of elongate yellowish acuminate setae on interstriae, alternating with the sets of plumose setae (Figure 4e); epipleura incomplete, covered by

short plumose setae. Ventral region of thorax with integument yellowish to dark brown. Prosternum with whitish plumose setae; 1.7 times longer than the coxal width; postocular lobes indistinct. Metepisternum with whitish plumose setae. Metasternum with distinct central concavity extending into abdomen, with whitish plumose setae next to concavity border and lateral region; whitish sparse elongate setae on center and more sparsely interspersed with plumose setae on lateral region (Figure 4f).

Abdomen. Ventrites I–II connate, concave at center; covered by whitish setae; margins of concavity with row of elongate setae; very short plumose setae at base and sides. Ventrites III–V covered by whitish setae, elongate in central region, without plumose setae. Ventrite V trapezoidal, slightly sinuose on apex (Figure 4g).

Male terminalia (Figure 6). Pygidium (tergum VIII) about 0.8 times as wide as long along midline, with anterior margin straight, and posterior margin rounded; with very large setae concentrated from median region to apex; ventral flap wide, with posterior margin slightly serrate (Figure 6f). Sternum VIII composed of two lateral plates separated by membrane, each laterally acuminate and curved anteriorly; posterior margin curved, with 6–8 setae (Figure 6d). Sternum IX (spiculum gastrale) with apodeme about 1.3 times as long as aedeagus length; apically acute, and slightly expanded to sides, with two hemisternites separated by a membrane (Figure 6e). Tegmen about 1.4 times longer than aedeagus; tegminal apodeme slender, sinuate; with two parameres fused along most of their length, apically rounded, each arm apically covered with several setae (Figure 6c). Aedeagus (Figures 6a–b) 3.7 times longer than wide, slightly constricted at middle, funnelling and rounded at apex; ventral plate strongly sclerotized with several sensilla forming transverse rows on apical third. Apodemes subequal to aedeagus in length. Endophallus with bifurcate pocket containing microtrichia next to basal sclerite; one pair of triangular lateral sclerites and one elongate median sclerite near apex, closing ostium.

Female. As males in general aspect, differing in the following features: Body size 2.4–3.1 mm. Rostrum 0.8–0.9 times shorter than pronotum; width at apex subequal width at base. Pronotum 0.9–1.1 times wider than length of pronotum. Prosternum length 1.4–1.7 times width of procoxae. Metasternum with slight sulcus in basal region. Femora without elongate ventral setae on basal third. Tibiae without mucro. Scutellum longer than wide. Elytra 1.5 times wider pronotum, 1.9 times longer than wide, 2.5–3.2 times as long as pronotum. Ventrites strongly convex; ventrites I–II connate at the middle, without depression in the center; ventrite V triangular, rounded at apex (Figure 4h)**.**

Female terminalia (Figure 7). Sternum VIII, including apodeme, about 3.8 times longer than coxites; lamina occupying posterior third; lateral arms sclerotized, with one row of elongate setae near external margin, and very short setae on distal region of lamina; lamina medially membranous; distal region of lamina sagittate, with setae forming two rows; apodeme of sternite 8 straight, distally bifurcated, and gradually lighter towards apex (Figure 7d). Coxites sclerotized, as long as lamina of sternite 8, slender, apically with tiny setae, baculi subparallel, elongated, gradually less sclerotized distally (Figure 7a). Styli cylindrical, inserted at external lateral margin of each coxite; surface with serrate texture, apparently without setae (Figures 7a–b). Bursa copulatrix elongate, constricted on distal region which is slender. Spermatheca curved, about 1.3 times longer than wide; *cornu* (cr) slightly curved; *collum* (cl) slightly constrict on apex; *ramus* (ra) very short; *ramus* and *collum* pointing approximately in same direction (Figure 7e).

Mature larvae (Figures 8–10).

Length: 1.6–1.8 mm. *Head* (Figures 8b–c). Sclerotized, free; head capsule round, light yellow to yellowish-brown; mandibles dark brown; clypeus and labrum slightly darkened. Epicranial suture (ES) distinct, 0.5 times as long as head length. Frontal suture (FS) distinct, complete, V-shaped.

Median endocarina present, extended to middle of frons. One pair of convex stemmata present on each side, posterior pair of stemmata sometimes present. Antennae (Figure 9c) exposed, one-segmented, with conical accessory sensory appendage (*acap*), and minute processes. Catapophyses distinct and in the same plane as frons. Hypopharyngeal bracon membranous. Epicranium with five pairs of dorsal epicranial setae (*des 1–5*); two pairs of lateral epicranial setae (*les1–2*) located next to anterior angle of head capsule; two pairs of ventral epicranial setae (*ves*1–2); four pairs of minute posterior epicranial setae (*pes1–4*) forming an oblique row next to posterior margin of head. Frons containing five pairs of frontal setae (*fs*1–5), *fs1*, *fs2*, and *fs3* smaller than *fs4* and *fs5*. Clypeus (Cl) (Figures 9a–b) transverse, lateral margins subparallel, anterior margin sinuate, with three pairs of clypeal setae (*cls*), *cls1*, and *cls3* longer than *cls2*, which is very small. Labrum (Lm) (Figure 9a) transverse, anterior margin sinuate, with three pairs of labral setae (*lms*1–3), *lms3* smaller than *lms1* and *lms2*, that are similar in length. Epipharynx (Figure 9b) trapezoidal, almost truncate anteriorly, with four anteromedian setae (*ams1–4)* close together; three pairs of anterolateral setae (*als*1–3); two pairs of median setae (*msp*1–2); subparallel labral rods (*lr*), slightly curved outwards anteriorly. Mandibles (Figures 9f–g) triangular, symmetrical, strongly sclerotized, tridentate apically, the basalmost tooth smallest, ventrally with two central mandibular setae (*mds*1–2), two minute sensilla proximal to *mds1*, dorsally with one sensillum near internal margin. Maxillae with cardo transverse, subtriangular; stipes elongated with three long setae, one very short seta, and three sensilla on ventral side; mala rounded, ventrally with five elongated setae on apex (Figure 9d), and seven spatulate setae arranged in a row dorsally (Figure 9e); palpifer with two-segmented membranous maxillary palp (MxP), proximal palpomere subequal in length and wider than distal one, with one seta and two sensillae on ventral side; distal palpomere elongated, with one sensillum at base and eleven minute setae on apical region. Labial palps (LbP) (Figure 9d) two-segmented, proximal palpomere transverse, wider than distal one, with one sensillum; distal palpomere elongated,

conical, with one sensillum at base and nine minute setae at apex. Prementum (PrMT) (Figure 9d) rounded on sides, with three pairs of setae, median pair long, located near lateral margins, basal pair and apical pair short; premental sclerite (PrmS) slightly sclerotized, trident-shaped. Postmentum (PMt) (Figure 9d) with three pairs of postmental setae (*pms*1–3) and two pairs of sensilla.

Thorax (Figures 9h, 10a, d, g). Pro-, meso-, and metathorax transverse; prothorax longer than meso- and metathorax, with 11 pronotal setae (*prns* 1–11) on each side; pronotum with two rectangular, sub-contiguous sclerites, each one with six *prns* (*prns*1–6); lateral margin with *prns*7–10 forming a curved row, *prns*10 furthest, prns7–8 smaller; pedal area (Figure 10d) with six pedal setae (*pdas*1–6), *pdas*2–5 very short; ventropleural region of prothorax (Figure 10h) with two setae (*vpls*1–2); mediosternal fold (Figure 10e) with one mediosternal seta (*msts*). Prothoracic spiracle (Figure 9h) bicameral, peritreme rounded; air tubes annular, with twelve annuli. Meso- and metathorax: prodorsum of meso- and metathorax (Figures 10a, g) each with one pair of prodorsal setae (*prs*) long. Postdorsal area of meso- and metathorax (Figures 10a, g) with four pairs of postdorsal setae (*pds*); meso- and metathorax with two alar setae (*as*1–2), *as*1 very short (Figure 10g); pedal area with six pedal setae (*pdas*1–6; Figures 10d, g); ventropleural region with one seta (*vpls;* Figures 10d, g); mediosternal fold with one seta (*msts*; Figure 10d).

Abdomen (Figures 8a, 9i–j, 10b, c, e, f, h, i). Eight pairs of bicameral spiracles (Figure 9i), smaller than prothoracic spiracle, but with same form and structure, with six annuli; last pair very close, located dorsally on abdominal segment eight. Segments I–VII each with four folds (folds I, II, III and IV); segment VIII with three folds; segment IX reduced; segment X circular and ventral, anus subterminal surrounded by six prominent lobes. Lateral fold (fold I) developed on segments II–VII, narrow, without setae, indistinct on segment VIII (Figures 8a, 10h–i). Chaetotaxy similar on segments I–VII: prodorsum (Figures 10b, c, h, i) with one prodorsal seta (*prs*); postdorsum (Figures 10b, c, h, i) with four postdorsal setae (*pds*), two long and two very short; two epipleural setae (*eps*)

on epipleuron , *eps* 1 shorter than *eps* 2; ventropleural lobe (Figures 10b, c, h, i) with two setae (*vpls*); laterosternal region (Figures 10c, e, h, i) with two setae (*lsts*1–2); mediosternal fold (Figures 10h–i) with two minute setae (*msts* 1–2). Abdominal segment VIII (Figure 10i) with dorsal spiracles very close, with 12 annuli, directed backward (Figure 9j); two pairs of postdorsal setae (*pds*) next to spiracles, one pair long and the other one very short; fold III of abdominal segment VIII with three dorsal setae (*ds*1–3); abdominal segment X with two setae located on lateroposterior anal lobe (Figure 10i).

Pupae (Figure 11).

Length: 1.8–2.1 mm. Adecticous and exarate. Whitish-cream coloured; with long, curved setae on head, rostrum, thorax, abdomen, and femora; body setae placed on long tubercles, except those of anterior region of rostrum, and femora; tubercles of pronotum, meso-, and metathorax larger than abdomen, except those of tergites VI–VII (tVI–VII).

Head (Figure 11a–b) completely covered by pronotum in dorsal view; one pair of vertical setae (vs); one pair of supraorbital setae (*sos*) located near lateral eye margin, and one pair of orbital setae (*os*) located on internal eye margin. Rostrum (Figure 11b) surpassing mesocoxae, with one pair of post-antennal setae (*pas*), and one pair of rostral setae (*rs*).

Thorax. Pronotum (Figure 11a) transverse, conical; one pair of suprapical setae (*sas*), two pair of discal setae (*ds*1–2), two pairs of lateral setae (*ls*1–2), and four pairs of posterolateral setae (*pls*1–4). Mesothorax (Figure 11a) with two pairs of mesonotal setae (*msN*) placed on tubercles located at sides of rounded scutellum. Metathorax (Figure 11a) longitudinally sulcate and divided into two parts, each side with one pair of metanotal setae (*mtN*) similar to mesothorax arranged in transverse row and moderately separated. Legs (Figures 11a–b). Each femur with one femoral seta (*fes*) inserted in a small tubercle.

Abdomen (Figure 11a). Nine segments visible dorsally, segments I–VI with three pairs of discotergal setae (*dsT*) subequal in length and placed on elevated tubercles, discotergal setae 3 (*dsT3*) located on lateral elevated area; segments III and IV slightly wider than others; segments VI and VII longer than others, segment VII twice as long as segment VI and with posterior margin rounded; tubercles of segment VII slightly longer than others; segments VIII and IX partially visible dorsally, without setae; segment IX with pseudocerci (*pc*) pedunculate and partially darker than other parts of the body. Seven annular spiracles placed at margins of segments I–VII, visible dorsally.

Sexual dimorphism. Usually, the abdominal segments of males are narrower than females in dorsal view. Female with small round convexity located on each side of sternum on the ninth abdominal segment (Figure 11c).

Etymology

The species name refers to the Brazilian Cerrado, a hotspot of biodiversity where *C. saxatilis*, the host plant of *U. cerradensis*, is distributed and that corresponds to the possible general distribution of the weevil species based on host plant distribution. The specific epithet *cerradensis* means “from Cerrado”, and is used as a noun in apposition.

Distribution

Udeus cerradensis is known only from the type locality of Barra do Garças, Mato Grosso, Brazil.

DISCUSSION

Here we describe a new species of *Udeus* and provide the first thorough description of immature stages for a Neotropical Eugnomini. Adults share the main external diagnostic characters with other species of *Udeus* while being easily distinguished by colour and pilosity. Like other species of Eugnomini, there is marked sexual dimorphism with a mucronate tibia in males only (Champion 1902; Kuschel 1952; Bondar 1957; Cawthra 1966) and a central metasternal concavity extending into the first and second ventrites in males (Champion 1902). New sexually dimorphic characters reported here include longer setae at the base of tibiae and femora in males and a markedly distinct shape of ventrite V, trapezoidal in males and triangular in females. Because of the lack of detailed descriptions of mouthparts and genitalia, these cannot be compared to other Neotropical eugnomines. More broadly, exodont mandibles are rare within Curculioninae (Caldara *et al.* 2014) and, when studied, have been reported in a few Curculionini, e.g., *Ergania gibba* Pascoe (Clarke *et al.* 2019), and eugnomines such *Meriphus* Erichson, *Myossita* Pascoe, *Orpha* Pascoe, and *Omoides* (Marshall 1937; Cawthra 1966). Unlike the endodont mandibles in *Udeus* mentioned in the key to Meriphina (Cawthra, 1966; Figure 12c), *U. cerradensis* has an exodont mandible, with only one apical tooth (Figure 12a), similar to *Omoides validus* Kuschel (Figure12b). The male genitalia is similar to other eugnomines, with the aedeagus constricted medially and curved in lateral view, the endophallus with irregular sclerites, and the tegminal parameres proximally fused (Cawthra 1966; Mazur 2014; Mazur 2017; Mazur 2019). On the other hand, the study of female genitalia revealed some interesting features. In contrast to *Meriphus* and *Myossita* (Cawthra 1966), we observed the presence of styli in *U. cerradensis*. Moreover, the coxites are sclerotized with each presenting a baculum (*sensu* Lyal 2022). These structures are not explicitly described in descriptions of other Eugnomini, but May (1993) generally mentions a sclerotized ovipositor in females. This degree of

sclerotization suggests that the ovipositor, rather than the mandibles, is used to prepare oviposition sites. In addition to adult morphology, the first description of an immature supports the close relationship between Neotropical and Australian eugnomines. Larvae of *U. cerradensis* resemble New Zealand Eugnomini described by May (1993). Differences include the number of postdorsal setae on abdominal segment VIII, and setae on the anal lateral fold. In *U. cerradensis*, there are four postdorsal setae instead of three, and two setae on the anal fold instead of three. The 12 annuli of spiracles of the prothorax and abdominal segment VIII are similar to *Hoplocneme* White and *Oreocalus* May with 10–12 annuli, and *Scolopterus* White with 12–14 annuli, whereas in other Eugnomini there are 6–8 annuli (May 1993). In summary, our detailed morphological study presents additional evidence of a close relationship between Neotropical and Australian eugnomines, while also revealing variable characters with potential phylogenetic and functional relevance within the group.

Even though host plants of *Udeus* have been considered as uncertain in the English literature (Caldara *et al.* 2014 and citations therein), this information has been available in Portuguese for several decades. Bondar (1957) described two species of *Udeus* from aborted inflorescences of two species of *Cecropia*, reporting for the first time the host plants for the genus. Andrade (1984) described the development of immatures and adults of *Ophtalmoborus* sp. Schoenherr (now *Anthobius* Schoenherr) in *C. lyratiloba* Miq. (now *C. pachystachya* Trécul) in Rio de Janeiro, Brazil. Based on the relatively poor-quality photographs and descriptions presented, we believe it to be a species of *Udeus* instead. Without this photo, it would be impossible to recognize the error: this is one example of how proper documentation in addition to checklists for poorly known taxa can enhance our knowledge on weevil flower visitors (Haran *et al.* 2023). Moreover, it highlights how literature reviews may miss important data if focused on a single language, with demonstrated negative impacts in biodiversity studies (Amano *et al*. 2021; Konno *et al*. 2020). It is remarkable

that such a specialized interaction with abundant and iconic plants has been overlooked. The genus *Cecropia* is composed of species popularly known as trumpet tree (English), embaúba (Portuguese) or guarumo (Spanish). Very abundant both in natural and disturbed areas in the Neotropics, they are widely known for their mutualistic association with ants of the genus *Azteca* Forel (Berg & Franco-Rosselli 2005; Dejean *et al.* 2012; Treiber *et al.* 2016). Species of *Udeus* are likewise quite abundant in nature but are very rare in collections. All species with known hosts (Bondar 1957) are highly species-specific, including *U. cerradensis*. This high host-specificity and larval breeding on adult hosts contrasts with other eugnomines. Specialized relationships with hosts are known in a few Australian genera, such as *Gonoropterus* Broun and *Myossita* associated with inflorescences and fruits, *Nyxetes* Pascoe which develops in galls of *Clematis* L. (Ranunculaceae), *Hoheria* A. Cunn. (Malvaceae), and *Nestegis* Raf. (Oleaceae) (May 1993; Cawthra 1966; Caldara *et al.* 2014), and *Pactola kuscheli* Mazur, recently recorded causing damage in *Agathis montana* de Laub. (Araucariaceae) (Mazur *et al.* 2016). Other Neotropical eugnomines such as *Omoides* and *Rhopalomerus* exhibit broad host ranges, having been collected in several species of plants of different botanic families (Kuschel 1952; Cawthra 1966), while *Pedetinus* seems to be more restricted, with collections registered in a few species of *Leandra* Raddi (Melastomataceae) (A. Lira, personal information). Given the high diversity of *Cecropia*, with 61 valid species distributed throughout the Neotropical region, and especially diverse near the Andes (Berg & Franco-Rosselli 2005), we expect that the number of new species of *Udeus* will increase in the coming years.

The *Cecropia* species observed here shares many of the putative traits related to beetle and weevil pollination: fragrant yellow flowers organized in larger inflorescences, dioecy, and crepuscular anthesis (Haran *et al.* 2023). However, species of *Cecropia* are generally believed to be wind-pollinated (Berg & Franco-Rosselli 2005). Because a species of *Udeus* has been implicated as a pollinator of *Cecropia* before (Andrade 1984), we tested whether this was the case here. Weevils

are strongly attracted to staminate flowers, which are fragrant and provide food for adults in the form of pollen and also breeding sites within floral tissues. Both direct observations and sticky traps failed to find evidence that *U. cerradensis* is also attracted to pistillate flowers. Therefore, it is unlikely that *U. cerradensis* is a relevant pollinator of *Cecropia saxatilis*. The presence of branched setae has been suggested as a trait associated with weevil pollination more generally (de Medeiros *et al.* 2019; de Medeiros & Farrell 2020; Haran *et al.* 2023), but here we show a non-pollinator abundantly covered by this kind of setae. We conjecture that these hairs may instead have a defensive function, as pollen-covered weevils were inconspicuous to us as collectors, and this may also be the case for visual predators. The fact that pistillate flowers provide no reward to weevils does not prevent the possibility of pollination by them: in palms there are many cases of pollination by beetles with odour mimicry between staminate and pistillate inflorescences and no rewards in the latter (Barfod *et al.* 2011; Haran *et al.* 2023). We note that our study has been conducted in a species of *Cecropia* found in open environments, while previous reports of weevil pollination have been done in rainforests. Therefore, it is possible that there is variation between species of *Cecropia* in the relevance of specialized weevil pollinators, and environmental conditions may favour different pollination agents.

While most of the weevil-focused literature highlights their interactions with host plants or parasitoids (Oberprieler 2014; Oberprieler *et al.* 2007), weevils are inserted in a larger community and are also attacked by generalist predators. Larvae of *Udeus* are endophytic, a trait generally thought to be a key adaptation of weevils that enables escape from predation (Oberprieler *et al.* 2007). However, here we demonstrate predation by behaviourally flexible predators such as social wasps. Herbivorous and carnivorous habits are well documented in Vespidae, rendering them excellent insect control agents in agricultural contexts (Prezoto *et al.* 2019; Elizalde *et al.* 2020): insects in several orders are the predominant prey items (Brock *et al.* 2021). Predation on

Curculioninae weevil larvae by social wasps has been previously documented: *Pachodynerus brevithorax* (Saussure) (Eumeninae) (Torezan-Silingardi 2011), and *Brachygastra lecheguana* (Latreille) (Polistinae) (Alves-Silva *et al.* 2013) prey on larvae of *Anthonomus* Germar (Curculioninae) inside flower buds of *Banisteriopsis malifolia* (Nees and Mart.) B. Gates (Malpighiaceae), also in the Cerrado. Our observations add to these and highlight that endophytic larvae may be targeted by generalist predators and also that weevil populations may be significantly impacted by interactions other than those traditionally considered for the taxon.

The natural history observations carried out here are part of our larger ongoing effort to document Neotropical eugnomines and the *Udeus*-*Cecropia* interaction. This is a fascinating highly specialized system, with potential for expanding our understanding of the evolution of insect-plant interactions. Documentation of this diversity and details of their natural history are a fundamental step to unleash this potential.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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APPENDIX - Figures

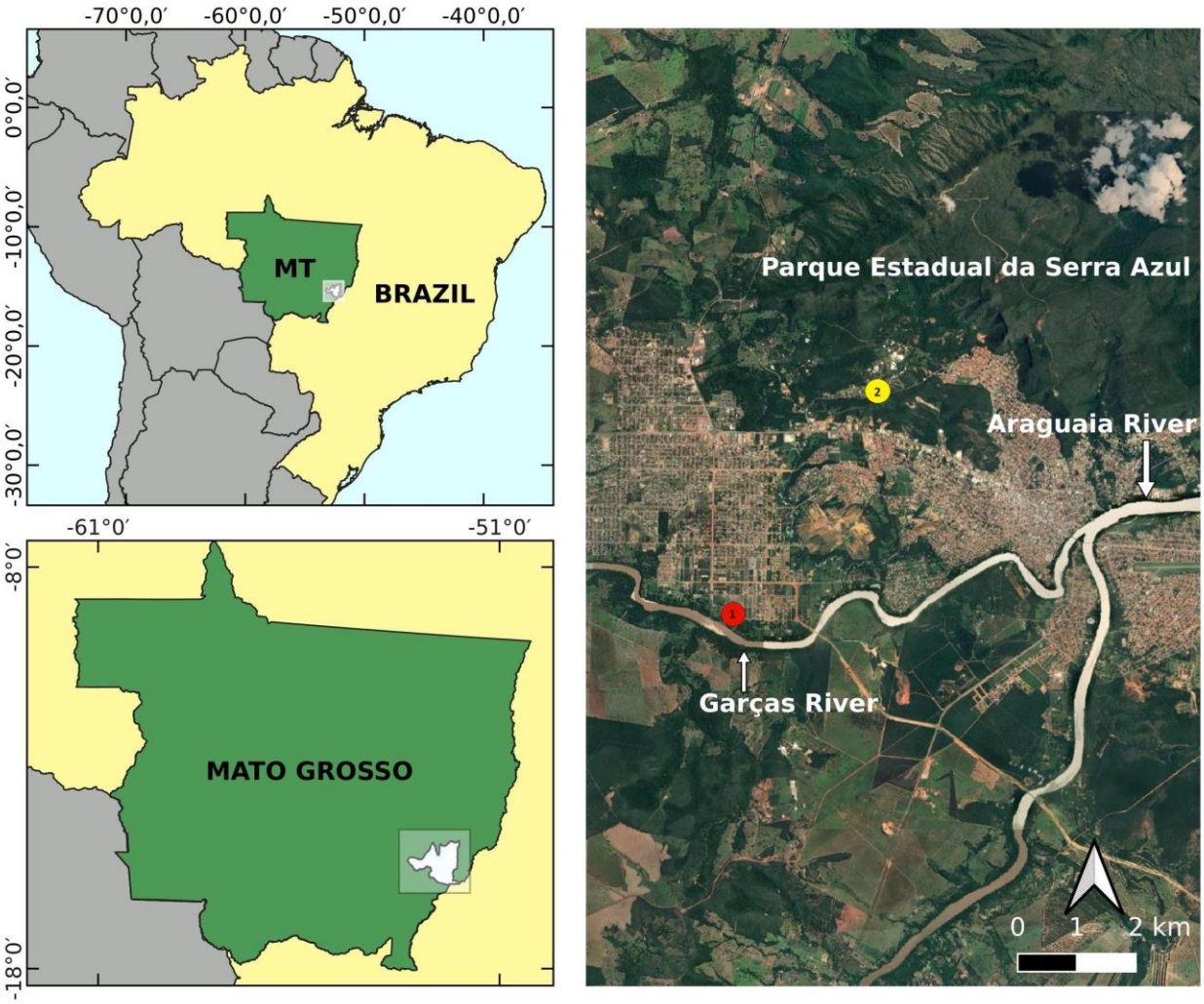

FIGURE 1 Collection sites of *Udeus cerradensis* sp. nov. in Barra do Garças, Mato Grosso, Brazil. The red circle corresponds to first observation point, at 6 kilometers West from PESA, and the yellow point corresponds to second observation point, at 2.5 km West from PESA.

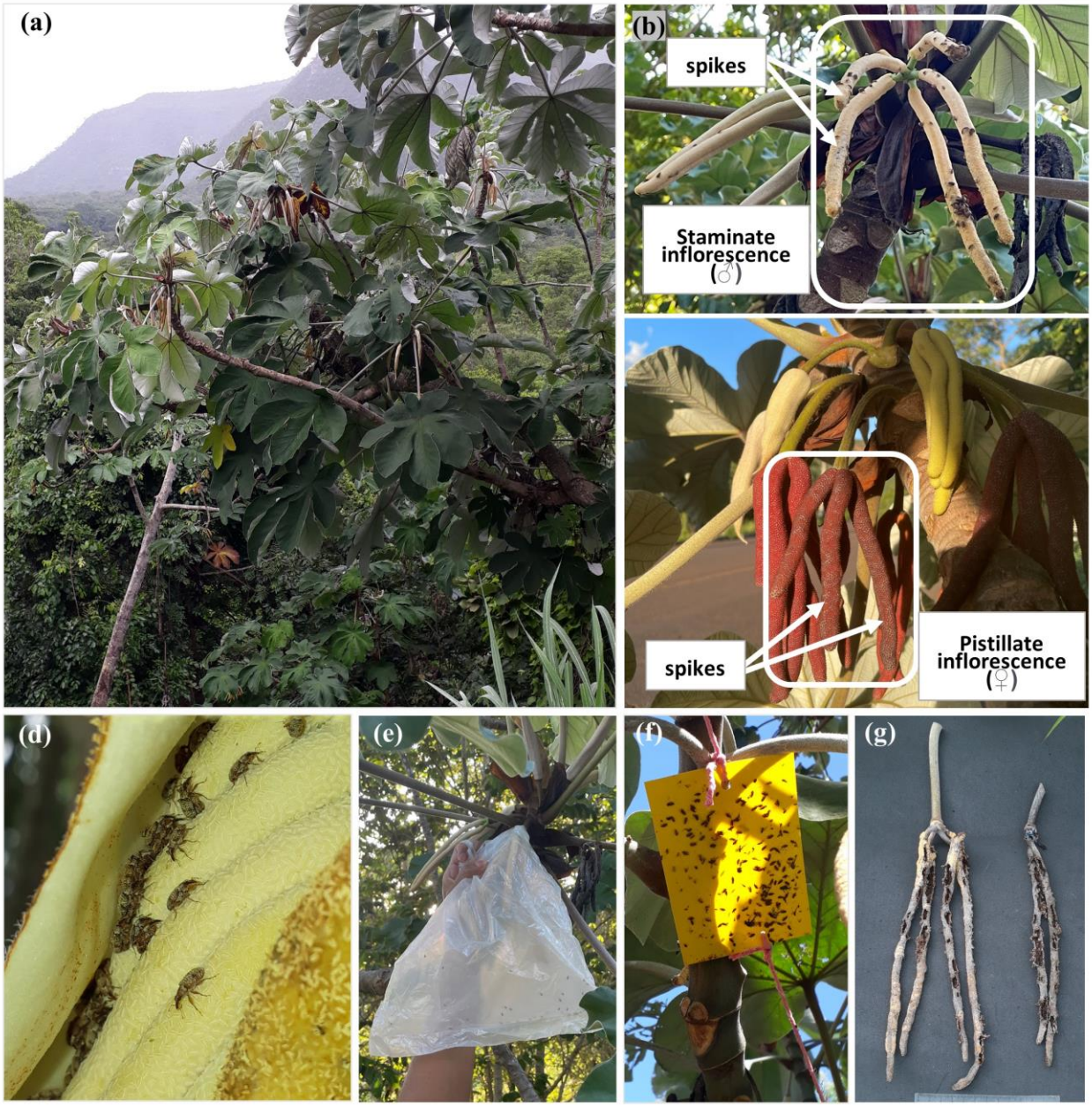

FIGURE 2 (a) Male plant of *Cecropia saxatilis* in a collection area; (b) staminate inflorescences of *C. saxatilis*; (c) pistillate inflorescence of *C. saxatilis*; (d) *Udeus cerradensis* sp. nov. adults in staminate inflorescences of *Cecropia saxatilis*; (e) *Udeus cerradensis* collected by bagging method in a staminate inflorecence of *C. saxatilis*; (f) *Udeus cerradensis* sp. nov. collected in sticky trap; (g) foraging signs of *Synoeca surinama* in male (i. e. staminate) inflorescences of *Cecropia saxatilis*.

FIGURE 3 *Synoeca surinama* foraging on staminate inflorescences of *Cecropia saxatilis*.: (a) wasp searching for *Udeus cerradensis* sp. nov. larva; (b) capturing a larva; (c) manipulating a larva; (d) flying with captured larva between the mandibles.

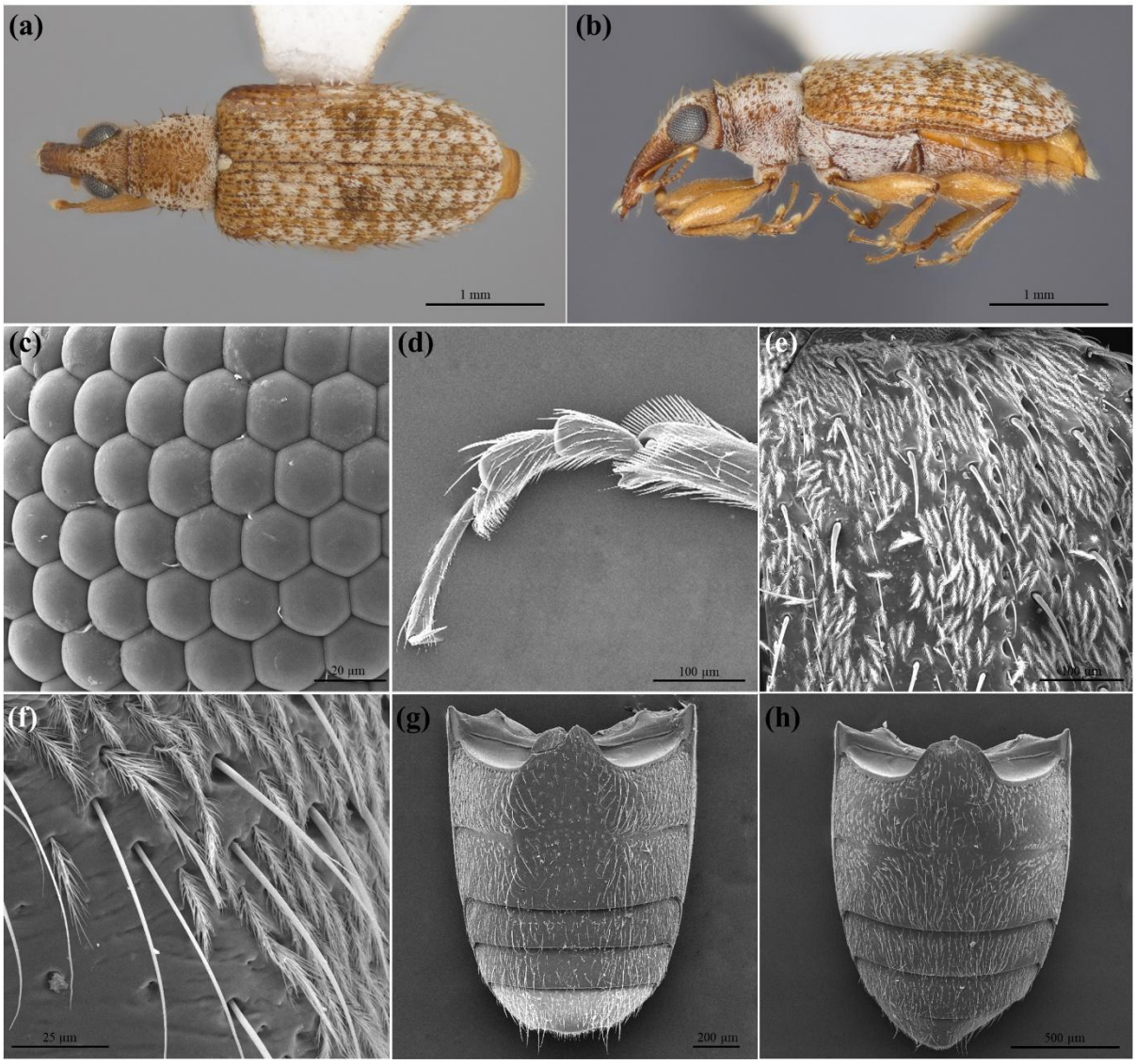

FIGURE 4 General morphology of *Udeus cerradensis* sp. nov.: (a) dorsal *habitus*, paratype male **(**FMNHINS 4429817); (b) lateral *habitus*, paratype male **(**FMNHINS 4429817); (c) microsetae between ommatidia; (d) apex of metatibia and metatarsus of male; (e) Elytral vestiture; (f) lateral of metasternum; (g) abdominal ventrites of male; (h) abdominal ventrites of female.

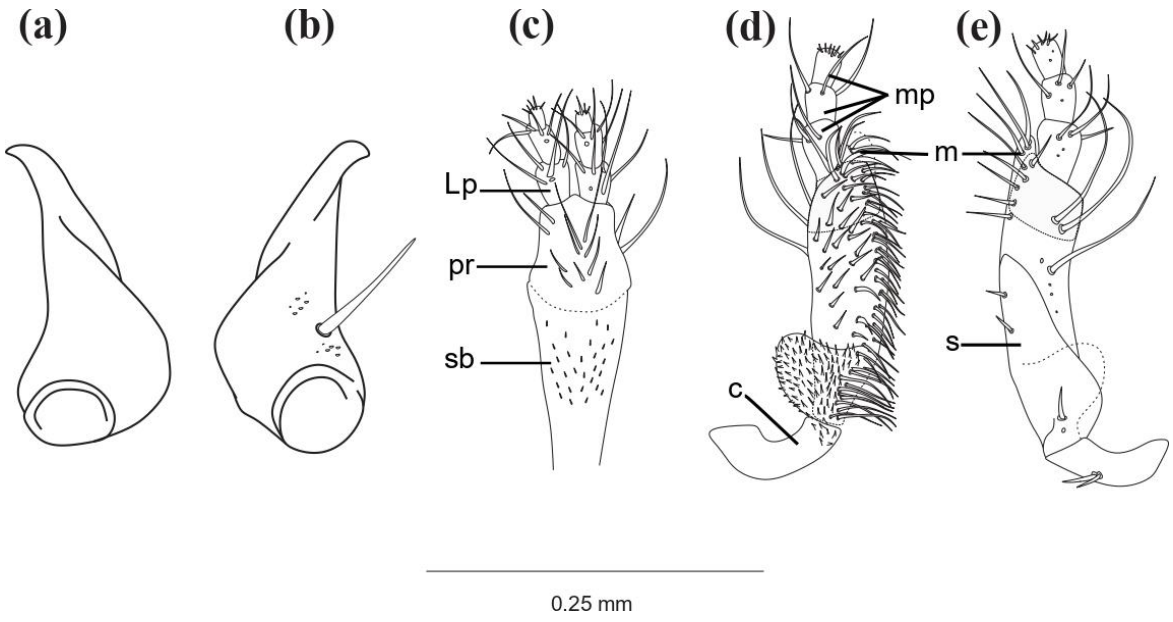

FIGURE 5 Mouthparts of *Udeus cerradensis* sp. nov.: (a) left mandible in dorsal view; (b) left mandible in ventral view; (c) labium in ventral view; (d) left maxilla in dorsal view; (e) left maxilla in ventral view. Legends: c, cardo; Lp, labial palps; m, mala; mp, maxillary palps; s, stipe; sb, submentum; pr, prementum.

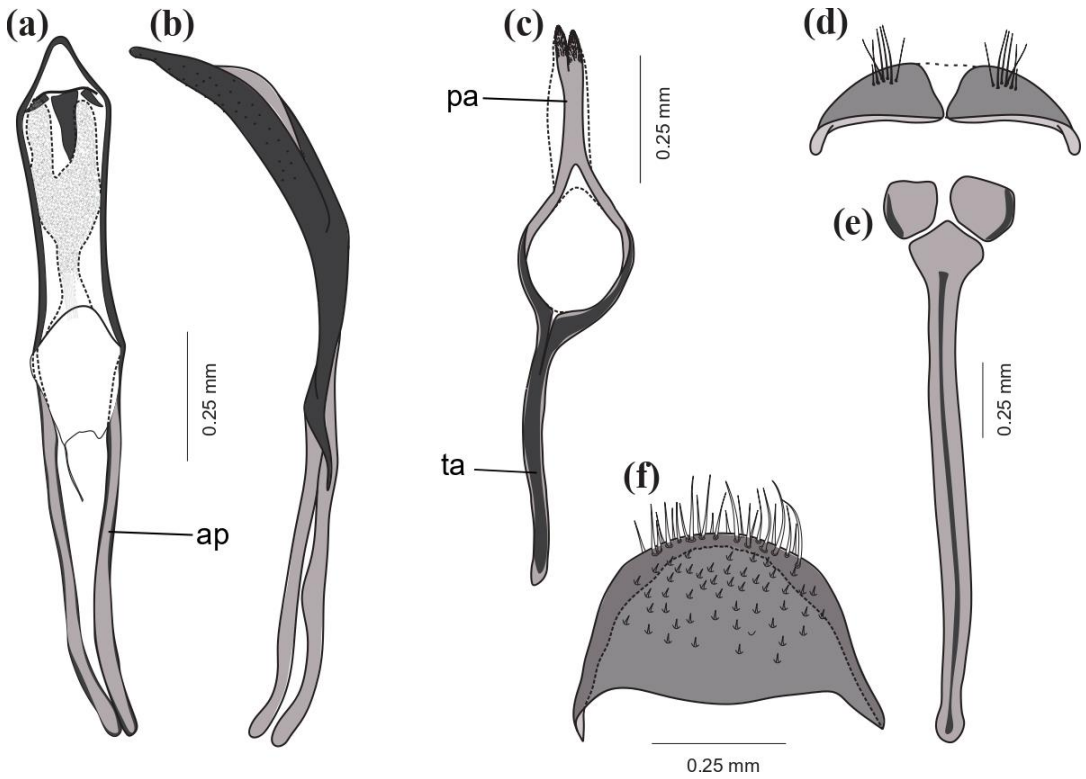

FIGURE 6 Male terminalia of *Udeus cerradensis* sp. nov.: (a) aedeagus in dorsal view; (b) aedeagus in lateral view; (c) tegmen; (d) sternum VIII; (e) spiculum gastrale; (f) pygidium. Legends: ap, apodemes; pa, parameres; ta, tegminal apodemes.

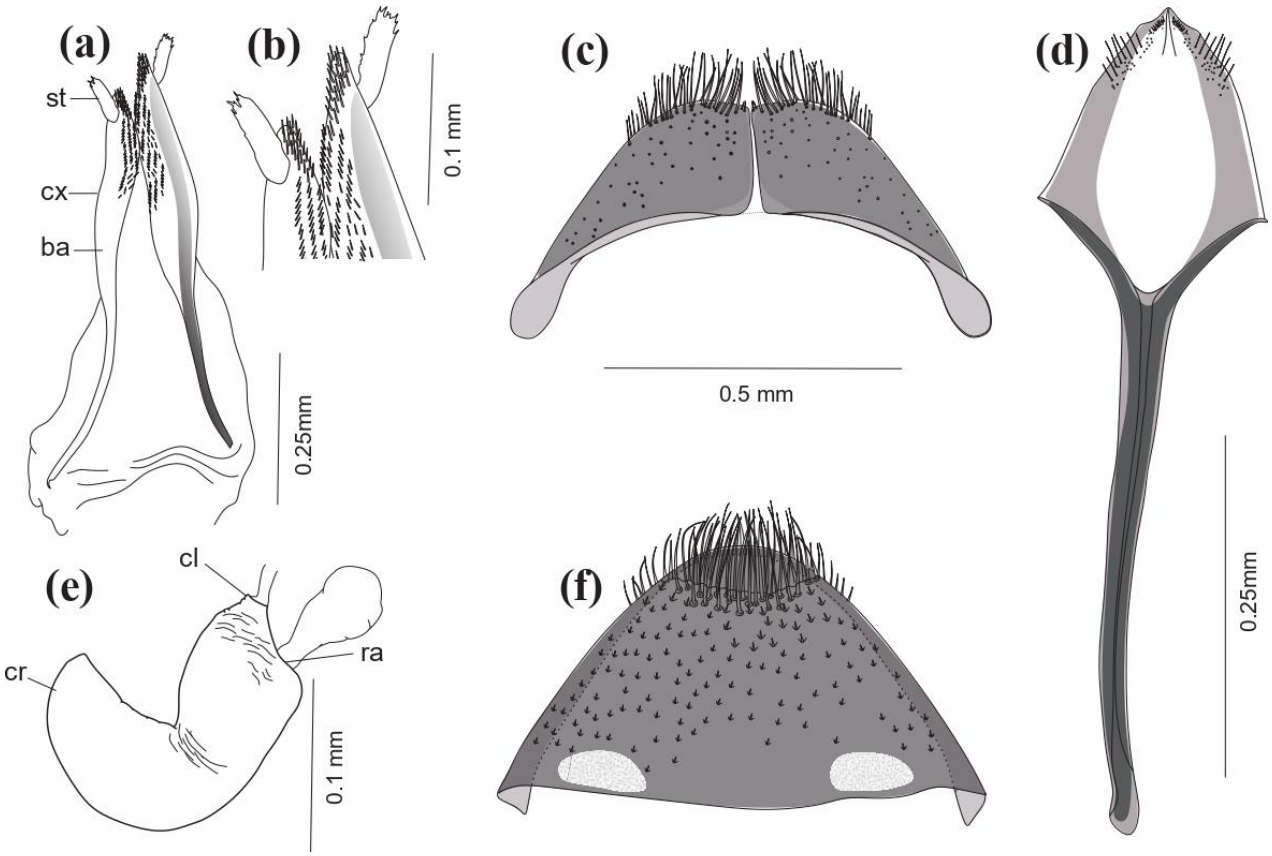

FIGURE 7 Female terminalia of *Udeus cerradensis* sp. nov.: (a-b) coxites and styli; (c) tergum IX; (d) sternum VIII; (e) spermatheca; (f) pygidium. Legends: ba, baculum; cl, collum; cr, cornu; cx, coxite; ra, ramus; st, stylus.

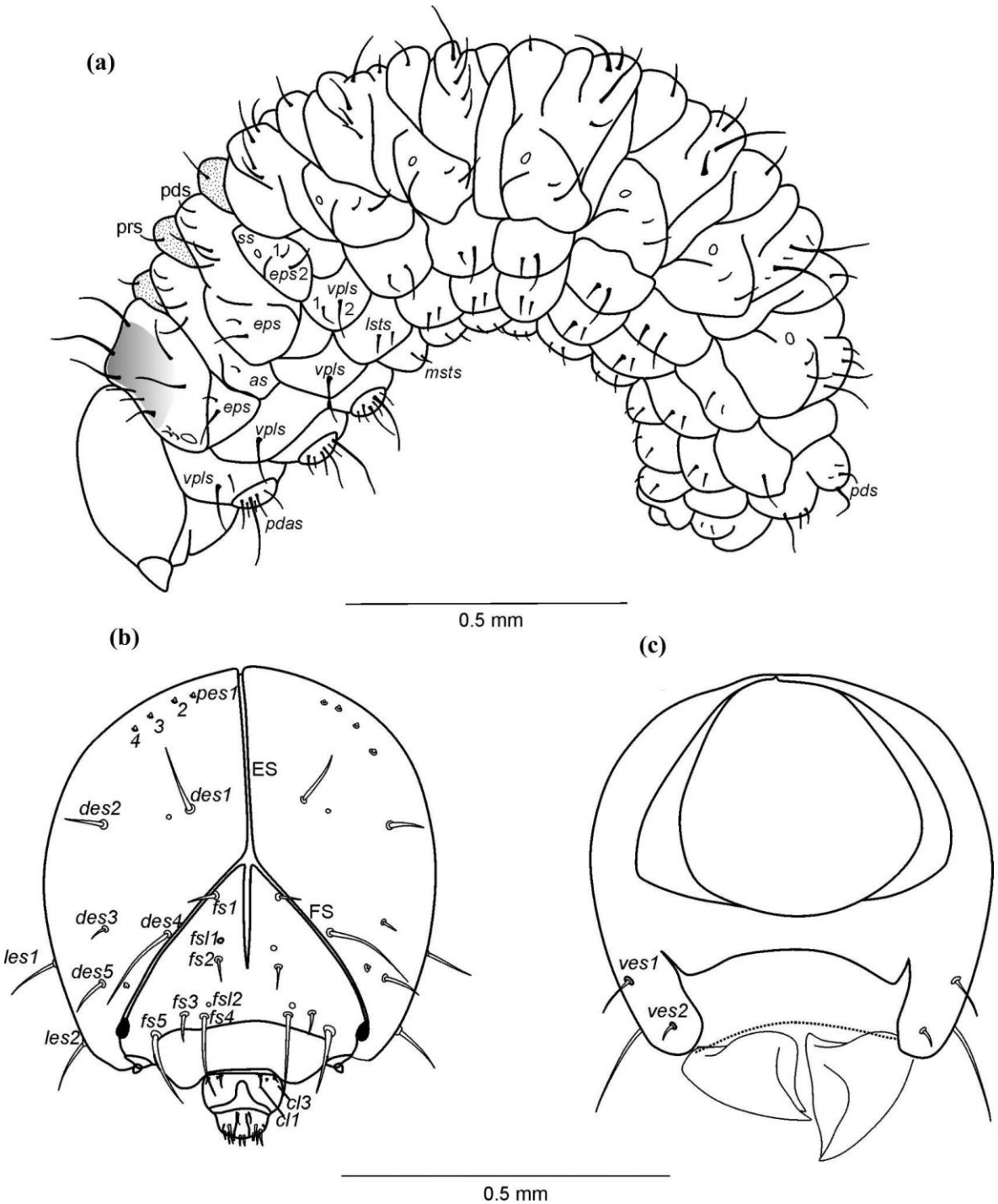

FIGURE 8 *Udeus cerradensis* sp. nov. larva: (a) lateral *habitus*; (b) head capsule in frontal view; (c) head capsule in posterior view. Legends [seta(ae), s.]: as, alar s.; cl, clypeal s.; des, dorsal epicranial s.; eps, epipleural s.; fs, frontal s.; les, lateral epicranial s.; lsts, laterosternal s.; mesosternal s.; pdas, pedal s.; pds, postdorsal s.; pes, posterior epicranial s.; prs, prodorsal s.; ves, ventral epicranial s.; vpls, ventropleural s.; ES, Epicranial suture; FS, Frontal suture.

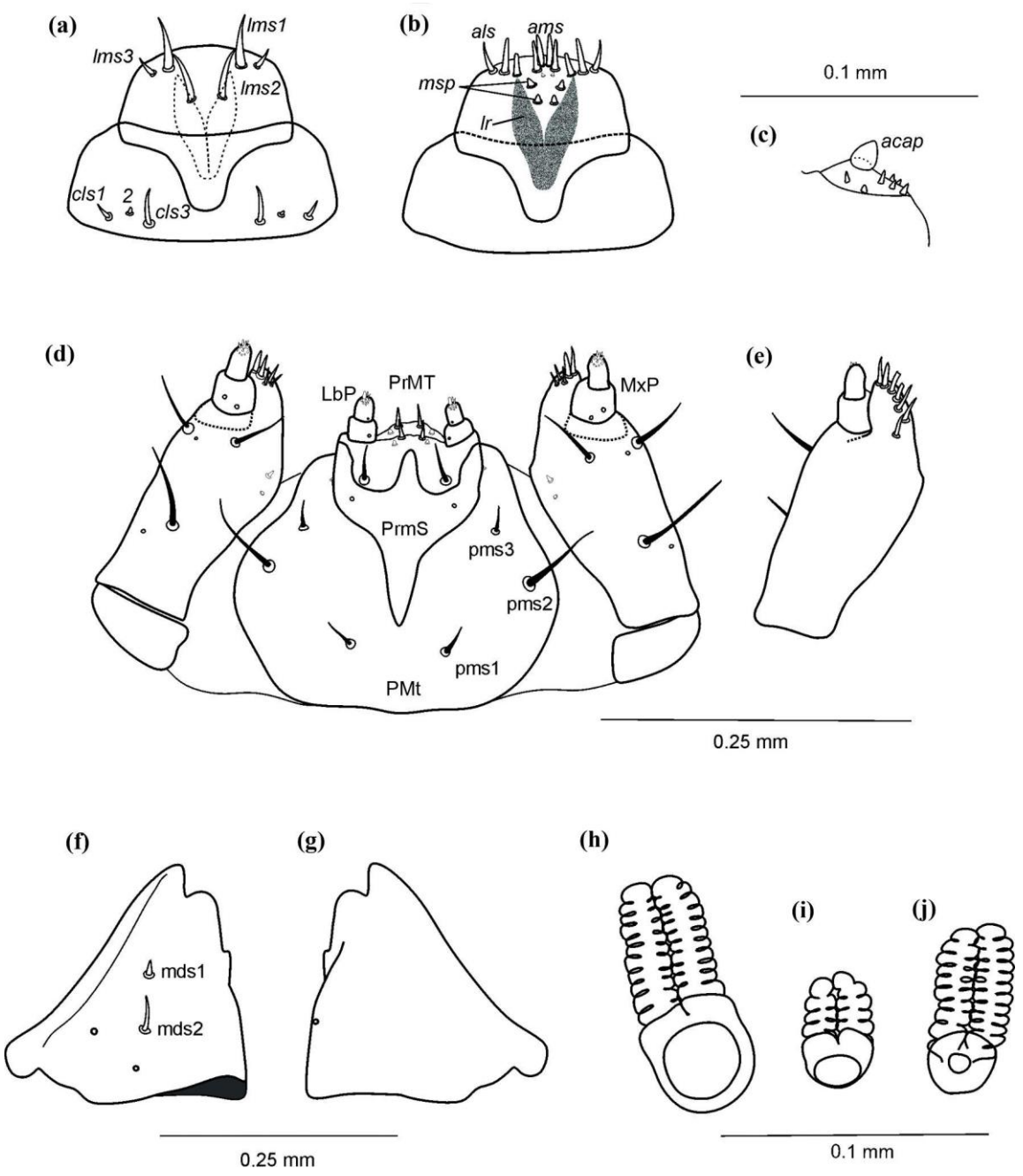

FIGURE 9 *Udeus cerradensis* sp. nov. mature larva: (a) clypeus and labrum; (b) epipharynx; (c) antenna; (d) maxillolabial complex; (e) maxillae in dorsal view; (f) mandible in ventral view; (g) mandible in dorsal view; (h) prothoraxic spiracle; (i) abdominal spiracle I; (j) abdominal spiracle VIII. Legends [seta(ae), s.]: mds, mandibular s.; pms, postmental s.; Mxp, maxillary palp; PmT, postmentum; PrmS, premental sclerite; PrmT, prementum.

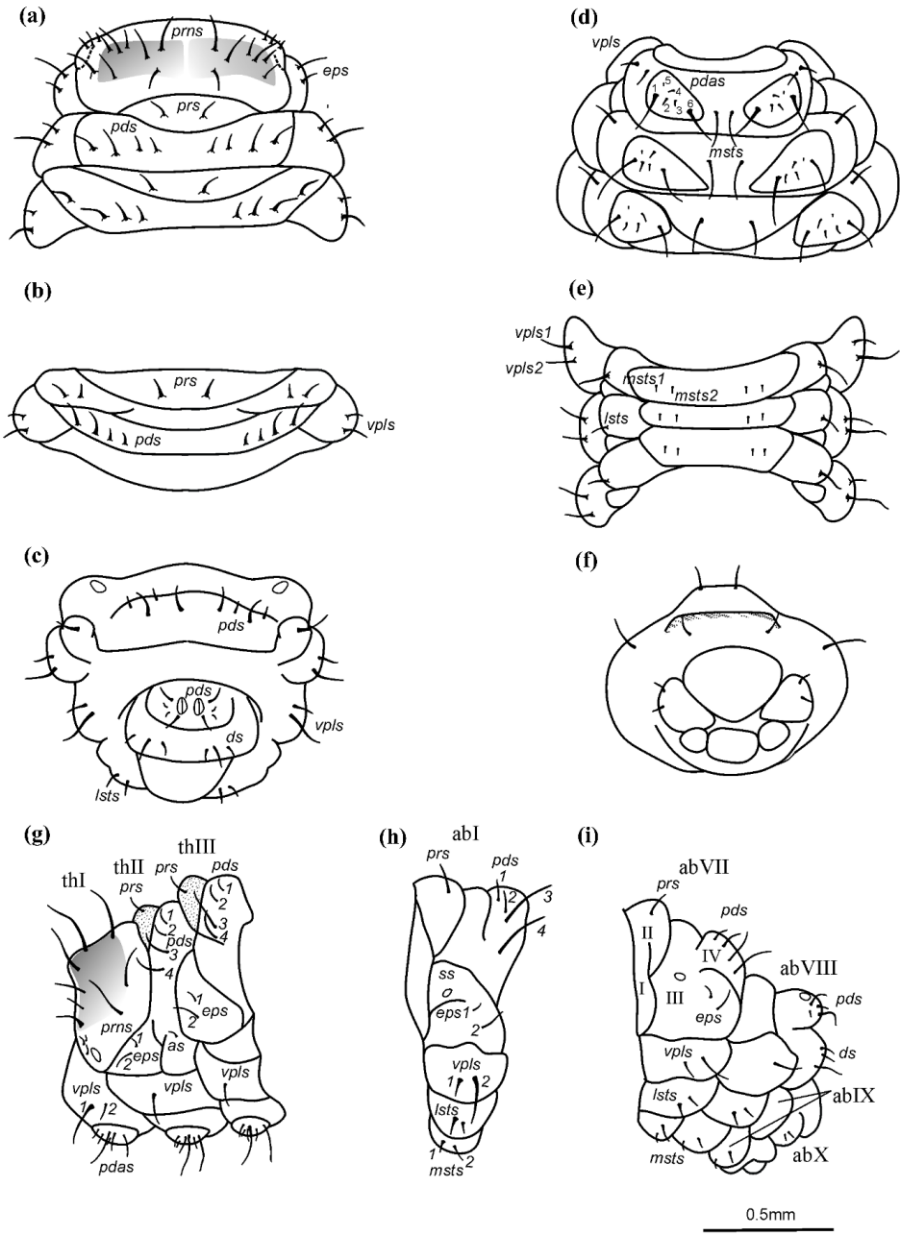

FIGURE 10 Morphology and chaetotaxy of *Udeus cerradensis* sp. nov. larva.: (a) thoracic segments in dorsal view; (b) first abdominal segment in dorsal view; (c) last abdominal segments in dorsal view; (d) thoracic segments in ventral view; (e) first abdominal segment in ventral view; (f) last abdominal segments in ventral view; (g) thoracic segments in lateral view; (h) first abdominal segment in lateral view; (i) last abdominals segments in lateral view. Legends [seta(e): s.]: as, alar s.; ds, discal s.; eps, epipleural s.; lsts, laterosternal s.; msts, mesosternal s.; pdas, pedal s.; pds, postdorsal s.; prns, pronotal s.; prs, prodorsal s.; vpls, ventropleural s.; ab, abdominal segment; th, thoracic segment.

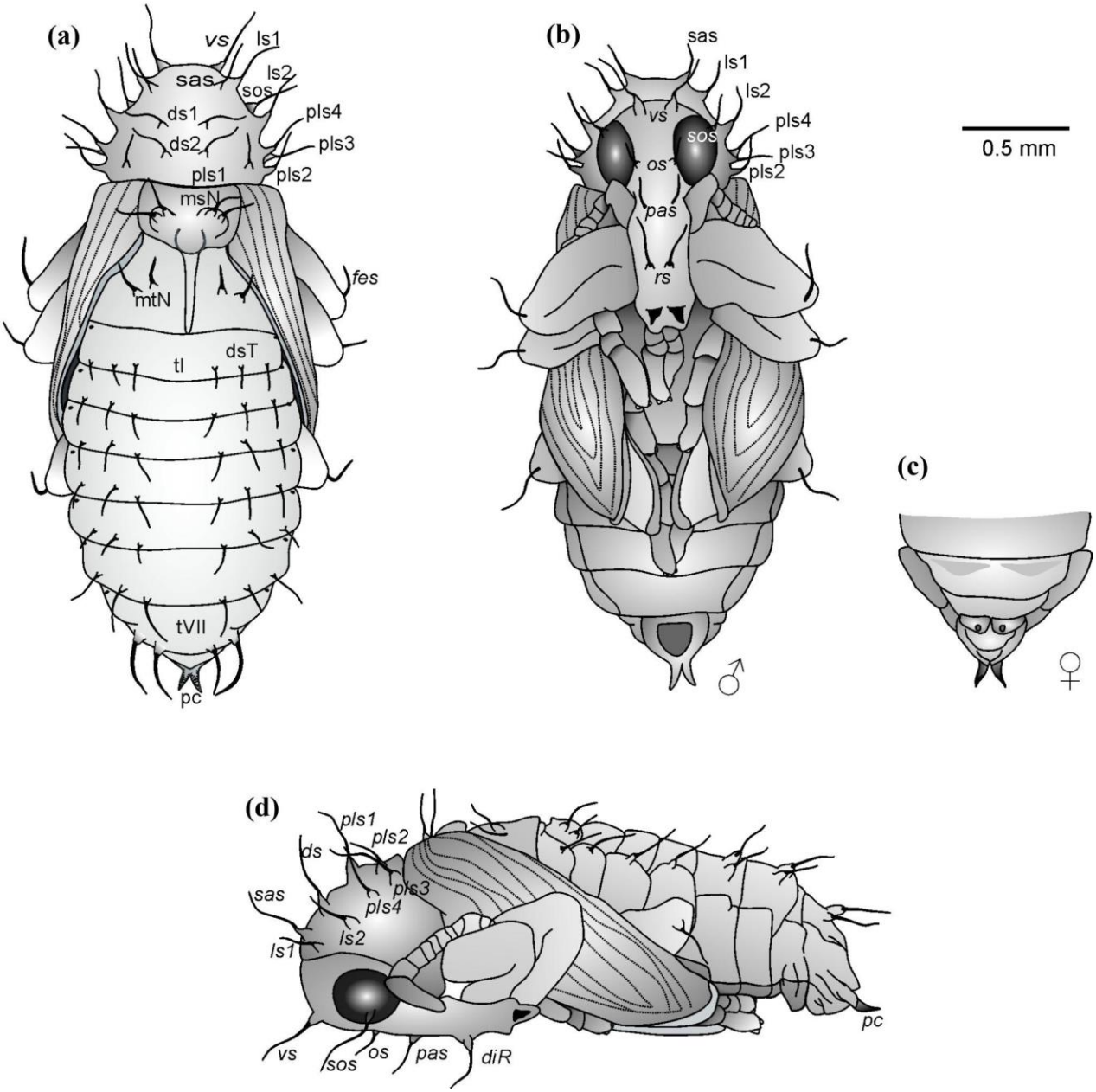

FIGURE 11 *Udeus cerradensis* sp. nov. pupa.: (a) dorsal *habitus*; (b) ventral *habitus*; (c) last abdominal segments of female; (d) lateral *habitus*. Legends [seta(e): s.]: diR, ds, discal s.; dsT, discotergal s.; fes, femoral s.; ls, lateral s.; os, orbital s.; pas, posterolateral s.; pls, posterolateral s.; rs, rostral s.; sas, suprapical s.; sos, supraorbital s.; vs, vertical s.; pc, pseudocerci; msN, mesonotal s.; mtN, metanotal s.

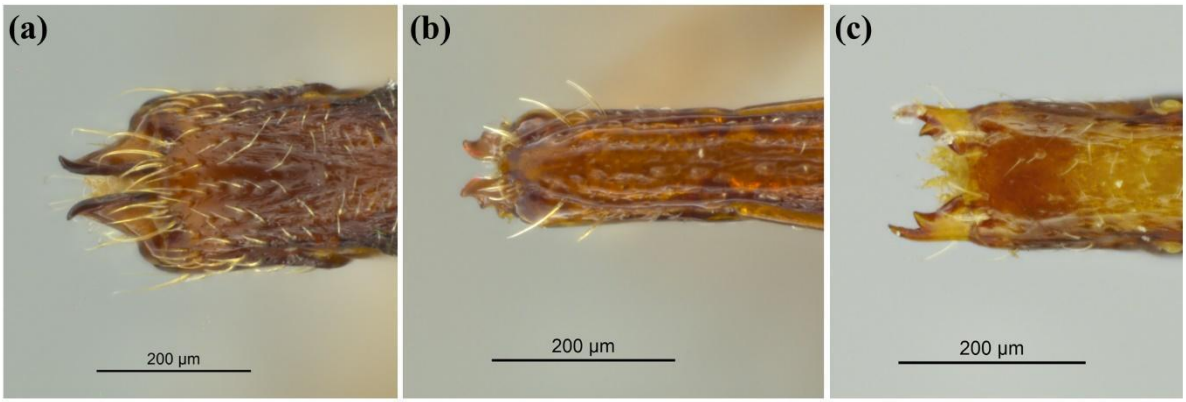

FIGURE 12 Mandibles in Neotropical Eugnomini : (a) exodont mandibles in *Udeus cerradensis* sp. nov. ; (b) exodont mandibles in *Omoides* sp. ; (c) endodont mandibles in *Udeus eugnomoides*.

CAPÍTULO 3

TAXONOMIC REVISION OF *Udeus* CHAMPION, 1902 (CURCULIONIDAE, CURCULIONINAE, EUGNOMINI), A GENUS OF NEOTROPICAL FLOWER WEEVILS [1]

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[1]Lira, A.O, de Medeiros, B.A.S & P.C. Grossi. Taxonomic revision of U*deus* Champion, 1902 (curculionidae, curculioninae, eugnomini), a genus of Neotropical weevils. Zootaxa.

Taxonomic revision of *Udeus* Champion, 1902 (Curculionidae, Curculioninae, Eugnomini), a genus of Neotropical flower weevils

Abstract

The tribe Eugnomini comprises weevil flower visitors with a Gondwanan distribution. The most diverse Neotropical genus is *Udeus* Champion, 1902, with a specialized association with flowers of *Cecropia* Loefl., currently including 12 valid species. The limited historical attention received by this genus might have been an impediment to studies on their interactions with host plants and their role in pollination. To fill this gap, here we produce the first comprehensive taxonomic revision of the genus. We consolidate taxonomy by establishing *Udeus fonsecai* Voss, 1941 as senior synonym for *U.deus cecropiae* (Bondar, 1957) and *Udeus sergioi* (Bondar, 1957) and *Udeus longicollis* Voss, 1941 as a senior synonym for *Udeus martiniquensis* Rheinheimer, 2019. We additionally describe 21 new species (*Udeus* sp. nov. 3, *Udeus* sp. nov. 5, *Udeus* sp. nov. 6, *Udeus* sp. nov. 7, *Udeus* sp. nov. 8, *Udeus* sp. nov. 10, *Udeus* sp. nov. 11, *Udeus* sp. nov. 12, *Udeus* sp. nov. 15, *Udeus* sp. nov. 16, *Udeus* sp. nov. 17, *Udeus* sp. nov. 18, *Udeus* sp. nov. 19, *Udeus* sp. nov. 20, *Udeus* sp. nov. 21, *Udeus* sp. nov. 22, *Udeus* sp. nov. 23, *Udeus* sp. nov. 24, *Udeus* sp. nov. 25, *Udeus* sp. nov. 26, *Udeus* sp. nov. 27), including the descriptions of external morphology, male and female genitalia, and host plant information. With the new species and new synonyms, the diversity of the genus now amounts to 26 species. We find that *Udeus*, and Neotropical eugnomines in general, are not only much more diverse than previously considered but also widely distributed throughout the entire Neotropical region.

Key words: *Cecropia*, Curculionoidea, systematic, flower visitor, weevil.

Introduction

Udeus Champion, 1902 stands as the most diverse genus among the four neotropical genera of Eugnomini. The genus was characterized by Champion (1902) presenting eyes large, head convex, femora clavate armed with a tooth, tarsi long and slender, body covered with fine pubescence. It has received very little taxonomic attention since then. The type species, *Udeus eugnomoides* Champion, 1902 is one of the twelve valid species currently classified in the genus, which includes also *Udeus muticus* Hustache, 1929; *Udeus variabilis* Hustache, 1939; *Udeus fonsecai* Voss, 1941; *Udeus longicollis* Voss, 1941; *Udeus cecropiae* (Bondar, 1957); *Udeus sergioi* (Bondar, 1957); *Udeus behnei* Rheinheimer, 2018; *Udeus bifasciatus* Rheinheimer, 2018; *Udeus moraguesi* Rheinheimer, 2018; *Udeus martiniquensis* Rheinheimer, 2019, and *Udeus cerradensis* Lira, de Medeiros & Grossi, 2024. The genus is distributed in South America, Central America, and the Caribbean (O'Brien & Wibmer 1982, Wibmer & O'Brien 1986, Rheinheimer 2018, Rheinheimer 2019). *Udeus* remained taxonomically stable until Wibmer & O'Brien (1986) synonymized *Moracetribus* to *Udeus*, and consequently *M. cecropiae* Bondar, 1957, and *M. sergioi* Bondar, 1957 to *U. cecropiae* and *U. sergioi*. The most recent *Udeus* species from French Guiana and Martinique were described by Rhinheimer (2018, 2019) following a 61-year hiatus since Bondar (1957) described two species from Brazil. Apart from descriptions, *Udeus* has received scarce mention in other studies and was poorly represented in entomological collections around the world.

In contrast to the scant knowledge on the systematics, ecology and evolution of these weevils, their host plants are iconic Neotropical plants that historically receive considerable attention. Species of *Udeus* present an intrinsic association with the inflorescences of *Cecropia* Loefl. (Urticaceae), reported in the literature for the first time by Bondar (1957). In the description of the genus *Moracetribus* (now a junior synonym of *Udeus*), Bondar (1957) anticipated a

significant expansion of this genus based on its host plant diversity. In fact, at this moment all *Udeus* species with known host plants are associated with single species of *Cecropia* (Lira *et al.* in press), indicating a high degree of specialization even for flower visiting weevils (Haran *et al.* 2023). Assuming that most species of *Cecropia* are associated with these weevils, we should expect a large diversity remaining to be discovered, considering that there are approximately 61 described species in the genus *Cecropia* (Berg & Rosseli 2005).

Although it is not clear if *Udeus* are pollinators, they share many traits with other weevil pollinators, for example their small size, yellowish coloration, crepuscular activity, specialization on flowers, presence of plumose setae, larval breeding in decaying flower tissues (Haran *et al.* 2023; Lira *et al.* 2024). However, in most instances, there is no specific information on the role of these flower visitors as pollinators. Mendonça (2014) suggested that *Udeus* acts as a pollinator of *Cecropia glaziovii* Snethl. based on visitation patterns to both pistillate and staminate flowers. On the other hand, we recently studied the interaction between *Udeus cerradensis* Lira, de Medeiros & Grossi, 2024 and its host *Cecropia saxatillis* Snethl. in detail (Lira et al. 2024). In this case, we found that weevils are abundant as adults in staminate flowers but found no evidence of visitation to pistillate flowers. It is likely that pollination efficiency and the dependency of species of *Cecropia* on weevil pollination varies between species and environmental contexts. A better understanding of the taxonomy of *Udeus* is fundamental for the development of the required ecological studies.

In this study, we aim to update the taxonomic knowledge of *Udeus* through the revision of the genus, including a review of the literature, a comprehensive search in natural history collections, and study of types. This resulted in new synonyms and the description of 21 new species, providing information on host plants and biological aspects of *Udeus*-*Cecropia* associations, in addition to significantly expanding knowledge about the geographic distribution of this neotropical genus. We

additionally identify gaps for further study, such as putative species complexes that could be target of molecular studies on speciation.

Material and methods

Morphological study

Adult morphology was examined from pinned specimens under a stereomicroscope. Female and male terminalia were dissected, slide-mounted, and examined in an optical microscope Olympus BX41 and Zeiss 508 DOC stereomicroscope with an eyepiece reticle. For dissections, adults were left for 15-30 minutes in soapy hot water, then dissected with fine-tipped tweezers and micro pins. Female and male terminalia, after being removed from the abdomen, were incubated in warm 10% KOH for a few minutes to digest soft tissue and mounted in permanent slides using "Downs' gel" (polyvinyl lactophenol) (Downs 1943; Salmon 1947), a water-soluble mounting media. Illustrations were prepared based on images taken under a microscope Olympus BX41 with a Moticam Pro 285B and the Motic Images software. In a few cases, illustrations were traced in the CorelDraw package. Habitus photos were taken using a Microptics system composed of a Canon EOS 6D camera, P-51 Camlift Controller 2.8, and Canon Eos Utility. The photos were stacked with Helicon Focus 6.5.2.0 and edited using Adobe Lightroom 5 and Adobe Photoshop CS 5. We obtained scanning electron micrographs with a TESCAN VEGA3 to examine the vestiture and ornamentation of the head, antennae, metasternum, elytra, legs, and ventrites. Measurements were taken directly of two or three males and two or three females, considering the length variation in the entire material, using a Zeiss 508 DOC stereomicroscope with an eyepiece reticle, following measurements taken by de Medeiros & Vanin (2020). Terminology for adults follows Franz (2006); Wanat (2007) for male genitalia; Howden (1995), and Gíron & Franz (2010) for female genitalia.

In most cases, morphological characters have been scored in a table and natural language descriptions have been generated with the assistance of the large language model ChatGPT version 4 (OpenAI, San Francisco, USA) followed by manual revision. We used the most complete description of a *Udeus* species, in this case, *U. cerradensis*, as a template to describe new species, and the interactive tool GPTaxonomist (de Medeiros, in prep) to generate the initial prompts. Using the description of *U. cerradensis* the GPTaxonomist returns a prompt requesting ChatGPT to extract all characters and their states in the description in a table with one character per line containing a single property of a given structure (shape, color, aspect, position, vestiture, punctuation, setation, etc.). The table was constructed in two columns following specifications. Column 1 comprised the character name, with the following format: semaphoront; major body area; specific body area; more specific body area, if any; property (units, if any). The column 2 detailed the observed states. The table included body size and the characters organized by head, thorax, and abdomen. Additionally, the GPTaxonomist provided a table as a reference for the expected output. The table constructed based on the *U. cerradensis* description was used to construct a character table for all new species, maintaining the more important characters, and the states of the characters were manually included after specimens examination.

In the subsequent phase, the GPTaxonomist generates a prompt soliciting a taxonomic description utilizing the character table data. This prompt instructs ChatGPT to formulate a taxonomic description of high quality suitable for publication in natural language. Furthermore, it mandates consistency with descriptions of similar taxa, providing a template for reference. Finally, the prompt requests the ChatGPT to adhere to guidelines such as publication-quality description, telegraphic language, English language, and others to avoid errors in the description. Any descriptions generated by ChatGPT were reviewed and corrected as needed to ensure accuracy.

Examined material

We examined type material for almost all species, except *U. muticus, U. behnei, U. bifasciatus,* and *U. moraguesi.* These are arguably deposited at MNHN but could not be found by the collection staff. Specimens in the following collection were examined as part of this study: Coleção Entomológica do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (CEIOC); Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, Brazil (CERPE); Coleção Entomológica da Universidade Federal de Pernambuco (CEUPE); Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Brazil (DZUP); American Museum of Natural History, New York, USA (AMNH); Charles W. O'Brien Collection, Arizona State University, Tempe, USA (ASUCOB); Natural History Museum, London, UK (BMNH); Field Museum of Natural History, Chicago, USA (FMNH); Museo de Invertebrados G.B. Fairchild, Universidad de Panama, Panama (MIUP); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN); National Museum of Natural History, Washington, USA (USNM).

Additionally, new type material of new species will be deposited in the following institutions: Australian National Insect Collection, Australia (ANIC); Canadian Museum of Nature, Canada (CMN); Seção de Entomologia, Coleção Zoológica, Universidade Federal de Mato Grosso, Brazil (CEMT); National Museum Bloemfontein, South Africa (NMB); New Zealand Arthropod Collection, New Zealand (NZAC); Museum of Natural History, University of Wrocław, Poland (MNHW).

From 2020 to 2022, we conducted multiple collections in Brazil, including the states of Pernambuco, Mato Grosso, Goiás, Manaus, Pará, and Rio de Janeiro, as well as in Panama, to collect *Udeus* specimens on different *Cecropia* species. The primary method involved manual

collections by bagging inflorescences, targeting adult specimens directly from male inflorescences. Additional adult specimens were obtained by rearing larvae from aborted staminate inflorescences. Finally, we also used sticky traps placed next to both male and female inflorescences of *Cecropia* for two to seven days. Taxonomic identification of *Cecropia* species was conducted by an expert in *Cecropia* taxonomy, MSc. Daniel Aguiar, following Berg & Franco-Rosselli (2005), and also based on Croat (1978). Specimens collected were initially deposited in the "Coleção Entomológica da Universidade Federal Rural de Pernambuco" (CERPE) and Field Museum of Natural History (FMNH).

Taxonomy

Eugnomini Lacordaire, 1863

Udeus Champion, 1902

Udeus Champion, 1902: 139 (description); O'Brien & Wibmer 1982: 89 (catalog); Wibmer & O'Brien 1986: 110 (catalog).
Moracetribus Bondar, 1957: 257 (description); O'Brien & Wibmer 1982: 89 (synonym).

Type species: *Udeus eugnomoides* Champion, 1902 (by monotypy).

Diagnosis. *Udeus* can be distinguished from other Eugnomini mainly by the elongate tarsi (Fig. 1E), with all tarsomeres together being almost always longer than the metatibia (Fig. 29). Moreover, the last tarsomere is the longest. The following characters additionally define the genus: antennal funicle with first article wider and longer than others (Fig. 1D); large eyes (Fig. 1B), with elongate yellowish setae near the internal margin of each eye (Fig. 1B); pronotum with transversal sulcus on median region, with a strong apical constriction, with distinct yellowish elongated setae forming rows on sides, near apical constriction, and in some cases on center of pronotal disc; base of

pronotum with plumose setae; tibiae mucronate on males; elytral interstriae with a row of elongate yellowish acuminate setae interspersed with short setae similar those from striae (Fig. 1H); ventrites I and II connate. *Udeus* is quite similar to Australian eugnomines such as *Ancyttalia* Zimmerman, 1994, and *Eugnomus* Schoenherr, 1847. The similarity with *Ancyttalia* is evident by length, generally yellowish color, evident mucro on males, and interstriae with decumbent setae contrasting with background vestiture (Zimmerman, 1994), and with *Eugnomus* by the general aspect of the body, with vestiture similar, and large flexible maxillae (Cawthra 1966). Among Neotropical eugnomines, *Udeus* is most similar to *Omoides* by the mucro present in males and absent in females (Kuschel, 1952). However, *Udeus* can be easily distinguished from these genera by the diagnostic characters above.

Redescription. Male. Body size: 1.6–4.9 mm. Rostrum 0.7–1.5 times as long as pronotum; almost always wider at apex than at base; without or with one median longitudinal carina (Fig. 1A), almost always located from basal region to near apex, sometimes extending to interorbital region; scrobe oblique, directed ventrally, reaching or almost reaching anterior eye margin (Fig. 1B); apex with scarce elongate setae; elongate and decumbent setae arranged transversely from antennal insertion to base of the rostrum (Figs. 1A, B, D); sometimes with plumose setae concentrated at base; with or without small longitudinal sulcus near median carina in both sexes. Eyes almost always higher than wide, 1.1–1.3 times as high as wide; 1.0–2.7 times more separated above than below; with microsetae between ommatidia (Fig. 1C); with one to six elongate yellowish setae near internal margin of each eye (Fig. 1B). Antennae long, slender; scape straight with apex dilated, almost always extending to posterior eye margin; funicle almost always with seven antennomeres, first always wider than others and 1.2–2.3 times longer than antennomere II; club three-segmented, 1.7–

4.0 times longer than wide (Figs. 1A, 1D, 28). Mandibles almost always endodont, symmetric, with one, two, or more commonly three teeth.

Thorax. Pronotum transverse; 1.0–1.3 times wider than long; lateral margins subparallel, with relatively deep transversal sulcus on median region; apically strongly constricted; disc with setae in distinct or discrete punctation; almost always with plumose setae forming a transversal band on base (Figs. 2A, 5A, 7A, 10A); with yellowish elongated setae sparsely distributed forming rows on sides, near apical constriction, and in some cases on center of pronotal disc (Figs. 2A, 3C, 5A–B, 6A–B). Procoxae contiguous; pro- and mesocoxae covered with plumose and non-ramified setae (Figs. 4C, 5C, 7C, 8C, 9C, 10C, 11C, 12C, 13C). Femora with well-defined ventral tooth, with a set of elongate setae ventrally, almost always concentrated on basal third. Tibiae mucronate on males, compressed, internal margin of metatibiae almost always slightly sinuose, covered with elongate setae in apical third (Fig. 29)**.** Tarsi elongate, 0.9–1.4 times as long as metatibiae; first tarsomere usually longer than tarsomere II, tarsomere III very short and bilobate, last tarsomere usually longer than I; claws simple and divergent (Fig. 29). Scutellum triangular, small, almost always covered with plumose setae (Figs. 2A, 3A, 4A, 5A, 6A, 7A, 8A, 9A, 10A, 11A, 12A, 13A). Elytra 1.8–4.0 times longer than wide; 1.3–1.9 times wider and 2.6–3.5 longer than pronotum; humeri rounded; lateral margins subparallel; with 10 punctate striae with tiny setae inserted in each puncture; interstriae covered with setae similar those from striae; with a row of elongate yellowish acuminate setae almost always on odd interstriae; epipleura incomplete, covered with setae. Prosternum covered with plumose or non-ramified setae; postocular lobes indistinct. Mestepisternum well delimited, almost always covered with plumose setae intercalated with scarce non-ramified setae. Metasternum with distinct central concavity extending into abdomen, with plumose or non-ramified setae next to concavity border and lateral region.

Abdomen. with five ventrites; ventrites I–II fused (Fig. 4C, 5C), concave at center; ventrites III-IV shorter than others; ventrite V with different patterns of setae. Pygidium covered. *Male terminalia* with sternum VIII composed of two lateral plates separated by a membrane; sternum IX (spiculum gastrale) almost always straight (Fig. 2J); tegmen delicate, usually with parameres fused and tegminal apodeme slender (Fig. 2I); aedeagus 1.2–13 times longer than wide, with ventral plate strongly sclerotized with several sensilla (Fig. 2G); apodemes longer or smaller than median lobe (Fig. 2G); endophallus with a pocket containing microtrichae,sometimes bifurcate on apex.

Female terminalia with pygidium triangular, longest setae concentrated near to apex (Fig. 4D); sternum VIII with apodeme slender and straight, lateral arms sclerotized (Fig. 4F); coxites when visible elongate and sclerotized on laterals (Figs. 8G–H); style almost always not visible; spermatheca curved; *cornu* (cr) slightly curved; *collum* (cl) slightly constrict on apex; *ramus* (ra) very short; *ramus* and *collum* pointing approximately in same direction (Fig. 4E).

Sexual Dimorphism. Males of *Udeus* have a mucronate tibia (Fig. 29), sometimes very short, while the mucro is always absent in females. Males also bear a central metasternal concavity extending into the first and second ventrites; longer setae at the base of tibiae (Fig. 29) and femora when compared to females. A conspicuous difference in the shape of ventrite V is frequently observed, with a trapezoidal configuration in males and a triangular shape in females. In *Udeus* sp. nov. 6, *Udeus* sp. nov. 7, and *Udeus* sp. nov. 12, only males display modified metatibiae, characterized by expansions at the apex (Figs. 29F, G, I, K, M). While *Udeus* sp. nov. 10, *Udeus* sp. nov. 17, *Udeus* sp. nov. 19, and *Udeus* sp. nov. 22 are exclusively known from male specimens, we hypothesize that the modifications observed in ventrites and metatibiae likely represent sexual dimorphism.

Distribution. *Udeus* species inhabit a vast range extending from southern Brazil to Mexico. Throughout South America, they are encountered in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Paraguay, Peru, Suriname, and Venezuela. In Central America, *Udeus* species are documented in Belize, Costa Rica, Honduras, and Panama. Additionally, they have been observed in the Caribbean, including Guadeloupe, Martinique, and Trinidad (Fig. 30).

Host plants. *Udeus* species exhibit a specialized association with the inflorescences of *Cecropia*. In this study, we have identified 13 species of *Udeus* occurring in 11 species of *Cecropia* (Table 1). Although biological observations are lacking for the majority of *Udeus* species, we hypothesize that the specialized association with a specific *Cecropia* species is a recurring pattern.

Table 1. Summary of known host plant association in *Udeus*.

***Udeus* species**	**Host plant**
U. cecropiae	*Cecropia palmata*
U. longicollis	*Cecropia pachystachya, Cecropia concolor*
U. cerradensis	*Cecropia saxatilis*
U. variabilis	*Cecropia glaziovii, Cecropia hololeuca*
U. moraguesi	*Cecropia* sp.
Udeus sp. nov. 3	*Cecropia palmata*
Udeus sp. nov. 5	*Cecropia* sp.
Udeus sp. nov. 6	*Cecropia glaziovii, Cecropia hololeuca*
Udeus sp. nov. 7	*Cecropia ulei*
Udeus sp. nov. 8	*Cecropia latiloba, Cecropia membranacea*
Udeus sp. nov. 12	*Cecropia*
Udeus sp. nov. 24	*Cecropia longipes*
Udeus sp. nov. 27	*Cecropia obtusifolia*

***Udeus eugnomoides* Champion, 1902**

(Figures 2, 28A, 29A, 30A)

Udeus eugnomoides Champion, 1902: 139 (description); O'Brien & Wibmer 1982: 89 (catalog); Wibmer & O'Brien 1986: 110 (catalog).

Diagnosis. This species can be distinguished from other *Udeus* species by the uniform brown coloration of the body, large elytral punctation, and sparse thin setae on the body (Figs. 2A–F). *Udeus eugnomoides* is externally very similar to morphotypes of *U. cecropiae* (Fig. 5A) and *U. variabilis* (Figs. 3A, C) without elytral macules and *Udeus* sp. nov. 22 (Fig. 22A) but differs from these by the shiny integument and the shape of aedeagus.

Holotype. Male. GUADELUPE: Pantaleon, 1700 ft., Champion, NHMUK 015550232; B.C.A. Col. iv. 4. *Udeus eugnomoides*, Champ. Deposited in NHMUK, photography examined.

Description. Male. Body size: 2.2–2.4 mm. Head: Rostrum (Figs. 2A–F) 0.8 times shorter than pronotum; apex 1.1 times wider at base than at apex; integument color brown; longitudinal carina absent; scrobes reaching eye margin; apex with scarce elongate setae; setae arranged transversely from antennal insertion to near base on laterals, glabrous and smooth in median line; eyes (Figs. 2A–F) subequal in height and width, about 2.5 times more separate above than below; integument brown, similar to rostrum; covered with setae non-ramified, with 1 elongate yellowish setae on posterior inner margin of each eye; plumose setae laterally and ventrally. Antennae (Fig. 28A) with first antennomere 1.7 times longer than II, antennomere II subequal in length to antennomeres IV and VI, 1.3 times longer than antennomeres III, V, and VII subequal in length, club three-segmented, 2.8 times longer than wide. Mandibles endodont, symmetrical, 1.75 times longer than wide, with 3 teeth on internal margin.

Thorax. Pronotum (Figs. 2A–F) transverse, 1.1 times longer than wide, with parallel lateral margins and shallow transverse sulcus on median region; integument brown, similar to head; covered with yellowish short setae on disc, with whitish plumose setae at base, and six yellowish elongated setae next to apical constriction. Profemora with elongate scarce setae ventrally on base; metatibiae evenly covered with sparse setae, denser apically near mucro (Fig. 29A). Tarsus (Fig. 29A) elongate, 0.9 times shorter than metatibiae; first tarsomere 1.2 times longer than II, tarsomere II 1.6 times longer than tarsomere III; last tarsomere longer than rest, 1.5 times longer than tarsomeres I. Scutellum (Figs. 2A, C, F) 1.1 times wider than long, brown, covered with short whitish plumose setae; elytra 3.5 times longer than wide, 1.7 times wider and 3.3 times longer than pronotum, with subparallel lateral margins, brown, covered by short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae; humeri rounded, similar color to elytra. Ventral region with integument brown, similar to dorsal color, sometimes slightly darker than dorsal region. Prosternum with scarce non-ramified setae. Metasternum with whitish plumose setae and fewer elongate non-ramified setae medially. Metasternum with distinct central concavity extending into abdomen, densely covered with whitish non-ramified setae.

Abdomen with ventrites I–II covered by yellowish non-ramified setae, scarcer on center, longer on border of posterior margin of ventrite II; ventrites III–V covered by yellowish non-ramified setae, longer on center of posterior margin; ventrite V triangular, rounded on border. Terminalia. Pygidium (tergum VIII) (Fig. 2K) as wide as long along midline; anterior margin straight; posterior margin rounded; elongate setae on apex, shortest setae posteriorly. Sternum IX (spiculum gastrale) (Fig. 2J) as long as aedeagus; straight, with two hemisternites separated by a membrane. Tegmen (Fig. 2I) 0.6 times shorter than aedeagus; tegminal apodeme slightly curved on apex; parameres fused. Aedeagus (Figs. 2G–H) 7.5 times longer than wide on base, margins parallel, slightly ampliate at base; apex acute, slightly rounded on sides; ventral plate sclerotized.

Apodemes 1.1 times longer than median lobe. Endophallus with a pocket containing microtrichae bifurcated on apical region.

Female. Body size: 2.4–2.5 mm. Rostrum 0.8 times shorter than pronotum; width at apex subequal to width at base; pronotum 1.2 times wider than long. Femora with elongate ventral setae, present but scarce. Scutellum 1.1 times wider than long. Elytra 1.9 times wider than pronotum, 3.3 times longer than wide, and 3.8 times longer than pronotum. Ventrites convex; ventrite V triangular, rounded at apex. Terminalia not examined.

Examined material. Type material: Paratype. Female, Guatemala, Pantaleon, 1700 ft., Champion, NHMUK 015550232; B.C.A. Col. iv. 4. *Udeus eugnomoides*, Champ. Deposited in NHMUK, photography examined. **Other material.** COSTA RICA: Punta Coto Brus, Est. Biol Las Alturas, 8 57 N, 82 52 W, 31mar.2002, A. Cline (10 sex indet. ASUCOB). PANAMA: Cerro Jefe, 900m, 9.15N, 79.21W, K. Joplin (1 sex indet. ASUCOB); Bocas del Toro, Miramar, sea level, 82 15 W, 9 N, 16mar.1979, H. Wolda (1 sex indet. ASUCOB).

Distribution. *Udeus eugnomoides* is distributed across Mexico, Guatemala, Costa Rica, and Panama (Fig. 30A).

Host plant. Unknown.

Remarks: The description of *U. eugnomoide*s mentions six antennomeres in the funicle, which deviates from the typical pattern of seven antennomeres observed in most species within the genus. Upon closer examination of the holotype (male) and the paratype (female) photographs (Figs. 2C–F), it becomes apparent that determining the precise number of antennomeres is challenging due to the low quality of the images. In light of this limitation, we hypothesize that *U. eugnomoides* indeed

possesses seven antennomeres in the funicle, suggesting that Champion was mistaken in counting the antennomeres in the species description.

***Udeus variabilis* Hustache, 1939**

(Figures 3, 30A)

Udeus variabilis Hustache, 1939: 61 (description); Wibmer & O' Brien 1986: 110 (catalog).

Diagnosis. This species can be distinguished from other *Udeus* species by the denser setae on the body (Figs. 3–C, E), and aedeagus with apex acute. *Udeus variabilis* is very similar to *U. eugnomoides* (Fig. 2), *Udeus* sp. nov. 21 (Fig. 21) and *Udeus* sp. nov. 22 (Fig. 22).

Redescription. Male. Body size: 2.0–2.1 mm. Head: Rostrum (Figs. 3B–E) 0.8 times shorter than pronotum, 1.1 times wider at base than at apex; integument ochre to brown; longitudinal carina absent; scrobes almost reaching eye margin; apex with scarce elongate setae; setae arranged transversely from antennal insertion to near base on laterals, glabrous and smooth in median line; eyes 1.1 higher than wide, 2.1 times more separated below than above; integument ochre to brown, similar to rostrum; with setae non-ramified, inserted on discrete punctation above eyes and in interorbital region, with one to three elongate yellowish setae on inner margin of each eye; plumose setae laterally and ventrally. Antennae (Fig. 3E) with first antennomere two times longer than II, antennomere II subequal in length to antennomeres IV and VI, 1.3 times longer than antennomeres III, V, and VII subequal in length, club three-segmented, 2.5 times longer than wide. Mandibles endodont, symmetrical, with 3 teeth on internal margin, 1.4 times longer than wide.

Thorax: Pronotum (Figs. 3A–E) transverse, subequal in length and width, lateral margins parallel, with distinct transverse sulcus on median region; integument brown, similar to head,

covered with yellowish short setae distributed in distinct punctation on disc; base with whitish plumose setae; 4-8 yellowish elongated setae next to apical constriction and 2-3 laterally. Pro- and mesocoxae covered with plumose setae denser externally and scarce non-ramified setae. Femora with elongate scarce setae ventrally on base. Metatibiae with internal margin slightly sinuous on base, evenly covered with sparse setae, denser apically near mucro. Tarsus elongate (Figs. 3A–B), 1.1 times longer than metatibiae; first tarsomere 1.2 times longer than II, tarsomere II two times longer than tarsomere III; last tarsomere longer than rest, 1.6 times longer than tarsomeres I. Scuttelum (Figs. 3A, C) as long as wide, brown, covered with plumose setae; elytra 3.5 times longer than wide, 2.9 times wider and 1.6 times longer than pronotum, with subparallel lateral margins, brown to dark brown, sometimes with two complete or incomplete dark bands in basal and postmedian region, covered by non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in all interstriae or just in odd interstriae; humeri rounded, brown. Ventral region with integument brown, similar to dorsal color, sometimes darker than dorsal region. Prosternum with scarce ramified setae. Metepisternum with whitish plumose setae and fewer elongate non-ramified setae medially. Metasternum with distinct central concavity extending into abdomen, with denser whitish plumose setae merged with scarce elongate non-ramified setae next to concavity border, and scarce yellowish non-ramified setae on center.

Abdomen: Ventrites I–II covered by yellowish non-ramified setae, scarcer on center; ventrites III–V covered by yellowish non-ramified setae, longer on center of posterior margin; ventrite V trapezoidal, straight on apex. Terminalia. Pygidium (tergum VIII) 1.2–1.9 times as wide as long along midline; anterior margin straight; posterior margin rounded; elongate setae on apex, shortest setae posteriorly. Sternum IX (spiculum gastrale) 0.6 times shorter than aedeagus; straight, with two hemisternites separated by a membrane, curved on apex. Tegmen 0.6 times shorter than aedeagus; tegminal apodeme slightly curved on apex. Aedeagus (Figs. 3F–K) 7.7 times longer than

wide in median region, slightly constricted in middle; apex slightly cute; ventral plate sclerotized. Apodemes 0.8 times shorter than median lobe. Endophallus with a pocket containing microtrichae on apical region.

Female not described.

Examined material. Type material: Syntypes. BOLIVIA: no data, no locality, Coll. Kraatz (2# MNHN EC14223, EC14224).

Other material: BOLIVIA: Santa Cruz: Rio Marmore, 2 km N. mouth of Rio Chapare, 31jul.1965, J.K. Bouseman (1 sex indet. AMNH), 3.7 km SSE Buena Vista, Hotel Flora & Fauna, 430 m, 14-19Oct2000, M.C. Thomas (1 m# ASUCOB). BRAZIL: São Salvador, Bot. Inst., 28jan.1959, A.M.Nadler (5 sex indet. AMNH); Espírito Santo: Iúna, 20.3142°S, 41.8189°W, 21.iii.2022, B. Clarkson (6 sex indet. CERPE); Rio de Janeiro: Itatiaia, Pq. Nac. Itatiaia, Trilha das borboletas, 22.4486°S, 44.6067°W, 18.xii.2021, B. Clarkson (28 sex indet. CERPE), Nova Friburgo, Deyr (1 sex indet. MCZ), Represa Rio Grande, Guanabara, iv.1972, M. Alvarenga (2 sex indet. DZUP), vii.1972, F.M. Oliveira (1 sex indet. DZUP), Rio de Janeiro, Botafogo, 10.xi.2021, E.S. Grossi (8 sex indet. CERPE), Rio de Janeiro, Nova Friburgo, Braunes, 22.281S, 42.512W, i.2022, P.C. Grossi (10 sex indet. CERPE), Rio de Janeiro, Nova Friburgo, SansSouci, 22.287S, 42.521W, i.2022, P.C. Grossi (10 sex indet. CERPE); Rondônia: 62 km. SW. Ariquemes, Fzda. Rancho Grande, 5-17Sep1993, JE. Eger, UV trap (3 m# ASUCOB), 22Aug1993, U. Schmitz (1 m# ASUCOB), 8-20Nov1994, JE. Eger (1 m# ASUCOB). ECUADOR: Napo: vic. Puerto Misahueli, 6-19Sep1998, J.E. Eger (1 m# ASUCOB). PERU: Tingo Maria, 10jul.1968, CW & L O'Brien (1 m# ASUCOB), Loreto 100m Iquitos, 25Dec2005, RW Westerduijn (1 m# ASUCOB), Madre de Dios, Tambopota Wild life Reserve, 30 km SW Pto Maldonado, 1-14Oct1982, JJ Anderson (1 m# ASUCOB).

Distribution. This species is distributed along South America, from Ecuador to southeastern Brazil, passing through Peru and Bolivia (Fig. 30A).

Host plants. Specimens from Rio de Janeiro (Brazil) were collected in male inflorescences of *C. glaziovii* and *C. hololeuca.*

Remarks. The specimens examined exhibit diverse morphological variations (Figures 3A–E). Conversely, specimens from Ariquemes, Rondônia; Tingo Maria, Peru; and Santa Cruz, Bolivia, despite their geographic dispersal, share a common yellowish integument and external appearance. However, a distinguishing feature observed in the Bolivian specimens is the elongation of the last tarsomere. As mentioned by Hustache (1939) in the original description, the observed morphological diversity across specimens collected throughout South America suggests that *U. variabilis* may represent a species complex necessitating additional work. Hustache examined seven specimens and noticed variations in coloration among them. Unlike those we examined from Rio de Janeiro (Figure 3D) and the types (Figure 3E) that exhibit incomplete dark bands in the median and basal or lateral regions of the elytra, specimens from Rondônia, Peru, Bolivia, and Ecuador lack macules on the elytra. Furthermore, the types display less dense and more elongated setae on the interstriae, while their ventral region appears darker compared to other examined specimens. Moreover, there were disparities in the distribution of setae. Specimens from Rondônia and Bolivia displayed elongated setae arranged in a continuous row across all interstriae, contrasting with other specimens where they were only present on the odd interstriae. Notably, despite sharing a similar aedeagus structure with a slightly acute apex, specimens from Bolivia possess a more elongated median lobe (Figure 3F), which is not widened at the base and lacks a distinct constriction in the median region observed in specimens from Peru (Figue 3H) and Brazil (Figure 3J).

The distribution of *U. variabilis* appears to be extensive (Figure 30A), but Hustache (1939) has examined only specimens from Bolivia. The considerable range of variations and similarities observed among the specimens does not provide sufficient confidence to definitively classify them as *U. variabilis*. Both morphological and molecular analyses will be necessary for accurately delineating this species complex. It is prudent to defer the designation of lectotype and paralectotypes until additional studies have been conducted. Notably, although putative female specimens were analyzed, they have not been included in the description since females appear to be morphologically indistinguishable from other species such as *Udeus* sp. nov. 19, *Udeus* sp. nov. 21, *Udeus* sp. nov. 22, *Udeus* sp. nov. 26.

***Udeus longicollis* Voss, 1941**

(Figures 4, 28B, 29B, 30B)

Udeus longicollis Voss, 1941: 208 (description). Wibmer & O' Brien 1986: 110 (catalog).
Udeus martiniquensis Rheinheimer, 2019: 108 **(new synonym).**

Diagnosis. *Udeus longicollis* can be distinguished from other *Udeus* by the dark border of scrobes (Fig. 4B); elongated elytra (Figs. 4A–B); large eyes (Figs. 4B–C); head in dorsal view including eye margins with the same width of the pronotum; laterals of the pronotum straight; mesosternum with a set of elongate setae between the coxae; apex of aedeagus bifurcate, with an indentation on apical third (Fig. 4G). This species is morphologically closer to *Udeus* sp. nov. 24 (Figure 24), *Udeus* sp nov. 25 (Figure 25), and *Udeus* sp. nov. 26 (Figure 26), by the format of elytra, longer than others. *Udeus longicollis* resembles *Udeus* sp. nov. 8 (Figure 11) and non-spotted variation of *U. variabilis* (Figure 3C), with the same uniform ochre colour.

Redescription. Male. Body size: 2.4–2.5 mm. Head: Rostrum (Fig. 4B) 0.8 times shorter than pronotum; 1.2 times wider at base than at apex; with integument yellowish, dark brown on scrobes;

slightly rugose, without median carina, punctuation visible; scrobe oblique, directed downward reaching near eye margin; covered with yellowish setae, except on median region, apex with longest setae; decumbent setae arranged transversally from antennae insertion to base of rostrum. Eyes 1.1 times higher than wide; 2 times more separated above than below. Head yellowish color, covered by yellowish non-ramified setae dorsally, and plumose setae on lateral and ventral region; a row of four or five elongate and yellowish setae near to inner margin of each eye. Antennae (Fig. 28B) with scape straight, apex dilated, extends behind to the anterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 1.9 times longer than antennomere II; antennomere II 1.7 times longer than antennomeres III, V and VII subequal in length and 1.2 times longer than IV and VI, subequal in length; club three-segmented, 2.6 times longer than wide. Mandibles 1.5 times longer than wide, with three teeth.

Thorax: Pronotum (Figs. 4A–B) flat, as long as wide, transverse, lateral margin parallel, with transversal sulcus on median region; strong apical constriction; integument yellow to brown color; covered by yellowish setae, except the basal line of whitish plumose setae; three yellowish elongate setae sparsely on lateral margin, three erected setae directed forward on the apical border on each side, without elongate setae on center of disc. Legs. Integument yellowish. Pro- and mesocoxae covered with setae, some plumose. Femora with teeth well defined ventrally. Tibiae (Fig. 29B) mucronate, compressed, almost straight. Tarsus (Fig. 29B) elongate, 1.1 times longer than metatibiae; tarsomeres I and II subequal in length, two times longer than tarsomere III; last tarsomere longer than rest, 1.6 times longer than tarsomeres I and II. Scutellum triangular, subequal in length; covered with simple setae, and plumose setae on borders. Elytra (Figs. 4A–B) with yellowish to brown uniform color; humeri rounded; lateral margins subparallel; 3.8 times longer than wide; three times longer and 1.7 times wider than pronotum; interstriae covered with short yellowish setae, with a row of elongate setae on odd interstriae and in the second stria on apical

third; striae slightly depressed, with large punctuation, some punctuations contiguous; epipleura covered with scarce simple setae. Ventral region (Fig. 4C) of thorax with integument yellowish to brown. Prosternum covered with scarce non-ramified setae. Mesosternum with scarce plumose setae, and a set of elongate setae concentrated between coxae. Metasternum with transversal roughness on concavity central, that is smooth; densely covered with setae on lateral, and a row of plumose setae on posterior border above metacoxae.

Abdomen (Fig. 4C): Ventrites I-II connate in the middle; with a larger depression in the center. Ventrites covered with yellowish setae; length. Terminalia. Pygidium (tergum VIII) (Fig. 4K) 2 times as wide as long along midline; anterior margin straight; posterior margin rounded; elongate setae on apex, shortest setae posteriorly. Sternum IX (spiculum gastrale) (Fig. 4I) as long as aedeagus; straight, with two hemisternites separated by a membrane, curved on apex. Tegmen (Fig. 4J) 0.6 times shorter than aedeagus; tegminal apodeme slightly curved on apex; parameres fused on base, membranous apically, covered with several spicules. Aedeagus (Figs. 4G–H) 4.6 times longer than wide in median region, slightly constricted in middle, expanding to extremes; border of apical third with an indentation; bifurcated apex; ventral plate sclerotized. Apodemes 0.7 times shorter than median lobe. Endophallus with a pocket containing microtrichae arranged in two longitudinal bands on apical region.

Female. Body size: 2.2–2.8 mm. Rostrum 0.9 times shorter than pronotum; 1.1 times wider at base than at apex. Pronotum subequal in length and wide. Pro- and mesofemora with elongate setae on the base. Metatibiae compressed, slightly sinuose basally. Scutellum subequal in length and width. Metasternum with sulcus slight, in the basal region. Elytra 3.5 times longer than wide; 3.8 times longer and 1.8 times wider than pronotum. Ventrites slightly convex; ventrites I and II connate in middle without depression in the center; ventrite V triangular, rounded on apex. Terminalia. Tergum VIII (pygidium) (Fig 4D) triangular, anterior margin straight; rounded apex,

slightly rough border; long setae on apical third, shorter posteriorly. Sternum VIII (Fig. 4F), including apodeme, about 3.6 times as long as coxites; lamina occupying posterior third; lateral arms and a central band sclerotized; apex almost truncate, slightly sinuose with a row of setae surrounded basally by sensilla. Coxites thin, elongate, 6.4 times longer than wider. Styli minutes, inserted externally on lateral border of coxites. Spermatheca (Fig. 4E) curved, about 2 times as long as wide; *ramus* and *collum* pointing in the same direction.

Examined material. Type material: Lectotype (m#): PARAGUAY: no locality, no date, Kraatz coll., deposited at Museum National of History Natural, Paris, France.

Other material: 25m#, 16f#, BELIZE: Cayo District nr. Teakettle Bank, Pooks Hill, 7jul.2003, CR Bartlett (ASUCOB). BOLIVIA: S. Cruz, Saaverdra Res. Sta., 22mar.1978, CR Ward & CW O`Brien, UV trap (ASUCOB); Santa Cruz: 5 km SSE Buena Vista Hotel Flora & Fauna, 63°N, 17°E, 440mm, 10-22Oct2004, J.E. Eger, at UV, MV and Incandescent lights (CERPE), Ingenio la Belgica, 40 km N. Santa Cruz, 20jan.1980, L. Stange, Black ligth trap (FMNH), Saavedra Res. Sta, 3abr.78, H. Serrate, UV trap (ASUCOB). BRAZIL: RO: 62 km. SW. Ariquemes, Fzda. Rancho Grande, 5-17Sep1993, JE. Eger, UV trap (ASUCOB), 18-set.-92, U. Schmitz, UV trap (ASUCOB), 15-set.-94, U. Schmitz, UV trap (ASUCOB), 6-15Dec1990, JE. Eger, UV trap (ASUCOB), 3-15Dec1996, JE Eger, MV & Black Lights (ASUCOB). COSTA RICA: [no state given]: Guan. 3 km SE R. Naranjo, 20jan.1992, F.D. Parker (ASUCOB), jan.1992, F.D. Parker (CERPE). GUATEMALA: [no state given]: 6 mi. W. Amatitlan, 8jun.1974, G.B. Marshall, at light (ASUCOB), Peten Parque Natural Ixpanpajul, 18-out.-06, R. Turnbow (ASUCOB), Zacapa rd. to San Lorenzo, 14-out.-06, R. Turnbow (ASUCOB), 15-out.-06, R. Turnbow (CERPE). HONDURAS: [no state given]: Siguat. Hond., 23-ago.-74, Fco Lega colector (ASUCOB). MEXICO: Santa Cruz: Fortin de las Flores, 11jul.1964, Ing. Daniel Rabago, blacklight trap

(ASUCOB), 17mar.1964, Ing. Daniel Rabago, blacklight trap (ASUCOB). PANAMA: [no state given]: Bocas del Toro, Miramar, sea level, 9°N, 82°E, 26-out.-79, H. Wolda, UV trap (ASUCOB), 28-dez.-78, H. Wolda, UV trap (CERPE), 31jan.1979, H. Wolda, UV trap (ASUCOB), 23mar.1979, H. Wolda, UV trap (ASUCOB), Canal Zone, Barro Colorado Is., 25-ago.-78, H. Wolda, UV trap 3 (36 m.high) (ASUCOB), 24-mai.-76, H. Wolda, UV trap 3 (26m high) (ASUCOB), 3-ago.-76, H. Wolda, UV trap 3 (26m high) (CERPE), 15jul.1978, H. Wolda, UV trap 1 (3m high) (ASUCOB), 5jun.1978, H. Wolda, UV trap 3 (26m high) (ASUCOB), 16jun.1977, H. Wolda, UV trap 1 (3m high) (ASUCOB), 29nov.1977, H. Wolda, UV trap 3 (26m high) (ASUCOB), Panama, El Llano-Carti Rd. 12 km., mv + bl, 27jun.1997, R. Turnbow (ASUCOB), Panama, Las Cumbres, 17-set.-76, H. Wolda, UV trap (ASUCOB), 29-out.-76, H. Wolda, UV trap (ASUCOB), 22-out.-76, H. Wolda, UV trap (ASUCOB), 2jan.1977, H. Wolda, UV trap (ASUCOB), 13jun.1978, H. Wolda, UV trap (ASUCOB), 6-set.-76, H. Wolda, UV trap (ASUCOB), 20nov.1976, H. Wolda, UV trap (ASUCOB).

Distribution. *Udeus longicollis* is the species with the widest distribution in the Neotropics, occurring from Mexico to southern Brazil, including Belize, Guatemala, Honduras, Costa Rica, Panama, Martinique, and Bolivia.

Host plant and notes on biology. We collected *U. longicollis* in Goiás, Mato Grosso, Bahia, Pernambuco, and Paraná states (Brazil) in staminate inflorescences of *C. pachystachya* and *C. concolor* in Manaus, Amazonas state. Similarly to *U. cerrandensis* (Lira et al. in press), the larvae develop within the male inflorescences, feeding on the internal tissue, where pupate until emerging as adults. Monitoring plants of *C. pachystachy*a in Recife (Brazil), few adults were observed per inflorescences, mating, and eating pollen. Minuscule cylindrical eggs were observed on the base of the petiole of staminate inflorescences. No specimen was registered in pistillate inflorescences. The

wide distribution of *U. longicollis* exceeds the distribution limits of *C. pachystachya*, consistently associated with this species in Brazil. The distribution of *C. pachystachya* is limited to Brazil from the south of the Amazon basin, through the central and eastern parts of the country, extending to Paraguay and northern Argentina. Therefore, *U. longicollis* possibly has an alternative host in Central America outside the region of occurrence of *C. pachystachya*.

Remarks. In the description of *U. fonsecai*, Voss (1941) referenced *Udeus longicollis* when comparing the morphology of these species. Voss suggested that *U. fonsecai* was described by Hustache during this comparison, without specifying the location of the type material. However, *U. longicollis* is not attributed to Hustache but was recognized as a valid species by Wibmer & O'Brien (1986). Consequently, the concise description of *U. longicollis* provided by Voss during his comparison with *U. fonsecai* serves as the original description of *U. longicollis*. We have identified a specimen at MNHN labeled as *U. longicolli*s, collected by Kraatz, which we believe to be the holotype.

In this study, we synonymize *U. martiniquensis* to *U. longicollis* based on an examination of type photographs and original descriptions. While Rheiheimer (2019) provided a comprehensive description of *U. martiniquensis*, an examination of the genitalia was absent. Several diagnostic characters omitted in the original description are presented in the redescription: tegument of rostrum near scrobes darker; head covered by yellowish non-ramified setae dorsally, and plumose setae on the lateral and ventral region; a row of four or five elongate and yellowish setae near to inner margin of each eye; pronotum with the basal line of whitish plumose setae; three yellowish elongate setae sparsely on lateral margin, three erected setae directed forward on the apical border on each side; metasternum with transversal roughness on concavity central. Sexual dimorphism is apparent, characterized by ventrites I-II connate in the middle, with a larger depression in the center, a set of

elongate setae between median legs, and a short mucro on tibiae in males. Females exhibit a larger body size than males, with ventrites slightly convex.

Several specimens of *U. longicollis* are distributed in collections in Brazil and the US labelled as *Phytotribus embaubae* (*nomen nudum*) (see Remarks under *U. cecropiae* for more details).

***Udeus fonsecai* Voss, 1941**

(Figs. 5, 28C, 29D, 30G)

Udeus fonsecai Voss, 1941: 207 (description).
Udeus cecropiae (Bondar, 1957: 258) (**new synonym** *);Moracetribus cecropiae* Bondar, 1957: 258 (description); *Udeus cecropiae* Wibmer & O'Brien 1986: 110 (catalog) .
Udeus sergioi Bondar (1957 : 260) (**new synonym***); Moracetribus sergioi* Bondar, 1957: 260 (description); *Udeus sergioi* Wibmer & O'Brien 1986: 110 (catalog).

Diagnosis. This species can be recognized by the robust and short rostrum (Fig. 5B), with a median longitudinal carina, head with a posterior line of plumose setae, as well as ventrally and on laterals, plumose setae at the base of the pronotum and ventrally on thorax (Figs. 5B–C); elytra with strong punctuation (Fig. 5A), elongate setae in all interstriae contrasting with small other setae, similar those of the striae; striae slightly sinuose on basal third where there is a slight depression; apex of the pygidium exposed dorsally; tarsus elongate with the last tarsomere very large. *Udeus cecropiae* shares with *U. variabilis* (Fig. 3), *Udeus* sp. nov. 20 (Fig. 20), and *Udeus* sp. nov. 22 (Fig. 22) similar variations in elytra coloring with two transversal bands on base and postmedian region, sometimes with a longitudinal band intersecting them.

Redescription. Male. Body size: 2.3–2.4 mm. Head: Rostrum (Fig. 5B) 0.8 times as long as pronotum, 1.1 times wider at base than at apex; integument yellowish to dark brown; with longitudinal carina; scrobes almost reaching eye margin; apex with scarce elongate setae; setae

arranged transversely from antennal insertion to near base on laterals; eyes 1.1 times wider than height, about 2.3 times more separate above than below; integument yellowish to dark brown, similar to rostrum; covered with setae unramified, with four elongate yellowish setae on internal margin of each eye; plumose setae laterally and ventrally. Antennae (Fig. 28C) with first antennomere 1.6 times longer than II, antennomere II 1.7 times longer than antennomeres III, V, and VII subequal in length, antennomeres IV and VI subequal in length and 0.8 shorter than II; club three-segmented, 2.1 times longer than wide. Mandibles endodont, symmetrical, 1.2 times longer than wide, with three teeth on internal margin.

Thorax: Pronotum (Figs. 5A–F) transverse, 1.1 times wider than long, with parallel lateral margins, slightly rounded, and distinct transverse sulcus on median region; integument yellow to dark brown; covered with short yellowish setae on disc, with whitish plumose setae at base, and six yellowish elongated setae next to apical constriction. Profemora with elongate scarce setae ventrally on base; metatibiae (Fig. 29D) evenly covered with sparse setae, denser apically near mucro. Tarsus (Fig. 29D) elongate, 0.9 times shorter than metatibiae; first tarsomere 0.9 times shorter than II, tarsomere II two times longer than tarsomere III; last tarsomere longer than rest, 2.4 times longer than tarsomeres I. Scutellum (Fig. 5A, D–F) as long as wide, brown, covered with short whitish plumose setae; elytra 3.7 times longer than wide, 2.9 times wider and 1.5 times longer than pronotum, with subparallel lateral margins, uniformly yellowish or dark brown, sometimes with two complete or incomplete dark bands in basal and postmedian region, or only incomplete dark bands on postmedian region, covered by short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in all interstriae; humeri rounded, dark or yellowish. Ventral region (Fig. 5C) with integument similar to dorsal color, sometimes slightly darker than dorsal region. Prosternum with scarce and short ramified setae. Metasternum with whitish plumose setae

and fewer elongate non-ramified setae medially. Metasternum with distinct central concavity extending into abdomen, covered with whitish non-ramified setae.

Abdomen with ventrites I–II covered by yellowish non-ramified setae, scarcer on center, slightly longer on laterals; ventrites III–V covered by yellowish non-ramified setae, longer on center of posterior margin; ventrite V trapezoidal, straight on border. Terminalia. Pygidium (tergum VIII) (Fig. 5J) subequal in length and width; anterior margin straight; posterior margin rounded; elongate setae on apical half, shortest setae posteriorly. Sternum IX (spiculum gastrale) (Fig. 5I) 0.7 times shorter than aedeagus; straight, with two hemisternites separated by a membrane. Tegmen 0.6 times shorter than aedeagus; tegminal apodeme slightly curved on apex; parameres fused, membranous apically. Aedeagus (Figs. 5G–H) 6.5 times longer than wide on base, slightly constricted in middle, apex rounded; ventral plate sclerotized. Apodemes 0.8 times shorter than median lobe. Endophallus with a pocket containing microtrichae on apical region.

Female. Body size: 2.5–2.8 mm. Rostrum 0.8 times shorter than pronotum; subequal in width at apex and base; pronotum 1.1 times wider than long. Femora with elongate ventral setae, present but scarce. Scutellum as long as wide. Elytra 3.7 times longer than wide, 3.2 times longer, and 1.5 times wider than pronotum. Ventrites convex, ventrite V triangular, rounded at apex. Terminalia not examined.

Morphological variations. There is significant variation in color pattern. For example, in a single population from Recife, Pernambuco we find individuals with elytra almost completely yellowish, with dark bands on the base, median line, and longitudinally intersecting these bands, or with elytra completely black (Figs. 5A–F). This large level of polymorphism has also been observed in a few species of other weevil flower visitors, such as *Anchylorhynchus tremolerasi* Hustache, 1937 (de Medeiros & Vanin 2020).

Examined material. Type material: Syntipes: BRAZIL: no locality, no data, G. Bondar (8 sex indet. FMNH), Bahia: 10Jan1951, G. Bondar (15 sex indet. FMNH), Bahia, xii.1950 (438 sex indet. AMNH).

Other material: BRAZIL: Amazonas: Manaus, UFAM, 3.10042°S, 59.9831°W, 30.vi.2022, D.P.P. Aguiar (37 sex indet. CERPE); Pará: Baião, 2.71258°S, 49.0051°W, x.2022, N.L. Medeiros (5 sex indet. CERPE); Pernambuco: Camaragibe, 8°N, 34°E, 28.iii.2021, A.O. Lira (13 sex indet. CERPE), Camaragibe, Aldeia, Cond. Divinópolis, 7.96345°S, 35.0037°W, 1-31.xii.2020, Grossi & Parizotto (26 sex indet. CERPE), Camaragibe, Aldeia, Km 14, 7°N, 35°E, xii.2019, P.C. Grossi (125 sex indet. CERPE), xi.2019, P.C. Grossi (2 sex indet. CERPE), Camaragibe, Aldeia, Km 9, 7°N, 35°E, xii.2019, P.C. Grossi (28 sex indet. CERPE), Recife, 10-25.ix.2021, A.O. Lira & P.E. Oliveira (4 sex indet. CERPE), 16.i.2015, Silva, F.M. (10 sex indet. CERPE), 29.viii-07.ix.2021, A.O. Lira & P.E. Oliveira (3 sex indet. CERPE), 12-21.ix.2021, A.O. Lira & P.E. Oliveira (2 sex indet. CERPE), Recife, 28°N, 34°E, 10-25.ix.2021, A.O. Lira & P.E. Oliveira (4 sex indet. CERPE), Recife, BR 101, 8.01685°S, 34.941°W, 05-20.x.2021, A.O. Lira & P.E. Oliveira (375 sex indet. CERPE), Recife, V, 8°N, 34°E, 22.vii-09.viii.2021, A.O. Lira & P.E. Oliveira (61 sex indet. CERPE).

Distribution. This species is distributed from the western region to the northeast of Brazil, in open habitats in the states of Amazonas, Pará, Pernambuco, and Bahia.

Host plants. We collected this species in Pernambuco, Pará, and Amazonas states in male inflorescences of *C. palmata*. Bondar (1957) mistakenly described new species based on material collected in male inflorescences of *C. cinerea* Mig. and *C. adenopus* Mart. in Bahia state, both species synonymized with *C. pachystachya* (see remarks).

Remarks. We propose here the synonym between *U. cecropiae* and *U. sergioi* based on examining of type material and descriptions of both species (Bondar 1957), as well we synonymized *U. cecropiae* with *U. fonsecai* following the examing of the description and photography of holotype of *U. fonsecai*.

Bondar deposited dozens of specimens denominated cotipes in the Instituto Biológico da Bahia, Instituto Biológico de São Paulo, NMNH, AMNH, and FMNH. Before publishing the descriptions of *U. cecropiae* and *U. sergioi*, Bondar deposited specimens labeled as *Phytotribus cecropiae* and *P. embaubae*, which he later deemed *in litt.*, therefore invalid names, and which would correspond to *U. cecropiae* and *U. sergioi*, respectively. Upon examination, we observed discrepancies within this material. Cotipes labeled as *U. cecropiae, U. sergioi,* and *P. cecropiae* are consistent with the same species. However, specimens labeled as *P. embaubae* correspond to a different species, specifically *U. longicollis*.

While Bondar collected specimens labeled as *P. embaubae*, the descriptions, and illustrations provided for *U. sergioi* do not correspond to this species. Instead, they resemble the variant lacking elytral macules seen in *U. cecropiae*, bearing some resemblance to *U. longicollis*. Furthermore, specimens designated by Bondar as cotypes of *U. sergioi* match the variation lacking macules observed in *U. cecropiae*. Additionally, we noted potential errors in host assignments for *U. cecropiae* and *U. sergioi*. The first insights about the association of *Udeus* with their host plant, *Cecropia*, were provided by Bondar, and correspond to additional differences between *U. cecropiae* and *U. sergioi*, according to the author. *Udeus cecropiae* was reared from falling staminate inflorescences of *C. cinera*, while *U. sergioi* was associated with *C. adenopus*. Both *Cecropia* species were synonymized with *C. pachystachya*, the senior synonym. However, in our collections from *C. pachystachya*, we consistently found an association with only *U. longicollis*, whereas *U.*

cecropiae was linked with *C. palmata*. This leads us to question the accuracy of Bondar's identification of the host plants.

In summary, our reevaluation suggests that *U. cecropiae* and *U. sergioi* likely represent variations of the same species. Furthermore, we propose that Bondar erroneously attributed the host of another species, *U. longicollis* (previously labeled as *P. embaubae*), to the descriptions of *U. cecropiae* and *U. sergioi*. While Bondar's study remains valuable for understanding host associations, revisions to taxonomic attributions are necessary based on our findings.

Regarding the proposed synonymy with *U. fonsecai*, a thorough examination of the type photograph and the detailed external morphology description by Voss (1941) reveals striking similarities with the variant of *U. cecropiae* that lacks elytral macules. There are minor discrepancies observed in the density of pronotal setae, with the holotype exhibiting slightly denser setae.

***Udeus cerradensis* Lira, de Medeiros & Grossi, 2024**

(Figures 6, 29C, 30A)

Diagnosis. *Udeus cerradensis* is easily distinguished from other *Udeus* species by the exodont mandible with one apical tooth; the presence of whitish plumose setae on the elytral interstriae (Fig. 6A), pronotum, prosternum, and head (Fig. 6B); incomplete band on the middle of elytra darker than rest of elytra; and antennomere V of the funicle shortest. This species resembles to morphotype of *U. cecropiae* with spots on the median region of elytra (Fig. 5A).

Host plant. *Udeus cerradensis* is associeted with *C. saxatilis* Snethl.

Distribution. This species is limited to grassland areas and, until now only known from the type locality, in Barra do Garças, Mato Grosso, Brazil.

Remarks. For a complete description of adult and immature stages, see Lira *et al.* (2024).

***Udeus* sp. nov. 3 Lira & de Medeiros**

(Figures 7, 28D, 29E, 30C)

Holotype: Male. BRAZIL: Pernambuco: Recife, UFRPE, Transrural, 8.01944°S, 34.9471°W, 13.xi.2021, A.O. Lira, manual, in *Cecropia palmata* (CERPE1210).

Diagnosis. *Udeus* sp nov 3 is distinguished from other *Udeus* species by the dark longitudinal bands on the basal half of the elytra forming diverse patterns (Figs. 7–F); longer antennomeres in funicle (Fig. 28D); unique aedeagus with lateral margins compressed ventrolaterally; female with pigydium with apex serrate, with a large spine centrally (Fig. 7H). This species is similar in length to *Udeus* sp. nov. 6 (Fig. 9), as well as the integument of morphotypes without macules.

Description. Male. Body size: 3.2–3.6 mm. Head: Rostrum (Figs. 7A–F) 1.2 times longer than pronotum; 1.1 times wider at base than at apex; integument yellowish to dark brown; longitudinal carina absent; scrobe reaching eye margin; apex with elongate setae mainly on ventral region; ventral region with a dense arrangement of setae from base to apex; base with sparse, unramified setae inserted on distinct punctation. Eyes 1.2 times higher than wide; 1.8 times more separated above than below. Head with integument yellowish to brown, simple setae on dorsal region and short and plumose setae laterally at base; a row of five elongate setae near to internal margin of each eye; interorbital region slightly depressed. Antennae (Fig. 28D) with scape straight, apex dilated, extends near to posterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 1.2 times longer than antennomere II; antennomere II subequal in length antennomere III; antennomeres IV and V subequal in length and 0.8 times shorter than II and III;

antennomeres VI and VII shortest, subequal in length, about 0.7 times shorter than II and III; club three-segmented, three times longer than wide. Mandibles endodont, symmetric, with three teeth on internal margin.

Thorax. Pronotum (Figs. 7A–F) transverse, convex dorsally, margins parallel, subequal in length and width; color similar to head; disc pronotal slightly punctuate, with delicate sulcus on laterals; strong apical constriction; covered by short yellowish setae from apex to near base, directed towards the center on the basal third; short whitish plumose setae on the base and lateral regions; one erected setae directed backward close to the basal border on laterals, three erected setae directed forward on the apical border on each side, two closest and the other far away on lateral margin, and two pair of erected setae on disc center. Legs. Pro- and mesocoxae covered by whitish plumose setae externally, with scarce non-ramified setae near to trochanter, internally. Femura with strong teeth ventrally, with elongate setae from base to tooth. Tibia compressed, almost straight, with internal margin slightly, elongate setae on the apical third; with short mucro. Tarsus (Fig. 29E) elongate, almost tibia length; tarsomere I 1.1 times longer than II, tarsomere III 0.4 times shorter than I; last tarsomere longer than rest, 1.2 times longer than tarsomere I. Scutellum (Figs. 7A, D, F) triangular; subequal in length and width; integument dark brown; entirely covered by whitish plumose setae. Elytra (Figs. 7A, B, D, F) with most of integument yellowish, with dark bands forming diverse color patterns; lateral margins subparallel; 3.7 times longer than wide; 3.1 times longer and 1.7 times wider than pronotum; interstriae covered with tiny yellowish setae, with a row of elongate, erected and long sparse setae inserted after small tubercles; striae with rounded punctuations, with tiny setae similar to those of interstriae inserted above each punctuation; epipleura and interstriae 10 with plumose setae. Ventral region (Fig. 7C) of thorax with integument yellowish; short withish plumose setae on prosternum, mesosternum, and lateral and basal region of metasternum. Prosternum and metepisternum covered with plumose setae intercalated with

scarce elongate setae. Metasternum with incomplete carina on center of basal region; withish elongate setae sparse in the center, gradually interspersed with plumose setae on lateral.

Abdomen (Fig. 7C). Ventrites covered by yellowish setae, with straight posterior margins; ventrites I and II connate at the middle, with suture visible, and depression in the center; ventrite V trapezoidal, straight on apex. Terminalia: Pygidium (tergum VIII) (Fig. 7N) 1.7 longer than wide on base, with laterals expanded in flaps; anterior margin straight and posterior margin rounded; setae very large concentrated from median region to apex and smaller setae on base. Sternum IX (spiculum gastrale) (Fig. 7 M) with apodeme 0.7 times smaller than aedeagus; straight with apex sinuous; with two hemisternites separated by a membrane. Tegmen (Fig. 7L) 0.7 times shorter than aedeagus; terminal apodeme slender, slightly sinuous, apex curved in lateral view. Aedeagus (Figs. 7J–K) 9.1 times longer than wide at base, subparallel margins, funneling to the apex; margins ventrolaterally compressed, rounded apex; ventral plate strongly sclerotized with several sensilla. Apodemes 1.3 times shorter than median lobe. Endophallus with a pocket containing microtrichae.

Female (Figs. 7D–E). Body size: 3.3–3.8 mm. Rostrum (Fig. 7E) 1.2 times longer than pronotum, apex subequal to base in width. Pronotum subequal or 1.1 times wider than length. Pro- and mesofemora with elongate setae on the base. Metatibiae compressed, slightly sinuose basally. Scutellum subequal in length and width. Metasternum with sulcus slight, in the basal region. Elytra 3.5 times longer than wide; 3.1 times longer and 1.7 times wider than pronotum. Ventrites slightly convex (Fig. 7E); ventrites I and II connate in middle without depression in the center; ventrite triangular, slightly sinuose centrally on apex. Terminalia. Tergum VIII (pygidium) (Fig. 7H) triangular, anterior margin straight; rounded apex, serrate, with a large spine centrally; long setae apically, small setae from base to near to apex. Sternum VIII (Fig. 7G), including apodeme, 6.7 times longer than coxites, with elongate setae on apex concentrated on central border. Coxites and

styli not visible. Spermatheca (Fig. 7I) 1.4 times longer than wide; *cornu* strongly curved; *collum* and *ramus* in the same direction.

Examined material. Type material. Paratypes: BRAZIL: Pará: Baião, 2.71258°S, 49.0051°W, x.2022, N.L. Medeiros, manual (3m#, 3f# CERPE); Pernambuco: Camaragibe, Aldeia, Cond. Divinópolis, 7.96345°S, 35.0037°W, 1-31.xii.2020, Grossi & Parizotto, manual (1f# CERPE); Camaragibe, Aldeia, Km 9, 7°57'23.6"S, 35°00'54"W, xii.2021, P.C. Grossi (5m#, 6f# CERPE); Recife, UFRPE, CEGOE, -8.01717, -34.94929, 17.xi.2021, A.O. Lira, manual (3m#, 2f# CERPE); UFRPE, Transrural, 8.01944°S, 34.9471°W, 13.xi.2021, A.O. Lira, manual (12m#, 11f# CERPE); UFRPE, 08°01’02.5”S, 34°56’56.6”W, 10Dec2022, A.O. Lira, manual, in *Cecropia palmata* (1m#, 1f# NMB; 1m#, 1f# ANIC; 1f# MNHW; 1m#, 1f# CMN; 1m#, 1f# NZAC; 1m#, 1f# BMNH; 1m#, 1f# MCZ; 1m#, 1f# AMNH; 1m#, 1f# ASUCOB; 1m#, 1f# USNM; 1m#, 3f# FMNH); Dois Irmãos, 8°01'9.2" S, 34°57'13.7" W, 27.iv.2020, P.E. Oliveira (1f# CERPE); Várzea, 8°01'41.9"S, 34°57'18.2"W, 22.vii-09.viii.2021, A.O. Lira & P.E. Oliveira (3m#, 3f# CERPE).

Distribution. This species is known from Brazil occurring in open habitats in the Amazon Forest in Pará, and Atlantic Forest in Pernambuco state.

Host plants and notes about biology. We collected *Udeus* sp. nov. 3 in *Cecropia palmata* in open areas from the Atlantic Forest in Pernambuco state, as well as in the Amazon Forest in Pará state. Notably, this species exhibited coexistence with morphotypes of *U. variabilis* in staminate inflorescences specifically in Pernambuco (Brazil). While rearing larvae from inflorescences we noted that *Udeus* sp. nov. 3 developed significantly faster than compared to *U. variabilis*. *Udeus* sp. nov. 3 emerged from the inflorescences a few days after the emergence of the coexisting species.

Remarks. *Udeus* sp nov. 3 exhibits notable morphological variations in the pattern of bands on the elytra. While certain specimens display no pigmentation on the elytra (Fig. 7F), others exhibit dark-colored longitudinal bands partially covering the interstriae from the humeri to the postmedian region in varying patterns (Figs. 7A, D). Remarkably, these variations were observed among specimens originating from the same inflorescences.

***Udeus* sp. nov. 5 Lira & de Medeiros**

(Figures 8, 30D)

Holotype: Male. BRAZIL: Rio de Janeiro: Itatiaia, Pq. Nac. Itatiaia, Trilha das borboletas, 22.448°S, 44.606°W, 18.xii.2021, B. Clarkson (CERPE).

Diagnosis. *Udeus* sp. nov. 5 can be distinguished from other *Udeus* species by the yellowish coloration, incomplete carina on the rostrum, elongated setae of the head, pronotum, and interstriae bifurcate apically (Fig. 1H). This species resembles *Udeus* sp 8 (Fig. 11) by the length, and body coloration.

Description. Male. Body size: 2.1 mm. Rostrum (Fig. 8A–C) 1.5 times longer than pronotum, apex subequal to base in width; integument yellowish, sometimes dark brown on scrobes; with an incomplete longitudinal carina; scrobe reaching eye margin; apex with elongate setae; decumbent setae arranged transversely from near to antennae insertion to base of rostrum. Eyes (Fig. 8A–C) 1.2 times higher than wide; 2 times more separated above than below; with microsetae between ommatidia. Head with integument yellowish, covered with setae non-ramified on dorsal region, scarce plumose setae near to apical border, abundant on laterals; a row of five elongate setae apically bifurcate near to internal margin of each eye. Antennae with scape straight, apex dilated, extends behind to anterior margin of eye; funicle seven segmented, antennomere I longer and wider than

others, 1.7 times longer than antennomere II; antennomere II 1.3 times longer than antennomeres III, VI and VI, subequal in length; antennomeres V and VII subequal in length, shortest, 0.3 times shorter than antennomere I; club three-segmented, 2.1 times longer than wide. Mandibles endodont, symmetric, with three teeth on internal margin, 1.3 times longer than wide.

Thorax: Pronotum (Fig. 8A–C) transverse, 1.1 times wider than long; lateral margins parallel, with shallow transversal sulcus on middle region; strong apical constriction; color similar to head; densely punctuate, with non-ramified yellowish setae from apex to near base, directed towards the center, whitish plumose setae on the base and lateral regions, one erected elongate setae close to the basal border on center, three erected setae directed forward on sides, three erected setae directed forward on the apical border on each side. Pro- and metacoxae covered with simple and plumose setae. Femora with strong teeth and scarce elongate setae on base ventrally. Tibiae mucronate, compressed; metatibiae with internal margin slightly sinuose on base. Tarsus elongate, subequal to metatibiae length; first tarsomere 1.1 times longer than II, tarsomere II two times longer than tarsomere III, last tarsomere longer than rest, 1.4 times longer than tarsomere I. Scutellum triangular, 1.1 times longer than wide, covered with whitish plumose setae. Elytra (Figs. 8A–B) 3.5 times longer than wide, 3.1 times longer, and 1.6 times wider than pronotum; humeri rounded, lateral margins subparallel, integument entirely yellowish, or with a transversal band in middle, the beginning of the elytral suture, and last interstriae dark brown color; interstriae covered with non-ramified and short setae, striae punctuate with yellowish setae inserted above each punctuation a little longer than those of interstriae, a row of elongated yellowish bristles between the shorter setae on the odd interstriae. Epipleura incomplete and covered with scarce non-ramified setae. Ventral region (Fig. 8C) of thorax with integument yellowish to dark brown; whitish plumose setae on prosternum, mesosternum, and lateral of metasternum. Metasternum with transversal roughness on concavity central, that is smooth and covered with scarce simple setae.

Abdomen (Fig. 8C): Ventrites punctuate, covered with yellowish simple setae denser on laterals than center. Ventrites I-II connate in the middle; with a large depression in the center. Ventrite V trapezoidal, straight on apex. Terminalia. Pygidium (tergum VIII) (Fig. 8M) transverse, 2.1 times wider in base than long along midline; anterior margin straight, and posterior margin rounded; long setae near to apex, shorter posteriorly; ventral flap with bifurcated spicules in posterior border. Sternum IX (spiculum gastrale) (Fig. 8L) straight, subequal in length to aedeagus; anteriorly expanded in triangular form, with two hemisternites separated by a membrane. Tegmen (Fig. 8K) 0.7 times shorter than aedeagus; tegminal apodeme straight; parameres fused, lateral border membranous, apex membranous, with sparse setae. Aedeagus (Fig. 8I–J) 5.9 times longer than wide at base, laterals parallel, apex slightly acute, rounded. Apodemes 0.6 times smaller than aedeagus length. Endophallus with a pocket with microthichae in all extension of aedeagus close to ostium; longer microtrichae on apex than those on base.

Female. Body size: 2.1–2.4 mm. Rostrum 1.3 times longer than pronotum. Pronotum subequal in length and width. Femora without elongate setae ventrally on basal third. Tibiae without mucro. Scutellum 1.3 times wider than long. Elytra 4.1 times longer than wide, 3.1 times longer, and 1.6 times wider than pronotum. Ventrites strongly convex; ventrites I-II connate at the middle, without depression in the center; ventrite V rounded at apex. Terminalia. Tergum VIII (pygidium) (Fig. 8D) subtriangular, 1.6 times wider on base than longer on midline; anterior margin sinuose centrally, posterior margin rounded; long setae concentrated apically, short setae posteriorly. Tergum IX composed of two plates connected on posterior border, separated by a central membrane on center; apical margin almost truncate, slightly sinuose on surface; long setae on apical third. Spermatheca (Fig. 8E) curved, 1.5 times longer than wide; *cornu* slightly curved; *ramus* and *collum* pointing in the same direction.

Examined material. Type material. Paratypes: BRAZIL: Rio de Janeiro: Itatiaia, Pq. Nac. Itatiaia, Trilha das borboletas, 22.448°S, 44.606°W, 18.xii.2021, B. Clarkson (6m#, 11f# CERPE), Nova Friburgo, ix.2017, P.C. Grossi (4m#, 3f# CERPE).

Distribution. This species is known from Rio de Janeiro, Brazil (Figure 30D).

Host plant. *Cecropia* sp.

***Udeus* sp. nov. 6 Lira & de Medeiros**

(Figs. 9, 28E, 29F, 30B)

Holotype: Male. BRAZIL: Rio de Janeiro: Nova Friburgo, Braunes, 22.281°S, 42.512°W, i.2022, P.C. Grossi, manual (CERPE).

Diagnosis. This species is distinguished from other *Udeus* by the dimorphism on metatibiae of males, internally with a triangular expansion near to center, covered with setae modified in spines on the border, and flattened apex covered with setae on borders (Fig. 28F). Additionally, the ventrite V of males is covered with abundant rigid setae forming a triangular area in the center (Fig. 9C), the tegmen contains parameres fused into a rectangular format (Fig. 9H), and the pygidium in males is one of the most elongate in the genus. The males of *Udeus* sp. nov. 6 exhibit a notable resemblance to those of *Udeus* sp. nov. 7 (Fig. 10), *Udeus* sp. nov. 12 (Fig. 14), *Udeus* sp. nov. 19 (Fig. 19), and *Udeus* sp. nov. 22 (Fig. 22), characterized by modified metatibiae, indicative of sexual dimorphism.

Description. Male. Body size: 3.3 mm. Rostrum (Figs. 9A–C) 0.9 times shorter than pronotum; apex 1.1 times wider than base; integument yellowish to dark brown; with median carina, and

smooth roughness on median region longitudinally; scrobe almost reaching eye margin; apex with scarce elongate setae; yellowish, sparse, non-ramified setae, inserted on distinct punctation on base. Eyes (Figs. 9A–C) subequal in length and height; with microsetae between ommatidia. Head integument ochre to brown; with a visible fovea on central region, at the edge of posterior margin of eyes; with short yellowish setae and punctuations marked from base to region above eyes; a row of five setae elongate and yellowish near to internal margin of each eye. Antennae (Fig. 28E) with scape straight extends near to posterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 1.6 times longer than antennomere II; antennomere II 1.5 times longer than antennomere III and 1.3 times longer than IV; antennomeres V and VII subequal in length, shortest; club 2.3 times longer than wide. Mandibles endodont, symmetrical, with two teeth on internal margin.

Thorax: Pronotum (Figs. 9A–C) transverse; 1.1 times wider than long; lateral margins parallel, with sulcus relatively deep on the middle region; strong apical constriction; integument ochre to brown; punctuations well-marked, intercalated by smaller ones; covered by golden setae, except the basal line of whitish plumose setae; three erected, elongate, brown setae on lateral, three erected setae directed forward on the apical border on each side, two closest and the other far away on lateral margin, and two erected setae on disc center, near to median region. Pro- and mesocoxae with tiny plumose setae on the base and non-ramified setae on apex and trochanter. Femora with strong teeth ventrally, with scarce elongate setae on base ventrally; postfemur longer and broader than pro- and mesofemur. Pro- and mesotibiae mucronate, compressed, almost straight. Metatibiae (Fig. 29F) straight on basal third, dilated towards the apex; internally with a triangular expansion near to center, covered with setae modified in spines on the border; flattened apex, rounded border, internal margin with a row of elongate setae. Tarsus (Fig. 29F) elongate, as long as metatibiae, first tarsomere 1.1 times longer than tarsomere II; tarsomere III 0.3 times shorter than tarsomere I; last

tarsomere 1.3 times longer than I. Scutellum (Fig. 9A) triangular, 1.2 times wider than long; covered with dense yellowish plumose setae. Elytra (Fig. 9A) convex; 3.7 times longer than wide; 3.1 times longer, and 1.7 times wider than pronotum; integument ochre to brown; humeri rounded, lateral subparallel from base to apical third; interstriae covered by yellowish setae; striae strongly punctuate with yellowish setae inserted above each punctuation a little longer than those of interstriae, a row of elongate yellowish setae among the shorter setae; base of epipleura with plumose setae. Ventral region (Fig. 9C) of thorax with color of integument similar to the dorsal region; yellowish plumose setae on prosternum, mesosternum, and lateral of metasternum. Metepisternum covered with plumose setae, with a row of elongate and non-ramified setae on median region. Metasternum with a deep central concavity on base, delimited by two elevations located above metacoxae; with yellowish sparse setae on center, more elongated on external border of elevations.

Abdomen (Fig. 9C). Ventrites I-II connate in the middle, with a smooth depression in center; lateral margin of ventrite I slightly sinuose; all ventrites covered with sparse yellowish setae; ventrite V with central region with a dense tuft of spine setae. Terminalia. Tergum VIII (pygidium) (Fig. 9J) subtriangular, 1.2 times longer than wide at base. Sternum IX (spiculum gastrale) (Fig. 9I) thin and straight, 1.2 times longer than aedeagus, anteriorly expanded in a triangular form, with two hemisternites separated by a membrane. Tegmen (Fig. 9H) 0.7 times smaller than aedeagus; tegminal apodeme slightly curved; parameres fused, lateral border membranous; apex membranous, slightly sinuous, with sparse setae. Aedeagus (Figs. 9F–G) 5.7 times longer than wide, slightly constricted in middle; with apical third narrower than half length of wider region of aedeagus; rounded apex, with several sensilla in the apical half. Apodemes 2.1 times shorter than aedeagus. Endophallus with several spicules on apical third ending near to ostium.

Female. Body size: 3.2–3.5 mm. Rostrum subequal in length pronotum; apex subequal to wide base. Pronotum 1.1 times wider than long. Pro- and mesofemora with elongate setae on the base. Tibiae compressed, almost straight, without mucro. Scutellum 1.1 times wider than long. Metasternum with depression in the central region, delimited by two elevations moderately elevated. Elytra 3.4 times longer than wide; 3.6 longer and 1.9 times wider than pronotum. Ventrites slightly convex; ventrites I-II connate at the middle, with posterior margins visible, without depression in the center; ventrite V depressed on laterals, with two carinas from center to apex, with two projections like spines on apex. Terminalia. Tergum VIII (pygidium) (Fig. 9D) triangular, anterior margin almost straight, apical margin rounded with long setae along apical surface, very short setae in direction to anterior border. Sternum VIII, including apodeme, about 4.8 times longer than coxites; lamina occupying posterior half, lateral arms sclerotized; with a row of setae along lateral margins to apex; lamina mesally membranous; apical region of lamina acute, with a clear separation of arms; apodeme slightly curved on posterior half, apically bifurcated, gradually narrower towards apex. Coxites and styli not visible. Spermatheca (Fig. 9E) curved, 1.6 times longer than wide; *cornu* slightly curved; *ramus* and *collum* pointing in the same direction.

Examined material. Type material. Paratypes: BRAZIL: Rio de Janeiro: Itatiaia, Pq. Nac. Itatiaia, Trilha das Borboletas, 22.4486°S, 44.6067°W, 18.xii.2021, B. Clarkson, manual (5m#, 4f# CERPE; 2m#, 1f# FMNH; 1m# USNM; 1m# ASUCOB; 1m# MCZ; 1f# NZAC), Nova Friburgo, ix.2017, P.C. Grossi, manual (5f# CERPE), Nova Friburgo, Braunes, 22.281°S, 42.512°W, i.2022, P.C. Grossi, manual (5m#, 3f# CERPE), Nova Friburgo, SansSouci, 22.287°S, 42.521°W, i.2022, P.C. Grossi, manual (2f# CERPE). **Santa Catarina**: Florianópolis, 16.1.2003, Neves, E. (2m#, 2f# DZUP).

Distribution. This species is known from Brazil in Rio de Janeiro and Santa Catarina states (Fig. 30B).

Host plant. *Udeus* sp. 6 was collected on staminate inflorescences of *C. glaziovii* (Santa Catarina and Rio de Janeiro) and *C. hololeuca* (Rio de Janeiro).

Remarks. The specimens from Santa Catarina correspond to those cited by Mendonça (2014) observed in pistillate and staminate inflorescences of *C. glaziovii*. However, despite this reference, field verification of adult visitation to female inflorescences proved inconclusive. Conversely, specimens collected in Rio de Janeiro predominantly align with collections from male inflorescences.

***Udeus* sp. nov. 7 Lira & de Medeiros**

(Figures 10, 28F, 29G, 30D)

Holotype: BRAZIL: Amazonas: Manaus, Residencial Morada dos Nobres, Ponta Negra, 3019590°S, 60.0789°W, m#, 03.iv.2022, D.P.P. Aguiar, manual (CERPE).

Diagnosis. This species shares a similar dark color of the elytra with *Udeus* sp. nov. 19, *Udeus* sp. nov. 24, and *Udeus* sp. nov. 27, and shares a deep concavity on metasternum with elevated borders with *Udeus* sp. nov. 10, *Udeus* sp. nov. 19, *Udeus* sp. nov. 20, *Udeus* sp. nov. 23, *Udeus* sp. nov 24, and *Udeus* sp. nov. 27. *Udeus* sp. nov. 7 is distinguished from other *Udeus* by the color of legs, with the apex of femora, and base of tibiae darker (Figs. 10A–C). Males can be distinguished from others *Udeus* with sexual dimorphism by the metatibiae, dilated on apex in two dilated flaps with

elongated setae on border (Fig. 29G), and aedeagus with long median lobe, 2.3 times longer than apodemes (Figs. 10G–H).

Description. Male. Body size: 2.8 mm. Head: Rostrum (Figs. 10 A–C) subequal in length to pronotum, 1.1 times wider in apex than base; slightly curved on apex; integument dark brown to black; slightly rugose, without median carina; scrobe oblique, directed downward almost reaching eye margin; densely covered with whitish setae; decumbent setae arranged transversally on median region, and directed backward to eyes on the base. Eyes (Figs. 10 A–C) 1.3 times wider than height; 1.7 times more separated above than below; interorbital region slightly depressed, with dense whitish setae; three or four longest forming a row near to inner margin of each eye. Head with integument similar to rostrum; setae non-ramified on region above the eyes, and plumose setae on lateral and ventral region. Antennae (Figs. (Figs. 10 A–C, 28F) yellowish, with scape straight surpassing the posterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 1.4 times longer than antennomere II and 2.3 times longer than antennomere V; antennomere II 1.2 times longer than antennomere III, IV and VI subequal in length; antennomeres V shortest; club 3.2 times longer than wide.

Thorax: Pronotum (Figs. 10 A–C) transverse; 1.1 times wider than long; lateral subparallel, with transversal sulcus deep located on middle region; strong apical constriction; integument similar to head; covered with short whitish setae, a row of plumose setae on base, denser towards to lateral; one yellowish elongate setae near to posterior border laterally, three erected setae directed forward on the apical border on each side, two closest and the other far away on lateral margin, and two pair on center of the disc. Legs. Pro- and mesocoxae covered by plumose setae, internally with scarce non-ramified setae; trochanter with long whitish setae and shortest setae surrounded. Femora yellow with apex dark brown, strong teeth ventrally. Profemur length. Tibiae yellowish, dark brown on

basal third. Pro- and mesotibiae mucronate, compressed, almost straight. Metatibiae (Fig. 28G) modified, straight on base, dilated on apex in two dilated flaps with elongated setae on border. Tarsus (Fig. 28G) yellowish; tarsomere I 1.7 times longer than tarsomere II and 1.6 times longer than last tarsomere; tarsomere III 0.2 times shorter than tarsomere I; last tarsomere 1.1 times longer than II. Scutellum triangular, length and width subequal; covered with whitish plumose setae. Elytra (Fig. 10A–B) 3.5 times longer than wide; 1.6 wider and 3.1 times longer than pronotum; integument dark brown to black; humeri rounded, lateral margins subparallel; interstriae covered with short whitish setae, with a row of elongate yellowish setae in the odd interstriae inserted on small tubercles, sometimes one or two setae on interstriae 4, 6 and 8 on elytral median region, apex of interstria 2 with some elongate setae; striae punctuate, with whitish setae similar to those of interstriae inserted above each punctuation; interstria 10 and median region of interstria 9 with plumose setae. Ventral region (Fig. 10C) of thorax with integument dark brown; whitish plumose setae on prosternum, mesosternum and lateral of metasternum. Metasternum with a central concavity, delimited by two elevations, with scarce whitish setae on center.

Abdomen (Fig. 10C): Ventrites I-II connate in the middle, with a depression in center; length; ventrite V trapezoidal, with posterior margin straight. Genitalia. Pygidium (tergum VIII) (Fig. 10J) triangular, 1.4 times wider than long on base, with anterior margin straight, and posterior margin rounded; scarce long setae in apical half, shorter in basal half; ventral flap with bifurcated spicules in posterior border. Tegmen 0.6 times shorter than aedeagus; terminal apodeme slender, straight. Aedeagus (Figs. 10G–H) 7.7 times longer than wide at base; margins parallels, apex rounded; ventral plate sclerotized. Median lobe 2.3 times longer than apodemes. Endophallus with a pocket of microthrichae on apical half.

Female. Body size: 2.8–3.0 mm. Rostrum 0.9 times shorter than pronotum; apex subequal in width in apex and base. Pronotum 1.1 times wider than long. Tibiae compressed, almost straight,

without mucro. Scutellum 1.1 times wider than long. Metasternum with a central concavity, delimited by two elevations. Elytra 3.9 times longer than wide; 3.2 times longer, and 1.5 times wider than pronotum. Ventrites slightly convex, covered with whitish setae; ventrites I-II connate at the middle, without central depression; ventrite V depressed on lateral of the basal border, with two projections on apex. Terminalia. Tergum VIII (pygidium) (Fig. 10D) triangular, anterior margin sligtly sinuose; rounded apex, slightly rough border; long setae on apical third, shorter posteriorly. Sternum VIII (Fig. 10F) with lamina occupying posterior third; lateral arms and a central band sclerotized, apex acute. Coxites tand styli not visible. Spermatheca (Fig. 10E) curved, 1.5 times as long as wide; *ramus* and *collum* pointing in the same direction.

Examined material. Type material. Paratypes: BRAZIL: Amazonas: Manaus, Residencial Morada dos Nobres, Ponta Negra, 3019590°S, 60.0789°W, 03.iv.2022, D.P.P. Aguiar, manual (3m#, 7f# CERPE; 1m#, 2f# FMNH; 1f# USNM; 1m#, 1f# ASUCOB; 1f# MCZ; 1f# NZAC).

Distribution. This species is known only from the type locality (Fig. 30D).

Host plant. This species was collected on staminate inflorescences of *C. ulei* Snethl.

***Udeus* sp. nov. 8 Lira & de Medeiros**

(Figs. 11, 30B)

Holotype: Male. BRAZIL: Amazonas: Manaus, Av. Theomario Pinto, Chapada, -3.092853, -60.028161, 20-29.xii.2021, D.P.P. Aguiar, manual (CERPE).

Diagnosis. *Udeus* sp. nov. 8 is distinguished from other *Udeus* species by the wide pronotum, wider than long, and subrectangular elytra, with apical curvature not abrupt (Fig. 11A). *Udeus* sp nov 8 is

similar to *U. longicollis*s (Figs. 4A–C) due to the yellowish color of the integument, and the length of the body.

Description. Male. Body size: 2.0–2.1 mm. Head: Rostrum (Figs. 11A–C) 0.9 times shorter than pronotum, apex subequal to base in width; integument light yellow, darker on apex; punctuate laterally, without median carina; scrobe covered with yellowish setae, except on median region longitudinally, longest setae in apex and near to anterior margin of scrobe; decumbent setae arranged transversally from antennae insertion to base of rostrum. Eyes (Figs. 11A–C) 1.2 times higher than wide. Head with integument light yellow, covered with marked punctuation, tiny yellowish setae dorsally and plumose setae laterally, an erect elongate dark brown seta near to posterior margin of each eye. Antennae (Figs. 11A, C) with scape straight, apex dilated, not extending after posterior margin of eye, funicle seven segmented; antennomere I longer and wider than others, 1.7 times longer than antennomere II; antennomere II, subequal in length with antennomeres IV and VI, and 1.3 longer than antennomeres II, V, and VII, which are subequal in length; club three-segmented, 2.6 times longer than wide. Mandibles endodont, symmetric, with three teeth on internal margin.

Thorax: Pronotum (Figs. 11A–C)transverse, 1.3 times wider than long; slightly convex, lateral margins parallel, with shallow transversal sulcus on median region; strong apical constriction; integument color similar to head; covered by short yellowish setae, except the basal band of whitish plumose setae; three yellowish elongate setae directed forward on the apical border on each side, one pair of elongate setae on center of disc, and an elongate seta on laterals, near to basal border. Legs with integument similar to the rest of the body. Pro- and metacoxae covered with plumose setae in external margin. Femora with teeth well defined ventrally. Tibiae mucronate, compressed; internal margin of metatibiae almost straight. Tarsus elongate, almost tibia length;

tarsomere I subequal in length with tarsomere II; tarsomere III 0.5 times shorter than tarsomere I; last tarsomere 1.5 times longer than I and II. Scutellum triangular, 1.1 times wider than long; covered with plumose setae, denser close to borders. Elytra (Figs. 11A–B) 3.5 times longer than wide, 3.5 times longer, and 1.5 times wider than pronotum; subrectangular, with lateral margins parallel from humeri to postmedian region, and apical region subrounded, almost trapezoidal; integument light yellowish; humeri rounded; interstriae covered with thin yellowish setae, with a row of elongate setae on odd interstriae; striae punctuate with yellowish setae inserted above each punctuation a little longer than those of interstriae; epipleura covered with simple setae. Integument of ventral region light yellow, similar to dorsal region, short whitish plumose setae on prosternum, longer on mesosternum, and lateral of metasternum (Fig. 11C). Metepisternum covered with plumose setae, with a row of elongate and non-ramified setae on median region. Metasternum with a deep central concavity on base, with yellowish elongate setae on center.

Abdomen (Fig. 11C): Ventrites covered with yellowish non-ramified setae denser on laterals than center. Ventrites I-II connate in the middle; with a large depression in the center. Ventrite V trapezoidal, straight on apex. Terminalia. Pygidium (tergum VIII) (Fig. 11J) 1.8 times wider than long, with anterior margin straight and posterior margin rounded; long setae on apex, shortest setae posteriorly. Sternum IX (spiculum gastrale) (Fig. 11I) slender, straight for most of its length, except for the apex curved. Tegmen 1.2 times longer than aedeagus; tegminal apodeme straight; paremeres fused, apically membranous, with sparse setae. Aedeagus (Figs. 11G–H)5.9 times longer than wide at base, lateral margins parallel, apex strongly acute. Median lobe subequal in length to apodemes. Endophallus membranous, with a pocket of microtrichae on half apical region.

Female. Body size: 2.1–2.2 mm. Rostrum 0.9 times shorter than pronotum. Pronotum 1.1 times wider than long. Femora without elongate setae ventrally on basal third. Tibiae without mucro. Scutellum 1.3 times wider than long. Elytra 4 times longer than wide. Ventrites strongly

convex; ventrites I-II connate at the middle, without depression in the center; ventrite V rounded at apex. Terminalia. Pygidium (Tergum VIII) (Fig. 11E) triangular, 1.4 times longer than wide at base; anterior margin straight, apical margin rounded, with long setae concentrated near to apex. Sternum VIII (Fig. 11D) including apodeme, 3.1 times longer than coxites; lamina occupying posterior half, lateral arms sclerotized; with a row of long setae along lateral margins to apex, and several sensilla under the setae; lamina mesally membranous; apical region of lamina truncate, with a clear separation of arms, with minute setae; apodeme straight, apically bifurcated, gradually narrower towards apex. Coxites elongated, 8.5 times longer than wide. Styli not visible. Spermatheca (Fig. 11F) curved, about 1.6 times longer than wide; *cornu* rounded, *ramus* and *collum* close, pointing approximately in the same direction.

Examined material. Type material. Paratypes: BRAZIL: Amazonas: Manaus, Av. Theomario Pinto, Chapada, -3.092853, -60.028161, 20-29.xii.2021, D.P.P. Aguiar, manual (27 sex indet. CERPE); Manaus, Conjunto Petro Aleixo, -3.075569, -59.983078, 19.iii.2022, D.P.P. Aguiar, manual (37 sex indet. CERPE); Manaus, Igarapé do São Raimundo, São Jorge, -3.113931, -60.033072, 02.i.2022, Aguiar, manual (10 sex indet. CERPE).

Distribution. This species is known only from Manaus, Amazonas state, Brazil (Fig. 30B).

Host plants. *Udeus* sp. 8 was collected in staminate inflorescences of *C. membranacea* Trécul and *C. latiloba* Miq.

Remarks. The specimens examined appear to be teneral. They were fixed a few moments after emerging from the pupa, maintaining a lighter coloration and limited sclerotization of internal tissues.

***Udeus* sp. nov. 10 Lira & de Medeiros**

(Figs. 12, 28G, 29H, 30H)

Holotype: Male. PERU: Loreto: 80 km N. Iquitos, Explornapo Lodge, 1 km fro Amazon R. on Rio Yanamono, 25-28Aug1992, J. Castner, P. Skelley (ASUCOB).

Diagnosis. *Udeus* sp. nov. 10 is distinguished from other *Udeus* species by the following characters: robust rostrum; long antennomeres I and II of funicle (Fig. 28G); robust metafemora, with a short spine ventrally; ventrites with elongate setae in central region; ventrite V convex, with a set of elongate setae centrally directed backward, forming a bifurcation on the proximal region (Fig. 12C); aedeagus slender, with two short lobes forming a bifurcation (Fig. 12D); parameres of the tegmen fused in almost length but bifurcated on apex (Fig. 12F). This species resembles a spotted variation of *U. cecropiae* (Figs. 5D–E), presenting a similar pattern of transversal bands on elytra, although *Udeus* sp. nov. 10 presents the posterior band oblique and interstriae densely covered with setae.

***Description*.** Male. Body size: 3.9 mm. Head: Rostrum (Fig. 12B) yellowish to brown, lacking longitudinal carina; slightly curved; scrobe almost reaching eye margin; apex with elongate setae denser dorsally; decumbent setae arranged transversely from antennal insertion to base and directed forward on apex; base with dense non-ramified setae concentrated. Eyes (Fig. 12B) 1.3 times higher than wide, 1.8 times more separated above than below. Head with integument color yellowish to dark brown; non-ramified setae concentrated from the base of rostrum to interorbital region; interorbital region setae longer than base of head. Antennae (Fig. 28G) with scape straight, apex dilated, extends near to posterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 1.6 times longer than antennomeres II and III which are subequal in length; antennomeres II and III 1.3 times longer than antennomeres IV, VI and VII, subequal in length;

antennomere V shortest, 0.4 times shorter than antennomere I; club three-segmented, 2.6 times longer than wide. Mandibles non-exodont, symmetric, as long as wide, with three teeth.

Thorax: Pronotum (Figs. 12 A–C) transverse, as long as wide, lateral margins subparallel, with shallow transversal sulcus on median region; tegument yellowish to brown; covered by three types of setae: whitish plumose on base, short yellowish decumbent directed to center, and yellowish elongated next to apical constriction, on margins, and in the center. Pro- and mesocoxae covered by plumose setae. Femora with a set of elongate setae on base. Pro- and mesotibiae with mucro; metatibiae (Fig. 29H) margin internally sinuous, elevated on center region. Tarsus (Fig. 29H) elongate; first tarsomere 1.3 times longer than II, tarsomere III 0.2 times shorter than I; last tarsomere damaged. Scutellum (Fig. 12 A) triangular, 1.1 times wider than long; integument yellowish to brown; covered with dense whitish plumose setae. Elytra (Figs. 12A–B) 3.5 times longer than wide, 3 times longer, and 1.7 times wider than pronotum; with two transversal dark bands, anteriorly on humeri region and middle region, and a longitudinal darker band on elytral suture; lateral margins subparallel; interstriae covered by dense non-ramified setae; striae punctate with tiny yellowish setae, similar to those interstriae, inserted in each puncture; setae on interstriae elongate yellowish setae bifid at apex on odd interstriae, alternating with sets of plumose setae; epipleura incomplete, covered by short plumose setae on anterior region and non-ramified setae posteriorly. Ventral region (Fig. 12C) yellowish to dark brown; prosternum with whitish plumose setae; metepisternum with whitish plumose setae; metasternum with a distinct, deep central concavity extending into the abdomen; vestiture next to concavity border short whitish plumose setae with some elongate non-ramified setae intercalated; center of metasternum with elongate yellowish non-ramified setae.

Abdomen (Fig. 12C): Ventrites I–II covered by whitish plumose setae on laterals and elongate yellowish setae on borders of concavity; Ventrites III–V covered by whitish setae, elongate

setae in central region, no plumose setae; Ventrite V laterally compressed, trapezoidal, straight on apex. Terminalia: Pygidium (Tergum VIII) (Fig. 12H) subequal in length and width at base; anterior margin curved; posterior margin rounded; setae dense elongate setae apically, sparse, and short anteriorly. Tegmen (Fig. 12F) shorter than aedeagus; tegminal apodeme slender, slightly sinuate on apex; parameres almost completely fused. Aedeagus (Figs. 12D–E) 13 times longer than wide at base; slender, apically bifurcate; ventral plate sclerotized with several sensilla on apical third. Endophallus with a pocket containing microtrichae from base to apex.

Female unknown.

Examined material. Type material. Paratypes: BRAZIL: Amapá: Serra Lombard Limão, 30Aug1961, J. & Bechyné, USNMENT01735800 (NMNH). Amazonas: Fonte Boa, Sep1975, F.M. Oliveira (ASUCOB). PARÁ: Pará-Utinga, 3Dec1960, Bechyné, USNMENT01735850 (NMNH). RONDÔNIA: 62 km SW Ariquemes, nr. FZDA Rancho Grande, 3-15Dec1996, JE Eger, UV trap (CERPE); creek 8 km. S of Cacaulandia, 21nov.1991, D. Petr, light trap, USNMENT01735841 (NMNH). Mato Grosso: Sinop, 12 31 S, 55 37 W, Oct1976, M. Alvarenga (ASUCOB). **PERU:** Loreto: 80 km N. Iquitos, Explornapo Lodge, 2#m (# specimens), 25-28Aug1992, J. Castner, P. Skelley (ASUCOB); 14 km NE Iquitos, 1#f, 16Feb1984, W. E. Clark (ASUCOB); Madre de Dios, nr. Puerto Maldonado, Posada Amazonas, lodge @RT ambopata, 12 48 115 S, 69 18.019 W, 07-10Oct2004, C. R. Bartlett (ASUCOB), Rio Tambopata Res; 30 air km. SW Pto Maldonado, 290 m, 2-5Nov1979, J.B. Heppner, USNMENT01735838 (NMNH); Junin between San Ramon de Pangoa and Boca de Kiatari, 40-5 km SE Satipo, 750 m, 4mar.1972, R.T. & J.C. Schuh (AMNH). **ECUADOR:** Napo: Limoncocha, on Rio Napo, 300 m, 15nov.1974, 15nov.1974, blacklight trap (ASUCOB); **COLOMBIA:** Meta: Restrepo, 02Oct1965, J. A. Ramos (ASUCOB); Amazonas: Leticia, 15-16Jan1973, C. R. Gilbert, blacklight trap (ASUCOB). **VENEZUELA:** T.F. Amazon.

Cerro de La Neblina Basecamp., 0°50'N, 66°10'W, 140 m, P.J. & P.M.Spangler, R.A. Faitoute, W.E. Steiner, USNMENT01735836 (NMNH). **GUYANA:** Bartica Demerara, 1933, USNMENT01735815-01735819 (NMNH); Mazaruni - Potaro District, Takutu Mountains, 6°15'N, 59°5'W, 3-10Dec1983, Earthwatch Expedition: W.E. Steiner & P.J. Spangler, USNMENT01735847 (NMNH); Bartica Brit., F.C.Bowdittch, MCZ-ENT00795561 (MCZ). **FRENCH GUIANA:** Amazon Nature Lodge 30 km SE Roura on Kaw Rd., 04 33.570 N, 052 12.433 W, 300 m, 5-19Feb2010, J.E. Eger, UV trap (ASUCOB).

Distribution. This species is widely distributed in South America, in French Guiana, Guyana, Venezuela, Colombia, Ecuador, Peru, and Brazil.

Host plant. Unknown.

Remarks. Many specimens of *Udeus* sp. nov. 10 were collected using light trap, and this species occurs in sympatry in Rondônia (Brazil) with *Udeu*s sp. nov. 11, *Udeus* sp. nov. 22, and *Udeus* sp. nov. 26. In Napo (Ecuador), *Udeus* sp. nov. 10 occurs in sympatry with *Udeus* sp. nov. 17, *Udeus* sp. nov. 19, *Udeus* sp. nov. 21 and *Udeus* sp. nov. 26. Putative females are not included in the description due to the morphological similarity to sympatric species.

***Udeus* sp. nov. 11 Lira & de Medeiros**

(Figs. 13, 30C)

Holotype: Male. PANAMA: Panama: km 7.5-9 Llano-Cariti Road, 28jul.1995, CW & L O'Brien (ASUCOB).

Diagnosis. *Udeus* sp. nov. 11 can be distinguished from other *Udeus* species by the dark rostrum (Fig. 13B), contrasting with the rest of the body which is ochre; integument bright; posterior half of funicle and club dark brown (Fig. 13A); antennomere VI of funicle wider than first antennomere; pronotum with straight border after apical constriction; scutellum U-shaped; postfemora with large teeth. This species is similar to *Udeus* sp. nov. 12 (Fig. 14) by the brightness of integument and coloration, and *Udeus* sp. nov. 15 (Fig. 15) by the scarce setae on integument.

Description. Male. Head: Rostrum (Fig. 13B) 1.3 times longer than pronotum, 1.2 times wider at apex than at base; integument dark brown; longitudinal carina absent; scrobe proximity to eye not reaching eye margin; apex with scarce elongate setae; setae short, scarce, and evenly arranged along rostrum; base with sparse, unramified setae inserted on discrete punctation; sulcus near median carina absent. Eyes (Figs. 13B–C) subequal in width and height. Head with integument ochre; setae sparse, short, non-ramified, inserted on discrete punctation above eyes and interorbital region. Antennae (Figs. 13A–C) with funicle seven segmented; antennomere I longer and wider than others, 1.3 times longer than antennomeres II; antennomere II 1.4 times longer than III and VI, subequal in length; antennomere V shortest, 0.3 times shorter than antennomere I; club three-segmented, 2.9 times longer than wide. Mandibles non-exodont, symmetric.

Thorax: Pronotum (Figs. 13A–C) transverse, 1.1 wider than long; lateral margins subparallel without transverse sulcus on median region; integument ochre; vestiture with abundant short, yellowish, unramified setae evenly distributed in discrete punctation. Pro- and mesocoxae covered by plumose and non-ramified setae. Femora with a set of scarce elongate setae on base. Tibiae with short mucro; internal margin of metatibiae slightly sinuose, with a set of elongate setae on apex. Postfemora with large teeth, larger than the others. Tarsus elongate, first tarsomere 0.8 shorter than II, tarsomere III 0.8 times shorter than I; last tarsomere longer than others, 1.7 times longer than

tarsomere I. Scutellum (Fig. 13A) 1.2 times longer than wide; with distal region rounded, in U-shaped; integument brown; covered with yellowish plumose setae. Elytra (Figs. 13A–B) 1.8 times longer than wide; humeri rounded, similar color of all elytra; lateral margins subparallel; interstriae covered by dense short non-ramified setae; striae punctate with tiny yellowish setae, similar to those in interstriae, inserted in each puncture; interstriae covered by dense short non-ramified setae; epipleura incomplete, covered by short setae. Ventral region (Fig. 13C) with integument yellowish. Prosternum with scarce yellowish non-ramified setae. Metepisternum covered with whitish plumose setae and fewer elongate setae. Metasternum with central concavity slight, extends into abdomen; yellowish non-ramified setae next to concavity border, scarce yellowish shorter non-ramified setae on center.

Abdomen (Fig. 13C): Ventrites I–II vestiture evenly covered by yellowish non-ramified setae; ventrites III–V evenly covered by yellowish non-ramified setae; ventrite V trapezoidal, straight on apex. Terminalia. Pygidium (Tergum VIII) (Fig. 13J) 1.4 times wider than long; anterior margin straight; posterior margin rounded; elongate setae concentrated on posterior half, more sparse on basal region. Sternum IX apodeme (spiculum gastrale) (Fig. 13I) 0.5 times shorter than aedeagus; apically acute. Tegmen 0.5 times shorter than aedeagus; tegminal apodeme slender, slightly sinuose on median region. Aedeagus (Figs. 13G–H) 8.8 times longer than wide at base; margins parallel from base to apical third, apex rounded laterally, with a short acute projection on center; ventral plate strongly sclerotized. Median lobe and apodemes subequal in length; endophallus with a pocket containing microtrichae on median region.

Female: Rostrum 1.3 times longer than pronotum. Pronotum 1.2 times longer than wide. Femora without elongate setae ventrally on basal third. Tibiae without mucro. Scutellum 1.3 times wider than long. Elytra 1.7 times longer than wide. Ventrites strongly convex; ventrites trapezoidal, slightly sinuous on apex. Terminalia. Tergum VIII (pygidium) (Fig. 1D) triangular, subequal in

length and width, anterior margin straight, rounded apex; covered with short setae, longer on apex. Sternum VIII (Fig. 13F), including apodeme, about 5 times as long as coxites; lamina occupying posterior third; lateral arms and a central band sclerotized; apex almost truncate. Coxites and styli not visible. Spermatheca (Fig. 13E) strongly curved, 2.4 times as longer than wide; *ramus* and *collum* pointing in the same direction.

Examined material. Type material. Paratypes: **PANAMA:** Panama: km 7.5-9 Llano-Cariti Road, 28jul.1995, CW & L O'Brien (1f# CERPE). San Blas, Nusangandi, 250-350 m (2m#, 1f#, 1 indet. sex FMNH), 26jul.1995, CW & L O'Brien, at light (1 FMNH); **BRAZIL:** Rondônia: 62 km SW Ariquemes, Fzda. Rancho Grande, 5-17Oct1993, JE. Eger, UV trap (1m# ASUCOB).

Distribution. This species is known from Panama, in Panama and San Blas provinces, and from Brazil in Rondônia state (Fig. 30C).

Host plant. Unknown.

***Udeus* sp. nov. 12 Lira & de Medeiros**

(Figs. 14, 28H, 29I, 30D)

Holotype: Male. PANAMA: Cólon: Gamboa, 9.119868, -79.698041, 01Jul2021, B.A.S. de Medeiros (FMNH).

Diagnosis. *Udeus* sp. nov. 12 can be distinguished from other *Udeus* species by mandibles with two internal teeth; pronotum with laterals rounded after apical constriction (Fig. 14A); elytra elongate with laterals parallel from humeri to apical third; femora with tiny ventral teeth, posfemur more robust, with center region of external margin elevated and internal margin straight; males with

metatibiae with a projection on apex anteriorly to mucro (Fig. 29I); singular aedeagus very constricted on apex and curved ventrally; the membranous junction between apodemes and median lobe, similar to an articulation (Figs. 14 G–H).

Description. Male. Body size: 2.2 mm. Head: Rostrum (Figs. 14B–C) 0.7 times shorter than pronotum; apex width subequal to base; integument brown; longitudinal carina absent; scrobe reaching posterior eye margin; apex with scarce elongate setae; setae decumbent, arranged transversely from antennal insertion to near base on laterals, directed backward on base, very scarce; longitudinally glabrous and smooth; base with sparse, non-ramified setae, inserted on distinct punctation. Eyes (Figs. 14A–C) 1.1 times higher than wide; 2 times more separated above than below. Head with integument brown, similar to rostrum; setae short, non-ramified, inserted on distinct punctation above eyes and in interorbital region, with 2-3 elongate, brownish setae near to inner margin of each eye, short plumose setae laterally and ventrally. Antennae (Fig. 28H) with scape straight extending beyond posterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 2.3 times longer than antennomere II; antennomere II and III subequal in length, 1.5 times longer than antennomeres III, V, VI, and VII which are subequal in length; club 2.3 times longer than wide; club 2.7 times longer than wide. Mandibles endodont, symmetrical, with two teeth, 1.2 times longer than wide.

Thorax: Pronotum (Figs. 14A–C) transverse; 1.3 times wider than long; lateral margins rounded, with shallow depression on median region; integument color ochre; covered with yellowish short setae scarcely distributed in distinct punctation on disc, scarcer on median line, scarce short whitish plumose setae laterally on base, four yellowish elongated setae next to apical constriction. Pro- and mesocoxae covered by non-ramified setae and scarce plumose setae. Femora evenly covered with scarce setae, with tiny ventral teeth; posfemur more ampliate, with external

margin very sinuose, with central region more elevated, and internal margin almost straight. Tibiae with mucro present, large on meso- and metatibiae; internal margin of metatibiae sinuose, with a projection on apex anteriorly to mucro, with a set of elongate setae immediately before the apical projection (Fig. 29I). Tarsus (Fig. 29I) elongate, almost tibia length; tarsomere I 1.4 times longer than II, tarsomere III 0.4 times shorter than I; last tarsomere longer than rest, 1.6 times longer than tarsomere I. Scutellum 1.2 times longer than wide; integument ochre; covered with non-ramified setae, plumose setae on borders. Elytra (Figs. 14A–B) 3.7 times longer than wide; 3.5 times longer, and 1.4 wider than pronotum; humeri rounded, similar color of elytra; lateral margins subparallel; interstriae covered by dense short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae, scarcely on apex near to elytral suture. Epipleura incomplete, covered by short setae. Integument of ventral region ochre, similar to pronotum (Fig. 14C). Prosternum with scarce whitish short plumose setae. Metepisternum basally covered with yellowish non-ramified setae, with very scarce plumose setae posteriorly. Metasternum with slight central concavity, extends into abdomen; scarce yellowish non-ramified setae near to concavity border, very scarce yellowish non-ramified setae on center.

Abdomen (Fig. 14C): Ventrites I–II covered by yellowish non-ramified setae, more elongate centrally on posterior margin. Ventrites III–V covered by whitish non-ramified setae, denser laterally. Ventrite V covered by yellowish non-ramified setae, with a row of elongate setae apically; trapezoidal, sinuose on apex. Terminalia: Pygidium (Tergum VIII) (Fig. 14K) 1.1 times wider than long; anterior margin almost straight, with a slight depression in center; posterior margin sinuose; setae elongate on lateral margins, sparser on median region, abundant shorter setae on apex. Ventral flap wide, with a large depression on central region. Sternum IX apodeme (spiculum gastrale) (Fig. 14J) 0.6 times shorter than aedeagus; apodeme anteriorly very expanded in lateral view; posteriorly slightly expanded to sides. Tegmen (Fig. 14I) 0.4 times shorter than aedeagus; tegminal apodeme

slender, straight; parameres fused, enlarged, apically slightly acuminate. Aedeagus (Figs. 14G–H) 10 times longer than wide at base; margins parallel from base to median third, funneling to apex, apex curved ventrally in lateral view; ventral plate strongly sclerotized. Median lobe 1.7 times longer than apodemes; membranous junction between apodemes and median lobe, similar to an articulation; endophallus with a pocket containing microtrichia on apex.

Female. Body size: 2.6 mm. Rostrum subequal in length to pronotum; width at apex subequal at base. Pronotum 1.4 times wider than long. Scutellum 1.2 times longer than wide. Elytra 4.8 times longer than wide; 1.3 times wider than pronotum; 4.2 times longer than pronotum. Ventrite V trapezoidal, apex rounded, centrally with a rounded projection between two triangular projections. Coxites and styli not visible. Spermatheca (Fig. 14E) 1.1 times wider than long; cornu slightly curved; *collum* reduced; *ramus* very short, pointing in the same direction as collum.

Examined material. Type material. Paratypes: **PANAMA:** Panama: Las Cumbres, 19May1976, H. Wolda, UV trap (1m# FMNH, 1 indet. sex ASUCOB); 2jun.1976, H. Wolda, UV trap (1 sex indet. FMNH). Cólon: Gamboa, 9.119868, -79.698041, 01Jul2021, B. de Medeiros (5 sex indet. FMNH).

Distribution. This species is known only from Panama (Fig. 30D).

Host plant. *Cecropia longipes* Pittier.

Remarks. In some specimens, the apodemes of the aedeagus and tegmen as well as spiculum gastrale are more robust.

***Udeus* sp. nov. 15 Lira & de Medeiros**

(Figures 15, 30D)

Holotype: Male. PANAMA: Panama: Cerro Campana, 1m#, 26may.1972, W. Bivin, USNMENT1735830 (USNM).

Diagnosis. This species can be distinguished from other *Udeus* species by the darker color of all body, bright tegument (Figs. 15A–C), scarce non-ramified setae; without longitudinal sulcus on pronotum; interstriae without a row of elongate setae intercalating with others (Fig. 15A).

Description. Body size: 3.8 mm. Head: Rostrum (Figs. 15A–C) 0.8 times shorter than pronotum; apex 1.1 times wider than base; integument black; longitudinal carina and sulcus absent; scrobe not reaching eye margin; apex with scarce elongate setae; decumbent setae arranged transversely from antennal insertion to base on laterals and directed forward on apex; base with sparse non-ramified setae. Eyes (Fig. 15A) 1.05 higher than wide; 1.5 times more separate above than below. Head with integument black; Setae concentration on the head is short, non-ramified, and scarce setae on interorbital region, with elongate bifurcate seta above eyes, one on each side. Antennae with funicle seven segmented; antennomere I longer and wider than others, 1.3 times longer than antennomere II; antennomere II 1.5 times longer than antennomeres III, antennomeres IV and VII subequal in length, 0.4 times shorter than antennomere I; antennomere V shortest, 0.2 times shorter than I; club 2.7 times longer than wide. Mandibles endodont, symmetric.

Thorax: Pronotum (Fig. 15A) transverse; subequal in length and width; lateral margins subparallel, without transversal sulcus on median region; integument black, covered by yellowish decumbent setae inserted in each punctuation evenly distributed. Pro- and mesocoxae covered by non-ramified setae. Femora with a set of elongate setae on the base. Tibiae with mucro; internal margin of metatibiae slightly sinuose, with a set of elongate setae in the apical third. Tarsus elongate, subequal in length to tarsomere II, tarsomere III 0.5 times shorter than I; last tarsomere

longer than rest, 1.5 times longer than tarsomere I. Scutellum with integument black, covered with yellowish non-ramified setae. Elytra (Figs. 15A–B) 1.9 times longer than wide; humeri rounded, lateral margins subparallel; interstriae covered with scarce non-ramified setae; striae punctate with tiny yellowish setae, similar to those on interstriae, inserted in each puncture; setae on interstriae without a row of elongate setae intercalating with others; epipleura incomplete, with scarce yellowish setae. Integument of ventral region of thorax dark brown (Fig. 15C); prosternum and metasternum covered with yellowish non-ramified setae; central concavity of metasternum distinct, extends into abdomen, bordered by yellowish elongate non-ramified setae; vestiture on the center scarce, with yellowish elongate non-ramified setae.

Abdomen (Fig. 15C): Ventrites length I–II covered with yellowish setae on laterals, shorter and scarcer on the concavity; ventrites III–V evenly covered by yellowish setae, with no plumose setae; ventrite V laterally compressed and trapezoidal, with straight apex. Terminalia: Pygidium (Tergum VIII) (Fig. 15K) width subequal to length; anterior margin straight; posterior margin rounded; setae concentrated on posterior half, longer apically. Sternum IX (Spiculum Gastrale) (Fig. 15J) 0.9 times shorter than aedeagus; apically expanded to sides, straight along length, slightly curved on apex. Tegmen (Fig. 15I) 0.6 times shorter than aedeagus; tegminal apodeme slender, straight; parameres fused. Aedeagus (Figs. 15G–H) 8.4 times longer; parallel on laterals, slightly constricted at middle, funneling and acute at apex; ventral plate sclerotized; median lobe 1.1 times longer than apodemes; endophallus with a pocket containing microtrichia on median region, bifurcated to apex.

Female. Body size: 4.3 mm. Rostrum 0.9 times shorter than pronotum; width subequal in apex and base. Pronotum 1.3 times longer than wide. Elytra 1.7 times longer than wide. Metasternum with sulcus slight, in the basal region. Femora with elongate ventral setae on the base. Ventrites convex, ventrite V trapezoidal, straight on apex. Terminalia. Tergum VIII (pygidium)

(Fig. 15D) triangular, 1.2 times wider than long, anterior margin straight, rounded apex; long setae on apical third, shorter posteriorly. Sternum VIII (Fig. 15F), including apodeme, about 4.3 times as long as coxites; lamina occupying posterior third; lateral arms and a central band sclerotized. Coxites and styli not visible. Spermatheca (Fig. 15E) curved, about 2.4 times as long as wide; *ramus* and *collum* not pointing in the same direction.

Examined material. Type material. Paratype: PANAMA: Panama: Cerro Campana, 16jul.1976, Wayne E. Clark, USNMENT1735829 (1f# USNM).

Distribution. This species is known only from the type locality (Figure 30D).

Host plant. Unknown.

Remarks. This distinct species of *Udeus* exhibits a remarkably bright integument with sparse setae. In the male specimen, the tarsi were damaged, and the mandibles were closed, precluding their description in this study.

***Udeus* sp. nov. 16 Lira & de Medeiros**

(Figs. 16, 30E)

Holotype: Male. PANAMA: Barro Colorado: Canal Zone, Barro Colorado Is., 5-May-77, Silberglied/Aiello, at light, USNMENT1735828 (USNM).

Diagnosis. This species can be distinguished from other *Udeus* species by the bright integument with scarce setae; pronotum with rounded margins without a transversal sulcus (Figs. 16A–B); epipleura without setae; interstriae without a row of elongate setae intercalating with others;

aedeagus singular, with median lobe contained large spines and apex robust and strongly curved in lateral view (Figs. 16D–E); apodeme of the spiculum gastrale expanded anteriorly visible in lateral view (Fig. 16F). This species resembles *Udeus* sp. nov. 18 (Fig. 18) and both species largely distinguished from other *Udeus* species by the format of pronotum, with rounded laterals, tegument bright with scarce setae, and elytra with divergent apex; the genitalia is closed, with apodeme of spiculum gastrale expanded on apex, and pygidium with a circular depression near the center.

Description. Body size: 4.9 mm. Head: Rostrum (Figs. 16A–C) 1.2 times longer than pronotum; 1.2 times wider at apex than at base; integument dark brown; longitudinal carina and sulcus absent; scrobe not reaching eye margin; apex with scarce elongate setae; setae short, scarce, and evenly arranged along the length; base with sparse, unramified setae inserted on distinct punctation. Eyes (Figs. 16A–C) 1.1 times wider than height; 1.7 times more separated above than below. Head with integument dark brown, setae sparse, short, non-ramified, and inserted on distinct punctation in interorbital region and above eyes. Antennae with funicle seven segmented; antennomere I longer and wider than others, 1.5 times longer than antennomere II; antennomere II subequal in length to VI, 0.9 times shorter than antennomeres III; antennomeres V shortest, 0.5 times shorter than I; club 1.6 times longer than wide. Mandibles endodont, symmetric, with two large teeth on internal margin.

Thorax: Pronotum (Figs. 16A–B) transverse; 1.2 times wider than long; lateral margins slightly rounded without a transversal sulcus; integument brown; covered with sparse, short, yellowish, unramified setae evenly distributed in discrete punctation. Pro- and mesocoxae covered by scarce plumose setae and abundant non-ramified setae. Femora with a set of scarce elongate setae at the base. Tibiae with a short mucro; metatibiae with an internal margin slightly sinuous, ampliated in direction of the apex, and a set of elongate setae in the apical third. Tarsus elongate,

first tarsomere 1.3 times longer than II and III, subequal in length; last tarsomere longer than rest, 2.1 times longer than tarsomere I. Scutellum (Fig. 16A) 1.4 times longer than wide; integument yellowish; covered with elongate yellowish setae. Elytra (Figs. 16A–B) 3.7 times longer than wide; 3.1 times longer, and 1.4 times wider than pronotum; integument brown; humeri rounded, subparallel lateral margins, similar color of elytra; one row of elongate setae distant from each other in interstriae, and punctate striae with tiny yellowish setae inserted in each puncture; epipleura without setae; integument of ventral region yellowish to light brown (Fig. 16C). Prosternum and metepisternum with yellowish non-ramified setae; central concavity on metasternum distinct, extending into the abdomen, with yellowish elongate non-ramified setae near the concavity border and scarce yellowish shorter non-ramified setae on the center.

Abdomen (Fig. 16C): Ventrites I–II covered by elongate yellowish setae on borders of concavity, more abundant than laterals; ventrites III–V covered by yellowish setae, denser in the lateral region, without plumose setae; ventrite V trapezoidal in shape, slightly sinuous on apex, with elongate yellowish setae on center directed backward, smaller on laterals. Terminalia: Pygidium (Tergum VIII) (Fig. 16G) 1.2 times wider than long, with a circular depression near the center; anterior margin straight, with laterals expanded into two lobes; posterior margin rounded; setae elongate and denser on apical third, directed to center; shorter and scarcer on median region, denser on laterals. Sternum IX (spiculum gastrale) (Fig. 16F) 0.7 times shorter than aedeagus; apodeme anteriorly very expanded in lateral view; posteriorly slightly expanded to sides. Aedeagus (Figs. 16D–E) 3.4 times longer; parallel on laterals, apex bisinuate, robust and strongly curved in lateral view; ventral plate strongly sclerotized; median lobe 1.1 times longer than apodemes; endophallus with a pocket with microtrichae and 9 larger spines distributed along extension.

Female unknown.

Examined material. Only the holotype was examined.

Distribution. This species is known only from the type locality (Fig. 30E).

Host plant. Unknown.

***Udeus* sp. nov. 17 Lira & de Medeiros**

(Figs. 17, 28I, 29J, 30C)

Holotype. Male. ECUADOR: Napo: vic. Puerto Misahueli, 1°N, 77°E, 500-580m, 6-19Sep1998, J.E. Eger (ASUCOB).

Diagnosis. *Udeus* sp. nov. 17 distinguishes from other *Udeus* species by the following characters: robust rostrum (Fig. 17B); femora with elongate setae from base to a ventral tooth; metatibiae abruptly dilated on the apex, with a set of elongate setae on each side of the dilatation (Fig. 29J); ventrites II-V with distinct centrally projections, ventrite V with a triple projection (Figs. 17B–C); pygidium with a large triangular projection centrally between two small triangular projections directed externally (Fig. 17F).

Description. Body size: 2.7–3.1 mm. Head: Rostrum (Fig. 17B) 0.8 times as long as pronotum; 0.9 times narrower at apex than at base; with integument light to dark brown; with a longitudinal carina present from interorbital region above eyes to median region; scrobes reaching near posterior eye margin; apex with scarce elongate setae; base with sparse, unramified setae inserted on distinct punctation; sulcus near median carina absent. Eyes (Figs. 17A–C) 1.05 times as high as wide; 1.4 times more separated above than below. Head with integument dark brown, lighter on interorbital region; posterior and interorbital regions with setae sparse, short, non-ramified, inserted on distinct

punctation. Antennae (Fig. 28I) with scape straight, apex dilated, extends near to posterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 1.2 times longer than antennomere II; antennomere II 2 times longer than antennomeres III, V and VII which are subequal in length; antennomeres IV and VI subequal in length and 1.3 times longer than III, V and VII; club three-segmented, 2.6 times longer than wide. Mandibles endodont, symmetric; 1.6 times longer in length-to-width ratio; with three teeth on internal margin.

Thorax: Pronotum (Figs. 17A–B) transverse; subequal in width and length; lateral margins subparallel with shallow transversal sulcus on median region; integument color yellowish to dark brown; vestiture covered with short whitish setae abundantly distributed in distinct punctation, base with ramified setae shorter on lateral than center. Procoxae and Mesocoxae covered by plumose setae and scarce non-ramified setae. Femora with a set of scarce elongate setae on base. Tibiae with short mucro. Metatibiae (Fig. 29J) with internal margin sinuose, abruptly dilated on apex, with a set of elongate setae on each side of the dilatation. Tarsus (Fig. 29J) elongate, subequal metatibiae in length; tarsomere I 1.2 times longer than II, tarsomere III 0.5 times shorter than I; last tarsomere longer than rest, 1.1 times longer than tarsomere I. Scutellum (Fig. 17A) 1.5 times longer than wide, integument brown, covered with whitish plumose setae. Elytra (Figs. 17A–B) 3.4 times longer than wide; 1.8 times wider and 3 times longer than pronotum; humeri rounded, same color as most of elytra; lateral margins subparallel; interstriae covered by dense short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae; striae punctate with tiny whitish setae, similar to those in interstriae, inserted in each puncture; epipleura incomplete, covered by short plumose setae on anterior region and non-ramified setae posteriorly. Ventral region (Fig. 17C) integument color similar to elytra. Prosternum with abundant yellowish short, ramified setae. Metepisternum covered with whitish plumose setae, with fewer elongate setae posteriorly. Metasternum with a distinct central concavity, extends into abdomen; vestiture next to

concavity border with short whitish plumose setae with some elongate non-ramified setae intercalated; vestiture on center with scarce elongate whitish non-ramified setae.

Abdomen (Fig. 17C): Ventrites I–II covered by whitish non-ramified setae, more elongate on borders of concavity than laterals on ventrite I, ventrite V trapezoidal, straight on apex, with a triple projection. Terminalia: Pygidium (Tergum VIII) (Fig. 17F) 1.1 times longer than wide; anterior margin slightly sinuose; posterior margin irregular, with a large triangular projection centrally between two small triangular projections directed externally; rounded laterally; elongate setae, densely concentrated on central projection and moderately concentrated on median region, scarce setae on basal third. Sternum IX (Spiculum Gastrale) (Fig. 17F) 0.9 times shorter than aedeagus, apically expanded to sides. Tegmen 0.7 times shorter than aedeagus; tegminal apodeme slender, straight. Aedeagus (Figs. 17D–E) 6.8 times longer than wide at base, slightly constricted at middle; apex straight, slightly rounded on laterals; apex flat in lateral view; ventral plate strongly sclerotized. Median lobe 1.6 times longer than apodemes. Endophallus with a bifurcate pocket containing microtrichia on apical half.

Female unknown.

Examined material. Paratypes: ECUADOR: Napo: vic. Puerto Misahueli, 1°N, 77°E, 500-580m, 6-19Sep1998, J.E. Eger (1m# CERPE; 2m# FMNH). **PERU:** Madre de Dios: nr. Puerto Maldonado, Posada Amazonas lodge@RTambopata, 12°N, 69°E, 7-10Oct2004, C.R. Bartlett (1m# ASUCOB).

Distribution. This species is known from Ecuador, in Napo, and from Peru, in Madre de Dios (Fig. 30C).

Host plant. Unknown.

Remarks. Despite the examining of putative female specimens, their inclusion in the description was omitted as they exhibit morphological traits indistinguishable from other species such as *U. variabilis*, *Udeus* sp. nov. 10, *Udeus* sp. nov. 19, and *Udeus* sp. nov. 21.

***Udeus* sp. nov. 18 Lira & de Medeiros**

(Figs. 18, 30C)

Holotype. Male. TRINIDAD: WI: Arima Valley, 800-1200 ft, 22Feb1966, J.G. Rozen (AMNH).

Diagnosis. This species can be distinguished from other *Udeus* species by the ventrite V with elongate yellowish setae and a sinuous apex with a central projection (Fig. 18C); metatibiae with large setae apically on both sides; pygidium with a large sulcus near the center (Fig. 18I); asymmetric tegmen (Fig. 18F); aedeagus singular, with apex curved dorsally (Fig. 18E). *Udeus* sp. nov. 18 shares with *Udeus* sp. nov. 16 (Fig. 16) the pronotum with rounded laterals, the tegument bright with scarce setae, and the elytra with divergent apex; the spiculum gastrale expanded on apex and pygidium with a circular depression near the center.

Description. Head: Rostrum (Figs. 18A–C) dark brown; lacking longitudinal carina; scrobe reaches eye margin; apex with scarce elongate setae; decumbent setae arranged transversely from antennal insertion to base on laterals, and directed forward on apex; base with scarce non-ramified setae; sulcus near median carina absent; integument color brown; non-ramified setae concentrated from the base of rostrum to interorbital region and laterally near eyes; interorbital region with longer setae than base of head. Antennae with funicle seven segmented; antennomere I longer and wider than others, 1.4 times longer than antennomere II; antennomere II 2,2 times longer than antennomeres III, 1.5 times longer than IV and VI, subequal in length, antennomere V shortest, 0.2

times shorter than antennomere I, antennomere VII almost length to VI; club three-segmented, 2.2 times longer than wide. Mandibles non-exodont and symmetric.

Thorax: Pronotum (Figs. 18A–B) transverse in shape; lateral margins subparallel, and slightly rounded on curvature after apical constriction; without transverse sulcus on median region; integument color brown; covered by yellowish elongate setae inserted in sparse punctuations, more sparse on median line of disc; procoxae and mesocoxae covered by non-ramified setae; femora evenly covered by elongate setae; tibiae with obsolete mucro; metatibiae with a slightly sinuous internal margin; metatibiae evenly covered by elongate setae; scutellum integument color brown; covered with dense yellowish setae; humeri rounded, elytral suture and apical region darker; elytra lateral margins subparallel; interstriae covered by scarce non-ramified setae; striae punctate with elongate yellowish setae, similar to those on interstriae, inserted in each puncture; interstriae with elongate brownish acuminate setae alternating with other setae; epipleura incomplete, with scarce yellowish setae; ventral region integument (Fig. 18C) color brown, slightly darker than dorsal region; prosternum and metepisternum covered with yellowish non-ramified setae; metasternum with distinct, deep central concavity extending into abdomen; vestiture next to the concavity border with yellowish elongate non-ramified setae; central region of metasternum with scarce yellowish elongate non-ramified setae.

Abdomen (Fig. 18C): Ventrites length I–II are evenly covered by yellowish non-ramified setae; ventrites III–V are covered by yellowish setae, denser in the lateral region, with no plumose setae; ventrite V with elongate yellowish setae and a sinuous apex with a central projection, trapezoidal. Terminalia: Pygidium (Tergum VIII) (Fig. 18I) 1.1 times longer, with a large sulcus near center; anterior margin straight; posterior margin rounded; setae elongate, concentrated posteriorly on laterals. Sternum IX (Spiculum Gastrale) (Figs. 18G–H) 0.8 times shorter than aedeagus; posterior region expanded in lateral view; anteriorly expanded to sides; with two

posterior plates fused. Tegmen (Fig. 18F) with tegminal apodeme sinuose, slightly amplified on apex; parameres sclerotized on base and centrally. Aedeagus (Figs. 18D–E) 8.7 times longer than wide at base; parallel on laterals, slightly constricted at middle, funneling at apex; apex acute, curved ventrally in lateral view; ventral plate sclerotized. Median lobe 1.7 times longer than apodemes; endophallus with a pocket containing microtrichia on basal half.

Female unknown.

Examined material. Paratype: Holotype. Male. TRINIDAD: WI: Arima Valley, 800-1200 ft, 19Feb1966, J.G. Rozen (AMNH).

Distribution. This species is known only from the type locality (Fig. 30C).

Host plant. Unknown.

Remarks. In the phylogeny of Eugnomini, the position of *Udeus* sp. nov. 16 and *Udeus* sp. nov. 18, forming a sister clade to the other *Udeus*, supports the morphological convergences observed in these two species and notable distinctions from other *Udeus* species, making them strong candidates to represent a new genus. This discovery presents convincing evidence for the possibility of these two species representing a new genus. However, further investigations are needed, including identification of the host plant of these taxa. As a result, we chose to maintain these species within the genus *Udeus*, pending further research.

***Udeus* sp. nov. 19 Lira & de Medeiros**

(Figs. 19, 28J, 29K, 30E)

Holotype: Male. ECUADOR: Napo: vic. Puerto Misahueli, 1°2’2.4”S, 77°39’49.2”W, 1650-1900 ft, 6-19Sep1998, J.E. Eger (ASUCOB).

Diagnosis. *Udeus* sp. nov. 19 can be recognized by black dorsal tegument (Figs. 19A–C); short and robust rostrum (Fig. 19B); antennae with escape, and proximal part of the funicle yellowish and distal part of the funicle and club dark (Figs. 19A–C); basal region of the femora, apical region of the tibiae and tarsi brown and rest darker (Figs. 19B–C)**;** metatibia with a dilatation on apex forming a dentiform projection on internal margin, with a set of elongate setae on external margin of the projection (Figs. 19A, 19C, 29K); ventrites III and IV bidentate centrally on posterior margin; pygidium with posterior margin rounded on laterals, with a depressed region on center. This species externally resembles to dark morphotypes of *U. cecropiae.*

Description. Male. Body size: 3.7 mm. Head: Rostrum (Fig. 19B) subequal in length to pronotum; 0.94 times narrower at apex than at base; integument dark brown, apex and median line lighter; with a longitudinal carina present from interorbital region above eyes to region of insertion of antennae; scrobes reaching near posterior eye margin; apex with scarce elongate setae; base with sparse, unramified setae inserted on distinct punctation; sulcus near median carina absent. Eyes (Fig. 19B) 1.3 times higher than wide; 2.3 times more separated above than below. Head integument dark brown, interorbital region lighter; posterior and interorbital regions with setae short, non-ramified, inserted on distinct punctation. Antennae (Figs. A–C, 28J) with scape straight, extending near posterior margin of eye; funicle seven segmented; antennomere I 1.2 times longer than antennomere II; antennomere II 2.2 times longer than antennomere III and V, subequal in length; antennomere IV subequal in length to antennomere VII and 1.2 times longer than antennomeres III and V; antennal club 2.2 times longer than wider. Mandibles endodont, 1.1 times longer than wide.

Thorax: Pronotum (Figs. 19A–B) transverse; subequal in width and length; lateral margins subparallel with transversal sulcus on median region; integument color dark brown; vestiture covered with whitish short setae abundantly distributed in distinct punctation, base covered with ramified setae shorter on lateral than center. Procoxae and Mesocoxae covered by plumose setae and scarce non-ramified setae, internal region glabrous. Femora with elongate very scarce setae ventrally. Tibiae with mucro present, distinct. Metatibiae (Fig. 29K) internal margin sinuose, near apex with a dilatation forming a dentiform projection internally, with a set of elongate setae on external margin of the projection. Tarsi, median region of femora and tibia with lighter integument. Tarsus (Fig. 29K) elongate, 0.9 times shorter than metatibiae; tarsomere I 0.7 times shorter than II, tarsomere III 0.7 times shorter than I; last tarsomere longer than rest, 1.7 times longer than tarsomere I and 1.1 times longer than tarsomere II. Scutellum (Fig. 19A) as long as wide; integument dark brown, covered with whitish plumose setae. Elytra (Figs. 19A–B) 3.6 times longer than wide; humeri rounded, similar color to elytra; lateral margins subparallel; interstriae covered by dense short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae; striae punctate with tiny whitish setae, similar to those in interstriae, inserted in each puncture; epipleura incomplete, covered by short plumose setae on anterior region and non-ramified setae posteriorly. Ventral region (Fig. 19C) integument color similar to elytra. Prosternum with abundant yellowish short, ramified setae. Metepisternum covered with whitish plumose setae, with fewer elongate setae posteriorly. Metasternum with a distinct central concavity, extends into abdomen, with one elevated projection rounded apically on posterior margin in each side; vestiture next to concavity border with whitish non-ramified setae and plumose setae intercalated; vestiture on center very scarce whitish non-ramified setae.

Abdomen (Fig. 19C): Ventrites I–II covered by whitish non-ramified setae. Ventrites III and IV bidentate centrally on posterior margin. Terminalia: Pygidium (Tergum VIII) (Fig. 19H) as long

as wide; anterior margin straight; posterior margin rounded on laterals, with a depressed region on center; setae elongate concentrated on posterior half, longer apically. Sternum IX (Fig. 19G) apodeme (spiculum gastrale) 0.7 times shorter than aedeagus; apically slightly acute. Tegmen (Fig. 19F) 0.6 times shorter than aedeagus; tegminal apodeme slender, slightly sinuous on apical region. Aedeagus (Figs. 19D–E) 9.1 times longer than wide at base; slightly constricted on median region, apex rounded slightly laterally, with a short acute projection on center; ventral plate strongly sclerotized. Median lobe 1.1 times longer than apodemes; endophallus with a pocket containing microtrichia on apical third.

Female unknown.

Examined material. Only the holotype was examined.

Distribution. This species is known from the type locality in Napo, Ecuador.

Host plant. Unknown.

Remarks. While putative female specimens were analyzed, they have not been included in the description due to their morphological similarity to other species such as *U. variabilis*, *Udeus* sp. nov. 10 and *Udeus* sp. nov. 21.

***Udeus* sp. nov. 20 Lira & de Medeiros**

(Figures 20, 30E)

Holotype: Male, BRAZIL: Amazonas: Estirão do Equador, Rio Javari, 4°33’S, 71°38’W, Oct1979, M. Alvarenga (ASUCOB).

Diagnosis. *Udeus* sp. nov. 20 can be recognized by the short body; general brownish color, with two transversal bands on elytra slightly darker than rest of elytra (Fig. 20A); rostrum short and robust (Fig. 20B); eyes very large; scutellum, coxae, base and, laterals of the pronotum, pro-, meso- and metasternum densely covered with whitish plumose setae; metatibiae with internal margin sinuose, near apex with a slight projection; third ventrite with a transversal projection in semicircle format covered with setae (Fig. 20C); tegmen without apparent parameres (Fig. 20F).

Description. Male. Body size: 1.6 mm. Head: Rostrum (Fig. 20B) 0.9 times shorter than pronotum; 0.9 times narrower at apex than at base; integument brown, apex and median line lighter; longitudinal carina absent; scrobes reaching near posterior eye margin; apex with scarce elongate setae; base with sparse, unramified setae inserted on distinct punctation. Eyes (Figs. 20A–C) 1.2 times wider than high; 1.4 times more separated above than below. Head integument brown, interorbital region lighter; setae concentration short, non-ramified, inserted on distinct punctation above eyes and in interorbital region; plumose setae laterally. Antennae with scape straight, extending near posterior margin of eye; funicle seven segmented; antennomere I longer and wider than others, 1.4 times longer than antennomere II; antennomere II 1.2 times longer than antennomeres III, IV, VI, and VII, which are subequal in length; antennomere V shortest, 0.4 times shorter than antennomere I; club three segmented, 3.8 times longer than wide. Mandibles symmetric, with teeth on internal margin, tiny external tooth apically; 1.7 times longer than wide.

Thorax: Pronotum (Figs. 20A–B) transverse; 1.1 times wider than longer; lateral margins subparallel with transversal sulcus on median region; integument color brown; vestiture covered with whitish short setae abundantly distributed in distinct punctation on disc, whitish plumose setae on base and lateral, more abundant on basal half. Pro- and mesocoxae covered by plumose setae externally, internal region with non-ramified setae. Femora with elongate scarce setae ventrally.

Tibiae with short mucro. Metatibiae internal margin sinuose, near apex with a slight projection; setation with a small set of elongate setae on external margin of projection and another set apically on internal margin. Tarsus elongate, 1.1 times longer than metatibiae; tarsomere I subequal in length to tarsomeres II and IV; tarsomere III 0.5 times shorter than tarsomeres I, II, and IV. Scutellum (Fig. 20A) 1.2 times longer than wide; integument color brown; vestiture covered with whitish plumose setae. Elytra (Figs. 20A–B) 3.2 times longer than wide; 1.5 times wider and 2.6 times longer than pronotum; humeri rounded, similar color to elytra, lateral margins subparallel; interstriae covered by dense short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae, and at base of second interstriae; striae punctate with tiny whitish setae, similar to those in interstriae, inserted in each puncture; epipleura incomplete, covered by short non-ramified setae. Ventral region (Fig. 20C) integument color similar to elytra. Prosternum with abundant whitish short plumose setae. Metepisternum covered with whitish plumose setae, fewer elongate setae posteriorly. Metasternum with slight central concavity, extends into abdomen; vestiture next to concavity border whitish non-ramified setae with plumose setae intercalated; vestiture on center scarce whitish non-ramified setae.

Abdomen (Fig. 20C): Ventrites I–II covered by whitish non-ramified setae. Ventrites III–V covered by whitish non-ramified setae on laterals, ventrite III with a semicircle projection on center, with a row of setae apically; ventrite IV very short. Ventrite V evenly covered by whitish non-ramified setae; trapezoidal, straight on apex. Terminalia: Pygidium (Tergum VIII) (Fig. 20G) 1.2 times wider than long; anterior margin straight; posterior margin rounded; elongate setae concentrated on posterior half, longer apically. Sternum IX apodeme (spiculum gastrale) 0.7 times shorter than aedeagus. Tegmen (Fig. 20F) 0.4 times shorter than aedeagus; tegminal apodeme slender, straight. Aedeagus (Figs. 20D–E) 7.4 times longer than wide at base; parallel on laterals,

funelling to apex truncate; ventral plate strongly sclerotized. Apodems 1.1 times longer than median lobe; endophallus with a pocket containing spicules in all extension.

Female unknown.

Examined material. Only the holotype was examined.

Distribution. This species is known only from the type locality in Amazonas, Brazil (Fig. 30E).

Host plant. Unknown.

***Udeus* sp. nov. 21 Lira & de Medeiros**

(Figs. 21, 28K, 29L, 30F)

Holotype: Male. ECUADOR: Napo: vic. Puerto Misahueli, 1°2’2.4”S, 77°39’49.2”W, 1650-1900 ft, 6-19Sep1998, J.E. Eger (ASUCOB).

Diagnosis. *Udeus* sp. nov. 21 can be recognized by the general color brownish, with the last antennomere of funicle, club, laterals of pronotum, pro-, meso- and metasternum, and pygidium darker; apex of metafemur and base of metatibiae darker; elytra with two transversal bands and epipleura darker (Figs. 21A–B); escape, most of the funicle, and legs yellowish; rostrum robust with a longitudinal carina on the median region; tarsus elongate, 1.2 times longer than metatibia (Fig. 29L); ventrites densely covered with elongate setae (Fig. 21C); pygidium with two strong projections on apex forming a concave region in the middle (Fig. 21H); apodeme of the spiculum gastrale very expanded anteriorly visible in lateral view (Fig. 21G); aedeagus bilobed on apex (Fig. 21D).

Description. Male. Body size: 2.5 mm. Head: Rostrum (Fig. 21B) subequal in length to pronotum; apex width subequal to base; integument brown, darker on laterals, with a longitudinal carina, without sulcus near median carina; scrobe not reaching eye margin; apex with scarce elongate setae; decumbent setae, transversely from antennal insertion to near base on laterals, base and interorbital region with denser non-ramified setae. Eyes (Fig. 21B) 1.3 times higher than wide; 2.4 times more separated above than below. Head integument brown, posterior region darker. Setae non-ramified, inserted on distinct punctation above eyes and in interorbital region, with 1 elongate brownish seta above near to inner margin of each eye, plumose setae laterally and ventrally. Antennae (Fig. 28K) with scape straight, extending near posterior margin of eye; funicle seven segmented; antennomere I 1.4 times longer than II; antennomere II 1.7 times longer than III; antennomere IV 1.2 times longer than III and 1.7 times longer than V and VII, which are subequal; antennomere VI, 1.1 times longer than II. Antennal club 2.4 times longer than wide. Mandibles endodont, symmetric, with 3 teeth on internal margin; 1.8 times longer than wide.

Thorax: Pronotum (Figs. 21A–B); transverse, 1.2 times wider than long; lateral margins parallel with transversal sulcus on median region; integument dark brown, lighter on disc; vestiture covered with yellowish short setae distributed in distinct punctation on disc, denser whitish plumose setae on base, four yellowish elongated setae next to apical constriction. Pro- and mesocoxae covered by non-ramified setae, denser internally and plumose setae denser externally. Tibiae with mucro, larger on protibiae. Metatibiae (Fig. 29L) with internal margin slightly sinuose; setation evenly covered with sparse setae, denser apically near mucro. Tarsus (Fig. 29L) elongate, 1.2 times longer than metatibiae; tarsomere I subequal to II in length; tarsomere III 0.6 times shorter than I and II; last tarsomere 1.3 times longer than I and II. Scutellum (Fig. 21A) as long as wide; integument brown; vestiture covered with whitish plumose setae. Elytra (Figs. 21 A–B) 2.9 times longer than wide; 1.9 times wider and 3.2 times longer than pronotum; humeri rounded, darker

brown; elytra with two darker bands, one on base and another on median region, elytral suture darker from base to median region, slightly depressed on final first band; lateral margins subparallel; interstriae covered by short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae and basally on interstriae II; striae punctate with yellowish setae, similar to those on interstriae, inserted in each puncture; epipleura incomplete, covered by short non-ramified setae. Ventral region (Fig. 21C) with integument dark brown on thorax, lighter on abdomen; prosternum with abundant whitish short plumose setae; metepisternum covered with whitish plumose setae and fewer elongate non-ramified setae medially. Metasternum with slight central concavity, extending into abdomen; vestiture next to concavity border with scarce yellowish non-ramified setae; vestiture on center with very scarce yellowish non-ramified setae, with transversal sulcus.

Abdomen (Fig. 21C): Ventrites I–II covered with elongate yellowish non-ramified setae, longer and denser on center. Ventrites III–V covered with elongate yellowish non-ramified setae, longer and denser on center. Ventrite V covered with elongate yellowish non-ramified setae, longer and denser on center and posterior border, shape trapezoidal, stronger convex on border. Terminalia: Pygidium (Tergum VIII) (Fig. 21H) 1.3 times longer than wide; anterior margin straight on median region, laterals expanded in half length of pygidium; posterior margin rounded on laterals, with two strong projections forming a concave region in the middle; setae elongate on posterior half. Sternum IX (Spiculum gastrale) (Fig. 21G) with apodeme 0.9 times shorter than aedeagus, apically rounded, straight, anteriorly very expanded in lateral view. Tegmen (Fig. 21F) 0.6 times shorter than aedeagus; tegminal apodeme slender, straight, slightly amplified on apex. Aedeagus (Figs. 21D–E) 9.6 times longer than wide, parallel from base to median third, funneling in median region; apex bilobed; ventral plate strongly sclerotized; apodemes 1.2 times longer than median lobe; endophallus with a pocket containing microtrichia on apical half.

Female unknown.

Examined material. Type material. Paratypes: **ECUADOR:** Napo: vic. Puerto Misahueli, 1°2’2.4”S, 77°39’49.2”W, 1650-1900 ft, 6-19Sep1998, J.E. Eger (1m# CERPE, 1m# FMNH).

Distribution. This species is known only from the type locality, in Napo, Ecuador (Fig. 30F).

Host plant. Unknown.

Remarks. Although putative female specimens were analyzed, they have not been included in the description since females appear to be morphologically indistinguishable from other species such as *Udeus* sp. nov. 10, *Udeus* sp. nov. 17, and *Udeus* sp. nov. 19.

***Udeus* sp. nov. 22 Lira & de Medeiros**

(Figs. 22, 28L, 29M, 30E)

Holotype. Male. BRAZIL: Rondônia: 62 km SW Ariquemes, Fzda. Rancho Grande, 5-17Sep1993, JE. Eger, UV trap (ASUCOB).

Diagnosis. *Udeus* sp. nov. 22 can be recognized by the general color of body yellowish (Fig. 22A); head with plumose setae laterally and ventrally; coxae, base of pronotum, pro-, mesosternum, lateral of metasternum and scutellum covered with whitish plumose setae; striae well punctate; interstriae slightly elevated; metatibiae with internal margin sinuose, slightly amplified on apex, with a comb of flat setae (Fig. 29M); last tarsomere longer than others (Fig. 29M); aedeagus with robust apodemes, almost straight apically (Figs. 22D–E). This species is closely similar to *U. variabilis*

but distinguished by the modification on the apex of the metatibiae, slightly expanded, with rigid setae.

Description. Male. Body size: 2.6 mm. Head: Rostrum (Figs. 22A–B) 1.1 times longer than pronotum; apex subequal to base in wide; integument brown; longitudinal carina absent; scrobe almost reaching eye margin; apex with scarce elongate setae; scarce setae decumbent, arranged transversely from antennal insertion to near base on laterals, directed backward on base, glabrous and smooth in median line. Eyes subequal in height and width; 1.8 times more separated above than below. Integument of head brown, with setae non-ramified, inserted on distinct punctation above eyes and in interorbital region, with 1 elongate brownish seta on base and another above near to inner margin of each eye; plumose setae laterally and ventrally. Antennae (Fig. 28L) with scape straight, extending near posterior margin of eye; funicle seven segmented; antennomere I longer than others, 2 times longer than II; antennomere II, III, and IV subequal in length, 1.2 times longer than V and VI, which are subequal; VII shortest, 0.3 times shorter than I; antennal club 2.6 times longer than wide. Mandibles endodont, symmetric, with 2 teeth on internal margin; 1.1 times longer than wide.

Thorax: Pronotum (Figs. 22A–B) transverse; 1.3 times wider than long; lateral margins parallel with deeply transversal sulcus on median region; integument color brown; covered with yellowish short setae distributed in distinct punctation on disc, scarce short whitish plumose setae on base laterally, denser in the middle, three yellowish elongated setae on laterals and four next to apical constriction. Pro- and mesocoxae covered by non-ramified setae internally and plumose setae denser externally. Femora with elongate scarce setae ventrally on meso and metafemora. Tibiae with mucro on pro and mesotibiae. Metatibiae (Fig. 29M) with internal margin sinuose, slightly amplified on apex, with a comb of flat setae; with a set of elongate setae from median region to

apex on internal margin. Tarsus (Fig. 29M) elongate, 0.9 times shorter than metatibiae; tarsomere I 1.2 times longer than II; tarsomere II 2 times longer than III; last tarsomere 1.7 times longer than I. Scutellum 1.1 times wider than long; integument brown; covered with whitish plumose setae. Elytra (Figs. 22A–B) 3.2 times longer than wide; 1.6 times and 3.3 times longer than pronotum; humeri rounded, similar color to elytra; lateral margins subparallel; interstriae covered by dense short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae on two-thirds since base, apical third with elongate setae in all interstriae; striae punctate with yellowish setae, similar to those on interstriae, inserted in each puncture; epipleura incomplete, covered by short non-ramified setae. Ventral region (Fig. 22C) integument color brown, similar to dorsal color; prosternum with whitish short plumose setae; metepisternum covered with whitish plumose setae and fewer elongate non-ramified setae medially. Metasternum with slight central concavity, extending into abdomen; vestiture next to concavity border with yellowish non-ramified setae; on center with very scarce yellowish non-ramified setae.

Abdomen (Fig. 22C): Ventrites I–II evenly covered by yellowish non-ramified setae; ventrites III–V covered by yellowish non-ramified setae evenly distributed; ventrite V covered by yellowish non-ramified setae, longer on center, trapezoidal, slightly sinuose on apex. Terminalia. Pygidium (Tergum VIII) (Fig. 22H) 2.3 times wider than long; anterior margin straight, laterals expanded; posterior margin rounded; setae elongate on posterior two-thirds. Sternum IX (Spiculum Gastrale) (Fig. 22G) apodeme 0.5 times shorter than aedeagus; apodeme apically expanded to sides, straight. Tegmen (Fig. 22F) 0.6 times shorter than aedeagus; tegminal apodeme slender, slightly curved on apex. Aedeagus (Figs. 22D–E) 9.3 times longer than wide at base, parallel from base to apex, apex rounded, slightly compressed; ventral plate sclerotized; median lobe 1.2 times longer than apodemes; endophallus with a pocket containing microtrichia on apical quarter.

Female unknown.

Examined material. Type material. Paratypes: BRAZIL: Rondônia: 62 km SW Ariquemes, Fzda. Rancho Grande, 5-17Sep1993, JE. Eger, UV trap (3m# ASUCOB).

Distribution. This species is known only from the type locality.

Host plant. Unknown.

Remarks. Although putative female specimens were analyzed, they have not been included in the description since females appear to be morphologically indistinguishable from other species such as *U. variabilis* and *Udeus* sp. nov. 26.

***Udeus* sp. nov. 23 Lira & de Medeiros**

(Figs. 23, 28M, 29N, 30F)

Holotype: Male. FRENCH GUIANA: Amazon Nature Lodge 30 km SE Roura on Kaw Rd., 4°33.570'N, 052°12.233'W, 300 m, 5-19Feb2010, J. E. Eger, UV trap.

Diagnosis. *Udeus* sp. nov. 23 can be recognized by the general color brownish, with two transversal dark bands on base and median region of elytra, and a longitudinal dark band on elytral suture from scutellum to median region (Figs 23A–B); coxae, scutellum, base of pronotum, prosternum, mesosterum, and metepisternum covered with whitish plumose setae (Figs. 23B–C); first tarsomere longer than others; pygidium subrectangular, with a depression on central region of ventral flap (Fig 23H); spiculum gastrale ampliate anteriorly and expanded to sides forming projection directed downward posteriorly (Fig 23G); aedeagus funneling to apical third, with apex strongly amplified in fan-shape (Figs 23D–E). This species shares with *U. moraguesi* from Guyane the general color and elytra, differing by the format of aedeagus. While *Udeus* sp. nov. 23 has the apex of the

aedeagus expanded laterally in a fan-shape, the apex of the aedeagus of *U. moraguesi i*s pointed. *Udeus* sp. nov. 23 is also very similar externally to *Udeus* sp. nov. 17 and *Udeus* sp. nov. 21 with dark spots on the base and median region of the elytra.

Description. Male. Body size: 2.3 mm. Body size. Head: Rostrum (Fig. 23B) 0.9 times shorter than pronotum; 0.9 times narrower at apex than at base; integument brown; longitudinal carina absent; scrobes reaching near posterior eye margin; apex with scarce elongate setae; base with sparse, non-ramified, setae inserted on distinct punctation directed backward; with a longitudinal sulcus on median region. Eyes (Figs. 23A–C) 1.1 times higher than wide; 1.8 times more separated above than below. Head integument brown, similar to rostrum; setae concentration short, non-ramified, inserted on distinct punctation above eyes and interorbital region; short plumose setae laterally. Antennae (Fig. 28M) with scape straight, extending near posterior margin of eye; funicle seven segmented, antennomere I 1.8 times longer than antennomere II; antennomere II 1.7 times longer than antennomere III and V, subequal in length; antennomeres IV, VI, and VII subequal in length, 1.3 times longer than antennomeres III and V; antennal club 4 times longer than wide. Mandibles endodont, symmetric, with three teeth on internal margin; 1.7 times longer than wide.

Thorax: Pronotum (Figs. 23A–B) transverse, 1.1 times wider than long; lateral margins subparallel with deeply transversal sulcus on median region; integument color brown; vestiture covered with yellowish short setae abundantly distributed in distinct punctation on disc, short whitish plumose setae on base; six yellowish elongated setae next to apical constriction, and one on each side basally. Pro- and mesocoxae covered by plumose setae and scarce non-ramified setae. Tibiae with mucro; metatibiae (Fig. 29N) with internal margin slightly sinuose basally; evenly covered with sparse setae, slightly denser apically. Tarsus (Fig. 29N) elongate, 1.1 times longer than metatibiae; tarsomere I 1.7 times longer than II; tarsomere II 1.8 times longer than III; last

tarsomere 0.8 times shorter than I. Scutellum (Fig. 23A) 1.1 times longer than wide; integument brown, covered with whitish plumose setae. Elytra (Figs. 23A–B) 1.8 times longer than wide, 1.6 times wider and 3.1 times longer than pronotum; humeri rounded, black; lateral margins subparallel; interstriae covered by dense short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae. Epipleura incomplete, covered by short plumose setae on anterior region and non-ramified setae posteriorly. Ventral region (Fig. 23C) integument color brown, similar to head. Prosternum with abundant whitish short plumose setae. Metepisternum with whitish plumose setae and fewer elongate setae medially. Metasternum with slight central concavity, extends into abdomen; whitish non-ramified setae with plumose setae intercalated next to concavity border; vestiture on center scarce whitish non-ramified setae.

Abdomen (Fig. 23C): Ventrites I–II covered by whitish non-ramified setae, more elongate centrally on posterior margin. Ventrites III–V covered by whitish non-ramified setae, longer centrally. Ventrite V covered by yellowish non-ramified setae, scarce medially; trapezoidal, sinuose on apex. Terminalia: Pygidium (Tergum VIII) (Fig. 23H) 2.4 times wider than long; anterior margin curved in C-shaped; posterior margin slightly sinuose, ventral flap with depression on central region. Pygidium with elongate setae, denser on posterior third, directed to depression; sparse on basal third. Sternum IX (spiculum gastrale) (Fig. 23G) apodeme 0.6 times shorter than aedeagus in length; apodeme acute posteriorly, expanded to sides forming projection directed downward; anteriorly amplified. Tegmen (Fig. 23F) 0.5 times shorter than aedeagus; tegminal apodeme slender, straight, slightly amplified on apex. Aedeagus (Figs. 23D–E) 7.5 times longer than wide at base, slightly constricted at middle, funneling to apical third; apex strongly amplified, straight on border; ventral plate sclerotized. Aedeagus with median lobe 1.8 times longer than apodemes. Endophallus with a pocket containing large spines on median region.

Female unknown.

Examined material. Type material. Paratypes: FRENCH GUIANA: Amazon Nature Lodge 30 km SE Roura on Kaw Rd., 4 33.570 N, 052 12 233 W, 300 m, 5-19Feb2010, J. E. Eger, UV trap (4m# ASUCOB, 1m# CERPE).

Distribution. This species is known only from the type locality, in Rondônia, Brazil (Figure 30F).

Host plant. Unknown.

Remarks. Females exhibiting striking morphological resemblance to males of *Udeus* sp. 23 were registered in the same locality. Despite their apparent similarity, these females were not formally described nor included in the list of examined specimens due to their shared characteristics with other known species. Future investigations hold promise for precisely delineating the taxonomic boundaries of these specimens. Notably, the undescribed females present a remarkable resemblance to the illustration featured in the description of *U. behnei* (Rheinheimer 2018).

***Udeus* sp. 24 Lira & de Medeiros**

(Figs. 24, 28N, 29O, 30F)

Holotype: Male. PANAMA: Cólon: Gamboa, P.N. Soberanía, Pipeline, 9.123519, -79.715566, 07Jul2021, B.A.S. Medeiros (FMNH).

Diagnosis. *Udeus* sp. nov. 24 can be recognized by its darker body, except antennae, metasternum, ventrites, and legs yellowish (Figs. 24A–C); longer elytra, 4 times longer than wide; metatibiae compressed medially; tarsus longer than metatibiae; interstriae with short setae, elongate yellowish acuminate setae apically on interstriae 2 and 10; metasternum with a large elevated projection on

each side; aedeagus with margins parallel from base to median third, funneling to apex, apex bilobed (Figs. 24G–H).

Description. Male. Body size: 2.4–2.5 mm. Head: Rostrum (Figs. 24A–C) 1.1 times longer than pronotum; apex and base subequal in length and width; integument brown, lighter apically; longitudinal carina absent; scrobe almost reaching eye margin; apex with scarce elongate setae; setae decumbent, arranged transversely from antennal insertion to near base on laterals, directed backward on base, denser; glabrous and smooth in median line and dorsally at apex. Eyes (Figs. 24A–B) subequal in height and width; 2.2 times more separated below than above. Head with integument dark brown; setae non-ramified, inserted on distinct punctation above eyes and in interorbital region, with 1 elongate and brownish seta near to inner margin of each eye posteriorly; longitudinally glabrous; plumose setae laterally and ventrally. Antennae (Fig. 28N) with scape straight, extending near posterior margin of eye; funicle seven segmented, first antennomere 1.7 times longer than antennomere II; antennomere II 1.4 times longer than antennomere III, V and VII, subequal in length; antennomeres IV and VI subequal in length, 1.5 times longer than antennomeres III, V and VII; antennal club 2.5 times longer than wide. Mandibles endodont, symmetric, with 2 teeth on internal margin; subequal in length and width.

Thorax: Pronotum (Figs. 24A–B) transverse; subequal in length and width; lateral margins parallel with deeply transversal sulcus on median region; integument dark brown; covered with short yellowish setae distributed in discrete punctation on disc, scarcer on median line; scarce short whitish plumose setae on base laterally; three yellowish elongated setae next to apical constriction. Pro- and mesocoxae covered by non-ramified setae, denser internally and scarce plumose setae denser externally. Elongate scarce setae ventrally on pro- and mesofemora. Tibiae with mucro; metatibiae sinuose on internal margin, depressed medially; with a set of elongate setae immediately

before mucro (Fig. 29O). Tarsus (Fig. 29O) elongate, 1.2 times longer than metatibiae; tarsomere I 1.4 times longer than II; tarsomere III 0.7 shorter than I; last tarsomere 1.3 times longer than tarsomere I. Scutellum subequal in length and width; integument brown; covered with whitish plumose setae. Elytra (Figs. 24A–B) 4 times longer than wide; 1.3 times wider and 2.7 times longer than pronotum; humeri rounded, similar color of elytra; lateral margins subparallel; interstriae covered by dense short non-ramified setae, with elongate yellowish acuminate setae apically on interstriae 2 and 10; striae punctate with yellowish setae, similar to those on interstriae, inserted in each puncture; epipleura incomplete, covered by short non-ramified setae. Ventral region integument (Fig. 24C) color brown laterally, ochre on center of meso- and metasternum and ventrites. Prosternum with scarce non-ramified setae. Metepisternum with whitish plumose setae and fewer elongate setae medially. Metasternum with distinct central concavity, extending into abdomen, with one large, elevated projection on each side; vestiture next to concavity border with yellowish non-ramified setae; vestiture on center with very scarce yellowish non-ramified setae.

Abdomen (Fig. 24C): Ventrites I–II covered by yellowish non-ramified setae, denser laterally. Ventrites III–V covered by yellowish non-ramified setae evenly distributed. Ventrite V trapezoidal, straight on apex. Terminalia. Pygidium (Tergum VIII) (Fig. 24J) 1.2 times longer than wide; anterior margin straight; posterior margin rounded; scarce elongate seta on median region and denser on ventral flap. Sternum IX (spiculum gastrale) (Fig. 24I) 0.7 times shorter than aedeagus, slightly sinuose, posteriorly acute. Tegmen 0.6 times shorter than aedeagus; tegminal apodeme slender, slightly curved and ampliate on apex; parameres bilobed, near each other, apically setose. Aedeagus (Figs. 24G–H) 6.2 times longer than wide at base; margins parallel from base to median third, funneling to apex, apex bilobed; ventral plate strongly sclerotized. Median lobe 1.3 times longer than apodemes; endophallus with a pocket containing microtrichia on apical half.

Female: Body size: 2.6 mm. Rostrum 1.1 times longer than pronotum; apex and base subequal in width. Pronotum subequal in length and width. Metasternum with slight sulcus in basal region, slightly elevated on laterals. Femora with scarce elongate ventral setae on pro- and mesofemora. Scutellum 1.1 times longer than wide. Elytra subequal in width to pronotum; 4.2 times longer than width; 3.3 times longer than pronotum length. Ventrites convex. Ventrite V trapezoidal, apex straight. Terminalia. Tergum VIII (pygidium) (Fig. 24D) triangular, 1.3 times wider than long, anterior margin straight, rounded apex, with a rougness on median line apically; long setae on apical third, directly to center region, short setae posteriorly. Sternum VIII (Fig. 24F), including apodeme, about 3.7 times as long as coxites; lamina occupying posterior third; lateral arms and a central band sclerotized. Coxites and styli not visible. Spermatheca (Fig. 24E) curved, about 1.8 times as long as wide; *ramus* and *collum* pointing in the same direction.

Examined material. Type material. Paratypes: PANAMA: Bocas del Toro: Corriente Grande, Rio Changuinola, 9°17'30"N, 82°32'41"W, 14Feb1980, H. Wolda (1 ASUCOB); Las Cumbres: 2Aug1976, H. Wolda (1f# ASUCOB); Canal Zone, Barro Colorado Is., 9Aug1977, W. Holda, UV trap 3 (26m high) (1# ASUCOB); Cólon: Gamboa, P.N. Soberanía, Pipeline, 9.123519, -79.715566, 07Jul2021, B.A.S. Medeiros (4 sex indet. FMNH). **BELIZE:** S.C. Mile 19 Southern Highway, 19Aug1977, CW & L O`Brien & Marshall (1m# CERPE).

Distribution. This species is known from Panama and Belize.

Host plant. Some specimens were collected in *C. obtusifolia* in Panama.

***Udeus* sp. nov. 25 Lira & de Medeiros**

(Figs. 25, 28O, 29P, 30F)

Holotype: Male. BOLIVIA: Santa Cruz: Prov. of San Esteban, Muyrina, 49Km N. of Santa Cruz, 1120 ft, 27nov.1959, R. B. Cumming, blacklight trap (ASUCOB).

Diagnosis. *Udeus* sp. nov. 25 can be recognized by the color of the body dark brown; eyes very large (Figs. 25A–C); funicle with six antennomeres; head with ventral and lateral region, pro-, meso-, metasternum with whitish plumose setae (Figs. 25B–C); tarsus elongate, 1.4 times longer than metatibiae; spiculum gastrale expanded to lateral on posterior region (Fig. 25F); aedeagus very curved laterally, slender apex (Figs. 25D–E).

Description. Male. Body size: 2.2 mm. Head: Rostrum (Fig. 25B) 0.8 times shorter than pronotum; apex and base subequal in width; integument brown; longitudinal carina absent; scrobe reaching eye margin; apex with scarce elongate setae; setae decumbent, transversely from antennal insertion to near base on laterals, base and interorbital region with denser elongate setae merging with plumose setae directed backward. Eyes (Figs. 25A–C) subequal in height and width; 2.5 times more separated above than below. Head with integument brown; setae non-ramified, inserted on distinct punctation above eyes and in interorbital region, with 2-3 elongate and brownish setae near to inner margin of each eye; denser plumose setae laterally and ventrally. Antennae (Fig. 28O) with scape straight, extending near posterior margin of eye; funicle six segmented; antennomere I 1.2 times longer than II; antennomere II, 1.2 times longer than III, 2 times longer than IV; antennomeres V and VI subequal in length and 1.3 times longer than IV. Antennal club 2.7 times longer than wide. Mandibles endodont, symmetric, with 2 teeth on internal margin; 1.2 times longer than wide.

Thorax: Pronotum (Figs. 25A–B) transverse; 1.1 times wider than length; lateral margins subparallel with depression on median region in each side; integument dark brown; covered with

short yellowish setae distributed in distinct punctation on disc; scarce short whitish plumose setae on base laterally, denser in the middle; two yellowish elongated setae next to apical constriction. Pro- and mesocoxae covered by denser plumose setae. Femora evenly covered with scarce setae. Tibiae with mucro; metatibiae (Fig. 29P) with internal margin slightly sinuose; evenly covered with sparse setae, slightly denser apically. Tarsus (Fig. 29P) elongate, 1.4 times longer than metatibiae; tarsomere I 1.05 times longer than II and 3.3 times longer than III, tarsomeres II and IV subequal in length. Scutellum (Fig. 25A) subequal in length and width; integument brown; covered with whitish plumose setae. Elytra (Figs. 25A–B) 3.4 times longer than wide; 3.2 times longer and 1.8 wider than pronotum; humeri rounded, similar color to elytra; lateral margins subparallel; interstriae slightly elevated, covered by dense short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae; striae punctate with yellowish setae, similar to those on interstriae, inserted in each puncture; epipleura incomplete, covered by short non-ramified setae. Ventral region (Fig. 25C) with integument brown, similar to dorsal color; prosternum with abundant whitish elongate plumose setae; metepisternum covered with whitish plumose setae. Metasternum with distinct central concavity, extending into abdomen; vestiture next to concavity border denser with whitish plumose setae merged with scarce elongate non-ramified setae, on center with scarce whitish non-ramified setae.

Abdomen (Fig. 25C): Ventrites I–II covered with elongate whitish non-ramified setae, denser on laterals. Ventrites III–IV covered by whitish non-ramified setae, denser laterally. Ventrite V covered by whitish non-ramified setae, denser laterally, shape trapezoidal, strongly convex on border. Terminalia. Pygidium (Tergum VIII) (Fig. 25G) 2 times wider than long; anterior margin straight, with laterals expanded in two lobes; posterior margin rounded; elongate setae concentrated on posterior half, scarcer centrally, longer apically. Sternum IX apodeme (spiculum gastrale) (Fig. 25F) 0.6 times shorter than aedeagus; expanded to laterals. Tegmen 0.6 times shorter than aedeagus;

tegminal apodeme slender, straight. Aedeagus (Figs. 25D–E) 10.6 times longer than wide at base; parallel on laterals on basal third, funneling to rounded apex; ventral plate strongly sclerotized. Median lobe 1.8 times longer than apodemes; endophallus with a pocket containing microtrichia on apical region.

Female unknown.

Examined material. Only the holotype was examined.

Distribution. This species is known only from type locality, in Santa Cruz, Bolivia (Fig. 30F).

Host plant. Unknown.

Remarks. This is the only *Udeus* species known with six antennomeres in the funicle. Champion (1902) described *Udeus* with six antennomeres in the funicle, but examining photos of type material, we can notice a slight junction between antennomeres II and III. The challenge in discerning the separation of these segments, owing to their diminutive size, may have contributed to confusion regarding the number of antennomeres.

***Udeus* sp. nov. 26 Lira & de Medeiros**

(Figs. 26, 28P, 29Q, 30H)

Holotype: Male. BRAZIL: Rondônia: 62 km SW Ariquemes, Fzda. Rancho Grande, 3-15Dec1996, JE. Eger, MV & black lights (ASUCOB).

Diagnosis. This species strongly resembles *Udeus* sp. nov. 25 (Fig. 25), but can be distinguished from it by the rostrum, interorbital region, pro- and mesocoxae, and metasternum without plumose

setae (Figs. 26B–C), the only elongate setae on the internal margin instead of two or three, longer acuminate setae in odd interstriae, the seven antennomeres in the funicle, the scutellum just partially covered with plumose setae, and the aedeagus with apex bilobed (Figs. 26D–E).

Description. Body size: 2.4 mm. Head: Rostrum (Fig. 26B) 0.9 times shorter than pronotum; apex 1.1 times wider at base than at apex; integument brown; longitudinal carina absent; scrobe not reaching eye margin; apex with scarce elongate setae; decumbent setae, arranged transversely from antennal insertion to near base on laterals; base and interorbital region with denser non-ramified setae. Eyes (Figs. 26A–C) subequal in height and width; 1.9 times more separate above than below. Integument color brown, similar to rostrum. Setae non-ramified, inserted on distinct punctation above eyes and in interorbital region, with 1 elongate brownish seta on posterior eye margin near to inner margin of each eye, plumose setae laterally and ventrally. Antennae (Fig. 28P) with scape straight, extending near posterior margin of eye; funicle seven segmented; antennomere I 1.7 times longer than II; antennomere II, 1.5 times longer than III; antennomere IV and VI subequal, 1.2 times longer than III; antennomere V subequal to VII and 0.3 times shorter than antennomere I. Antennal club 2.2 times longer than wide. Mandibles not visible.

Thorax: Pronotum (Fig. 26 A–B) transverse, as long as wide; lateral margins parallel with deep transversal sulcus on median region; integument brown, similar to head; vestiture covered with yellowish short setae distributed in discrete punctation on disc; with one line of whitish plumose setae on posterior margin; six yellowish elongated setae next to apical constriction. Pro- and mesocoxae covered by non-ramified and plumose setae. Femora evenly covered with yellowish setae, with scarce elongate setae on base ventrally. Tibiae with mucro. Metatibiae (Fig. 29Q) with internal margin slightly sinuous on base; setation evenly covered with sparse setae, denser apically. Tarsus elongate; tarsomere I subequal to II; tarsomere III 0.3 times shorter than I; last tarsomere

damaged. Scutellum (Fig. 26A) as long as wide, integument brown; covered with whitish plumose setae on borders. Elytra (Figs. 26A–B) 3.6 times longer than wide; 1.7 times wider and 3.1 times longer than pronotum; humeri rounded, similar color to elytra; lateral margins subparallel; interstriae covered by short non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae. Striae punctate with yellowish setae, similar to those on interstriae, inserted in each puncture; epipleura incomplete, covered by non-ramified setae. Ventral region (Fig. 26C) integument brown, similar to dorsal color; prosternum with scarce non-ramified setae; metepisternum vestiture whitish plumose setae and fewer elongate non-ramified setae medially. Metasternum with slight central concavity, extending into abdomen; vestiture next to concavity border with scarce yellowish non-ramified setae; vestiture on center very scarce yellowish non-ramified setae, with transversal sulcus.

Abdomen (Fig. 26C): Ventrites I–II covered by yellowish non-ramified setae, scarcer on center. Ventrites III–V covered by yellowish non-ramified setae evenly distributed. Ventrite V covered by yellowish non-ramified setae, longer on center; trapezoidal, stronger convex on border. Terminalia: Pygidium (Tergum VIII) (Fig. 26G) 1.2 times wider than long; anterior margin straight; laterals expanded; posterior margin rounded; setae elongate on posterior two-thirds. Sternum IX (Spiculum Gastrale) (Fig. 26F) apodeme 0.7 times shorter than aedeagus; apodeme slightly sinuose, posteriorly rounded. Aedeagus (Figs. 26D–E) 6.1 times longer than wide at base; parallel on laterals on basal third, slightly funneling to bilobate apex; apex with a smooth external depression in lateral view; ventral plate strongly sclerotized. Median lobe 1.4 times longer than apodemes; endophallus with a pocket containing microtrichae from median region to apex.

Female unknown.

Examined material. Type material. Paratype: ECUADOR: Napo: Limoncocha, on Rio Napo, 300 m, 13nov.1974, Boyce A. Drummond, blacklight trap (1m# ASUCOB).

Distribution. This species is known from Rondônia (Brazil), and Napo (Ecuador).

Host plant. Unknown.

Remarks. All known specimens of *Udeus* sp. nov. 26 were collected with light traps. Although putative female specimens were analyzed, they have not been included in the description since females appear to be morphologically indistinguishable from other species such as *Udeus* sp. nov. 22.

***Udeus* sp. nov. 27 Lira & de Medeiros**

(Figs. 27, 28Q, 29R, 30G)

Holotype: Male. PANAMA: Cólon: Gamboa, P.N. Soberanía, Pipeline, 9.123519, -79.715566, 07Jul2021, B.A.S. Medeiros, FMNH4429966 (FMNH).

Diagnosis. *Udeus* sp. nov. 27 can be recognized by elytra darker than rest (Figs. 27A–C); pronotum, head, metasternum, and ventrites brown lighter than elytra, legs yellowish; eyes too far above; head with plumose setae laterally and ventrally; metepisternum covered with plumose setae (Figs 27B–C).

Description. Male. Body size: 2.3–2.4 mm. Head: Rostrum (Fig. 27B) subequal in length to pronotum; apex width subequal to base; integument color dark brown; longitudinal carina absent; scrobe not reaching eye margin; apex with scarce elongate setae; scarce decumbent setae, arranged

transversely from antennal insertion to near base on laterals, directed backward on base, glabrous and smooth in median line. Eyes (Figs. 27A–C) subequal in height and width; 2.7 times more separate above than below. Integument of head color dark brown, similar to rostrum. Setae non-ramified, inserted on distinct punctation above eyes and in interorbital region, with 1 elongate yellowish seta on base and another above near to inner margin of each eye; plumose setae laterally and ventrally. Antennae (Fig. 28Q) with scape straight, extending near posterior margin of eye; funicle seven segmented; antennomere I 1.7 times longer than II; antennomere II, IV, and VI subequal in length, 1.3 times longer than antennomeres III, V, and VII, subequal in length; antennal club 2.4 times longer than wide. Mandibles endodont, symmetric, with 3 teeth on internal margin; 1.4 times longer than wide.

Thorax: Pronotum (Figs. 27A–B) transverse; 1.1 times longer than wide; lateral margins parallel with deep transverse sulcus on median region; integument color dark brown, similar to head; covered with yellowish short setae distributed in distinct punctation on disc, with one line of whitish plumose setae on posterior margin, three yellowish elongated setae on laterals, and four next to apical constriction. Pro- and mesocoxae covered by scarce unramified setae internally and plumose setae denser externally. Femora with elongate scarce setae ventrally. Tibiae with mucro. Metatibiae (Fig. 29R) with internal margin slightly sinuous on base; evenly covered with sparse setae, denser apically near mucro. Tarsus (Fig. 29R) elongate, as long as metatibiae; tarsomere I 1.1 times longer than II; tarsomere III 0.5 times shorter than I; last tarsomere 1.6 times longer than I. Scutellum 1.2 times wider than long; integument dark brown; covered with short whitish plumose setae on borders. Elytra (Figs. 27A–B) 3.9 times longer than wide; 1.5 times wider and 3.2 times longer than pronotum; humeri rounded, similar color of elytra; elytra dark brown; lateral margins subparallel; interstriae covered by non-ramified setae, with elongate yellowish acuminate setae distributed sparsely in odd interstriae. Striae punctate with yellowish setae, similar to those on

interstriae, inserted in each puncture; epipleura incomplete, covered by non-ramified setae. Ventral region (Fig. 27C) with integument color brown, slighter than dorsal color; prosternum with scarce plumose setae merged with very scarce non-ramified setae; metepisternum covered with yellowish non-ramified setae, plumose setae concentrated on anterior region. Metasternum with distinct central concavity, extending into abdomen, with one large, elevated projection on each side; vestiture next to concavity border with scarce yellowish elongate non-ramified setae and scarce yellowish elongate non-ramified setae on center. Metepisternum covered with whitish plumose setae.

Abdomen (Fig. 27C): Ventrites I–II covered by yellowish non-ramified setae, scarcer on center. Ventrites III–V covered by yellowish non-ramified setae evenly distributed. Ventrite V evenly covered by yellowish non-ramified setae; shape trapezoidal, straight on apex. Terminalia. Pygidium (Tergum VIII) (Fig. 27I) 1.2 times wider than long; anterior margin straight, laterals expanded; posterior margin rounded; setae elongate on posterior two-thirds. Sternum IX (Spiculum Gastrale) with apodeme 0.7 times shorter than aedeagus, slightly sinuose, posteriorly rounded. Aedeagus (Fig, 27G) 6.6 times longer than wide at base; parallel on laterals on basal third; apex rounded; ventral plate strongly sclerotized. Median lobe 1.9 times longer than apodemes; endophallus with a pocket containing microtrichia from median region to apex.

Female not described.

Examined material. Type material. Paratypes: PANAMA: Cólon: Gamboa, P.N. Soberanía, Pipeline, 9.123519, -79.715566, 07Jul2021, B.A.S. Medeiros (3# FMNH); Coclé: El Valle, Sendero India Dormida, 8.615735, -80.151478, 17Feb2022, B.A.S. Medeiros (6# FMNH).

Distribution. This species is known only from type locality.

Host plant. *Udeus* sp. nov. 27 was collected in staminate inflorescences of *C. obtusifolia* in rainforest.

Udeus muticus Hustache, 1929

Udeus muticus Hustache, 1929: 246 (description). Wibmer & O'Brien 1986: 110 (catalog).

Description provided by Hustache (translated from French): A pale, dull reddish color, covered with a fine and short yellow pubescence, silky and lying flat, denser, and more visible on the elytra. Head with obsolete punctures, pubescent. Rostrum with excessively fine and close punctures at the base, sparsely dotted and shiny towards the front. Prothorax slightly longer than wide, weakly narrowed and abruptly constricted towards the front, with indistinct punctures. Elytra oblong, about twice as wide and four times as long as the prothorax, striated and punctured, with flat interstices and very fine roughness. Underside finely punctured. Slender legs; femora claviform but unarmed; elongated tarsi, with the first article more than twice as long as wide. Length: 2.5-3 mm. M. Champion mentioned as a generic character: "femora armed with a triangular tooth"; except for this character, our species possesses all the other characteristics of the genus, especially those on the underside of the body; I believe that this character should be considered solely as specific. *Udeus muticus* differs from *U. eugnomoides*, a genotype described from Central America, by its slightly elongated shape, longer and differently shaped prothorax, absence of femoral teeth, and much longer tarsi. Gourbeyre (Dufau). 3 specimens (from my collection).

Distribution. Guadeloupe.

Remarks. Due to the impossibility of examining the type material, we provide the original description translated into English. The type material of Hustache species is typically housed at the MNHN in Paris (Horn et al. 1990); however, the specimens were not found in this collection. According to the descriptions by Hustache, *U. muticus* is distinguished from other *Udeus* species, including the new species described here, by the absence of a tooth on the femora. Only *Udeus* sp. 10 and *Udeus* sp. 12 exhibit minute teeth on the femora, making these species closer to the description of *Udeus muticus*.

***Udeus behnei* Rheinheimer, 2018**

Udeus behnei Rheinheimer, 2018: 19 (description).

***Udeus bifasciatus* Rheinheimer, 2018**

Udeus bifasciatus Rheinheimer, 2018: 19 (description).

***Udeus moraguesi* Rheinheimer, 2018**

Udeus moraguesi Rheinheimer, 2018: 20 (description).

Remarks for the Rheinheimer's species. The types corresponding to *U. behnei*, *U. bifasciatus*, and *U. moraguesi*, as documented in Rheinheimer (2018) were not found in MNHN. Given that direct examination of the specimen was not feasible, we recommend that future research include a thorough investigation of these specimens.

Discussion

This study offers a thorough reevaluation of the *Udeus* genus, marking a substantial advancement in both its diversity and our understanding of its biology. Our contribution includes the deposition of specimens in institutions across nearly all continents, alongside the identification

of previously unexplored material from entomological collections, abandoning the status of a rare genus (Lira et al. in press). Notably, the Charles O'Brien Collection (ASUCOB) merits special attention for housing a significant and previously undocumented diversity of *Udeus*, especially from the Amazon and Andean regions.

In terms of morphology, the recurrent color pattern found on the elytra, characterized by transverse bands or dark spots, poses a significant challenge in distinguishing between various species of *Udeus*, especially given their sympatric occurrence. Historically, variation in color patterns led authors to publish variations of the same species as distinct species, as evidenced by the synonyms proposed here for *U. cecropiae* and the *U. variabilis* species complex. In addition to morphotypes of the *U. variabilis* complex, this characteristic pattern is observed across *Udeus* sp. nov. 10, *Udeus* sp. nov. 17, *Udeus* sp. nov. 21, and *Udeus* sp. nov. 23. Distinguishing between these species beyond examining the aedeagus, and in some cases by the expansions in the posterior tibiae and occasional integumentary modifications of male ventrites, becomes exceedingly arduous. For many of these species, descriptions have been limited to males, as sexual dimorphism aids in delimitation. However, there are numerous female specimens awaiting classification, which could be facilitated using alternative methods such as molecular or targeted collections on their host plants.

The exaggerated ornaments on the tibiae and ventrites are not commonly documented in weevil literature but have been observed in other phytophagous beetles, such as *Lankaphthona* Medvedev, 2001 (Ruan *et al.* 2019), and *Haplosomoides* Duvivier, 1890 (Lee *et al.* 2011), both chrysomelids with an abdominal appendage, possibly having some role in copulation. The evolutionary rationale behind these modifications remains unclear, although sexual selection is strongly considered as a potential driving force.

The considerable number of species described in this study corroborates our idea that *Udeus* diversity follows the host diversity. The Andean region is regarded as the center of species richness and the center of speciation of *Cecropia*, especially the northern part of the Andes, in Colombia and Ecuador (Berg & Franco-Rosselli 2005). Despite our study encompassing a limited number of localities in the Andes, notably material sourced from targeted collections in Napo, Ecuador, it has led to the identification of five new species (*Udeus* sp. nov. 10, *Udeus* sp. nov. 17, *Udeus* sp. nov 19, *Udeus* sp. nov. 21, and *Udeus* sp. nov. 26), alongside several others awaiting formal description. The Napo province is recognized as a biodiversity hotspot and a particular endemism area with registers of high diversity and has recently been highlighted by an increasing number of new species described, for example in Coccinellidae (Szawaryn & Czerwiński 2022), Scarabaeinae (Espinoza & Noriega 2018), Elmidae (Linský et al. 2019), and Cerambycidae (Vlasak & Santos-Silva 2023). Concentrating efforts on collecting in these locations is crucial to further expand our understanding of *Udeus* diversity and deepens our understanding of diversification patterns and coevolution between *Udeus* and their hosts.

The intrinsic association with *Cecropia* figures as a potential source of discoveries in the evolution of flower visitors, although there is much to know about this relationship. For known *Udeus* species until this review, the association with *Cecropia* was registered to *U. cecropiae* and *U. sergioi* for the first descriptions of their biology provided by Bondar (1957). Besides this first report, the description of *U. moraguesi* from Guyane is the only study that includes its register in *Cecropia sp.* (Rheinheimer 2018). As previously stated, this study reinforces the specificity of *Udeus* with *Cecropia*, including registers to 13 species associated with 11 *Cecropia* species. Eight *Udeus* species were associated with a unique *Cecropia* species, while only *U. longicollis*, *U. variabilis*, *Udeus* sp. nov. 6, and *Udeus sp. nov. 8* occur in more than one *Cecropia*. In line with our initial attempt to test the pollination of *C. saxatilis* by *U. cerradensis* (Lira et al. 2024), we

repeated the experiments using adhesive traps and conducted daytime and nighttime monitoring in *C. pachystachya* and *C. palmata*, and adhesive traps in *C. membranacea*, *C. latiloba*, and *C. ulei*. All attempts failed to capture weevils in pistillate flowers. However, it is noteworthy that odor with a chemical composition commonly found in nature was detected in the female inflorescences of *C. palmata* (Arthur Maia, personal communication), potentially indicating attractiveness to floral visitors. Although the role as a pollinator remains under investigation, the presence of *Udeus* in various habitats, particularly Andean forests, suggests a potential unique contribution to pollination if this function is confirmed.

While the full extent of *Udeus* diversity remains to be fully elucidated, recent investigations have revealed several known species along with novel ones, documented in this study. Incorporating these findings into a comprehensive phylogenetic analysis of Eugnomini has provided valuable insights into their taxonomic relationships, with important implications for future studies on Neotropical Eugnomini diversity.

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APPENDIX - Figures

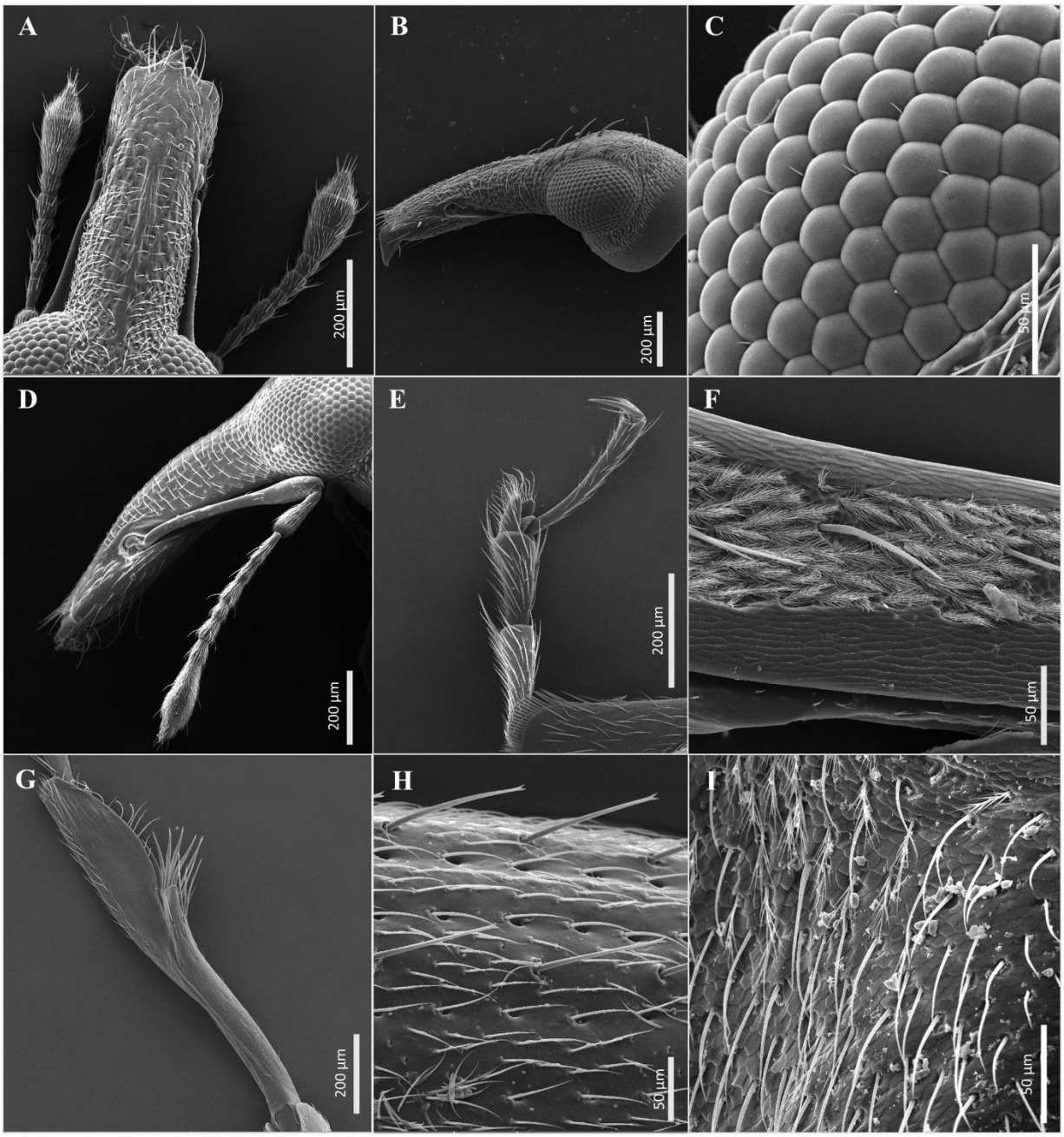

FIGURE 1. General morphology of *Udeus*. A rostrum in dorsal view. B head in lateral view. C ommatidia. D head and antennae in lateral view. E tarsus. F Mesepisternum. G metatibiae of *Udeus* sp. nov. 6. H setae in interstriae. I lateral of first ventrite.

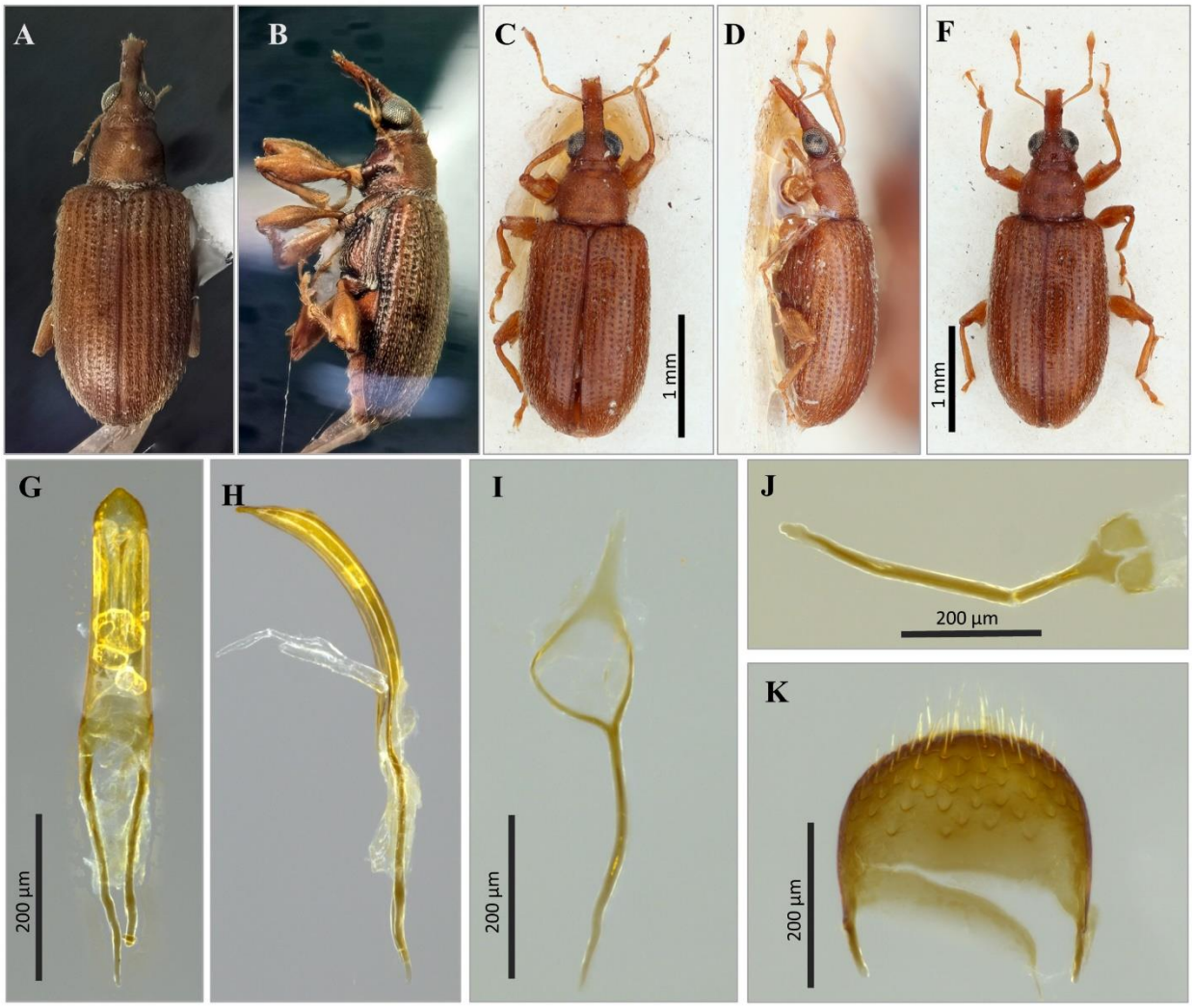

FIGURE 2. A–F *Udeus eugnomoides.* A–B dorsal and lateral habitus of a specimen from Costa Rica. C–D dorsal and ventral habitus of holotype (male) from Guadeloupe. E dorsal habitus of paratype (female) from Guadeloupe. F–J Male terminalia. F–G aedeagus in dorsal and lateral views. H tegmen. I sternum VIII. J pygidium.

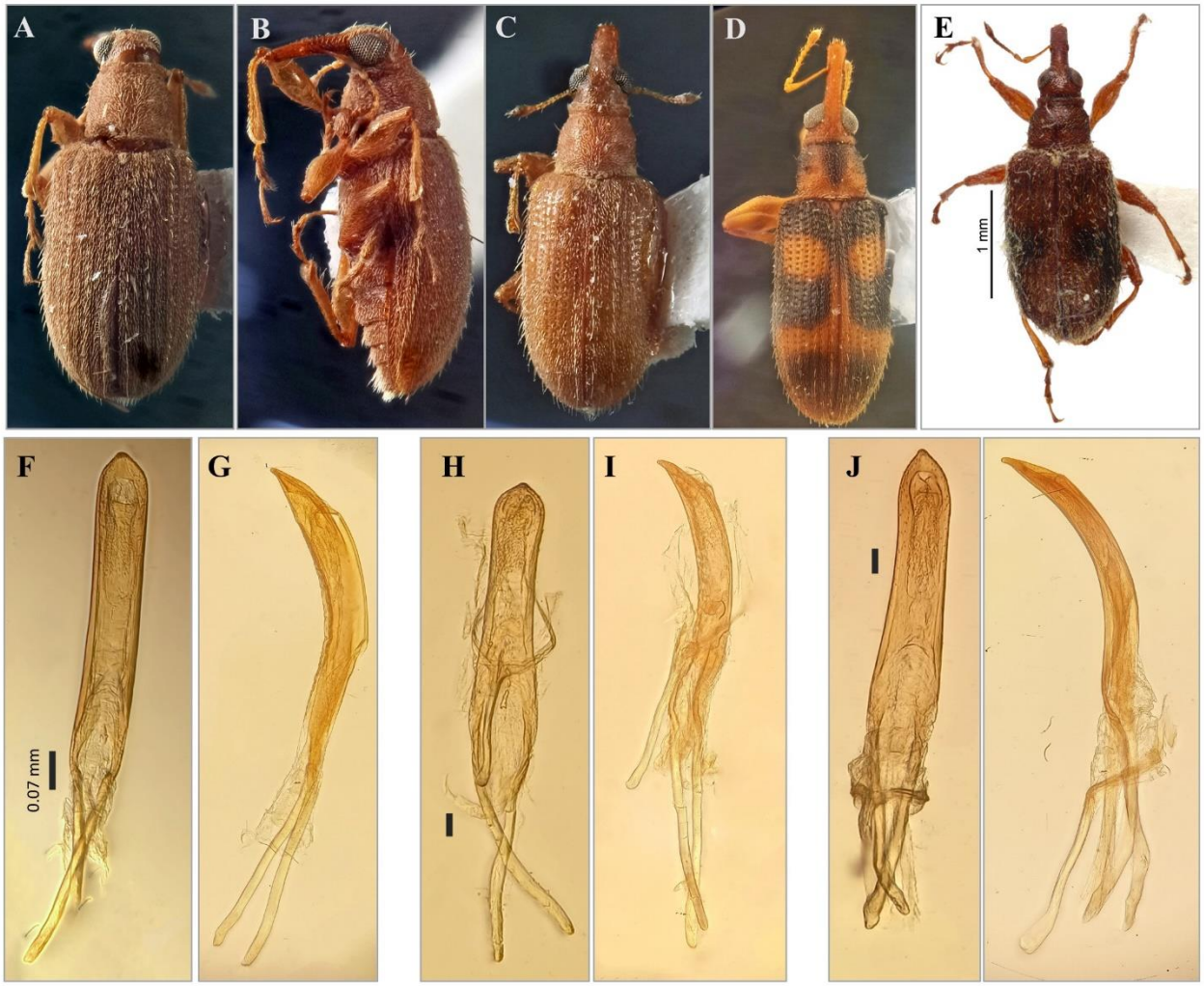

FIGURE 3. A–E *Udeus variabilis*. A–B dorsal and lateral habitus of a Bolivian specimen. C dorsal habitus of a Peruan specimen. D dorsal habitus of a Brazilian (from Rio de Janeiro) specimen. E dorsal habitus of syntipe from Bolivia. F–K Aedeagus of *U. variabilis.* F–G aedeagus in dorsal and lateral view of a Bolivian specimen. H–I aedeagus in dorsal and lateral view of a Peruan specimen. J–K aedeagus in dorsal and lateral view of a Brazilian specimen.

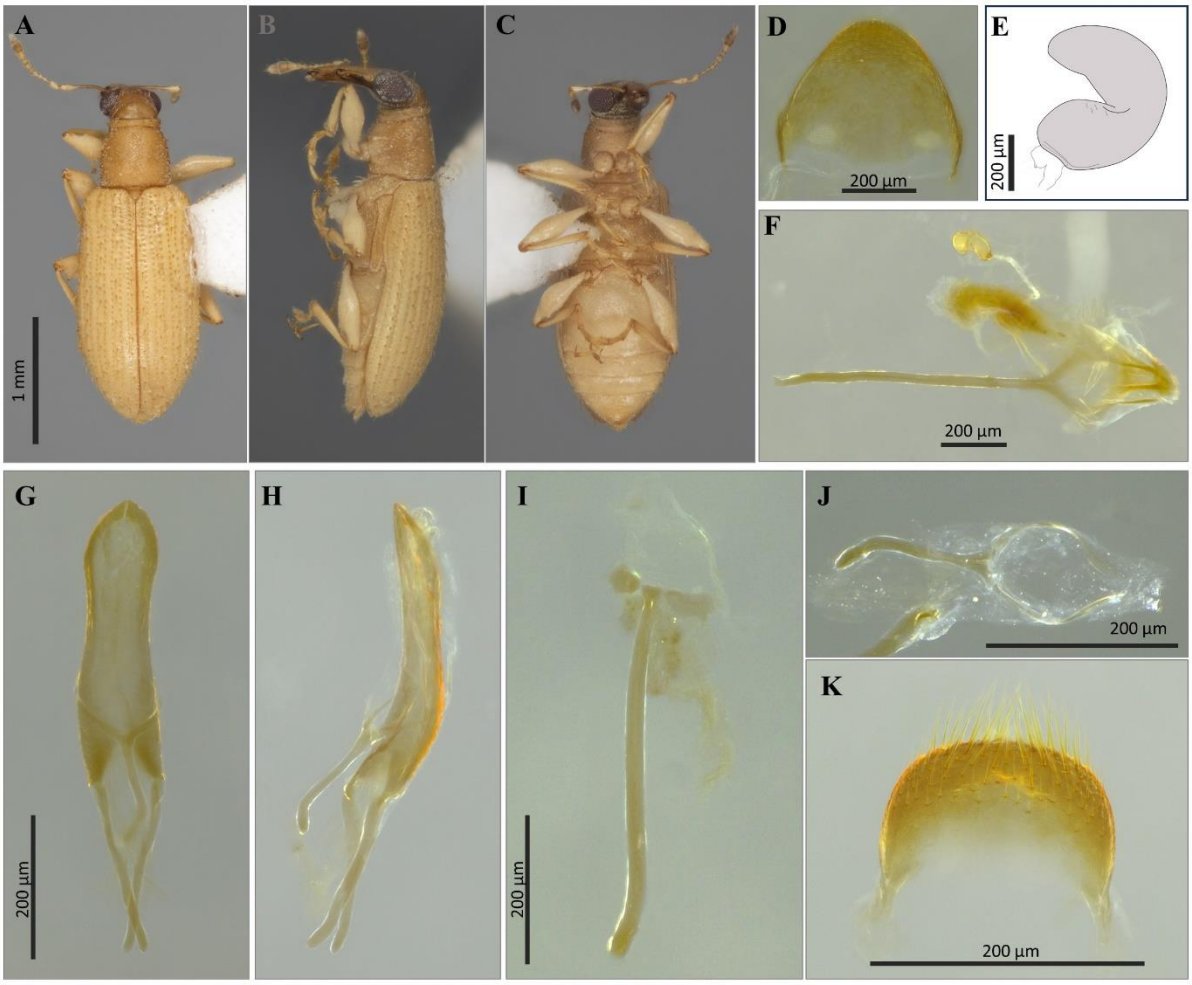

FIGURE 4. A–C *Udeus longicollis*. A dorsal habitus. B lateral habitus. C ventral habitus. D–F Male terminalia. G–H aedeagus in dorsal and lateral views. I sternum VIII. J tegmen. K pygidium.

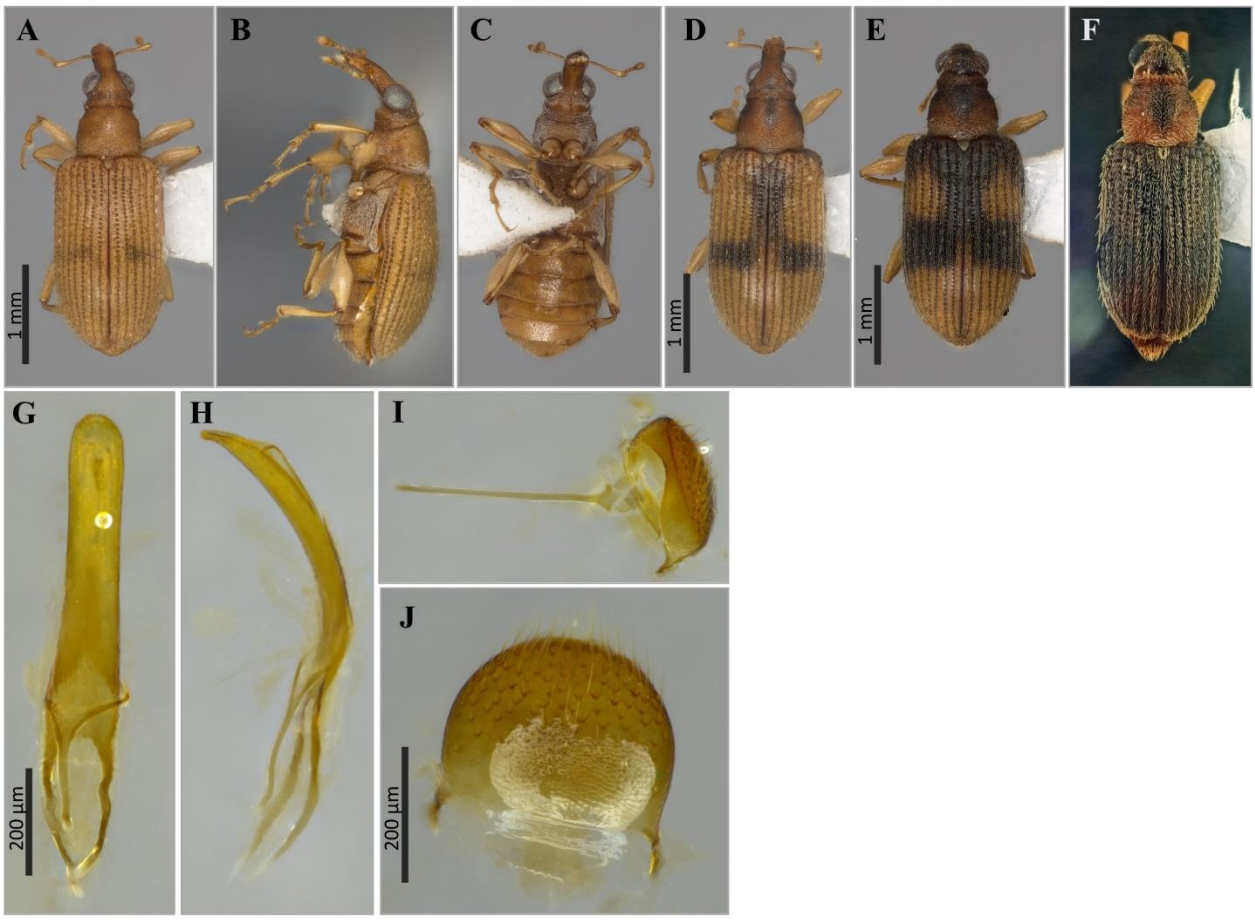

FIGURE 5. A–F *Udeus fonsecai.* A–C dorsal, lateral, and ventral habitus of paratype (female) from Pernambuco. D–E dorsal habitus of paratypes from Pernambuco. G–J Male terminalia. G–H aedeagus in dorsal and lateral views. I sternum VIII. J pygidium.

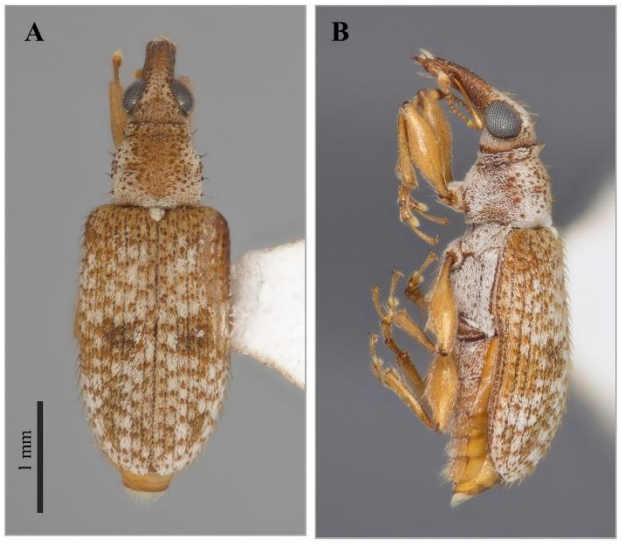

FIGURE 6. A–B *Udeus cerradensis.* A dorsal habitus. B lateral habitus.

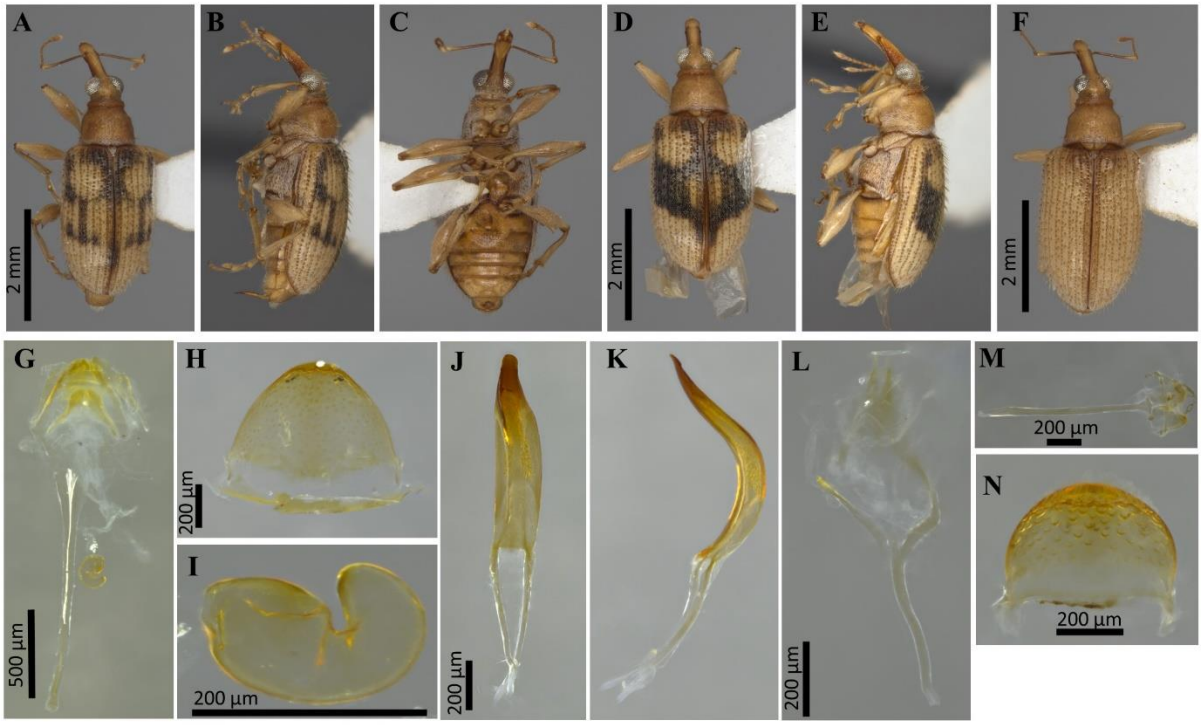

FIGURE 7. A–F *Udeus* sp. nov. 3. A–C dorsal, lateral, and ventral habitus of paratype (male) from Pernambuco. D–E dorsal and lateral habitus of paratype (female) from Pernambuco. F dorsal habitus of paratype from Pernambuco. G–I Female terminalia. G complete terminalia. H pygidium. I spermatheca. J–N Male terminalia. J–K aedeagus in dorsal and lateral views. L tegmen. M sternum IX. N pygidium.

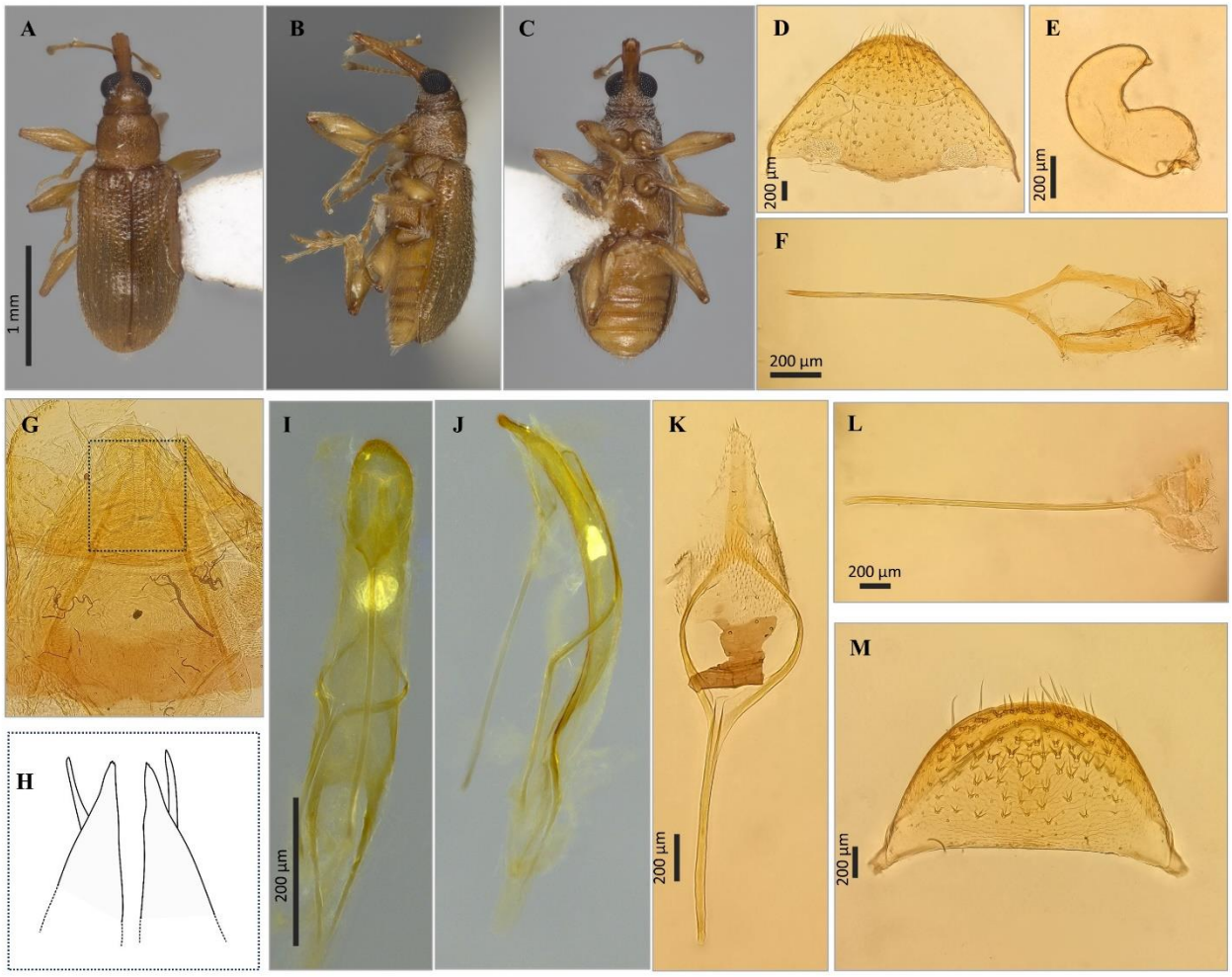

FIGURE 8. A–C *Udeus* sp. nov. 5. A–C dorsal, lateral, and ventral habitus of paratype. D–F Female terminalia. D pygidium. E spermatheca. F sternum VIII. G–H coxites and styli. I–M Male terminalia. I–J aedeagus in dorsal and lateral views. K tegmen. L Sternum IX. M pygidium.

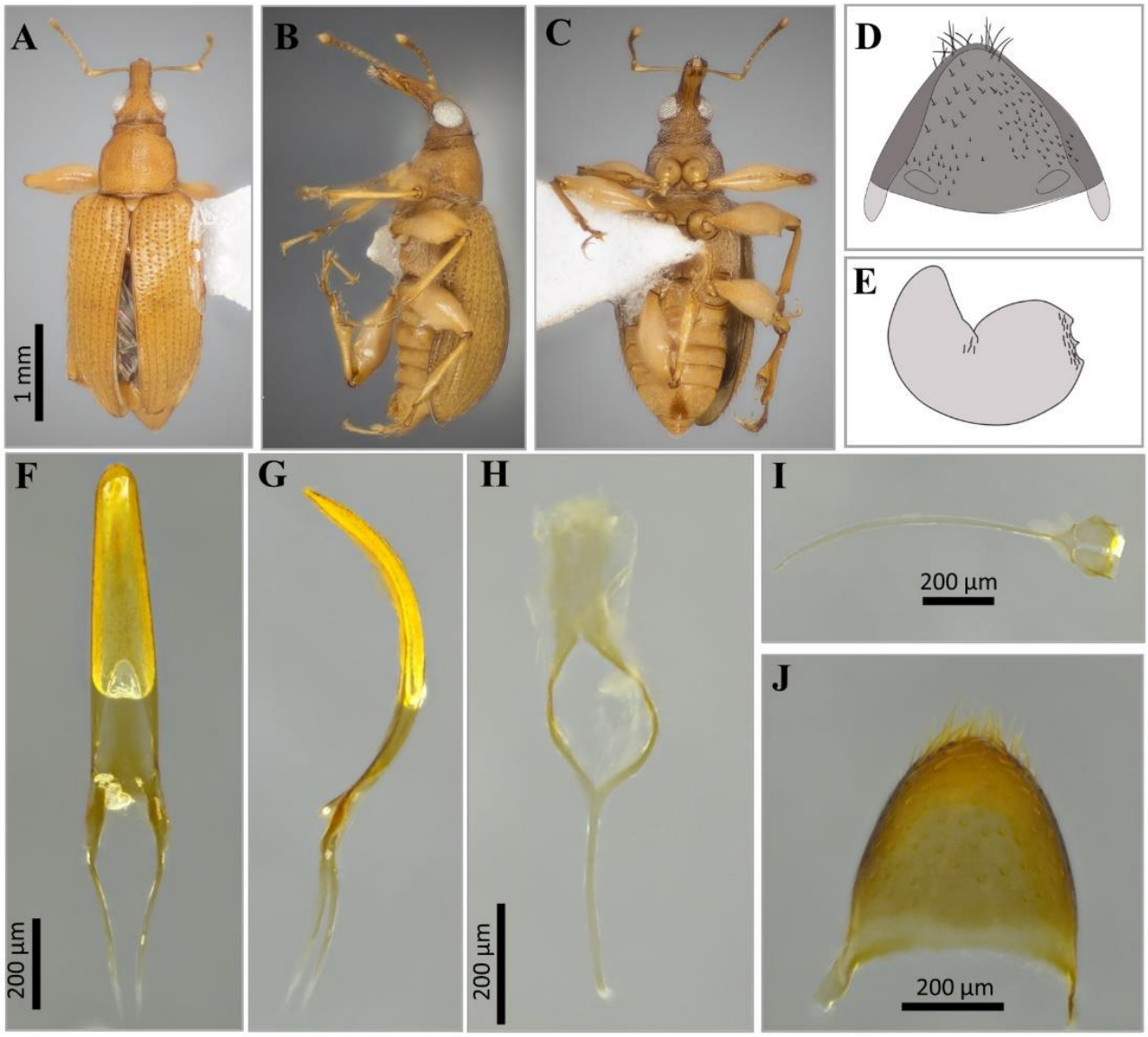

FIGURE 9. A–C *Udeus* sp. nov. 6. A–C dorsal, lateral, and ventral habitus of paratype. D–E Female terminalia. D pygidium. E spermatheca. F–J male terminalia. F–G aedeagus in dorsal and lateral views. H tegmen. I Sternum J. M pygidium.

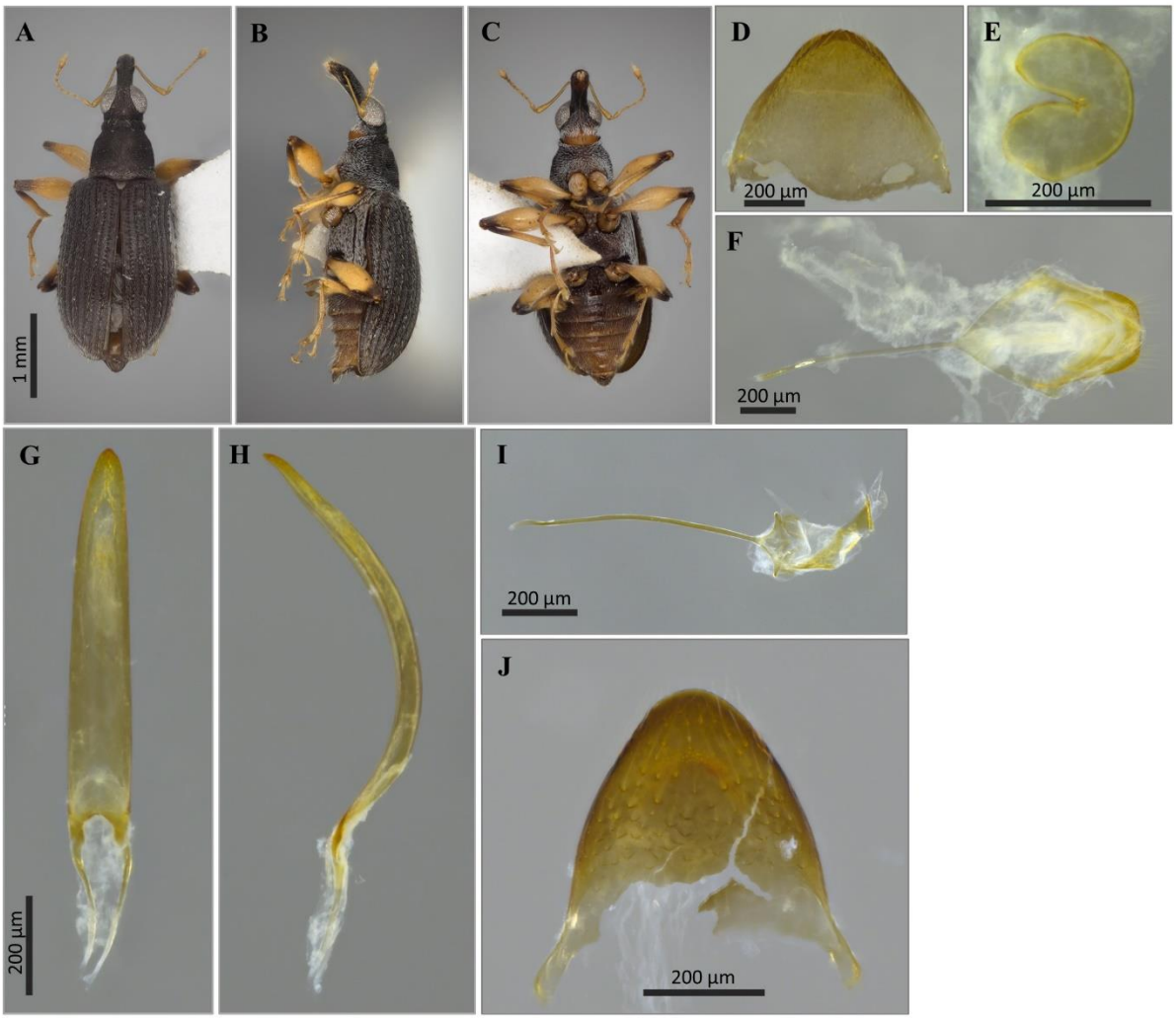

FIGURE 10. A–C *Udeus* sp. nov. 7. A–C dorsal, lateral, and ventral habitus of paratype. D–F Female terminalia. D pygidium. E spermatheca. F sternum VIII. G–J Male terminalia. G–H aedeagus in dorsal and lateral views. I Sternum IX. J pygidium.

FIGURE 11. A–C *Udeus* sp. nov. 8. A–C dorsal, lateral, and ventral habitus of paratype. D–F Female terminalia. D sternum VIII. E pygidium. F spermatheca. G–J Male terminalia. G–H aedeagus in dorsal and lateral views. I Sternum IX. J pygidium.

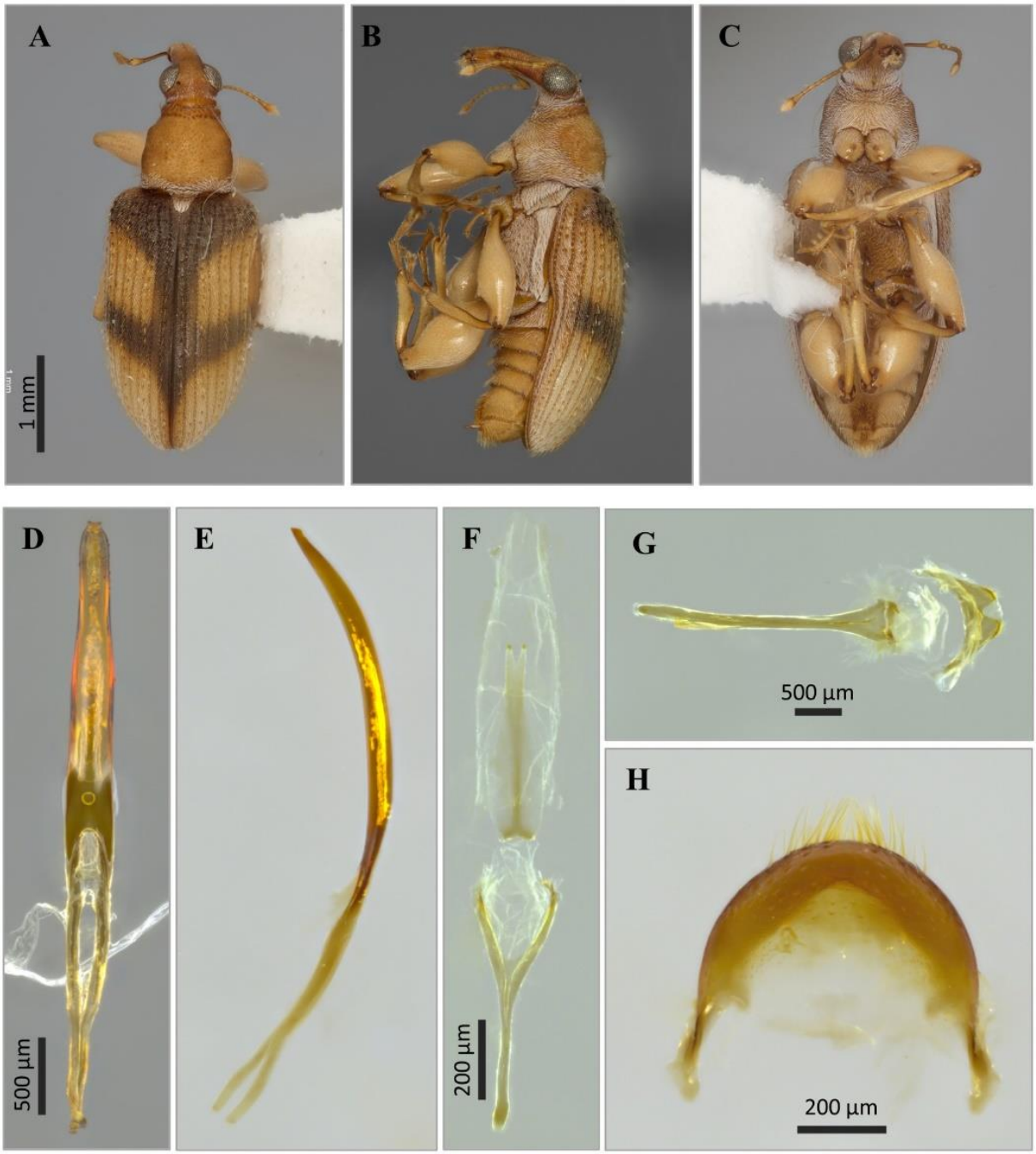

FIGURE 12. A–C *Udeus* sp. nov. 10. A–C dorsal, lateral, and ventral habitus of paratype. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F tegmen. G Sternum IX. H pygidium.

FIGURE 13. A–C *Udeus* sp. nov. 11. A–C dorsal, lateral, and ventral habitus of paratype. D–F Female terminalia. D pygidium. E spermatheca. F sternum VIII. G–J Male terminalia. G–H aedeagus in dorsal and lateral views. I Sternum IX. J pygidium.

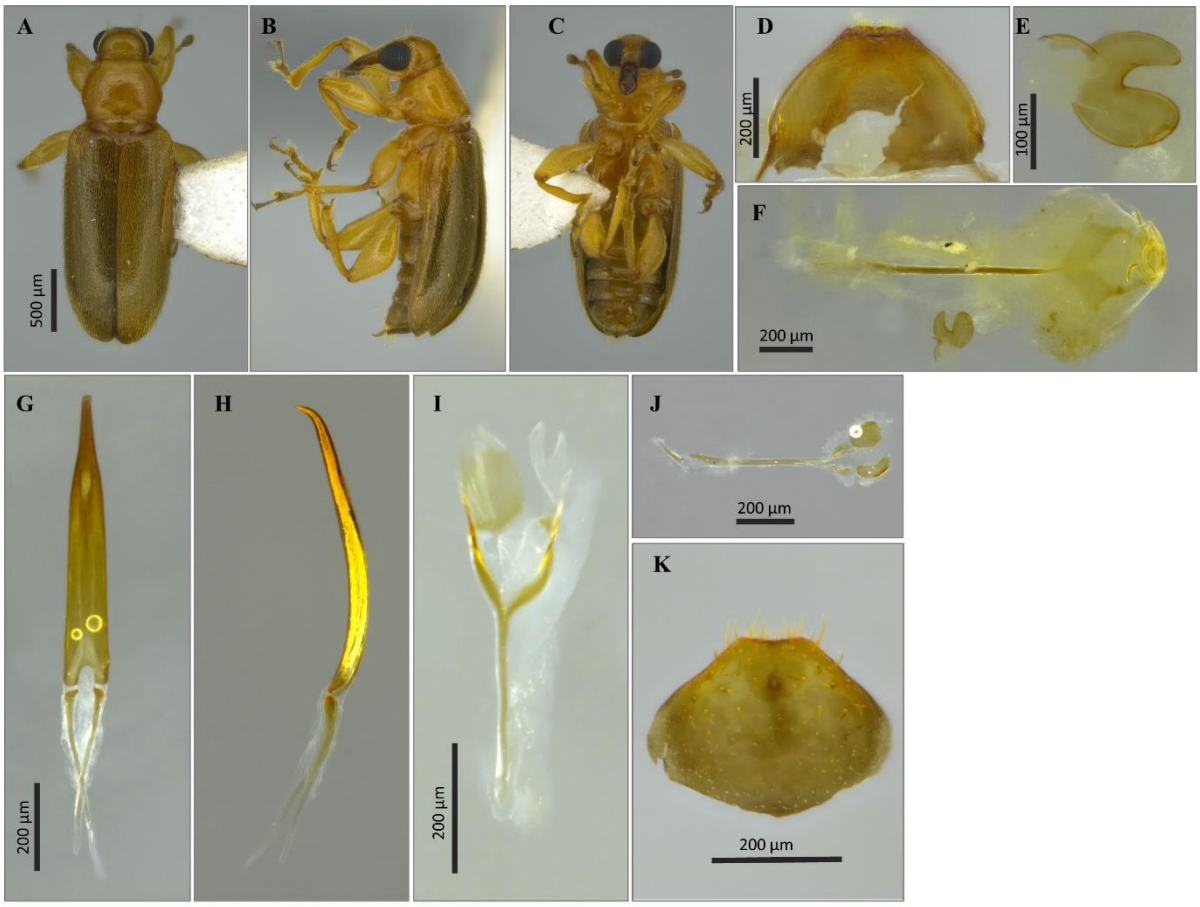

FIGURE 14. A–C *Udeus* sp. nov. 12. A–C dorsal, lateral, and ventral habitus of paratype. D–F Female terminalia. D pygidium. E spermatheca. F sternum VIII. G–K Male terminalia. G–H aedeagus in dorsal and lateral views. I tegmen. J Sternum IX. K pygidium.

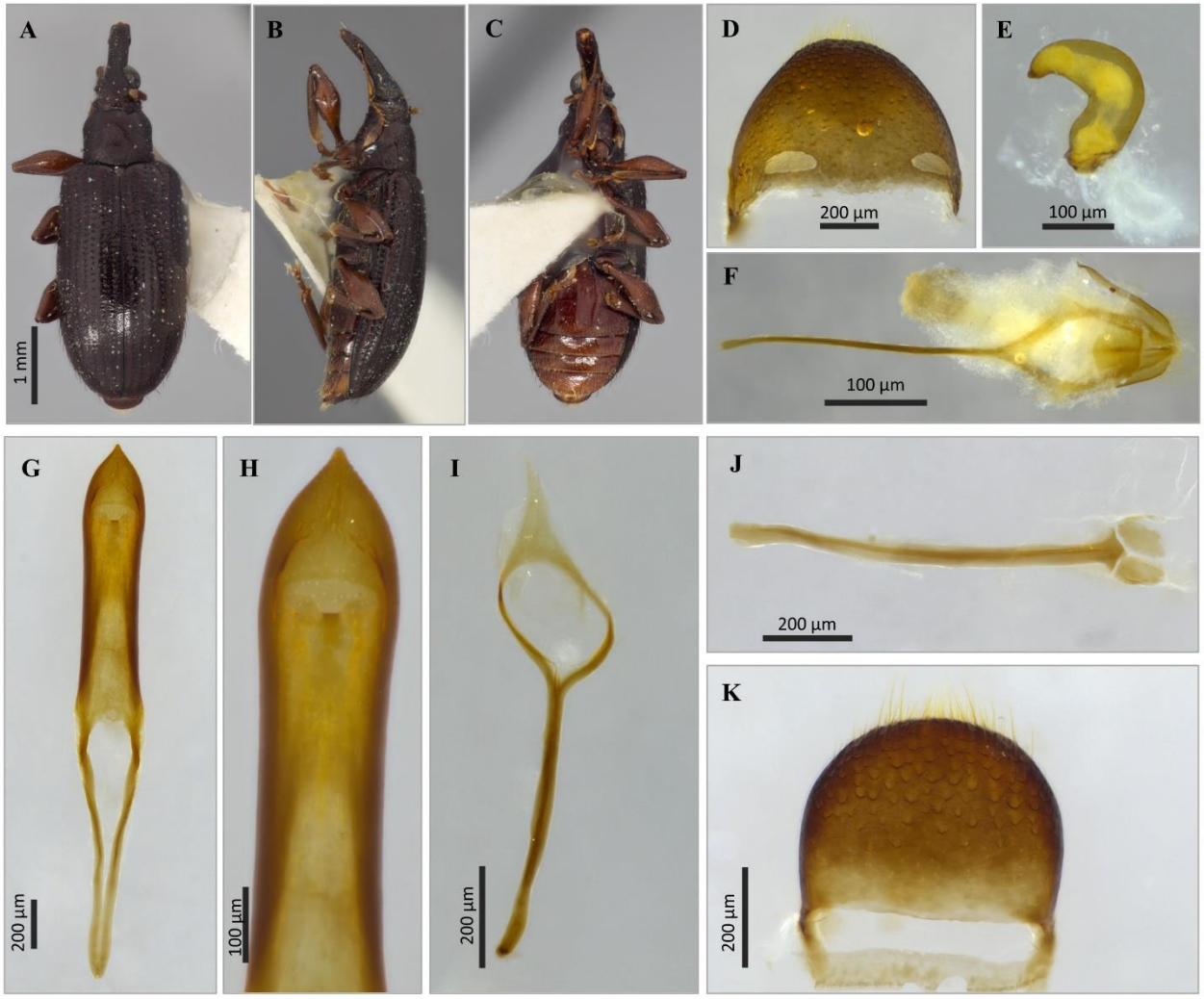

FIGURE 15. A–C *Udeus* sp. nov. 15. A–C dorsal, lateral, and ventral habitus of holotype. D–F Female terminalia. D pygidium. E spermatheca. F sternum VIII. G–K Male terminalia. G–H aedeagus in dorsal and lateral views. I tegmen. J Sternum IX. K pygidium.

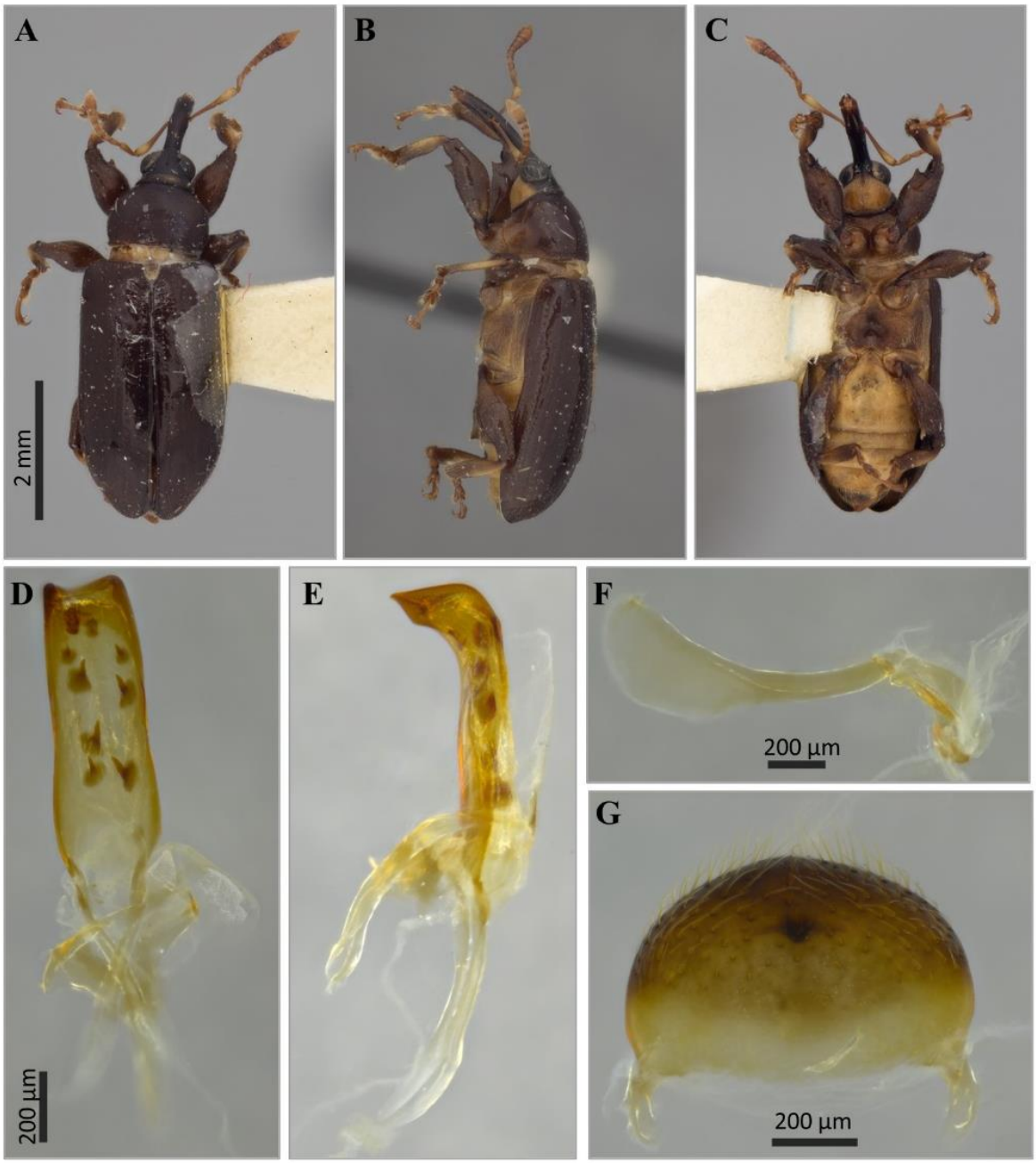

FIGURE 16. A–C *Udeus* sp. nov. 16. A–C dorsal, lateral, and ventral habitus of holotype. D–G Male terminalia. D–E aedeagus in dorsal and lateral views. F Sternum IX. G pygidium.

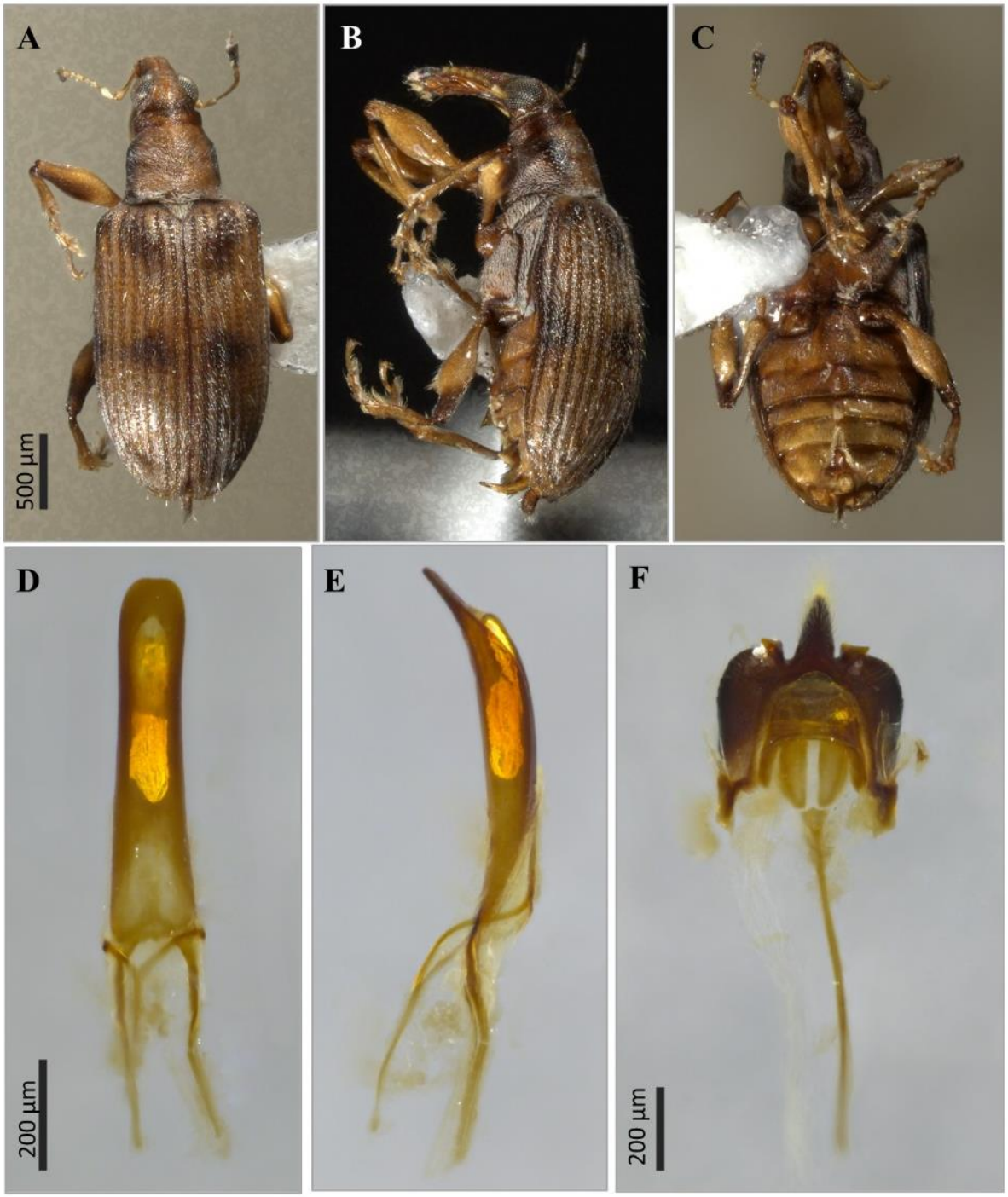

FIGURE 17. A–C *Udeus* sp. nov. 17. A–C dorsal, lateral, and ventral habitus of paratype. D–F Male terminalia. D–E aedeagus in dorsal and lateral views. F Sternum IX and pygidium.

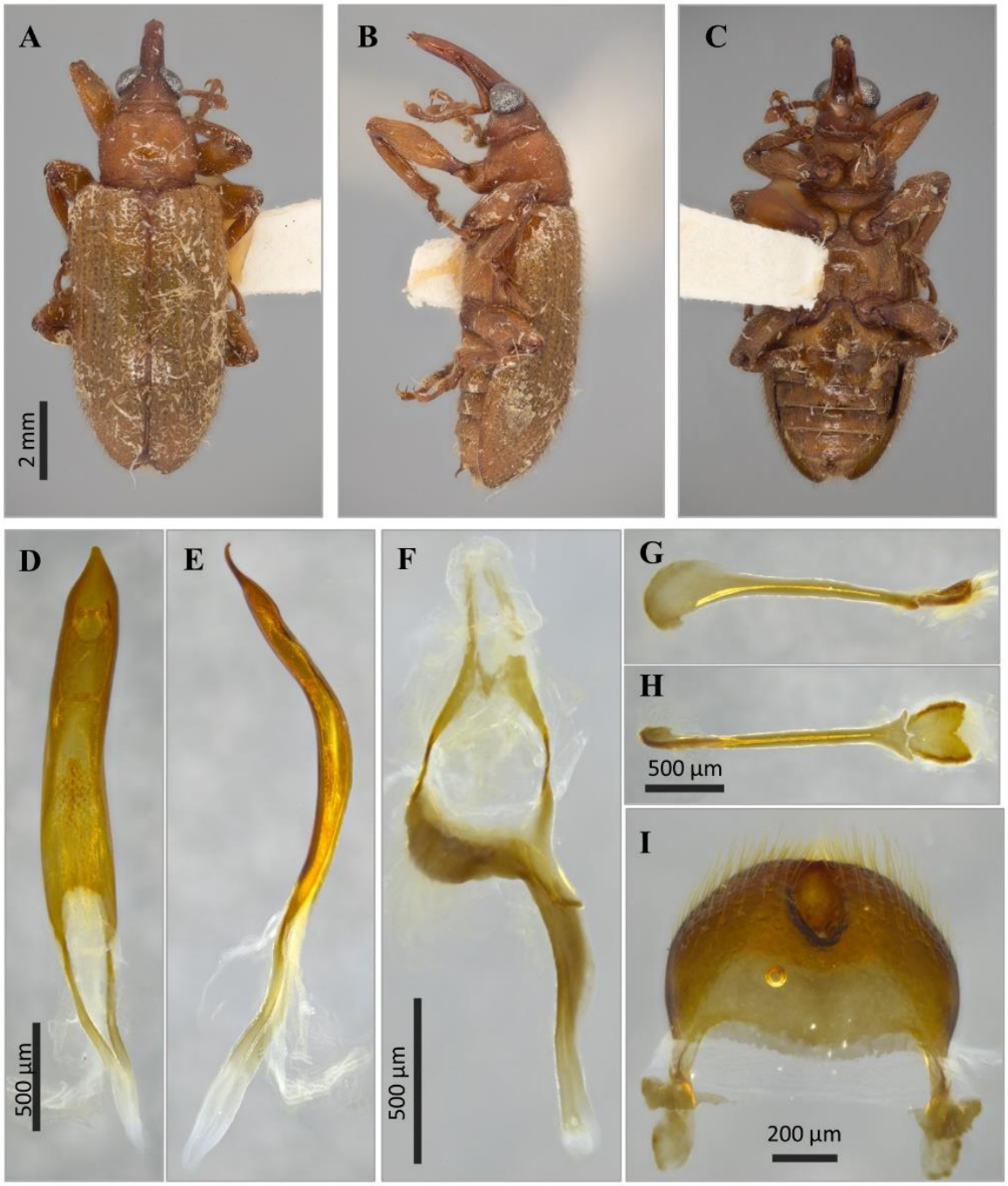

FIGURE 18. A–C *Udeus* sp. nov. 18. A–C dorsal, lateral, and ventral habitus of holotype. D–I Male terminalia. D–E aedeagus in dorsal and lateral views. F tegmen. G–H Sternum IX in lateral and dorsal views. I pygidium.

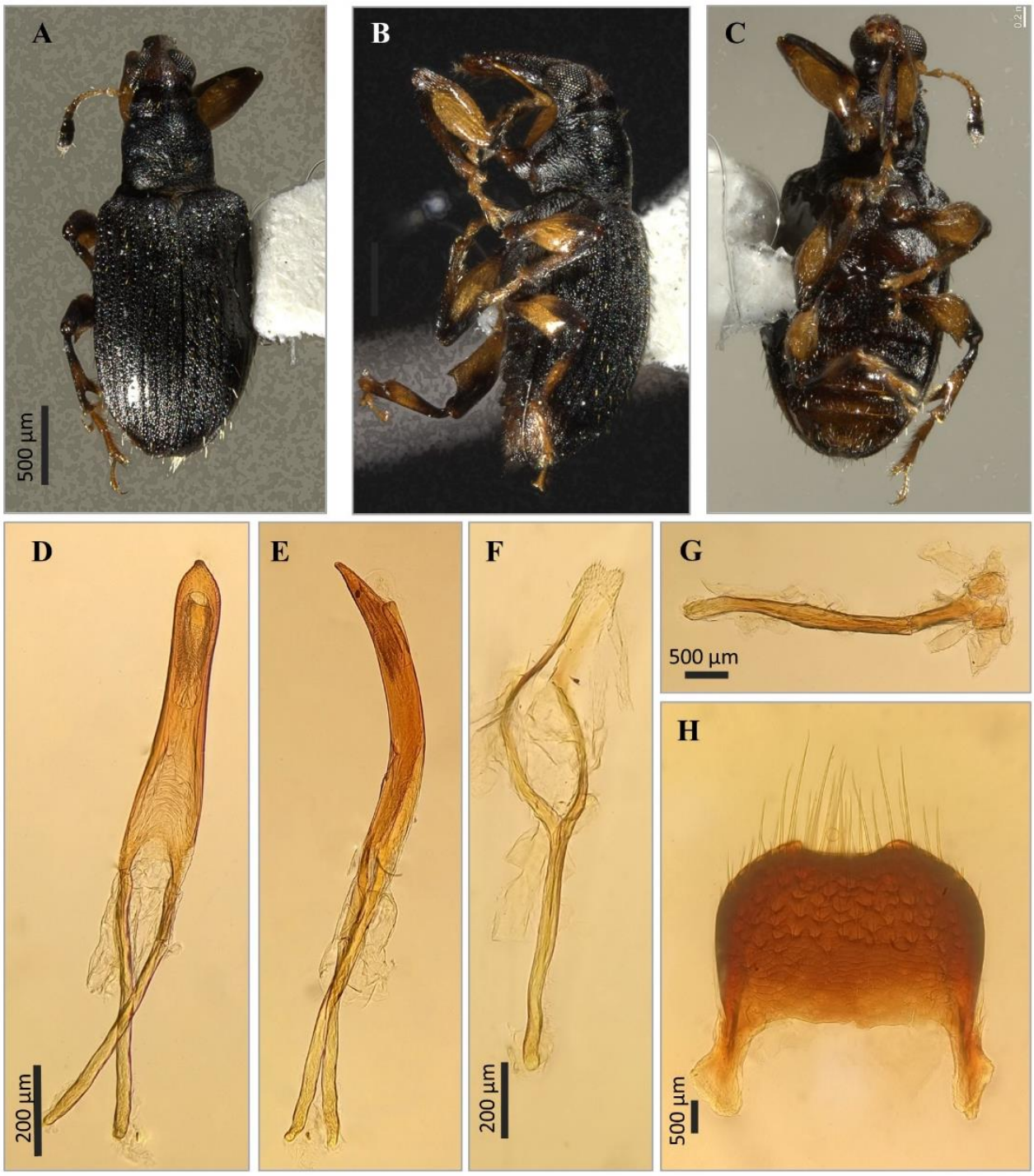

FIGURE 19. A–C *Udeus* sp. nov. 19. A–C dorsal, lateral, and ventral habitus of paratype. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F tegmen. G sternum IX. H pygidium.

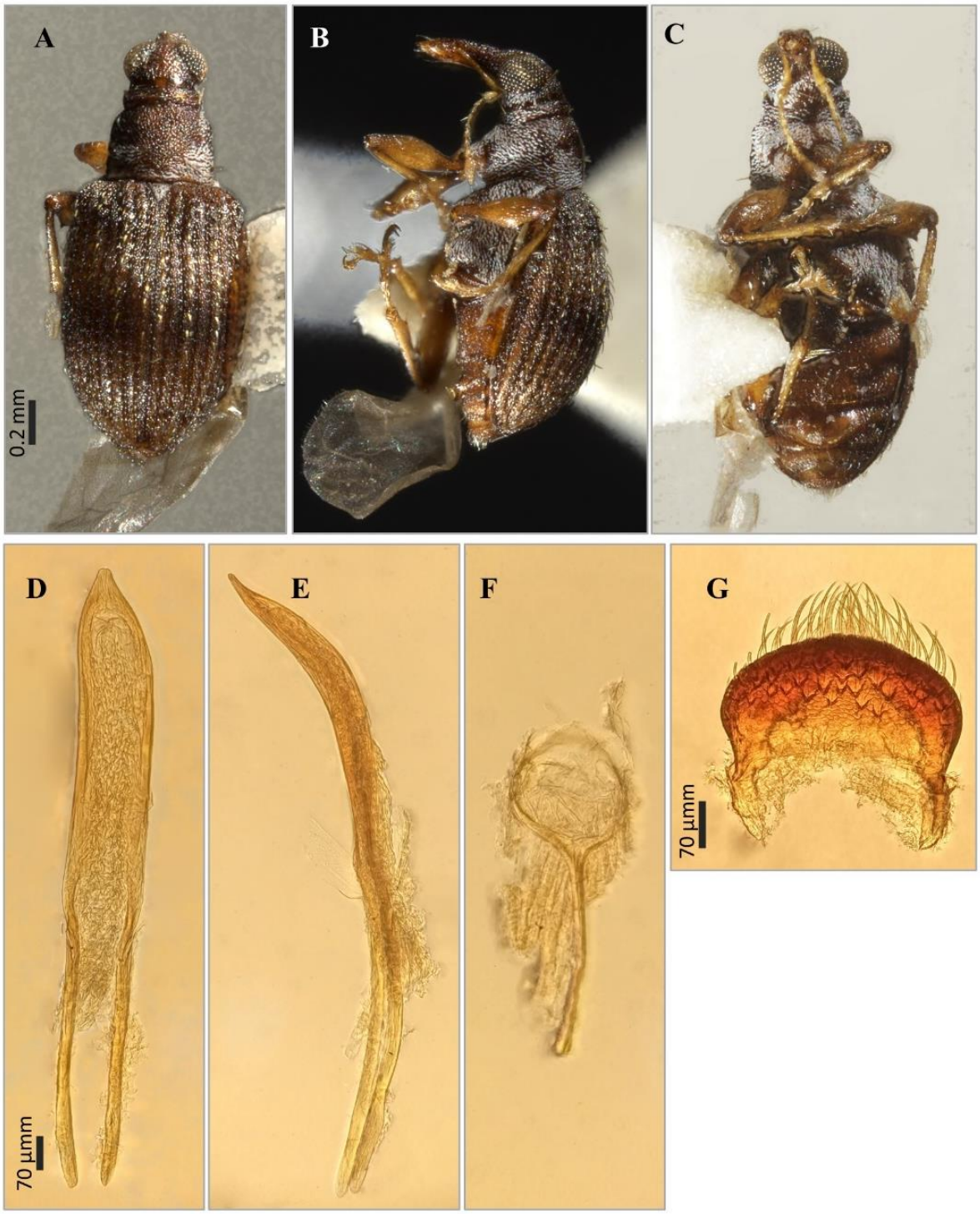

FIGURE 20. A–C *Udeus* sp. nov. 20. A–C dorsal, lateral, and ventral habitus. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F tegmen. G pygidium.

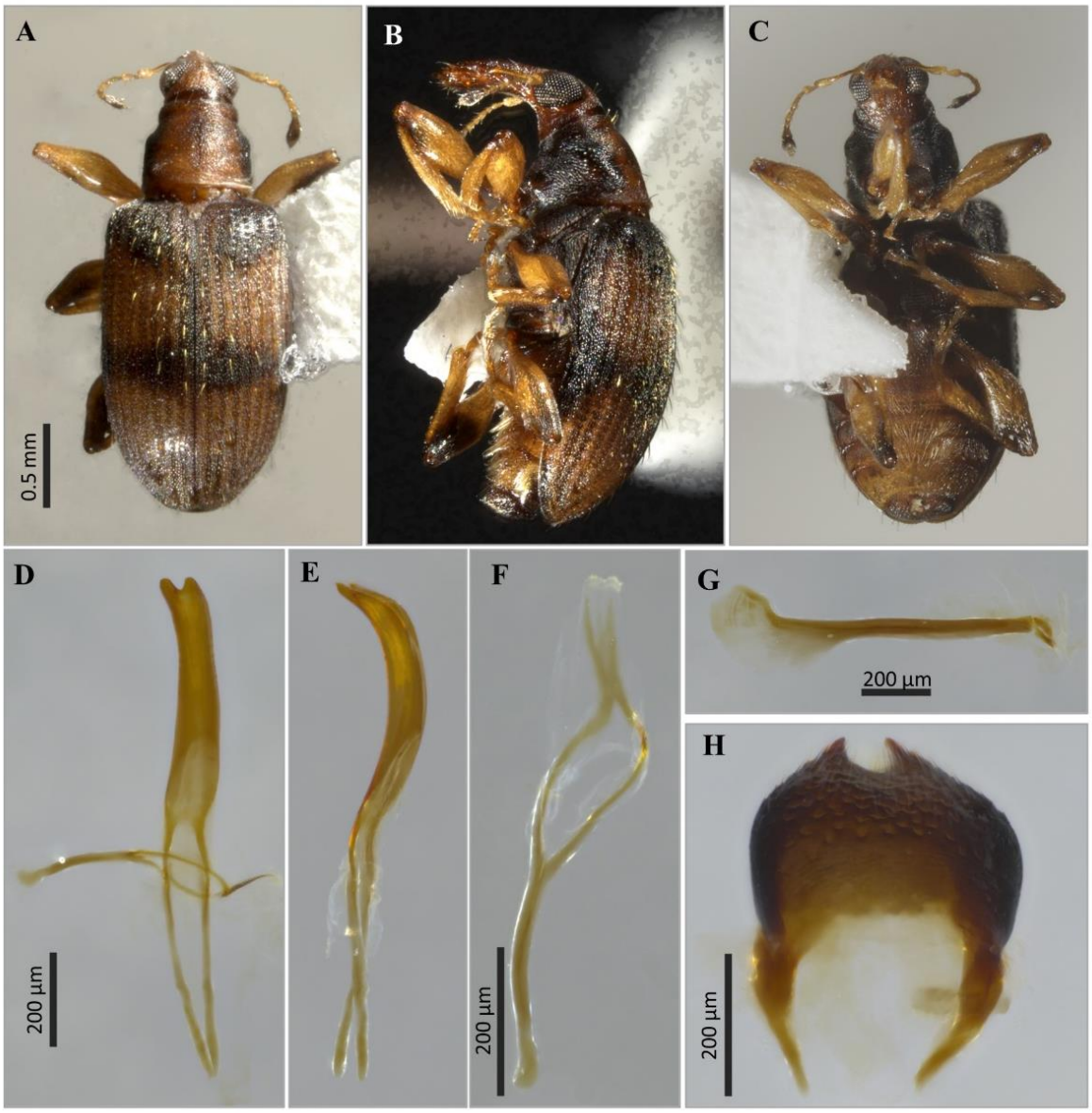

FIGURE 21. A–C *Udeus* sp. nov. 21. A–C dorsal, lateral, and ventral habitus. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F tegmen. G sternum IX. H pygidium.

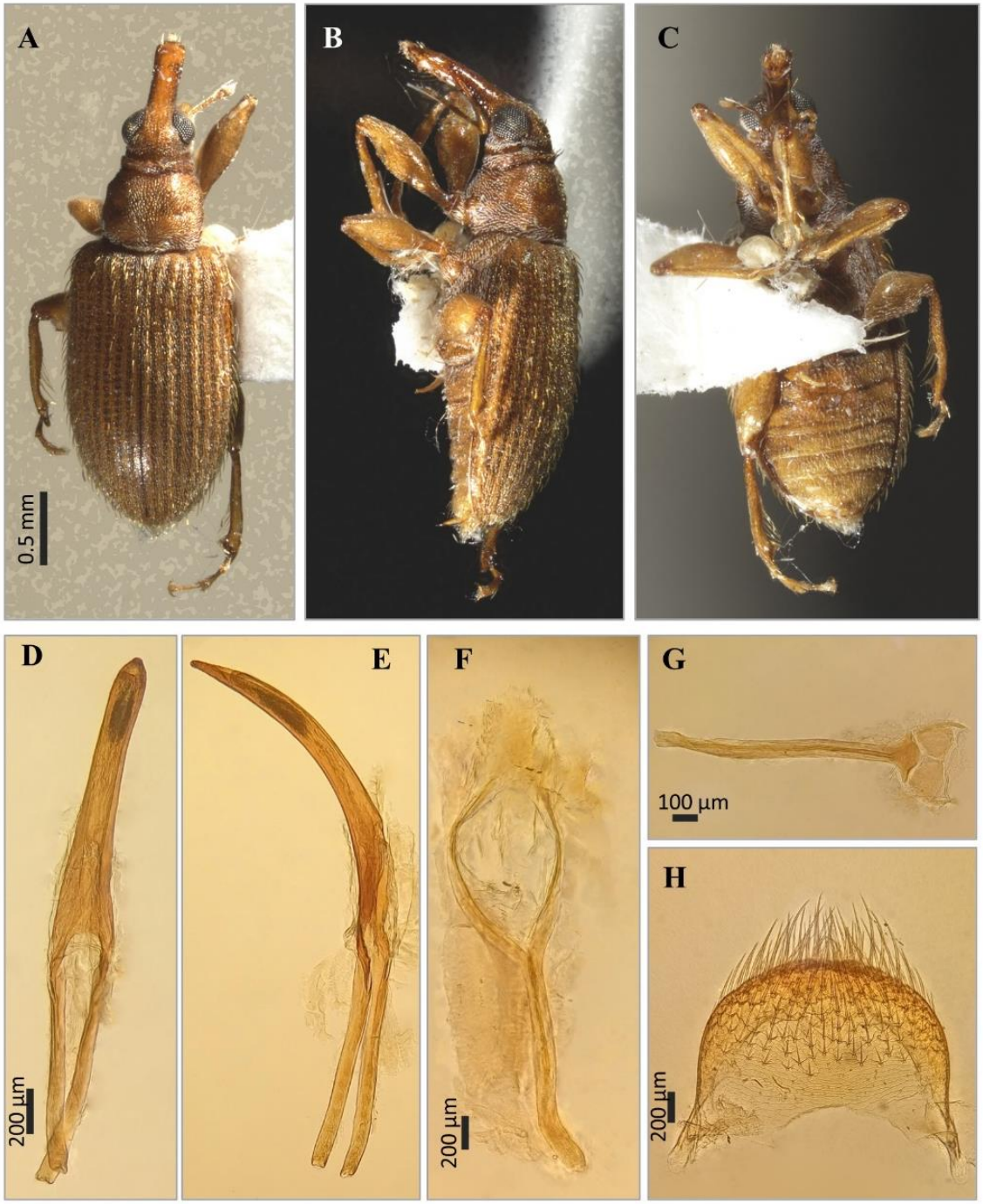

FIGURE 22. A–C *Udeus* sp. nov. 22. A–C dorsal, lateral, and ventral habitus. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F tegmen. G sternum IX. H pygidium.

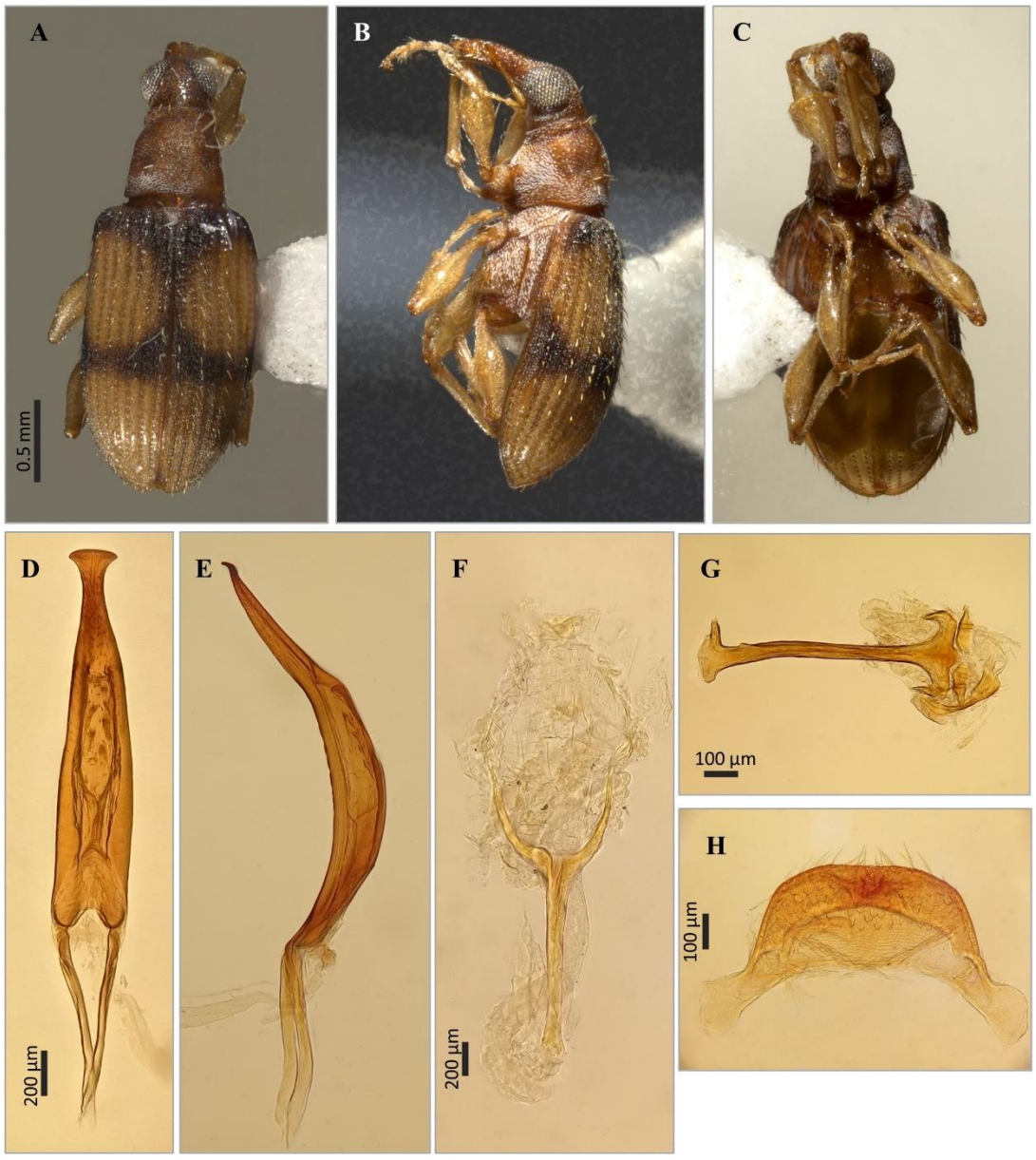

FIGURE 23. A–C *Udeus* sp. nov. 23. A–C dorsal, lateral, and ventral habitus. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F tegmen. G sternum IX. H pygidium.

FIGURE 24. A–C *Udeus* sp. nov. 24. A–C dorsal, lateral, and ventral habitus. D–F Female terminalia. D pygidium. E spermatheca. F sternum VIII. G–J Male terminalia. G–H aedeagus in dorsal and lateral views. I sternum IX. J pygidium.

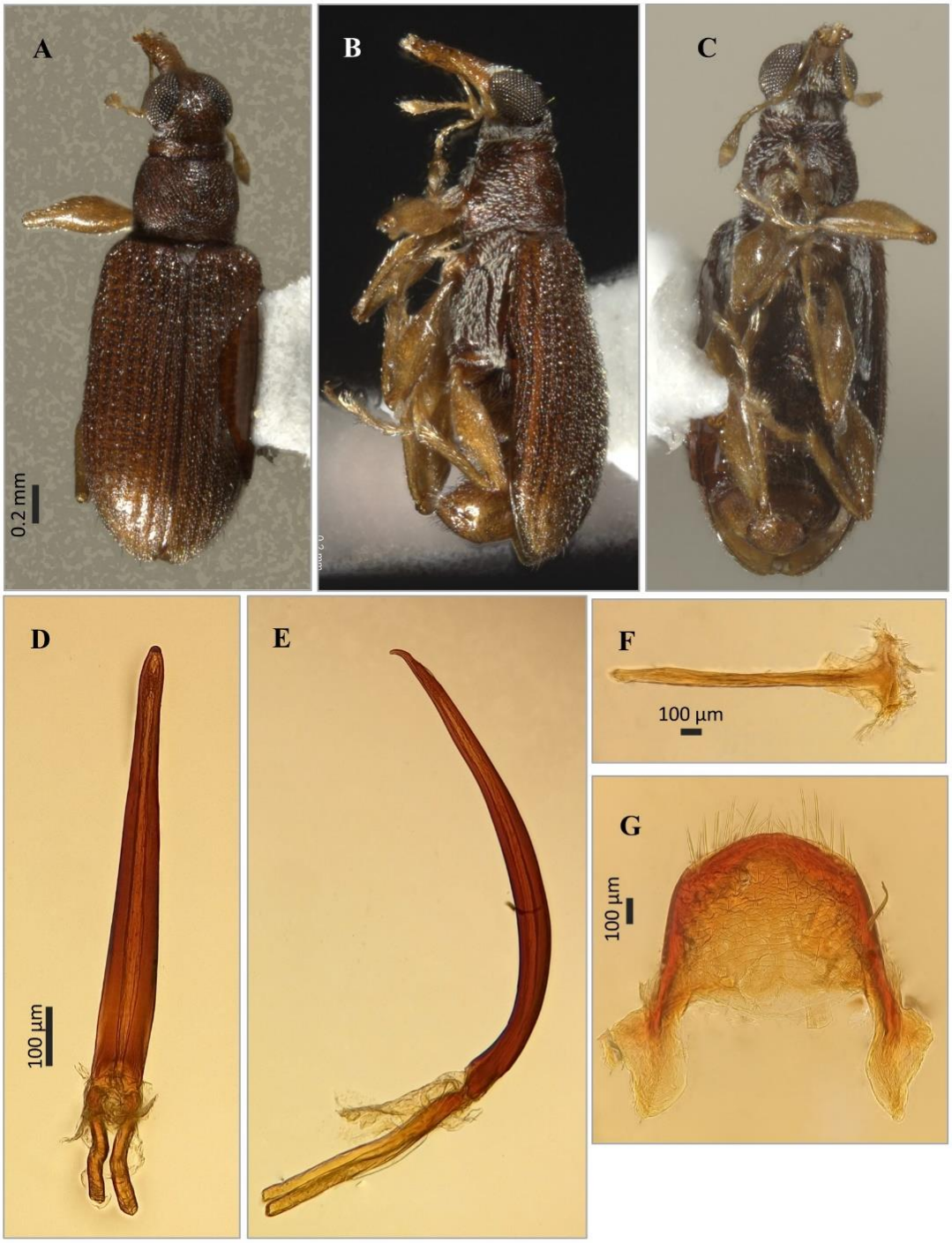

FIGURE 25. A–C *Udeus* sp. nov. 25. A–C dorsal, lateral, and ventral habitus. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F sternum IX. G pygidium.

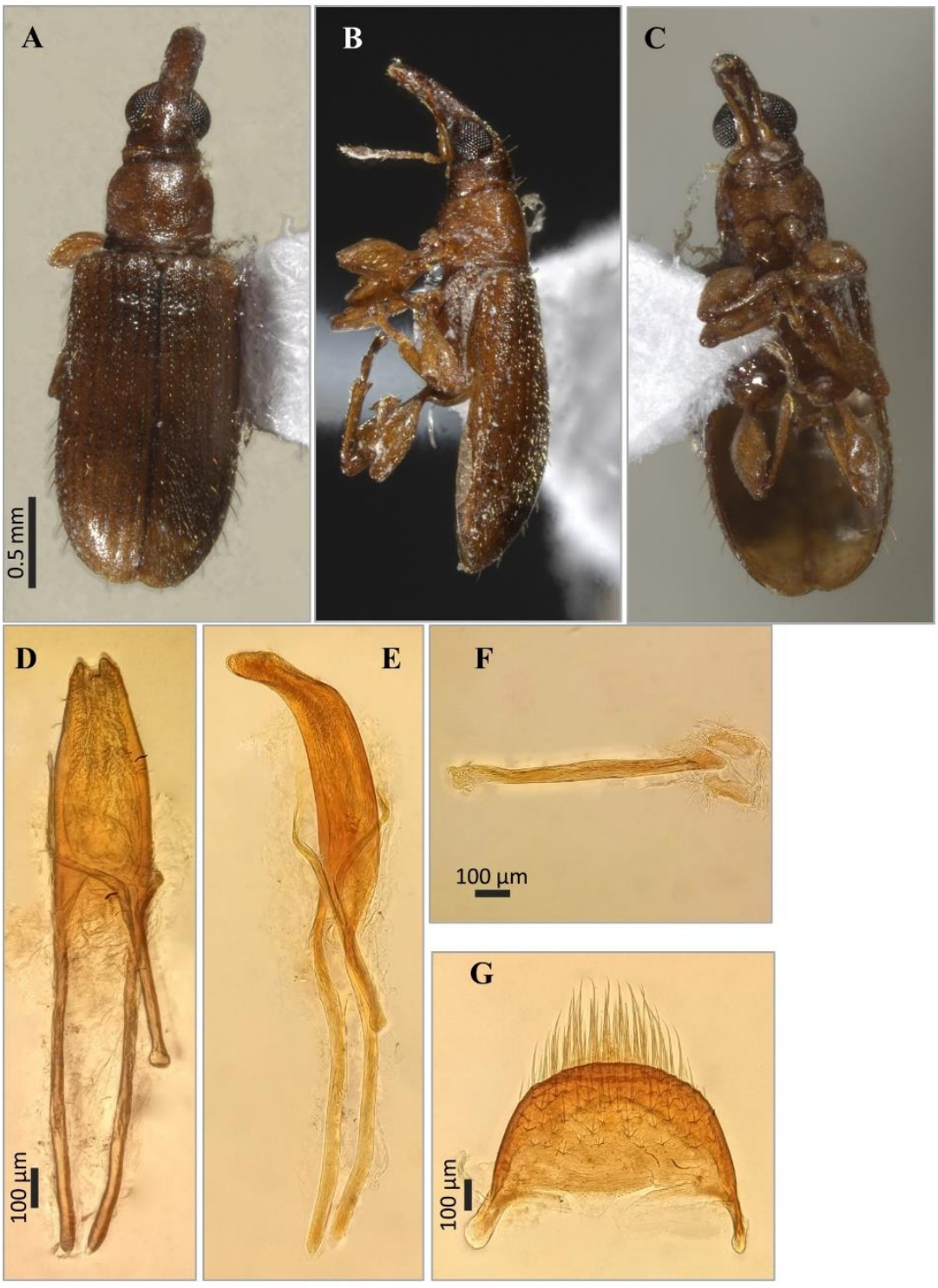

FIGURE 26. A–C *Udeus* sp. nov. 26. A–C dorsal, lateral, and ventral habitus. D–H Male terminalia. D–E aedeagus in dorsal and lateral views. F sternum IX. G pygidium.

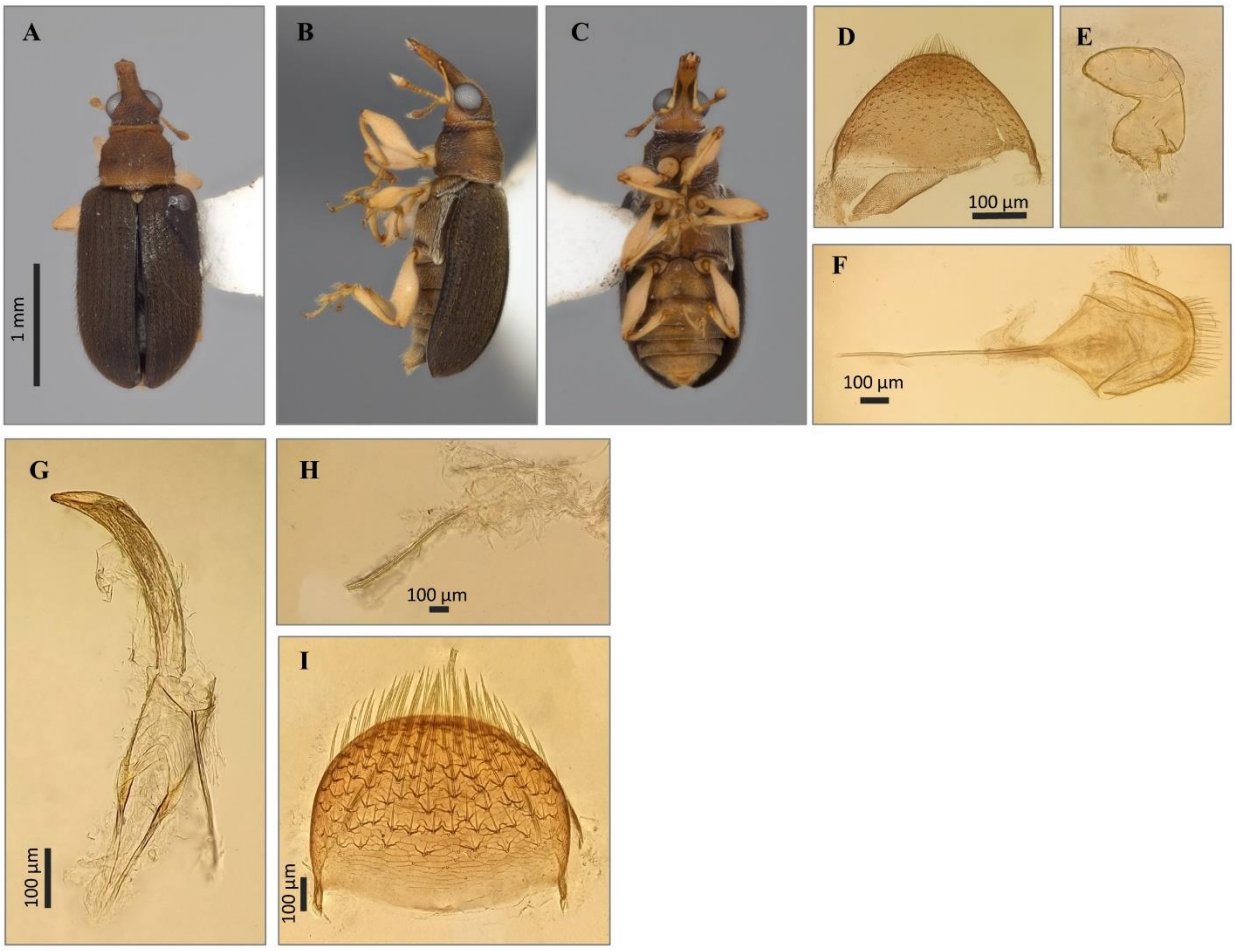

FIGURE 27. A–C *Udeus* sp. nov. 27.A–C dorsal, lateral, and ventral habitus. D–F Female terminalia. D pygidium. E spermatheca. F sternum VIII. G–J Male terminalia. G aedeagus. H sternum. IX. I pygidium.

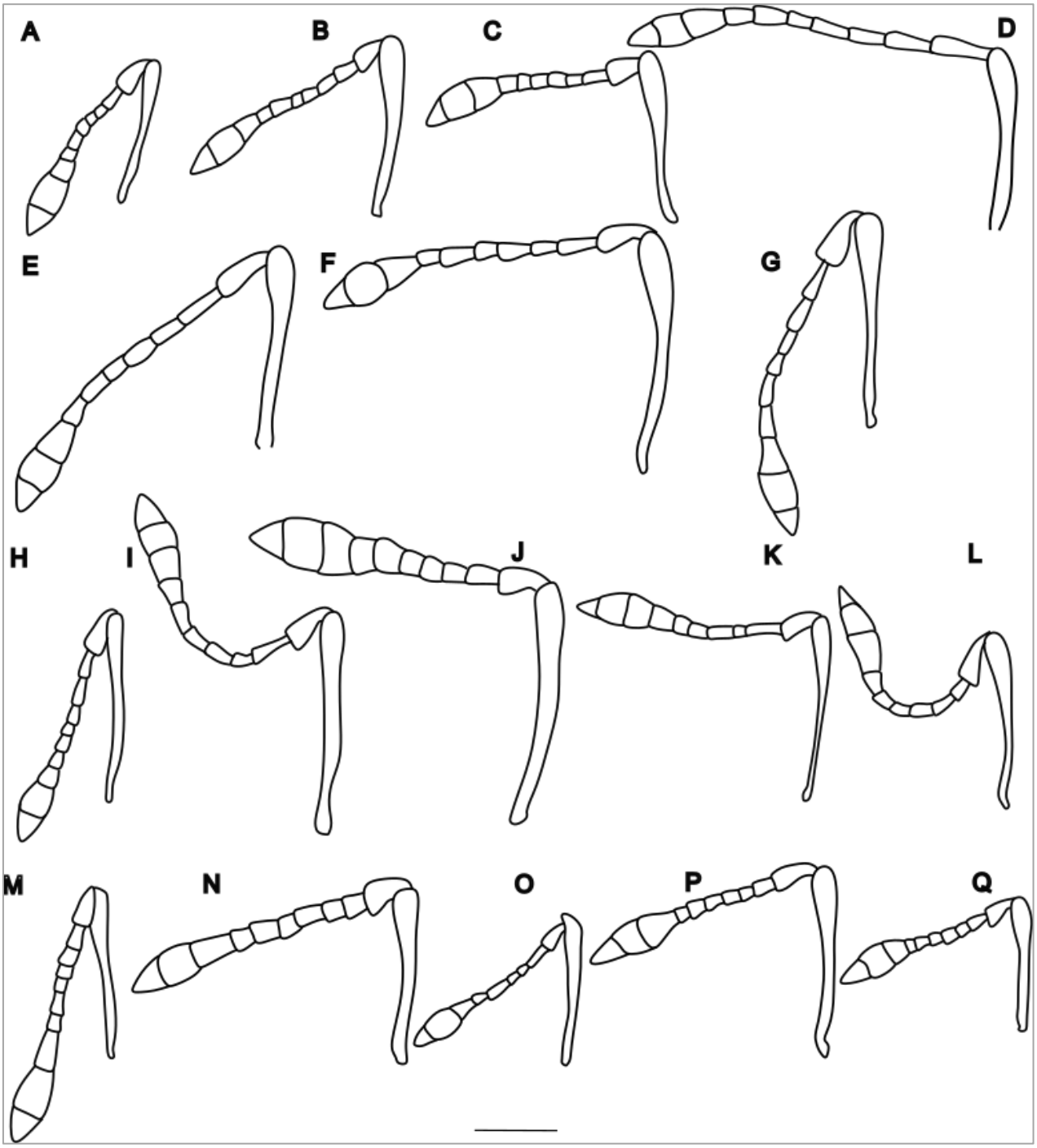

FIGURE 28. Antennae of males of *Udeus* species. A *U. eugnomoides*. B *U. longicollis*. C *U. cecropiae*. D *Udeus* sp. nov. 3. E *Udeus* sp. nov. 6. F *Udeus* sp. nov. 7. G *Udeus* sp. nov. 10. H *Udeus* sp. nov. 12. I *Udeus* sp. nov. 17. J *Udeus* sp. nov. 19. K *Udeus* sp. nov. 21. L *Udeus* sp. nov. 22. M *Udeus* sp. nov. 23. N *Udeus* sp. nov. 24. O *Udeus* sp. nov. 25. P *Udeus* sp. nov. 26. Q *Udeus* sp. nov. 27.

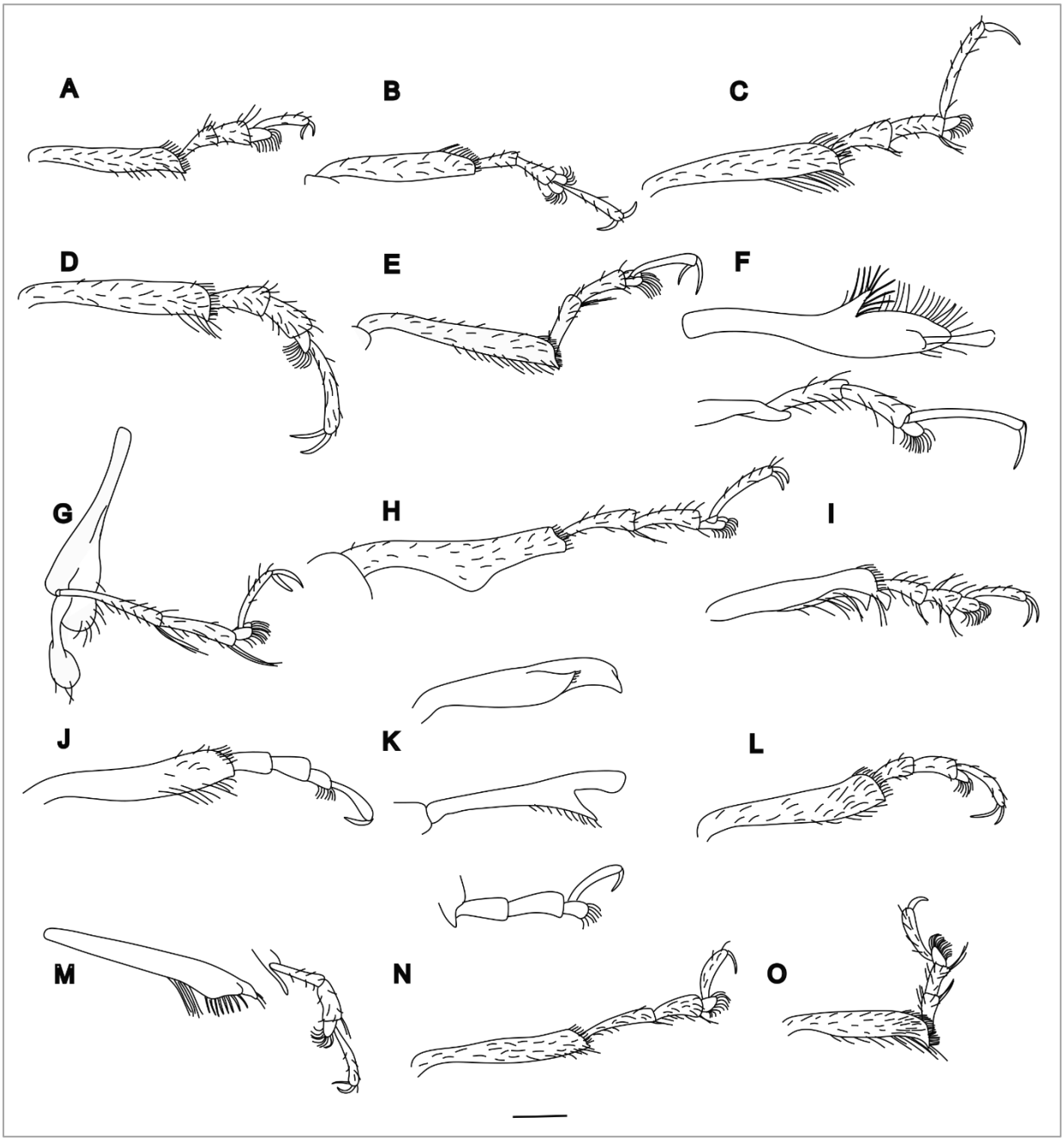

FIGURE 29. Metatibiae and metatarsus of males of *Udeus* species. A *U. eugnomoides*. B *U. longicollis*. C *U. cerradensis*. D *U. cecropiae*. E *Udeus* sp. nov. 3. F *Udeus* sp. nov. 6. G *Udeus* sp. nov. 7. H *Udeus* sp. nov. 10. I *Udeus* sp. nov. 12. J *Udeus* sp. nov. 17. K *Udeus* sp. nov. 19. L *Udeus* sp. nov. 21. M *Udeus* sp. nov. 22. N *Udeus* sp. nov. 23. O *Udeus* sp. nov. 24. P *Udeus* sp. nov. 25. Q *Udeus* sp. nov. 26. R *Udeus* sp. nov. 27.

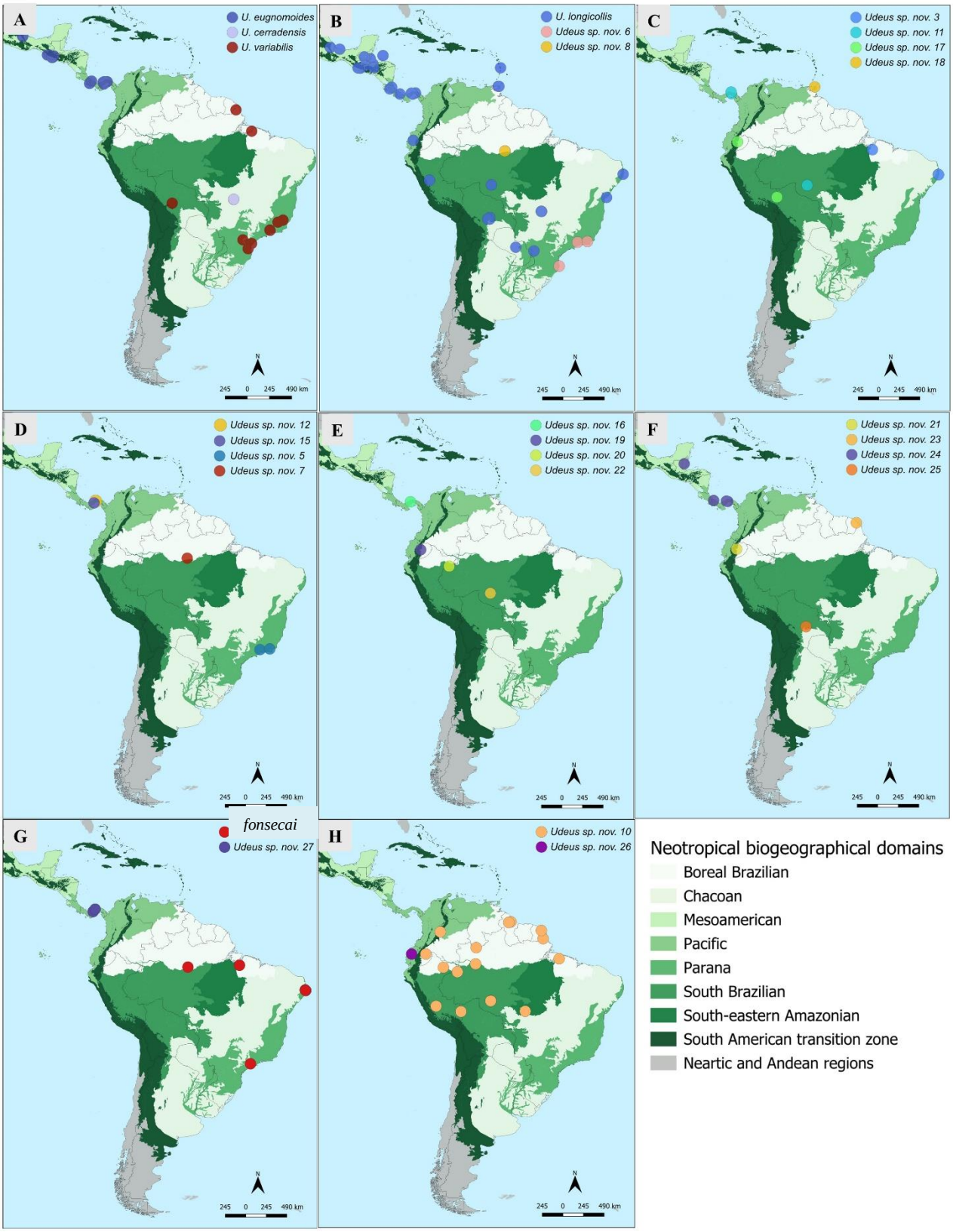

FIGURE 30. Geographical distribution of species of *Udeus* based on specimens examined.

CAPÍTULO 4

EVOLUTION AND PHYLOGENETIC RELATIONSHIPS AMONG THE WORLD EUGNOMINI FAUNA (COLEOPTERA, CURCULIONIDAE)[1]

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[1]Lira, A., Grossi, P., Souza, D.S., Leschen, R., Brown, S., Mazur, M., McKenna, D., Wanat, M., Escalona, H., Magland, A., Oberprieler, R., Haran, J. & B.A.S. de Medeiros. Evolution and phylogenetic relationships among the world Eugnomini fauna (Coleoptera, Curculionidae). Systematic Entomology.

Evolution and phylogenetic relationships among the world Eugnomini fauna (Coleoptera, Curculionidae)

Abstract

Eugnomini represents a small diverse tribe of flower weevils widely distributed across the Neotropics, Australasia, and Pacific islands. Despite their ecological significance as potential pollinators and florivores, there has been a notable absence of a comprehensive phylogenetic framework that allows an understanding of their evolutionary history and establishes a reliable classification. This study addresses this gap by presenting the first species-level phylogeny of a higher weevil taxon utilizing an extensive sampling of the global diversity of Eugnomini, employing Anchored Hybrid Enrichment to assess the monophyly of the tribe and elucidate its biogeographic history. Our phylogenomic analyses robustly supported the monophyly the subtribe Meriphina, while revealing the paraphyly of the subtribe Eugnomina and polyphyly of the tribe as currently defined, indicating a need for reassessment. Moreover, our broad taxonomic sampling facilitates the delineation of monophyletic genera and prompts a reevaluation of tribal diagnosis based on morphological traits in light of our phylogenetic findings. By delving into the internal relationships of Eugnomini, we briefly explored its biogeography, finding evidence for both vicariance and dispersals. This study underscores the importance of phylogenomic approaches in understanding the evolutionary history and morphological diversification in shaping the distribution and evolution of flower weevils and, more generally, the phytophagous insect biota.

Key words

Curculionoidea, biogeographic disjunction, Eugnomina, flower visitor, Meriphina, phylogeny, weevil.

Introduction

Since their origin in the Cretaceous, true weevils (Curculionidae) experienced a spectacular diversification to become one of the most diverse animal families today, comprising about 60,000 described species with a significant number yet to be discovered (Oberprieler et al. 2007; Oberprieler et al. 2014). This radiation has been attributed to their phytophagy and close interaction with flowering plant hosts, which also greatly diversified during this period (Oberprieler et al. 2007; Mckenna et al. 2009; Shin et al. 2018). Within the true weevil radiation, a notably diverse group corresponds to a clade of weevils closely associated with flowers and other reproductive structures, the subfamily Curculioninae (Caldara et al. 2014; Haran et al. 2023a). While we currently hold a comprehensive understanding of their diversification patterns at a large scale, the sheer diversity of these taxa has prevented us from understanding the details of their evolutionary history. For instance, although well-sampled species-level phylogenies for higher taxa can illuminate how weevils achieved their current distribution and diversity, these are often based on a handful of genes and lack sufficient support for robust inferences (Grebennikov 2022; Letsch et al. 2023). On the other end of the spectrum, weevil phylogenies with extensive gene sampling often have reduced species sampling (Baird et al. 2021), thus constraining the precision of taxonomic and biogeographical inferences. Notably, there is a lack of species-level phylogenies with phylogenomic sampling for any weevil higher taxon. Here, we address that gap by producing a species-level phylogeny for the flower weevil tribe Eugnomini (Curculionidae, Curculioninae), enabling an examination of both the global and local evolution of this taxon with Gondwanan distribution.

The Eugnomini comprises about 32 genera and 200 known species (Mazur 2017). With a strictly Gondwanan distribution, the greatest diversity is found in the Australian region (Australia, New Zealand, and New Caledonia), with a few representatives in the Neotropics (South America,

Central America, and the Caribbean) (Cawthra 1966; Caldara et al. 2014; Brown & Leschen 2018). While a few undescribed species have been noted from Southeast Asia (in Indonesia) and Pacific Islands (Fiji), no records currently exist for the Afrotropical region (Caldara et al. 2014; Mazur 2017; Brown & Leschen 2018). *Rhopalomerus* Blanchard, 1849 is the only genus with a disjunct distribution, with *Rhopalomerus tenuirostris* Blanchard, 1849 widely distributed across New Zealand and South America (Chile and Argentina) (Cawthra 1966; Alonso-Zarazaga & Lyal 1999), while most genera in New Zealand are endemic (Brown & Leschen 2018).

The common occurrence of Eugnomini with flowers is evident in the limited literature documenting their biology. Cawthra (1966) documented pollen grains in the digestive systems of *Eugnomus* Schoenherr, 1847, *Rhopalomerus*, *Icmalius* Broun, 1893, *Stephanorrynchus* White, 1846, *Meriphus* Erichson, 1842 and *Myossita* Pascoe, 1865, whereas several eugnomines were listed collected on angiosperm flowers and gymnosperm cones: *Rhopalomerus* species on *Brachyglottis rangiora* Buchanan (Asteraceae), *Weinmannia racemosa* L.f. (Cunoniaceae), *Leptospermum* J.R.Forst. & G.Forst. (Myrtaceae), *Astelia* Banks & Sol. ex R.Br. (Asteliaceae) and *Olearia* Moench (Asteraceae) species; *Stephanorrhynchus crassus* Broun, 1880 on *Pittosporum* Banks ex Gaertn. (Pittosporaceae) species; *Ancistropterus quadrispinosu*s White, 1846 on *Podocarpus dacrydioides* A. Rich. (Podocarpaceae) and *Melicytus ramiflorus* J.R.Forst. & G.Forst. (Violaceae); *Gonoropterus spinicollis* Broun, 1904 on *Olea lanceolata* Hook.f. (Oleaceae); *Eugnomus flavipilus* (Broun, 1883) on flowers of subalpine scrub; *Amylopterus pilosus* (Broun, 1877) on flowers of various forest shrubs. In New Zealand, *Kuschelysius* Broun & Leschen, 2018 was found associated with the flowers of *Dracophyllum traversii* Hook. f. (Ericaceae), *Celmisia armstrongii* Petrie (Asteraceae), and *Astelia nivicola* Ckn. ex Cheesm (Asteliaceae) (Broun & Leschen 2018), while *Stephanorhynchus lawsoni* Sharp, 187 and *Tysius bicornis* (Fabricius, 1781) feed on the pollen of several angiosperms (Kuschel 2012). In Neotropics, *Omoides* Boheman, 1859

is associated with several botanical families such as Salicaceae, Quillajaceae, Rosaceae, Lauraceae, Rhamnaceae, and Polygonaceae (Kuschel 1952). In Brazil, *Pedetinus* Faust, 1895 specimens were collected in *Leandra* spp. Raddi (Melastomataceae) (Aline Lira, personal information). *Rhopalomerus tenuirostris* is common on the flowers of *Baccharis sphaerocephala* Hook. & Arn. (Asteraceae), *Caldcluvia paniculata* D. Don. and *Eucryphia cordifolia* Cav. (both Cunoniaceae) (Kuschel 1952; Cawthra 1966), whereas *Udeus* Champion, 1902 species are specialized in *Cecropia* Loefl. (Urticaceae) (Bondar 1957, Lira et al. in press). The common association with flowers of different plants suggests that eugnomines may act as pollinators of at least some of their host plants, particularly when weevils are specialists. Species of the Neotropical genus *Udeus* share many traits with other weevil pollinators (Haran et al. 2023b) and are potential candidates to play a pollinator role in some species of *Cecropia* (Lira et al. in press). Likewise, endemic species of *Kuschelysius* may play an important role in the pollination of alpine plants in New Zealand (Broun & Leschen 2018).

While adults are attracted to live flowers and fruits, larvae of various genera develop in dead branches, trunks, and fruits of diverse plant species (Caldara et al. 2014). In New Zealand, the genus *Gonoropterus* Broun, 1904 develops in fruits of *Nestegis* Raf. (Oleaceae), *Nyxetes* Pascoe, 1870 inside galls of *Clematis* L. (Ranunculaceae), *Hoheria* A. Cunn. (Malvaceae) and *Nestegis* (May 1993). In Australia, *Myossita* Pascoe, 1865 reproduces in the reproductive structures and fruits of *Banksia* L.fil. (Proteaceae) (Caldara et al. 2014). In New Caledonia, *Pactola kuscheli* Mazur, 2016 was recently recorded causing damage in *Agathis montana* de Laub. (Araucariaceae), being the first confirmed pest for this plant (Mazur et al. 2016).

In light of the diversity and biological significance of Eugnomini, the tribe is poorly studied. The most comprehensive morphological study was conducted by Cawthra (1966), who provided diagnostic characters and a morphological definition for Eugnomini, and Mazur (2014) presented

the detailed classification history. Eugnomini is divided into Eugnomina and Meriphina subtribes. The latter differs from the first one by the exodont mandibles, mucronate tibiae in males, and simple, not divaricated claws (Cawthra 1966; Mazur 2014). Exclusive characters for the coherent distinction of all genera of the tribe have not yet been identified (Caldara et al. 2014). However, eugnomines are typically recognized by a combination of features, including (a) rostrum long and stout; (b) mandibles exodont; (c) maxillae flexible with long palps; (d) eyes large; (e) head elongate; (f) procoxae conical, contiguous; (g) femora with internal teeth; (h) tibiae mucronate; (i) tarsal claws free, simple to appendiculate; and (j) ventrites with straight posterior margins (Cawthra 1966; Caldara et al 2014; Broun & Leschen 2018). Recent attention has been directed toward the fauna of Eugnomini from New Caledonia, Pacific, and South America, resulting in an increased understanding diversity of the group (Mazur 2012; Mazur 2014; Mazur 2016; Mazur & Jezuita 2015; Mazur 2019; Brown & Leschen 2018; Rheinheimer 2018; Rheinheimer 2019; Lira et al. in press), including records of five fossil species in Baltic amber (Legalov 2016; Burkej & Legalov 2019; Legalov 2020a; Legalov 2020b). However, several other Australian species remain to await formal description (Pullen et al. 2014). Recent phylogenies of Curculionidae have sampled few eugnomines, with the monophyly of the tribe recovered when only New Zealand (Leschen *et al*. 2022; Haran *et al.* 2023a) or Australian (Gunter et al. 2016) taxa are included. However, a robust global molecular phylogenetic framework does not yet exist.

Here we establish, for the first time, a comprehensive molecular phylogeny of Eugnomini including a global selection of 149 species of the tribe employing anchored hybrid enrichment (AHE) (Lemmon et al. 2012). We combine our findings with morphology and geography information, to delimit the real diversity of Eugnomini and its biogeographic history.

Material and methods

Taxon sampling

This study includes a broad sampling of 26 valid Eugnomini genera representing more than 80% of the currently recognized genus diversity for the tribe (Figure 1). In total, we sequenced 203 samples from Eugnomini and other weevils putatively closely related to them. Eugnomini genera not represented include *Acanthopterus* Faust, 1889 and *Koghicola* Mazur, 2014 from New Caledonia; and *Goneumus* Marshall, 1937 and *Oropterus* White, 1846 from New Zealand. Three additional new genera were also included. This sampling corresponds to approximately 75% of fresh material resulting from recent collections in South America, Australia, New Zealand, and New Caledonia and preserved in 95% ethanol, and about 25% of pinned museum specimens (Table 1, Figure 2). Neotropical genera such as *Udeus*, *Omoides*, and *Pedetinus* have been extensively sampled, including most described species, as well Australian genera such as *Pactola*, *Stephanorhynchus*, and *Rhopalomerus*. To test the monophyly of Eugnomini, we included a broad outgroup sampling from the Curculioninae using sequences from Haran *et al.* (2023a). Voucher specimens of Eugnomini are deposited mostly at the Field Museum of Natural History (Table 1).

DNA extraction, library preparation, and sequencing

Genomic DNA was extracted from the abdomen or the whole specimen preserved in alcohol or pinned. In most cases, a non-destructive protocol was employed using the samples for the lysis step but not destroying body parts. In cases where many recently collected samples of the same species were available, we ground the whole specimen with a plastic pestle. Total genomic DNA was extracted from air-dried specimens using the OmniPrep kit (G Biosciences, St. Louis, MO) or the salting-out extraction protocol adapted from Sunnucks & Hales (1996) with an overnight lysis step in both cases. DNA amount and concentrations were estimated using a Qubit fluorometer, and DNA quality (degree of fragmentation/degradation and contamination with RNA) was assessed via gel

electrophoresis or the Agilent TapeStation system. DNA libraries were prepared using the KAPA HyperPlus Kit following the iTru system (Glenn *et al.* 2019). For high-molecular-weight samples, the enzymatic fragmentation was performed for 9 minutes at 37°C to obtain average insert sizes of 400–500 bp. For fragmented samples, this step was skipped. Libraries were prepared without size selection otherwise, using 0.9X SPRI beads during cleanup. Samples were indexed with dual 8 bp indexes. Indexed samples were pooled in pools of 22–24 samples. The pools were enriched using a myBaits Custom DNA-Seq kit (Biodiscovery, LLC dba Arbor Biosciences) with AHE probes designed for Coleoptera (Shin *et al.* 2018). The AHE libraries were paired-end (PE) sequenced on Illumina platform by Azenta Life Sciences using 150bp paired end reads.

Assembly and phylogenetic analysis

Paired-end Illumina data were cleaned, and adapters were removed using fastp (Chen et al. 2018). To construct a target file with protein sequences, we retrieve the protein set of *Anthonomus grandis grandis* from NCBI Genome (NCBI assembly GCF_022605725.1). This was the only high-quality curculionine genome available at the time of our analysis (Coehn et al. 2022) and constitutes a closer reference than weevil sequences used in prior AHE efforts (Shin *et al.* 2018; Haran *et al.* 2023a), likely decreasing problems such as paralogy. We used custom scripts to keep the longest isoform of each gene and then used *tblastn* to search these protein sequences against AHE probes using default parameters. We only kept in our final reference set the protein sequences that had a match to the probes. The assembly and retrieval of target loci were performed using HybPiper version 2.0 (Jhonshon *et al.* 2016) using this reference set. Samples with excessive missing data were visualized using Matrix Condenser (de Medeiros & Farrell 2018) and removed from the final dataset. Alignment of each gene was performed in MAFFT v.7.245 (Katoh *et al.* 2002).

A maximum likelihood (ML) tree with 1000 ultrafast bootstrap (Hoang et al. 2018) replicates for the concatenated matrix was estimated using IQ-TREE v2.1.3 (Nguyen *et al.* 2015) both for the unpartitioned aminoacid (AA) and the nucleotide (NT) datasets. The best model was found with in ModelFinder (Kalyaanamoorthy et al. 2017) as implemented in IQ-TREE. We additionally inferred separate gene trees for each locus using ModelFinder to select the best model for each locus. Finally, we assessed gene concordance factor (gCF) and site concordance factor (sCF) using IQ-TREE (Minh *et al.* 2020). While bootstrap values indicate measures of branch support and are applicable for robust inferences on phylogenetic trees, concordance factor values (gCF and sCF) are convenient for calculating the topological variation of the underlying data considering a given branch (Minh et al. 2020). The gCF (gene concordance factor) describes for each branch in a reference tree the proportion of inferred single-loci trees that contain that branch (Minh et al. 2020). In contrast, the sCF (site concordance factor) indicates the proportion of informative sites concordant with that branch (Mo et al. 2022). After a first tree was inferred, we additionally filtered samples showing very long branches and unexpected phylogenetic placement, repeating the analyses with the filtered dataset.

Results

A total of 203 samples were initially sequenced, with 23 of them being filtered from the final dataset due to signs of low-quality causing artifacts (Table 1). Twenty-one samples were removed after sequencing due to the high number of missing loci observed. Subsequently, two other samples (*Udeus* sp. 5 and *Philacta*) were excluded due to their unusual placement separated from other Eugnomini with very long branches and generally high level of missing data (93% and 77%, respectively). Additionally, seven outgroup samples from Haran et al. (2023a) with very long branches were removed from the final trees. Eugnomini samples included in the analyses have on

average 18% missing loci, while the filtered samples have on average 91% missing data. Most samples preserved with EtOH yielded high-quality sequences retained in the final dataset (143 of 149 total). Among dry pinned samples, success was more mixed but the majority of them still yielded sufficient data from inclusion in the final dataset (38 of 54 total).

In total, 669 loci were retained in the alignment. Both NT (Figure 3) and AA (Figure 4) trees recovered similar topology in most cases, with the NT tree having greater supports for most nodes. The NT dataset has bootstrap, gCF and sCF for nodes higher than AA dataset. The average bootstrap support for the nodes was 97% for NT dataset contrasting with 92% in AA tree. While gCF support to AA dataset was three times lower than NT tree (gCF NT= 40.3, gCF AA= 13.1), the average sCF supports have similar values, with NT dataset indicating slightly higher values than the AA dataset (sCF NT= 46.4, sCF AA= 44.7).

The NT analysis revealed two South American clades diverging on the base of the Eugnomini. The first clade comprises one undescribed Eugnomini from the Fiji Islands and *Omoides* from South America. The second one is represented by *Udeus*, sister to the remaining Eugnomini. The AA tree recovered just *the Udeus* clade and the indet. terminal from Fiji as older lineages, while *Omoides* was recovered outside Eugnomini. In addition to the two Neotropical basal clades, the third node in the NT tree includes the new genus from New Caledonia with all other terminals composed by specimens from Australia, New Zealand, New Caledonia, Vietnam, and *R. tenuirostris* from Chile. In AA dataset the third node merged the new genus from New Caledonia more closely related with taxa from New Caledonia and New Zealand. In the AA topology some taxa were recovered distant from Eugnomini (Figure 4), indicating potential artifacts in the analysis. *Kuschelysius, Meriphus fullo*, *Bothrophasis* sp. 3 and *Udeus longicollis* were recovered outside Eugnomini, merged with outgroups in clades of uncertain reliability. Additionally, *Omoides* was excluded from Eugnomini and recovered closer to *Pedetinus* in a weakly supported clade.

The ML tree reconstructed using the NT dataset was chosen to illustrate the resulting phylogenetic relationships (Figure 3). The monophyly of Eugnomini was not recovered in our analysis. The core Eugnomini comprises here almost all taxa currently recognized in the tribe, except *Pedetinus*, which was recovered outside of Eugnomini, closely related to Derelomini in a well-supported clade with maximum bootstrap. The monophyly of the subtribe Meriphina has maximum support, including *Myossita*, *Meriphus*, and *Orpha*, as suggested by Cawthra (1966), as well as *Meripherinus*. Otherwise, the subtribe Eugnomina was recovered as a polyphyletic group.

Like the neotropical clades *Omoides* and *Udeus*, the genera *Ancyttalia*, *Eugnomus*, and *Tysius* appeared as distinct, monophyletic groups with maximum bootstrap support. *Ancyttalia* was recovered as a sister clade of *Bothrophasis* + Meriphina robustly supported. *Eugnomus* is closely related to a clade comprising *Oreocallus*, *Icmalius*, New Genus 2, *Colabotelus* and New Genus 3, with internal relationships well supported in the NT tree but with weak support and different internal topology in the AA tree. Contrary to expectations, *Pactola* does not form a monophyletic clade but is merged with *Rasilinus* and *Pactolotypus* within a well-supported node of "short-nosed" eugnomines. This clade includes a recent grouping of *Pactola* from New Caledonia with *Rasilinus*, more distantly related to *Pactola* and *Pactolotypus* from New Zealand. *Stephanorrhynchus* appears polyphyletic, consistent with preliminary findings in other studies. The monophyletic clade comprising *S. lawsoni*, *S. nigrosparsus*, *S. brevipennis*, and *Stephanorrhynchus* sp. nov. is consistent with a recent revision that establishes a new genus. At the same time, the remaining *Stephanorrhynchus* species form another monophyletic group, sister to *Callistomorphus* (in both NT and AA datasets) and, together, sister to *Hoplocneme* (in NT tree). The genus *Rhophalomerus* is recovered as polyphyletic. Most *Rhophalomerus* species form a single, well-supported clade with two *Ancistropterus* species. *Rhopalomerus nobilis* forms a small clade with *Scolopterus* spp., while the validity of *R. tenuirostris* is questioned, particularly with the Chilean *R. tenuirostris*, closely

related to the Australian *R. piceosetosus*, together forming a sister clade to *R. tenuirostris* from New Zealand in NT tree. In AA tree similar relationship was recovered, however the New Zealander *R. tenuirostris* is moderately supported and closely related to *R. luctuosus*.

In a biogeographical context, Neotropical taxa are primarily clustered at the base of the tree, with only *R. tenuirostris* from Chile as a later branch closely related with Australian terminals. Australasian taxa form a derived node, except the Fijian terminal, which occupies a basal position. Most Australian terminals merged in a unique node, contrasting with the closely related New Caledonian and New Zealander taxa, which represent the most derived clades.

Discussion

While the majority of specimens sampled were originally preserved in ethanol, a notable portion consisted of pinned specimens from museum collections, which proved amenable to successful DNA sequencing. A considerable subset of these specimens, crucial for achieving the Eugnomini phylogeny were old and exclusively accessible via dry preservation. By being able to capture small fragments of degraded DNA, the AHE method has been used efficiently in the generation of genomic data from museum specimens (Lemmon et al. 2012; Breinholt et al. 2018; Toussaint et al. 2018; Toussaint et al. 2021). Otherwise, 70% of the samples removed after sequencing were dry-preserved samples. Since most of them were sourced from the same museum origin, it is plausible that prolonged storage under suboptimal conditions such as storage temperature, humidity, and sample history, led to diminished DNA integrity (Nunes et al. 2022), consequently resulting in a significant number of missing loci.

The phylogenetic trees have recovered maximum support in almost clades. Assessing the topology of Eugnomini, we observe that bootstrap values are 100% at higher nodes, except for the branch leading to the clade comprising most terminals from New Zealand and New Caledonia, as

well as the clade of Australian terminals (Meriphina and *Ancyttalia*) along with *Bothrophasis*, which has bootstrap support of 30% in NT tree compared with 77% in AA dataset. We can observe a wide range of values for gCF and sCF, with the values of sCF consistently greater than the values of gCF in NT dataset. Most nodes, including core Eugnomini, have gCF values lower than 33% (in NT dataset). This suggests conflicting signals in the gene trees arising from processes such as incomplete lineage sorting (Minh et al. 2020). The AA tree showed lower gCFs than NT tree. We attribute this due to the likely greater information content in nucleotide data for the level of divergence in our dataset. Similar to the case of gCF values much lower than sCF values, this conformation indicates the limitation of information in the alignments that generated the gene trees or random errors in the analyses (Minh et al. 2020). In summary, the high level of phylogenetic conflict in Eugnomini leads to challenges that can only be solved with large amounts of data and appropriate models, resembling challenges found in the weevil phylogeny more broadly (Shin et al. 2018; Haran et al. 2023a; Li et al. 2023).

Eugnomini was found to be non-monophyletic with strong support for the exclusion of *Pedetinus* (Figures 3, 4). Formerly in the Rhynchaeninae (O'Brien & Wibmer 1982; Wibmer & O'Brien 1989), *Pedetinus* was transferred to the Derelomini by Anderson (1989) and recently transferred from Derelomini to Eugnomini based in a morphological phylogeny of the Derelomini and outgroups (Franz 2006). In that case, *Pedetinus* has been recovered in a monophyletic group with the Neotropical eugnomine genera *Udeus* and *Omoides* (Franz 2006). However, our study suggests a compelling argument for reverting *Pedetinus* to Derelomini due to its robust association with *Notolomus* (Derelomini) within a well-supported clade. Nevertheless, it is important to note that the Derelomini have been found to be polyphyletic with phylogenomics, with its internal relationships still ambiguous (Haran *et al.* 2023a). This result also conflicts with morphological data finding a monophyletic Derelomini with exclusion of *Pedetinus* (Franz 2006). This outcome

underscores the inherent limitations of relying exclusively on morphological features to infer phylogenetic relationships. With the exception of *Pedetinus*, the monophyly of a core Eugnomini was recovered strong nodal support, consisted with earlier investigations with more limited sampling (Gunter *et al.* 2016; Leschen *et al.* 2022; Haran *et al.* 2023a). Consistent with Haran et al. (2023a), our findings reveal that Storeini is closely related to Eugnomini. However, our analyses demonstrate that in addition to Storeini, the tribes Derelomini and Ochyromerini form a strongly supported node, which is sister to Eugnomini. These tribes, similar to eugnomines, consist of floral visitor weevils that play roles in pollination systems (Haran et al. 2023b). While Derelomini and Ochyromerini are widely distributed, Storeini has a Gondwanan distribution (Alonso-Zarazaga & Lyal 1999). These discrepancies underscore the intricacies involved in delineating relationships within Curculioninae while at the same time highlighting evolutionary trends linking different groups of flower weevils.

The current subtribal classification of Eugnomini deserves to be reevaluated. Unlike Meriphina representing here a monophyletic group and initially supported by mandibular characters (Marshall 1937; Cawthra 1966), Eugnomina is not monophyletic and should be reevaluated considering morphological characters and the biogeographic history. Meriphina was characterized by several distinctive features including mucronate tibiae in males, oblique scrobes, a metafemur with a prominent tooth, and free, simple tarsal claws, but the exodont mandibles are the main morphological character for this classification (Marshall 1937; Cawthra 1966). *Meripherinus* classified in Camarotini (Alonso-Zarazaga & Lyal 1999), is now included in Eugnomini as suggested in Caldara *et al.* (2014). While the group comprising *Myossita*, *Meriphus*, and *Orpha* shares the feature of exodont mandibles, of particular importance is the fact that neotropical *Udeus cerradensis* Lira, de Medeiros & Grossi, 2024 and *Omoides* exhibit exodont mandibles (Kuschel 1952). Meriphina, comprising Australian genera, was found to be closely related to *Ancyttalia*,

which primarily consists of Australian species. Leveraging the phylogenetic relationships delineated in this study, we can reassess the morphology of current taxa, identifying characters that allow robust taxonomic delimitation. This, in turn, enables us to propose a revised arrangement of subtribes within Eugnomini.

Numerous Eugomini genera established in the 19th century necessitate thorough taxonomic reassessment. Among these, *Ancistropterus*, *Amylopterus*, *Gonoropterus,* and *Rhopalomerus* stand out as candidates for revision. The position of *An. brouni* in the tree, closely associated with *Amylopterus*, aligns with shared morphological traits observed within these taxa. Notably, *Amylopterus* exhibits strongly curved metatibiae, a character present in *An. brouni*. However, the absence of a tooth in the anterior femora, a defining feature of *Amylopterus*, contradicts the morphology of *An. brouni*. Despite these morphological disparities, *An. brouni* demonstrates a notable likeness to *Am. pilosus*, evident through their clustering within a well-supported clade. In contrast, *Ancistropterus* n. sp. *bispinosus* and *An. quadrispinosus* deviate from the typical pattern of curved tibiae, possessing a notably feeble anterior femoral tooth, and are associated with *Rhopalomerus* in the tree. These convergences underscore the imperative for reassessing diagnostic characters to delineate these genera accurately.

Drawing upon the present topology of Eugnomini, we can propose some scenarios to explain the origin and diversification of the tribe from a biogeographic perspective. Nevertheless, without conducting biogeographical analyses, particularly employing molecular dating, these speculative hypotheses will remain pending future confirmation. Like other taxa with strictly Gondwanan distribution (e.g., Wood *et al.* 2013; Kim & Farrell 2015; Malagon-Aldana *et al.* 2022), vicariance through the sequential breakup of Gondwana is traditionally employed to explain the disjunct distribution between Australasian and Neotropical taxa. However, given that oceanic islands New Caledonia and Fiji are within the distributional range of the Eugnomini, it is likely that dispersal

events have also played a significant role in shaping the biogeographic history of the tribe in these regions as they have for other groups (Cowie & Holland 2006; Grandcolas 2016). Moreover, all known eugnomine fossils are found in Baltic amber dating back to 48-33 Mya (Legalov 2016; Burkej & Legalov 2019; Legalov 2020a; Legalov 2020b), challenging a simple biogeographical pattern based merely on Gondwanan breakup and highlighting the role of extinctions in the achievement of the current distribution. Considering the South American origins, as evidenced by the basal Chilean *Omoides* clade in the phylogeny, vicariance events offer a compelling explanation for the current distribution pattern, with Australasian taxa likely dispersed across Antarctica (Sanmartín & Ronquist 2004). Nonetheless, elucidating the origin of the basal Fijian terminal presents a more intricate challenge due to the recent origin of Fiji and its complex geological history which indicates that the genesis of biodiversity in these localities hinges upon dispersal events (Cowie & Holland 2006; Neall & Trewich 2008; Grandcolas 2016). Several studies suggest that the oldest colonization of Fiji and New Caledonia is of Laurasian origin rather than being Gondwanan relicts (Monaghan et al. 2006; Balke et al. 2007; Sarnatt & Moreau 2011), in some cases with groups from southeast Asia originated by a Laraurasian ancestor and colonizing Pacific islands. Given the occurence of eugnomines in southeasoust Asia, and fossils from Baltic amber aligned with this hypothesis, we can not reject a relationship between species from the Northern and Southern hemispheres. In summary, the biogeographical history of Eugnomini is complex and necessarily included relevant vicariance, dispersal, and extinction events. These processes may have played pivotal roles in shaping the distribution patterns of Eugnomini, emphasizing the multifaceted nature of its evolutionary history.

Conclusion

This study marks the first comprehensive phylogeny at the species level with phylogenomic sampling in Curculionidae, shedding light on the intricate internal relationships within the tribe and its placement within Curculioninae. Our study now allows a morphological reassessment in light of the phylogenetic tree, allowing a more precise re-evaluation of the subtribal classification within the Eugnomini. Moreover, it provides a basis for a more reliable morphological analysis to infer whether known fossils belong to Eugnomini, supporting biogeographical inferences. Overall, this study advances our understanding of weevil phylogeny and underscores the importance of integrating phylogenomic approaches with biogeographic and morphological analyses to unravel the complex evolutionary history of this diverse group of insects.

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APPENDIX - Table and figures

Figure 1. Representative species of Egnomini (a) *Pedetinus* sp.; (b) *Omoides* sp.; (c) *Udeus cerradensis*; (d) *Udeus* sp. 16; (e) *Botrophasis* sp.; (f) *Ancyttalia* cf. *sydneyensis*; (g) *Orpha flavicornis*; (h) *Meriphus fullo*; (i) *Myossita* sp.; (j) *Kuschelysius hollowayae*; (k) *Tysius bicornis*; (l) *Scolopterus penicillatus*; (m) *Colabotelus dealbatus*; (n) *Eugnomus durvillei*; (o) *Oreocalus picigularis*; (p) *Icmalius abnormis*; (q) *Rhopalomerus tenuirostris*; (r) *Nyxetes bidens*; (s) *Hoplocneme hookeri*; (t) *Callistomorphus malleus*; (u) *Gonoropterus spinicollis*; (v) *Ancistropterus brouni*; (w) *Ancistropterus quadrispinosus*; (x) *Amylopterus prasinus*; (y) *Stephanorhyncus curvipes*; (z) *Rasilinus tchambicus*; (aa) *Pactolotypus subantarticus*; (ab) *Pactola variabilis.*

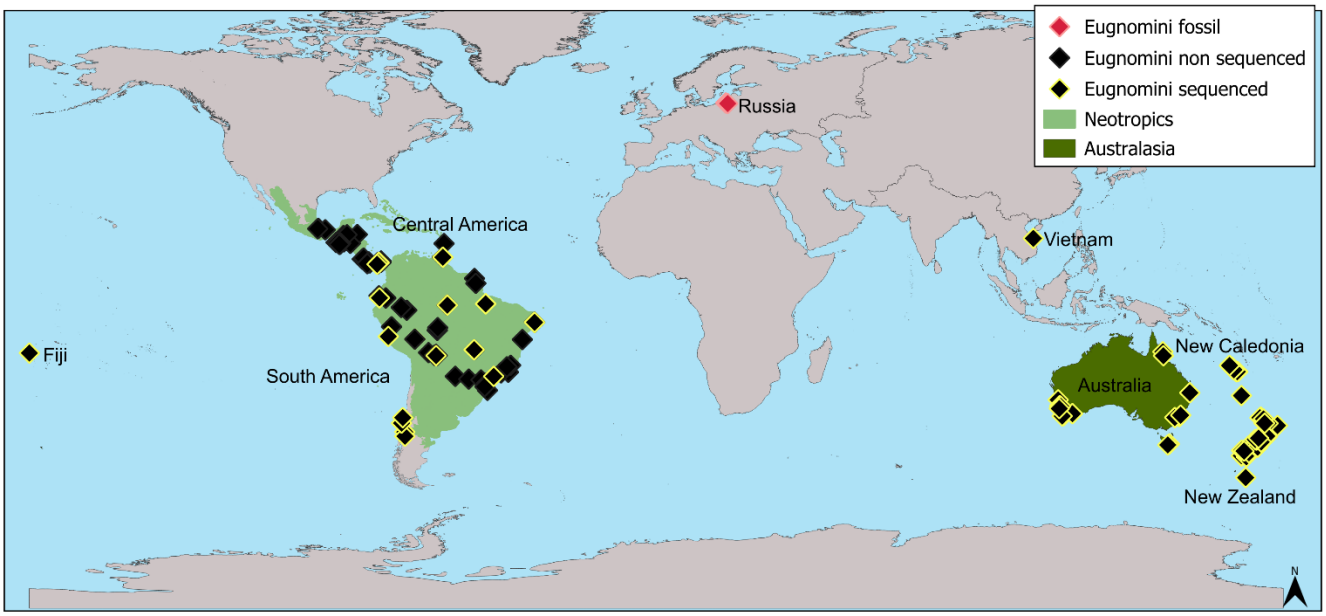

Figure 2. Geographical distribution of Eugnomini included in this study and known fossil occurrences.

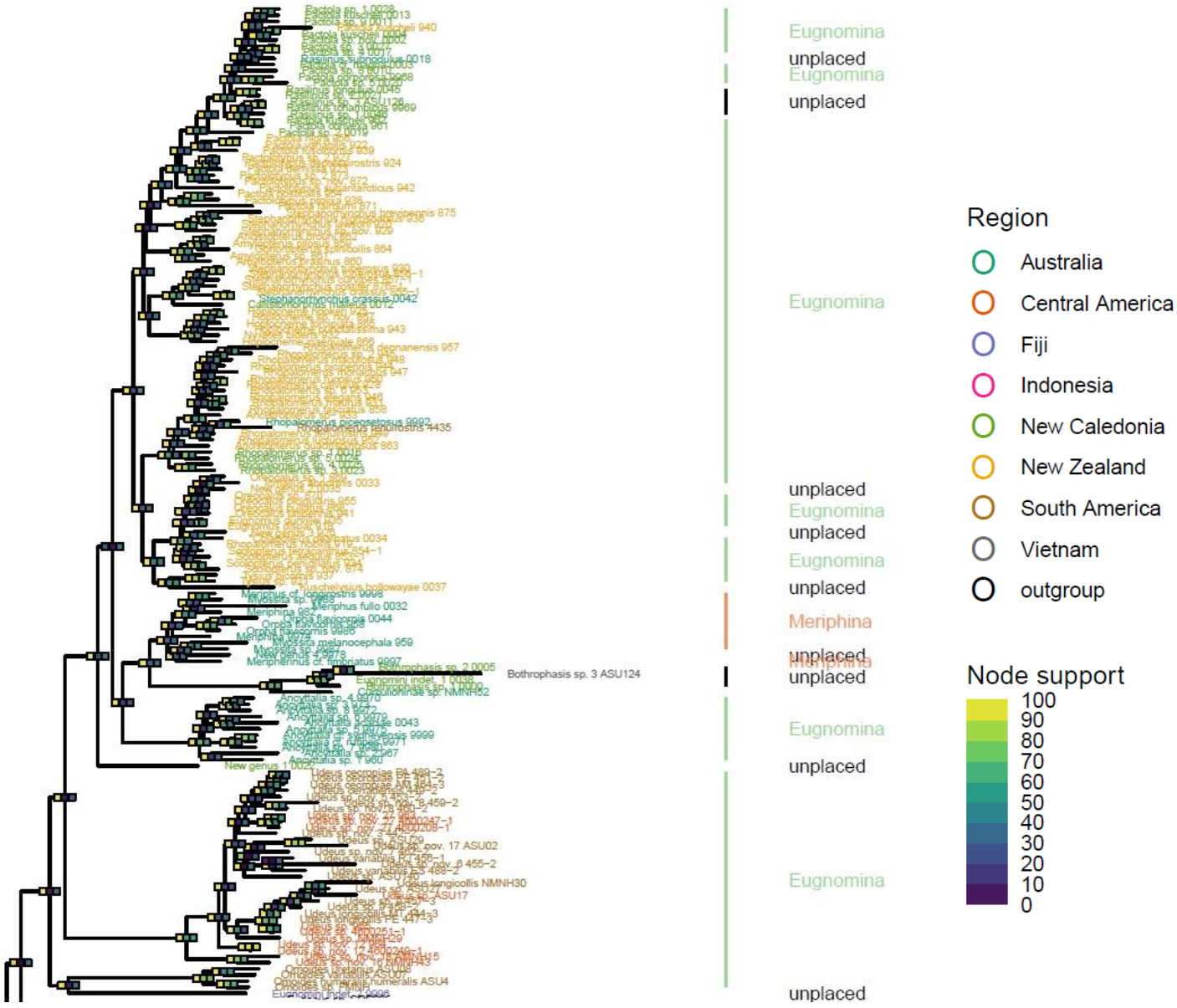

Figure 3. Maximum likelihood tree estimated in IQ-TREE for nucleotide dataset. Nodal support shown as a series of three color-coded boxes for each node: ultrafast bootstrap, gCF (gene concordance factor), and sCF (site concordance factor), respectively. Taxa in black font represent outgroups from Haran et al. 2023a, and taxa in colored font represent specimens included in sequencing in this study, with colors based on geographical region.

cont. Figure 3. Maximum likelihood tree estimated in IQ-TREE for nucleotide dataset. Nodal support shown as a series of three color-coded boxes for each node: ultrafast bootstrap, gCF (gene concordance factor), and sCF (site concordance factor), respectively. Taxa in black font represent outgroups from Haran et al. 2023a, and taxa in colored font represent specimens included in sequencing in this study, with colors based on geographical region.

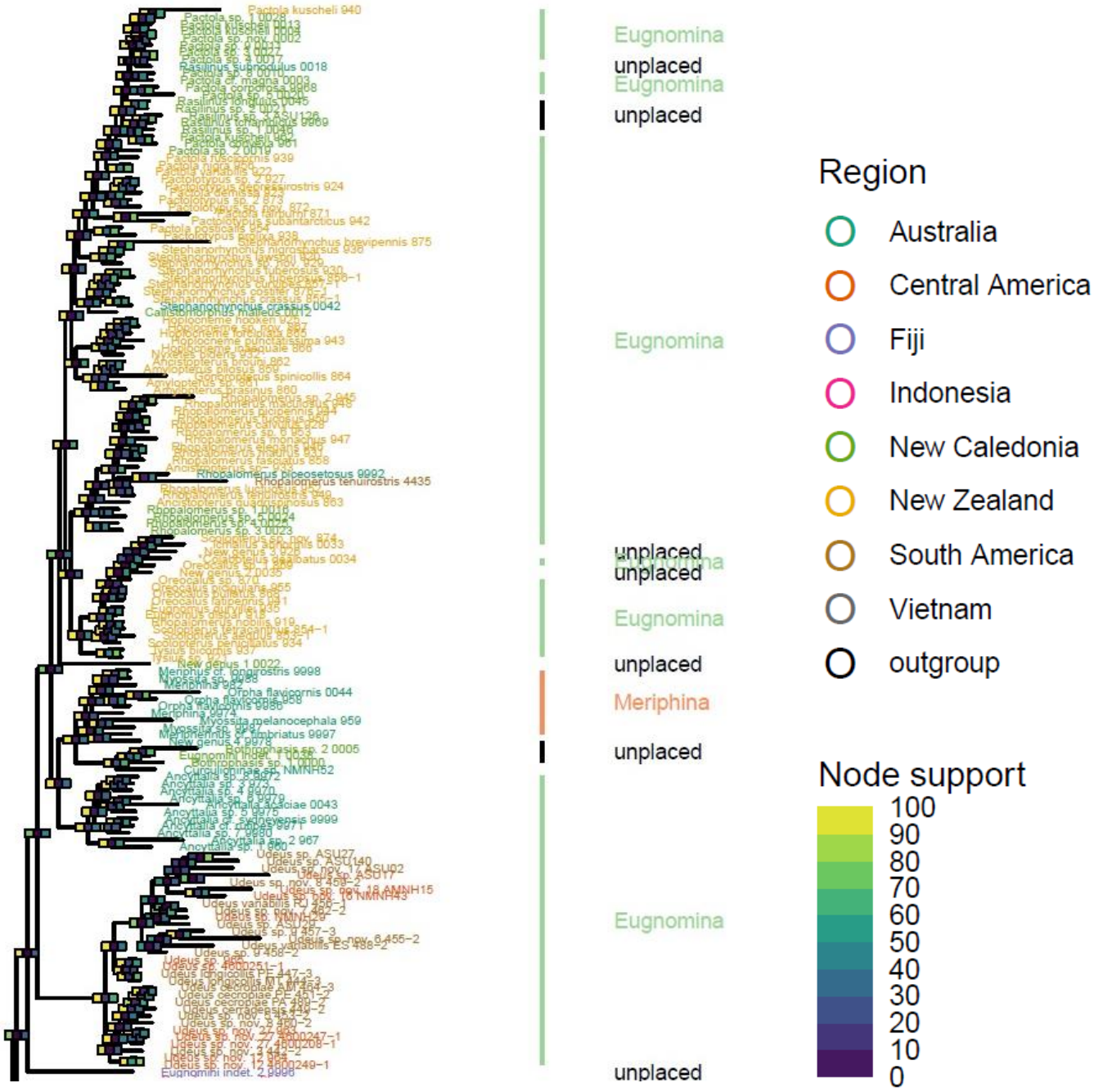

Figure 4. Maximum likelihood tree estimated in IQ-TREE for aminoacid dataset. Nodal support shown as a series of three color-coded boxes for each node: ultrafast bootstrap, gCF (gene concordance factor), and sCF (site concordance factor), respectively. Taxa in black font represent outgroups from Haran et al. 2023a, and taxa in colored font represent specimens included in sequencing in this study, with colors based on geographical region.

cont. Figure 4. Maximum likelihood tree estimated in IQ-TREE for aminoacid dataset. Nodal support shown as a series of three color-coded boxes for each node: ultrafast bootstrap, gCF (gene concordance factor), and sCF (site concordance factor), respectively. Taxa in black font represent outgroups from Haran et al. 2023a, and taxa in colored font represent specimens included in sequencing in this study, with colors based on geographical region.

Table 1. List of species of Eugnomini included on phylogenic analysis. The * indicates type species and the lines highlighted in bold indicate the samples excluding the analysis after sequencing.

Sampled taxon	Subtribe	Country	voucher ID	Museum	Preservation	Year	Sequencing
Amylopterus pilosus	Eugnomina	New Zealand	FMNH4429859	NZAC	EtOh	2011	Successful
**Amylopterus prasinus*	Eugnomina	New Zealand	FMNH4429860	NZAC	EtOh	-	Successful
Amylopterus sp.	Eugnomina	New Zealand	FMNH4429861	NZAC	EtOh	-	Successful
Ancistopterus brouni	Eugnomina	New Zealand	FMNH4429862	NZAC	EtOh	-	Successful
**Ancistopterus quadrispinosus*	Eugnomina	New Zealand	FMNH4429863	NZAC	EtOh	2011	Successful
Ancistropterus sp.	Eugnomina	New Zealand	FMNH4429933	NZAC	EtOh	2007	Successful
Ancyttalia acaciae	Eugnomina	Australia	FMNH4430043	NZAC	pinned	2019	Successful
Ancyttalia cf. *rufipes*	Eugnomina	Australia	FMNH4429971	ANIC	EtOh	2008	Successful
**Ancyttalia* cf. *sydneyensis*	Eugnomina	Australia	FMNH4429999	ANIC	EtOh	2008	Successful
Ancyttalia sp. 1	Eugnomina	Australia	FMNH4429960	NZAC	pinned?	2018	Successful
Ancyttalia sp. 2	Eugnomina	Australia	FMNH4429967	ANIC	EtOh	2023	Successful
Ancyttalia sp. 3	Eugnomina	Australia	FMNH4429973	ANIC	EtOh	2023	Successful
Ancyttalia sp. 4	Eugnomina	Australia	FMNH4429970	ANIC	EtOh	2019	Successful
Ancyttalia sp. 5	Eugnomina	Australia	FMNH4429975	ANIC	EtOh	2010	Successful
Ancyttalia sp. 6	Eugnomina	Australia	FMNH4429979	ANIC	EtOh	2012	Successful
Ancyttalia sp. 8	Eugnomina	Australia	FMNH4429972	ANIC	EtOh	2023	Successful
Ancyttalia sp. 7	Eugnomina	Australia	FMNH4429980	ANIC	EtOh	2010	Successful
Bothrophasis sp. 1	unplaced	New Caledonia	FMNH4430000	NZAC	EtOh	2023	Successful
Bothrophasis sp. 2	unplaced	New Caledonia	FMNH4430005	DBUO	EtOh	2005	Successful
Bothrophasis sp. 3	unplaced	Vietnam	FMNH4432046	ASUCOB	pinned	1970	Successful
Callistomorphus malleus	Eugnomina	New Caledonia	FMNH4430012	MNHW	EtOh	2008	Successful
**Colabotelus dealbatus*	Eugnomina	New Zealand	FMNH4430034	NZAC	EtOh	2011	Successful
Eugnomini indet. 1	unplaced	New Caledonia	FMNH4430038	FMNH	pinned	1962	Successful
Eugnomini indet. 2	unplaced	FIji Is.	FMNH4429996	ANIC	EtOh	2005	Successful
Eugnomus dispar	Eugnomina	New Zealand	FMNH4429918	NZAC	EtOh	-	Successful
**Eugnomus durvillei*	Eugnomina	New Zealand	FMNH4429935	NZAC	EtOh	2019	Successful
**Gonoropterus spinicollis*	Eugnomina	New Zealand	FMNH4429864	NZAC	EtOh	1985	Successful
Hoplocneme forcipiata	Eugnomina	New Zealand	FMNH4429865	NZAC	EtOh	-	Successful
**Hoplocneme hookeri*	Eugnomina	New Zealand	FMNH4429925	NZAC	EtOh	-	Successful

Hoplocneme inaequale	Eugnomina	New Zealand	FMNH4429866	NZAC	EtOh	-	Successful
Hoplocneme punctatissima	Eugnomina	New Zealand	FMNH4429943	NZAC	EtOh	2011	Successful
Hoplocneme sp. nov.	Eugnomina	New Zealand	FMNH4429867	NZAC	EtOh	-	Successful
**Icmalius abnormis*	Eugnomina	New Zealand	FMNH4430033	NZAC	pinned	1966	Successful
**Kuschelysius hollowayae*	unplaced	New Zealand	FMNH4430037	NZAC	pinned	1969	Successful
New genus 1	unplaced	New Caledonia	FMNH4430022	MNHW	pinned	2008	Successful
New genus 2	unplaced	New Zealand	FMNH4430035	NZAC	EtOh	2013	Successful
New genus 3	unplaced	New Zealand	FMNH4429926	NZAC	EtOh	-	Successful
New genus 4	unplaced	Australia	FMNH4429978	ANIC	EtOh	2010	Successful
**Nyxetes bidens*	Eugnomina	New Zealand	FMNH4429932	NZAC	EtOh	-	Successful
**Omoides humeralis humeralis*	Eugnomina	Chile	FMNH4432029	ASUCOB	pinned	1999	Successful
Omoides sp.	Eugnomina	Chile	FMNH4432009	FMNH	pinned	1982	Successful
Omoides uretanus	Eugnomina	Chile	FMNH4432033	ASUCOB	pinned	1999	Successful
Omoides variabilis	Eugnomina	Chile	FMNH4432032	ASUCOB	pinned	2001	Successful
Oreocalus latipennis	Eugnomina	New Zealand	FMNH4429941	NZAC	EtOh	2019	Successful
Oreocalus picigularis	Eugnomina	New Zealand	FMNH4429955	NZAC	EtOh	-	Successful
Oreocalus pullatus	Eugnomina	New Zealand	FMNH4429868	NZAC	EtOh	-	Successful
Oreocalus sp.	Eugnomina	New Zealand	FMNH4429870	NZAC	EtOh	-	Successful
Oreocalus sp. 1	Eugnomina	New Zealand	FMNH4429869	NZAC	EtOh	2011	Successful
Pactola cf. *magna*	Eugnomina	New Caledonia	FMNH4430003	NZAC	EtOh	2023	Successful
Pactola convexa	Eugnomina	New Caledonia	FMNH4429961	NZAC	EtOh	2023	Successful
Pactola corporosa	Eugnomina	New Caledonia	FMNH4429968	NZAC	EtOh	2023	Successful
Pactola demissa	Eugnomina	New Zealand	FMNH4429923	NZAC	EtOh	-	Successful
Pactola fairburni	Eugnomina	New Zealand	FMNH4429871	NZAC	EtOh	-	Successful
Pactola fuscicornis	Eugnomina	New Zealand	FMNH4429939	NZAC	EtOh	-	Successful
Pactola kuscheli	Eugnomina	New Caledonia	FMNH4429962	NZAC	EtOh	-	Successful
Pactola kuscheli	Eugnomina	New Caledonia	FMNH4430013	MNHW	EtOh	2008	Successful
Pactola kuscheli	Eugnomina	New Caledonia	FMNH4430004	DBUO	EtOh	2023	Successful
Pactola kuscheli	Eugnomina	New Zealand	FMNH4429940	NZAC	EtOh	2007	Successful
Pactola nigra	Eugnomina	New Zealand	FMNH4429956	NZAC	EtOh	2023	Successful
Pactola posticalis	Eugnomina	New Zealand	FMNH4429954	NZAC	EtOh	2023	Successful
Pactola sp. 1	Eugnomina	New Caledonia	FMNH4430028	MNHW	EtOh	2008	Successful
Pactola sp. 2	Eugnomina	New Caledonia	FMNH4430019	MNHW	EtOh	2008	Successful
Pactola sp. 3	Eugnomina	New Caledonia	FMNH4430027	MNHW	EtOh	2008	Successful

Pactola sp. 4	Eugnomina	New Caledonia	FMNH4430017	MNHW	EtOh	2008	Successful
Pactola sp. 5	Eugnomina	New Caledonia	FMNH4430020	MNHW	EtOh	2008	Successful
Pactola sp. 8	Eugnomina	New Caledonia	FMNH4430010	MNHW	EtOh	2008	Successful
Pactola sp. 9	Eugnomina	New Caledonia	FMNH4430011	MNHW	EtOh	-	Successful
Pactola sp. nov.	Eugnomina	New Caledonia	FMNH4430002	NZAC	EtOh	2023	Successful
**Pactola variabilis*	Eugnomina	New Zealand	FMNH4429922	NZAC	EtOh	2011	Successful
Pactolotypus depressirostris	Eugnomina	New Zealand	FMNH4429924	NZAC	EtOh	-	Successful
Pactolotypus prolixa	Eugnomina	New Zealand	FMNH4429938	NZAC	EtOh	-	Successful
Pactolotypus sp. 2	Eugnomina	New Zealand	FMNH4429873	NZAC	EtOh	-	Successful
Pactolotypus sp. 2	Eugnomina	New Zealand	FMNH4429927	NZAC	EtOh	-	Successful
Pactolotypus sp. nov.	Eugnomina	New Zealand	FMNH4429872	NZAC	EtOh	-	Successful
Pactolotypus subantarcticus	Eugnomina	New Zealand	FMNH4429942	NZAC	EtOh	-	Successful
Pedetinus sp. 1	unplaced	Chile	DZUP320930	DZUP	pinned	2001	Successful
Pedetinus sp. 2	unplaced	Chile	DZUP320944	DZUP	pinned	1986	Successful
Pedetinus sp. 3	unplaced	Chile	DZUP321995	DZUP	pinned	1972	Successful
Pedetinus sp. 4	unplaced	Chile	DZUP322084	DZUP	pinned	2001	Successful
***Philacta testaceae**	**Eugnomina**	**New Zealand**	**FMNH4430036**	**NZAC**	**pinned**	**-**	**Successful**
Rasilinus longulus	unplaced	New Caledonia	FMNH4430045	MNHW	EtOh	2010	Successful
Rasilinus sp. 1	unplaced	New Caledonia	FMNH4430046	MNHW	EtOh	2008	Successful
Rasilinus sp. 2	unplaced	New Caledonia	FMNH4430021	MNHW	EtOh	2010	Successful
Rasilinus sp. 3	unplaced	New Caledonia	FMNH4432048	ASUCOB	pinned	-	Successful
Rasilinus subnodulus	unplaced	Australia	FMNH4430018	MNHW	EtOh	2008	Successful
**Rasilinus tchambicus*	unplaced	New Caledonia	FMNH4429969	NZAC	EtOh	2023	Successful
Rhopalomerus calvulus	Eugnomina	New Zealand	FMNH4429928	NZAC	EtOh	-	Successful
Rhopalomerus dennanensis	Eugnomina	New Zealand	FMNH4429957	NZAC	pinned	1985	Successful
Rhopalomerus elegans	Eugnomina	New Zealand	FMNH4429946	NZAC	EtOh	-	Successful
Rhopalomerus fasciatus	Eugnomina	New Zealand	FMNH4429858	NZAC	EtOh	2011	Successful
Rhopalomerus fucosus	Eugnomina	New Zealand	FMNH4429950	NZAC	EtOh	-	Successful
Rhopalomerus luctuosus	Eugnomina	New Zealand	FMNH4429952	NZAC	EtOh	-	Successful
Rhopalomerus maculosus	Eugnomina	New Zealand	FMNH4429948	NZAC	EtOh	-	Successful
Rhopalomerus maurus	Eugnomina	New Zealand	FMNH4429931	NZAC	EtOh	-	Successful
Rhopalomerus monachus	Eugnomina	New Zealand	FMNH4429947	NZAC	EtOh	-	Successful

Rhopalomerus nobilis	Eugnomina	New Zealand	FMNH4429919	NZAC	EtOh	-	Successful
Rhopalomerus piceosetosus	Eugnomina	Australia	FMNH4429992	ANIC	EtOh	2010	Successful
Rhopalomerus picipennis	Eugnomina	New Zealand	FMNH4429944	NZAC	EtOh	-	Successful
Rhopalomerus sp. 1	Eugnomina	New Caledonia	FMNH4430016	MNHW	EtOh	-	Successful
Rhopalomerus sp. 2	Eugnomina	New Zealand	FMNH4429945	NZAC	EtOh	-	Successful
Rhopalomerus sp. 3	Eugnomina	New Caledonia	FMNH4430023	MNHW	EtOh	2008	Successful
Rhopalomerus sp. 4	Eugnomina	New Caledonia	FMNH4430025	MNHW	EtOh	-	Successful
Rhopalomerus sp. 5	Eugnomina	New Caledonia	FMNH4430024	MNHW	EtOh	2008	Successful
Rhopalomerus sp. 6	Eugnomina	New Zealand	FMNH4429953	NZAC	EtOh	-	Successful
**Rhopalomerus tenuirostris*	Eugnomina	Chile	FMNH4574435	FMNH	pinned	1978	Successful
Rhopalomerus tenuirostris	Eugnomina	New Zealand	FMNH4429949	NZAC	EtOh	-	Successful
Scolopterus aequus	Eugnomina	New Zealand	FMNH4429853.1	NZAC	EtOh	-	Successful
**Scolopterus penicillatus*	Eugnomina	New Zealand	FMNH4429934	NZAC	EtOh	-	Successful
Scolopterus sp. nov.	Eugnomina	New Zealand	FMNH4429874	NZAC	EtOh	-	Successful
Scolopterus tetracanthus	Eugnomina	New Zealand	FMNH4429854.1	NZAC	EtOh	2012	Successful
Stephanorhynchus brevipennis	Eugnomina	New Zealand	FMNH4429875	NZAC	EtOh	2011	Successful
Stephanorhynchus costifer	Eugnomina	New Zealand	FMNH4429876.1	NZAC	EtOh	-	Successful
Stephanorhynchus crassus	Eugnomina	Australia	FMNH4430042	NZAC	EtOh	2023	Successful
Stephanorhynchus crassus	Eugnomina	New Zealand	FMNH4429855.1	NZAC	EtOh	2019	Successful
**Stephanorhynchus curvipes*	Eugnomina	New Zealand	FMNH4429857.1	NZAC	EtOh	-	Successful
Stephanorhynchus lawsoni	Eugnomina	New Zealand	FMNH4429920	NZAC	EtOh	2018	Successful
Stephanorhynchus nigrosparsus	Eugnomina	New Zealand	FMNH4429936	NZAC	EtOh	2012	Successful
Stephanorhynchus sp. nov.	Eugnomina	New Zealand	FMNH4429929	NZAC	EtOh	-	Successful
Stephanorhynchus tuberosus	Eugnomina	New Zealand	FMNH4429856.1	NZAC	EtOh	-	Successful
Stephanorhynchus tuberosus	Eugnomina	New Zealand	FMNH4429930	NZAC	EtOh	-	Successful
Tysius bicornis	Eugnomina	New Zealand	FMNH4429937	NZAC	EtOh	2022	Successful
Tysius sp.	Eugnomina	New Zealand	FMNH4429921	NZAC	EtOh	2019	Successful
Udeus sp.	Eugnomina	Ecuador	USNMENT01735846	NMNH	pinned	2021	Successful
Udeus sp.	Eugnomina	Bolivia	FMNH4432043	ASUCOB	pinned	1980	Successful
Udeus cecropiae AM	Eugnomina	Brazil	FMNH4574464.3	CERPE	EtOH	2022	Successful
Udeus cecropiae PA	Eugnomina	Brazil	FMNH4574489	CERPE	EtOH	2022	Successful

Udeus cecropiae PE	Eugnomina	Brazil	FMNH4574451.2	CERPE	EtOH	2022	Successful
Udeus cerradensis	Eugnomina	Brazil	FMNH4574449.2	CERPE	EtOH	2022	Successful
Udeus longicollis MT	Eugnomina	Brazil	FMNH4574444.3	CERPE	EtOH	2022	Successful
Udeus longicollis PE	Eugnomina	Brazil	FMNH4574447.3	CERPE	EtOH	2021	Successful
Udeus sp.	Eugnomina	Panama	FMNH4600251.1	FMNH	EtOH	2021	Successful
Udeus sp.	Eugnomina	Panama	FMNH4429965	FMNH	EtOH	2021	Successful
Udeus sp.	Eugnomina	Brazil	FMNH4432053	ASUCOB	pinned	1997	Successful
Udeus sp.	Eugnomina	Panama	FMNH4432010	ASUCOB	pinned	1976	Successful
Udeus sp.	Eugnomina	Peru	FMNH4432044	ASUCOB	pinned	1992	Successful
Udeus sp.	Eugnomina	Panama	USNMENT01735825	NMNH	pinned	1964	Successful
Udeus sp. 9	Eugnomina	Brazil	FMNH4574457	CERPE	EtOH	2021	Successful
Udeus sp. 9	Eugnomina	Brazil	FMNH4574458.2	CERPE	EtOH	2021	Successful
Udeus sp. nov. 12	Eugnomina	Panama	FMNH4600249.1	FMNH	EtOH	2021	Successful
Udeus sp. nov. 12	Eugnomina	Panama	FMNH4429964	FMNH	EtOH	2021	Successful
Udeus sp. nov. 16	Eugnomina	Panama	USNMENT01735828	NMNH	pinned	1977	Successful
Udeus sp. nov. 17	Eugnomina	Ecuador	FMNH4432027	ASUCOB	pinned	1998	Successful
Udeus sp. nov. 18	Eugnomina	Trinidad	AMNH15	AMNH	pinned	1966	Successful
Udeus sp. nov. 27	Eugnomina	Panama	FMNH4600208	CERPE	EtOH	2022	Successful
Udeus sp. nov. 27	Eugnomina	Panama	FMNH4600247	CERPE	EtOH	2021	Successful
Udeus sp. nov. 27	Eugnomina	Panama	FMNH4429963	CERPE	EtOH	2022	Successful
Udeus sp. nov. 3	Eugnomina	Brazil	FMNH4574442	CERPE	EtOH	2021	Successful
Udeus sp. nov. 5	Eugnomina	Brazil	FMNH4574453	CERPE	EtOH	2022	Successful
Udeus sp. nov. 6	Eugnomina	Brazil	FMNH4574455.2	CERPE	EtOH	2021	Successful
Udeus sp. nov. 7	Eugnomina	Brazil	FMNH4574462.2	CERPE	EtOH	2022	Successful
Udeus sp. nov. 8	Eugnomina	Brazil	FMNH4574460.2	CERPE	EtOH	2022	Successful
Udeus variabilis ES	Eugnomina	Brazil	FMNH4574488	CERPE	EtOH	2022	Successful
Udeus variabilis RJ	Eugnomina	Brazil	FMNH4574456.1	CERPE	EtOH	2021	Successful
Udeus sp. nov. 8	Eugnomina	Brazil	FMNH4574459	CERPE	EtOH	2021	Successful
**Meriphus fullo*	Meriphina	Australia	FMNH4430032	NZAC	pinned	-	Successful
Meriphus cf. *longirostris*	Meriphina	Australia	FMNH4429998	ANIC	EtOH	2010	Successful
**Meripherinus* cf. *fimbriatus*	Meriphina	Australia	FMNH4429997	ANIC	EtOH	2021	Successful
Meriphina	Meriphina	Australia	FMNH4429982	ANIC	EtOH	2009	Successful
Myossita melanocephala	Meriphina	Australia	FMNH4429959	NZAC	pinned	2019	Successful

Myossita sp.	Meriphina	Australia	FMNH4429987	ANIC	EtOH	2019	Successful
Myossita sp.	Meriphina	Australia	FMNH4429988	ANIC	EtOH	2022	Successful
**Orpha flavicornis*	Meriphina	Australia	FMNH4429958	NZAC	pinned	2018	Successful
Orpha flavicornis	Meriphina	Australia	FMNH4430044	NZAC	pinned	2018	Successful
Orpha flavicornis	Meriphina	Australia	FMNH4429986	ANIC	EtOH	2012	Successful
Meriphina	Meriphina	Australia	FMNH4429974	ANIC	EtOH	2009	Successful
Strabonus sp. 1	NA	New Caledonia	FMNH4430014	MNHW	EtOH	2010	Successful
Strabonus sp. 3	NA	New Caledonia	FMNH4430015	MNHW	EtOH	2010	Successful
Strabonus sp. 2	NA	New Caledonia	FMNH4430026	MNHW	EtOH	2008	Successful
Strabonus sp.	NA	New Caledonia	FMNH4432051	ASUCOB	pinned	2010	Successful
***Scolopterus* sp.**	**Eugnomina**	**New Zealand**	**FMNH4432023**	**ASUCOB**	**pinned**	**1960**	**unsuccessful**
***Udeus* sp. nov. 15**	**Eugnomina**	**Panama**	**USNMENT01735830**	**NMNH**	**pinned**	**1972**	**unsuccessful**
Udeus sp. nov. 16	**Eugnomina**	**Brazil**	**FMNH4574465**	**CERPE**	**EtOH**	**2021**	**unsuccessful**
Omoides humeralis azarae	**Eugnomina**	**Chile**	**FMNH4432031**	**ASUCOB**	**pinned**	**1968**	**unsuccessful**
***Udeus* sp. nov. 11**	**Eugnomina**	**Panama**	**FMNH4432015**	**ASUCOB**	**pinned**	**1995**	**unsuccessful**
***Udeus* sp.**	**Eugnomina**	**Peru**	**FMNH4432011**	**ASUCOB**	**pinned**	**1964**	**unsuccessful**
***Udeus* sp.**	**Eugnomina**	**Panama**	**FMNH4432039**	**ASUCOB**	**pinned**	**1976**	**unsuccessful**
Omoides validus	**Eugnomina**	**Chile**	**FMNH4432028**	**ASUCOB**	**pinned**	**1972**	**unsuccessful**
***Pedetinus* sp.**	**Eugnomina**	**Chile**	**FMNH4432034**	**ASUCOB**	**pinned**	**1989**	**unsuccessful**
***Pactola* sp.**	**Eugnomina**	**New Caledonia**	**FMNH4430007**	**DBUO**	**EtOH**	**2003**	**unsuccessful**
***Udeus* sp. 12**	**Eugnomina**	**Panama**	**MIUP9**	**MIUP**	**pinned**	**1974**	**unsuccessful**
***Udeus* sp.**	**Eugnomina**	**Ecuador**	**FMNH4432017**	**ASUCOB**	**pinned**	**1998**	**unsuccessful**
***Rhopalomerus* sp. 2**	**Eugnomina**	**New Caledonia**	**FMNH4430008**	**MNHW**	**EtOH**	**2001**	**unsuccessful**
Pactola setacea	**Eugnomina**	**New Caledonia**	**FMNH4430006**	**DBUO**	**EtOH**	**2001**	**unsuccessful**
Meriphina sp.	**Meriphina**	**Australia**	**FMNH4430041**	**FMNH**	**pinned**	**-**	**unsuccessful**
***Pedetinus* sp.**	**unplaced**	**Costa Rica**	**FMNH4432052**	**ASUCOB**	**pinned**	**1987**	**unsuccessful**
***Pactola* sp. 6**	**Eugnomina**	**New Caledonia**	**FMNH4430009**	**DBUO**	**EtOH**	**2003**	**unsuccessful**
***Udeus* sp.**	**Eugnomina**	**Panama**	**FMNH4432014**	**ASUCOB**	**pinned**	**1995**	**unsuccessful**
Rhopalomerus antennalis	**Eugnomina**	**New Zealand**	**FMNH4429951**	**NZAC**	**EtOh**	**2007**	**unsuccessful**
Apionodes longipes	**NA**	**Laos**	**FMNH4432025**	**ASUCOB**	**pinned**	**1998**	**unsuccessful**
Anthonomini	NA	Chile	FMNH4432047	ASUCOB	pinned	2002	Successful
Conoderitae	NA	Indonesia	FMNH4429995	ANIC	EtOH	2001	Successful
Curculioninae sp.	NA	Australia	USNMENT01735870	NMNH	pinned	1990	Successful
Curculioninae sp.	NA	New Caledonia	FMNH4432045	ASUCOB	pinned	2001	Successful

Curculioninae sp.	NA	New Caledonia	FMNH4432050	ASUCOB	pinned	2000	Successful
Curculioninae sp.	NA	Indonesia	FMNH4429994	ANIC	EtOH	2001	Successful
Curculioninae sp.	NA	Australia	FMNH4429977	ANIC	EtOH	2008	Successful
Curculioninae sp.	**NA**	**New Caledonia**	**FMNH4432024**	**ASUCOB**	**pinned**	**1977**	**unsuccessful**
Curculioninae ssp.	**NA**	**New Zealand**	**FMNH4432049**	**ASUCOB**	**pinned**	**1960**	**unsuccessful**
Derelomini	NA	Australia	FMNH4429984	ANIC	EtOH	2010	Successful
Derelomini	NA	Indonesia	FMNH4429989	ANIC	EtOH	2001	Successful
Empolis cf.	NA	Australia	FMNH4429993	ANIC	EtOH	2011	Successful
Empolis cf.	NA	Australia	FMNH4429983	ANIC	EtOH	2010	Successful
Storeini	NA	Australia	FMNH4430039	FMNH	pinned	2004	Successful

CAPÍTULO 5

CONSIDERAÇÕES FINAIS

Neste estudo, adotamos uma abordagem integrativa, combinando dados morfológicos, biológicos, por meio da investigação da história natural, bem como a aplicação de métodos filogenômicos, visando esclarecer a diversidade e levantar hipóteses sobre a origem e diversificação da tribo Eugnomini que abriga uma rica diversidade de besouros de flores com uma distribuição estritamente gondwânica.

A utilização do método de enriquecimento híbrido ancorado permitiu estabelecer o não monofiletismo da tribo como é constituída atualmente, identificar as relações filogenéticas internas e explorar possíveis cenários para sua origem e diversificação ao longo da história evolutiva. Destaca-se a relevância da abordagem taxonômica do gênero *Udeus*, evidenciando uma diversidade ainda maior de Eugnomini na região Neotropical do que anteriormente estimado. Além de proporcionar informações biológicas valiosas, confirmando a especificidade desses besouros em relação às suas plantas hospedeiras. A delimitação taxonômica de Eugnomini e sua reavaliação morfológica agora podem ser definidas, respaldadas pelos resultados filogenéticos obtidos.

Este estudo tem o intuito de contribuir para a compreensão da história evolutiva da família Curculionidae, especialmente no que concerne às interações inseto-planta. Os próximos passos envolvem direcionar esforços para explorar a diversidade ainda desconhecida de Eugnomini na região neotropical, com especial atenção à região andina, investigando as relações com as plantas hospedeiras e somar esforços para a atualização taxonômica dos gêneros australianos permitindo assim aprofundar a compreensão da associação entre besouros visitantes florais e suas plantas hospedeiras, incluindo o papel desempenhado na polinização das mesmas.