IGOR DE SOUZA GONÇALVES

SISTEMÁTICA E FILOGENIA DE *CERACIS* MELLIÉ (COLEOPTERA: CIIDAE)

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ecologia, para obtenção do título de *Doctor Scientiae*.

Orientador: Cristiano Lopes Andrade

Coorientadoras: Lucimar Soares de Araujo
Vivian E. Sandoval Gómez

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“Without taxonomy to give shape to the bricks,

and systematics to tell us how to put them together,

the house of biological Science is a meaningless jumble.”

Robert M. May, Nature 347: 129–130, 1990

RESUMO

SOUZA-GONÇALVES, Igor de, D.Sc., Universidade Federal de Viçosa, março de 2021. **Sistemática e filogenia de *Ceracis* Mellié (Coleoptera: Ciidae).** Orientador: Cristiano Lopes Andrade. Coorientadoras: Lucimar Soares de Araujo e Vivian Eliana Sandoval Gómez.

Besouros são organismos fascinates e geralmente atrativos, ocorrendo nos mais variados hábitats, com exceção dos mares. A ordem Coleoptera é o táxon mais diverso da Terra, com mais de 400.000 espécies descritas e cerca de 180 famílias com espécies viventes, das quais 115 têm representantes no Brasil. Ciidae é a família mais diversa e abundante de besouros micetobiontes, com 756 espécies em 51 gêneros. Micetobiontes são aqueles que dependem de fungos como hábitat e alimento em todo o seu ciclo de vida, e são organismos importantes para estudos ecológicos e evolutivos. *Ceracis* Mellié é o segundo maior gênero de Ciidae, com maior diversidade nas áreas tropicais e subtropicais. Com o objetivo de compreender as relações sub- e supragenéricas de *Ceracis,* esta tese é dividida em quatro capítulos. No primeiro, o objetivo foi descrever sete novos gêneros, a maior parte com base em espécies descritas como *Ceracis*, e onze novas espécies de Ciidae da região Neotropical, fornecendo dados de distribuição geográfica, fungos hospedeiros, chaves de identificação e discutimos as afinidades morfológicas destes novos gêneros. No segundo capítulo, o objetivo foi descrever uma nova espécie de *Ceracis* da Guatemala e México, fornecendo dados de distribuição geográfica e fungos hospedeiros. No terceiro capítulo, o objetivo foi descrever uma nova espécie de *Ceracis* do Panamá, Colômbia, Costa Rica e Brasil, com dados de distribuição geográfica e fungos hospedeiros. No quarto capítulo, o objetivo foi testar pela primeira vez a monofilia de *Ceracis*, bem como suas relações sub- e supragenéricas, com base em análise filogenética morfológica. A partir dos resultados, concluimos que *Ceracis* é um gênero polifilético, com o grupo *furcifer* distanciado dos demais *Ceracis*, e sugere-se que as espécies do grupo *furcifer* devam compor um novo gênero.

Palavras-chave: Besouros. Ciidae. Filogenia. Morfologia.

ABSTRACT

SOUZA-GONÇALVES, Igor de, D.Sc., Universidade Federal de Viçosa, March, 2021. **Systematic and phylogeny of *Ceracis* Mellié (Coleoptera: Ciidae).** Advisor: Cristiano Lopes Andrade. Co-advisors: Lucimar Soares de Araujo and Vivian Eliana Sandoval Gómez.

Beetles are fascinating and generally attractive organisms, occurring in the most varied habitats, with the exception of the seas. The order Coleoptera is the most diverse taxon on Earth, with more than 400,000 species described and about 180 families with living species, of which 115 have representatives in Brazil. Ciidae is the most diverse and abundant family of micetobiont beetles, with 756 species in 51 genera. Micetobionts are the ones that rely on fungi as habitat and food throughout its life cycle, and are important organisms to ecological and evolutionary studies. *Ceracis* Mellié is the second major genus of Ciidae, and with most diversity at the tropical and subtropical areas. Aiming to understand the sub- and suprageneric relationships of *Ceracis*, this thesis is divided in four chapters. In the first, the aim was to describe seven new genera, mostly based on species described as *Ceracis*, and eleven new species of Ciidae from the Neotropical region. We provide data of geographical distribution and host fungi, identification keys and discussed morphological affinities of these new genera. In the second chapter, the aim was to describe a new *Ceracis* species from Guatemala and Mexico, providing data of geographical distribution and host fungi. In the third chapter, the aim was to describe a new *Ceracis* species from Panama, Colombia, Costa Rica and Brazil, with geographical distribution and host fungi data. In the fourth chapter, the aim was to test for the first time, the monophyly of *Ceracis*, as well as it sub- and suprageneric relationships with base on morphological phylogenetic analysis. From the results, we concluded that *Ceracis* is a polyphyletic genus, with the *furcifer* group, away from the other *Ceracis*, and it is suggested that species of *furcifer* group should compose a new genus.

Keywords: Beetles. Ciidae. Phylogeny. Morphology.

SUMÁRIO

INTRODUÇÃO GERAL

Besouros (Coleoptera: Insecta) são insetos fascinantes e geralmente atrativos (BEUTEL *et al.*, 2009). Estes organismos foram nomeados como grupo por Aristóteles no século IV A.C. (CROWSON, 1981) e devidamente caracterizados como insetos com asas em formato de estojo (ou élitros), do grego *koleon* = estojo (BEUTEL *et al.*, 2009). Coleópteros são altamente diversos, principalmente nas regiões tropicais e subtropicais, com mais de 400.000 espécies descritas (LAWRENCE & ŚLIPIŃSKI, 2013). Há cerca de 180 famílias de Coleoptera com espécies viventes (BOUCHARD *et al.*, 2011; LAWRENCE & ŚLIPIŃSKI, 2013), das quais pelo menos 115 possuem representantes no Brasil. Portanto, essa ordem compreende ~25% de todas as espécies conhecidas e ~40% de todos os insetos (ŚLIPIŃSKI *et al.*, 2011; MCKENNA *et al.*, 2015), sendo o táxon mais diverso de organismos da Terra. Os besouros exibem uma grande variedade de formas, tamanhos e estruturas corporais, refletindo em uma extensa varieadade de hábitats ocupados ao redor do mundo, com exceção dos mares (LAWRENCE & ŚLIPIŃSKI, 2013; MCKENNA *et al.*, 2015). Estes organismos desempenham as mais variadas funções ecológicas, valendo-se ressaltar predação e controle biológico de pragas na agricultura (*e.g.* Coccinellidae, Carabidae) (CHOCOROSQUI & PASINI, 2000; WYCKHUYS & O'NEIL, 2006; BEUTEL *et al.*, 2009; NEW, 2010), polinização (*e.g.* Cerambycidae, Cleridae, Melyridae e Scarabaeidae) (BERNHARDT, 2000) e ciclagem de nutrientes no solo (*e.g.* Scarabaeidae) (NEW, 2010). Além disso, representantes de algumas famílias podem causar sérios danos à agricultura e ao armazenamento de grãos (*e.g.* Chrysomelidae, Curculionidae e Tenebrionidae) (BEUTEL *et al.*, 2009; NEW, 2010).

A diversificação dos besouros nos mais variados hábitats foi possível devido a uma especializada co-evolução de hábitos alimentares (MCKENNA *et al.*, 2015). Dentre os mais variados hábitos alimentares encontrados neste táxon, vale destacar a granivoria, fitofagia, saprofagia, zoofagia, xilofagia, polenivoria, micofagia (ou fungivoria), endo- e ectopasaritismo, inquilinismo e parasitoidismo (CROWSON, 1981; LAWRENCE & NEWTON, 1982; LAWRENCE, 1989; LESCHEN *et al.*, 2010; LESCHEN & BEUTEL, 2014; BEUTEL & LESCHEN, 2016). A distribuição dos hábitos alimentares dentro das quatro subordens de Coleoptera (Archostermata, Myxophaga, Adephaga, Polyphaga) tende a suportar a hipótese que a saprofagia ou a micofagia foi o hábito ancestral dentro da ordem (LAWRENCE, 1989; HUNT *et al.*, 2007). Aproximadamente metade das 180 famílias de Coleoptera são primariamente micófagas ou se alimentam de material vegetal modificado por enzimas fúngicas, entretanto somente 25 destas famílias são estritamente micófagas (LAWRENCE, 1989).

A micofagia é o hábito de se alimentar do micélio (conjunto de hifas), estruturas reprodutivas (ascomas e basidiomas) ou esporos fúngicos (LAWRENCE, 1989; SCHIGEL, 2012). Muitas espécies de Leiodidae são consumidoras de esporos fúngicos na fase adulta, porém se alimentam de mixomicetos (Amebozoa: Myxogastria) enquanto são larvas; similar mudança de hábito alimentar na fase adulta é também conhecida para outros consumidores de esporos como Latridiidae, Nitidulidae e Sphindidae (SCHIGEL, 2012). Algumas famílias são associadas a ascomicetos (Fungi: Ascomycota), valendo ressaltar Clambidae, Cryptophagidae, Corylophidae, Phalacridae, Ptiliidae e Mycetophagidae (LAWRENCE, 1989; SCHIGEL, 2012). Besouros da ambrosia (Lymexilidae; Scolytinae e Curculionidae: Platypodinae) cultivam leveduras em túneis escavados na madeira, das quais se alimentam (LAWRENCE, 1989). Líquens também estão entre os recursos fúngicos utilizados por besouros, ressaltando-se espécies de *Orthocerus* Latreille (Zopheridae: Colydiinae), *Lichenobius* Holloway (Anthribidae: Anthribinae), *Amarygmus* Dalman (Tenebrionidae: Tenebrioninae), *Titaena* Erichson (Tenebrionidae: Tenebrioninae) (LAWRENCE, 1989) e *Nilio* Latreille (Tenebrionidae: Nilioninae) (ALOQUIO & LOPES-ANDRADE, 2016).

Há ainda uma gama de besouros chamados micetócolos (*sensu* SCHEERPELTZ & HÖFLER, 1948), que são os que estão associados aos basidiomas de macrofungos poroides decompositores de madeira (vulgarmente chamados de “orelhas-de-pau”) e macrofungos lamelados (chamados de cogumelos), ambos basidiomicetos (Fungi: Basidiomycota). Os organismos micetócolos tem sido alvo de um crescente interesse de estudo (HANSKI, 1989; JONSELL *et al.*, 1999; JONSEL & NORDLANDER, 2002; AMAT-GARCÍA *et al.*, 2004; GRAF-PETERS *et al.*, 2011; ARAUJO *et al.*, 2015). O interesse por esses organismos advém da sua alta diversidade, importância na degradação de macrofungos e da potencialidade para estudos ecológicos e evolutivos devido: i) seu comportamento (*e.g.* geralmente são gregários, com adultos e larvas construindo galerias e milhares de indivíduos cohabitando no mesmo fungo) (LAWRENCE & BRITTON, 1991; LAWRENCE, 1973; COSTA *et al.*, 1988); ii) fisiologia (*e. g.* desenvolvimento de mecanismos contra intoxicação pelos compostos químicos dos fungos) (MARTIN, 1979); e iii) características ecológicas (*e.g.* especialização na utilização de diferentes partes dos fungos) (LAWRENCE, 1989).

Os besouros e demais insetos micetócolos são divididos em três categorias, de acordo com seu grau de dependência do fungo (*sensu* SCHEERPELTZ & HÖFLER, 1948): i) micetoxenos, os quais visitam o fungo ocasionalmente, utilizando-o normalmente como refúgio ou por estarem próximos a recursos de interesse (*e.g.* Silphidae, Hydrophilidae, Scarabaeidae e Staphylinidae) (LAWRENCE, 1989); ii) micetófilos, que utilizam o fungo como recurso, abrigo ou forrageio em alguma fase do desenvolvimento (*e.g.* Anobiinae (Ptinidae); Endomychidae; Melandryidae; Mycetophagidae; Nitidulidae; Scaphidiinae, Aleocharinae e Tachyporinae (Staphylinidae); Trogossitidae e Tetratomidae) (LAWRENCE, 1989; SCHIGEL, 2009, 2012); e iii) micetobiontes, representando uma associação obrigatória com o fungo, uma vez que tanto adultos quanto larvas dependem exclusivamente do fungo como alimento (*e.g.* Diaperinae (Tenebrionidae), Dorcatominae (Ptinidae), Erotylidae e Ciidae) (JONSELL & NORDLANDER, 2002; KOMONEN, 2003; KOMONEN *et al.*, 2003). Essas categorias são artificiais e foram propostas antes dos avanços no conhecimento taxonômico, biológico e ecológico sobre insetos micetócolos que ocorreram desde a década de 1980.

Ciidae Leach, 1819

Ciidae é uma família de pequenos besouros com 756 espécies descritas, agrupadas em 51 gêneros (LAWRENCE, 2016, 2019; SOUZA-GONÇALVES *et al.*, 2018), apresentando uma distribuição geográfica cosmopolita com exceção dos polos (LAWRENCE & LOPES-ANDRADE, 2010). Besouros ciídeos estão divididos em duas subfamílias: i) Sphindociinae, que inclui uma única espécie norte-americana, *Sphindocis denticollis* Fall, 1917, que ocorre na costa norte da Califórnia (LAWRENCE, 1974; LAWRENCE, 2016); e ii) Ciinae, que abriga todas as demais espécies, atualmente dividida nas tribos Ciini Leach, Orophiini Thomson e Xylographellini Kawanabe & Miyatake (LAWRENCE, 2016). Entretanto, há evidências que sustentam monofilia somente de Xylographellini (LOPES-ANDRADE & GREBENNIKOV, 2015).

O ciclo de vida da maioria das espécies ocorre em basidiomas de macrofungos poroides (LAWRENCE, 1967). Esses besouros dependem exclusivamente dos basidiomas como alimento, abrigo, local de cópula e oviposição (LAWRENCE, 1973; NAVARRETE-HEREDIA, 1991; LAWRENCE & LOPES-ANDRADE, 2010; GRAF-PETERS *et al.*, 2011). A ocorrência desses organimos se dá normalmente em basidiomas de Ganodermataceae, Hymenochaetaceae, Polyporaceae, Thelephorarceae e outros fungos decompositores de madeira (LAWRENCE, 1971; LAWRENCE & LOPES-ANDRADE, 2010). Há poucos registros de ocorrência de adultos de ciídeos fora dos fungos, sendo os casos mais frequentes de espécies ápteras e/ou micrópteras em serapilheira (LAWRENCE, 1971; LOPES-ANDRADE, 2007a). Os besouros ciídeos apresentam uma importância ambiental essencial, uma vez que são parte no processo de degradação de macrofungos poroides (LAWRENCE, 1973; ORLEDGE & REYNOLDS, 2005; GRAF-PETERS *et al.*, 2011). Assim, participam na ciclagem de nutrientes, devolvendo ao ambiente os nutrientes retidos nessas estruturas reprodutivas, como zinco, nitrogênio, cádmio e outros elmentos, os quais ficariam indisponíveis na cadeia trófica, até que processos naturais mais lentos as degradassem (THUNES *et al.*, 2000; GRAF-PETERS *et al.*, 2011).

Os ciídeos são altamente afetados por modificações ambientais que interfiram na disponibilidade de basidiomas (JONSELL & NORDLANDER, 1995; FOSSLI & ANDERSEN, 1998; RUKKE, 2000; THUNES *et al.*, 2000; ARAUJO *et al.*, 2015). Muitas das espécies destes besouros são restritos a florestas ou fragmentos florestais bem preservados, não apresentando ocorrência em vegetações secundárias mesmo quando estas se encontram próximas a áreas extremamente bem preservadas (GUMIER-COSTA, 2004). Existem indícios de que ao menos duas espécies de ciídeos, *Falsocis brasiliensis* Lopes-Andrade, 2007 e *Ceracis cassumbensis* Antunes-Carvalho & Lopes-Andrade, 2011, estejam seriamente ameaçadas de extinção (LOPES-ANDRADE & LAWRENCE, 2011; ANTUNES-CARVALHO & LOPES-ANDRADE, 2011; ARAUJO & LOPES-ANDRADE, 2016), sendo que *Cer. cassumbensis* já foi incluída na lista de espécies ameaçadas com base em sua ocorrência conhecida somente de uma área de restinga (ICMBio, 2018). Entretanto, muitas outras espécies podem estar extintas ou mesmo ameaçadas de extinção por consequência da constante fragmentação florestal e perda de hábitat (ARAUJO *et al*., 2015). Contudo, ainda é difícil fazer uma análise de quanto se perde de espécies de Ciidae nas florestas tropicais, por causa da escassez de estudos principalmente com base histórica, que determinem o encolhimento das populações e a perda de espécies nesses ambientes (C. LOPES-ANDRADE *pers. comm.*).

***Ceracis* Mellié, 1849**

Na família Ciidae, *Ceracis* Mellié é o segundo maior gênero, atualmente com 52 espécies descritas (LAWRENCE, 2016; PECCI-MADDALENA & LOPES-ANDRADE, 2017; SOUZA-GONÇALVES & LOPES-ANDRADE, 2020). O gênero tem distribuição reportada para sete regiões biogeográficas (*sensu* MORRONE, 2015) (número de espécies por região entre parênteses; algumas dessas espécies ocorrem em mais de uma região, como descrito abaixo): Neotropical (34), Neártica (20), Oriental (5), Australiana (5), Paleártica (5), Etíope (1) e Cabo (1) (LAWRENCE, 1967; ABDULLAH, 1973; BLACKWELDER, 1945; ANTUNES-CARVALHO & LOPES-ANDRADE, 2011; ANTUNES-CARVALHO & LOPES-ANDRADE, 2013; PECCI-MADDALENA *et al*., 2014; LAWRENCE, 2016; PECCI-MADDALENA & LOPES-ANDRADE, 2017). A maioria das espécies está restrita a uma região biogeográfica, porém 16 espécies têm distribuição por mais de uma região (LAWRENCE, 1967; ANTUNES-CARVALHO & LOPES-ANDRADE, 2013; LAWRENCE, 2016; PECCI-MADDALENA & LOPES-ANDADE, 2017): i) Neotropical e Paleártica – *Cer. castaneipennis* (Mellié, 1849); ii) Oriental e Paleártica – *Cer. laminicollis* Miyatake, 1982; iii) Neotropical e Neártica – *Cer. californicus* (Casey, 1884), *Cer. cornifer* (Mellie, 1849), *Cer. curtus* (Mellié, 1849), *Cer. dixiensis* (Tanner, 1934), *Cer. minutus* Dury, 1917, *Cer. multipunctatus* (Mellié, 1849), *Cer. nigropunctatus* Lawrence, 1967, *Cer. pullulus* (Casey, 1898), *Cer. punctulatus* Casey, 1898, *Cer. quadricornis* Gorham, 1886, *Cer. schaefferi* Dury, 1917, *Cer. similis* Horn, 1894, *Cer. singularis* (Dury, 1917); e iv) Neotropical, Etíope, Cabo, Paleártica e Oriental – *Cer. tabellifer* (Mellié, 1849).

Ceracis é mais diverso nas regiões Neártica e Neotropical (PECCI-MADDALENA *et al.*, 2014), sendo esta última a região com maior diversidade, incluindo cerca de 40 morfoespécies já reconhecidas em coleções como novas para a ciência. Na região Neártica, a maioria das espécies tem sua ocorrência em florestas temperadas distribuídas do leste ao sul dos Estados Unidos, incluindo parte da costa do Golfo do México (LAWRENCE, 1967). Já na região Neotropical, as espécies estão em sua maioria distribuídas pelas florestas tropicais do centro-sul do México até o Brasil e incluindo as ilhas do mar do Caribe (LAWRENCE, 1967; ANTUNES-CARVALHO & LOPES-ANDRADE, 2013; PECCI-MADDALENA *et al.*, 2014; PECCI-MADDALENA & LOPES-ANDRADE, 2017). No Brasil, a maior parte do conhecimento da fauna de *Ceracis* está restrita a áreas de Mata Atlântica, sendo que neste bioma os trabalhos mais robustos foram focados basicamente no Sul (GRAF-PETERS *et al.*, 2011; GRAF *et al.*, 2018) e Sudeste (LOPES-ANDRADE, 2002; LOPES-ANDRADE *et al.*, 2002; GUMIER-COSTA *et al.*, 2003; ANTUNES-CARVALHO & LOPES-ANDRADE, 2013; PECCI-MADDALENA *et al.*, 2014; ARAUJO *et al.*, 2015; PECCI-MADDALENA & LOPES-ANDRADE, 2017). Trabalhos esporádicos abrangeram espécies ocorrendo em outras regiões geopolíticas ou biomas do Brasil (ANTUNES-CARVALHO & LOPES-ANDRADE, 2011; ANTUNES-CARVALHO & LOPES-ANDRADE, 2013; PECCI-MADDALENA & LOPES-ANDRADE, 2017).

Biologia de *Ceracis*

Adultos e larvas das espécies de *Ceracis*, assim como a maioria das espécies de Ciidae, vivem, alimentam-se e se respoduzem dentro de basidiomas de macrofungos poroides ou sobre o micélio dos mesmos, abaixo da casca de árvores mortas (LAWRENCE, 1967; LAWRENCE, 1971; ORLEDGE & REYNOLDS 2005; LAWRENCE & LOPES-ANDRADE, 2010). Ambos, adultos e larvas, constroem galerias dentro dos basidiomas, e a formação da pupa também ocorre dentro do mesmo

(COSTA *et al.*, 1988; LAWRENCE & LOPES-ANDRADE, 2010), deixando-o apenas para dispersar (OLIVEIRA *et al.*, 2013). São usualmente gregários e milhares de indivíduos podem cohabitar um mesmo basidioma (LAWRENCE & BRITTON, 1991). As fêmeas normalmente ovipõe continuamente por um longo período, podendo serem observadas sobreposições de gerações (LAWRENCE, 1973).

Devido ao fato de cohabitarem com os adultos, as larvas são facilmente encontradas e coletadas (SOUZA-GONÇALVES *et al.*, 2020). Entretanto, informações sobre morfologia, número de ínstares e sua duração são escassas na literatura (SOUZA-GONÇALVES *et al.*, 2020). As informações existentes até o momento incluem descrições completas, desenhos ou citações de características morfológicas gerais, porém são restritas a alguns gêneros como *Cis* Latreille, *Ennearthon* Mellié, *Octotemnus* Mellié, *Orthocis* Casey, *Porculus* Lawrence, *Ropalodontus* Mellié, *Sphindocis* Fall, *Sulcacis* Dury, *Xylographus* Mellié, e mais recentemente, *Hadreule* Thomson (SAALAS, 1923; BÖVING & CRAIGHEAD, 1931; ENTWISTLE, 1955; LAWRENCE, 1974; LAWRENCE, 1987; COSTA *et al.*, 1988; LAWRENCE, 1991; RÜHM & MILEWSKI, 1996; HOLTER *et al.*, 1999; THAYER & LAWRENCE, 2002; LAWRENCE & LOPES-ANDRADE, 2010; SOUZA-GONÇALVES *et al.*, 2020.). A única referência à larva de *Ceracis* na literatura é um desenho da visão dorsal da cabeça da larva de *Ceracis thoracicornis* (Ziegler, 1845) (como *Ennearthron thoracicorne*) (BÖVING & CRAIGHEAD, 1931).

As espécies de *Ceracis*, que possuem informações sobre dados biológicos na literatura, foram todas encontradas em fungos decompositores de madeira, principalmente em Polyporaceae *s. str.* (LAWRENCE, 1967; PECCI-MADDALENA *et al.*, 2014). A preferência por fungos hospedeiros é bem conhecida para a fauna de Ciidae Holártica (LAWRENCE, 1973; KAWANABE, 1995, 1996, 1998, 1999; ORLEDGE & REYNOLDS, 2005). Entretanto, informações para a fauna Neotropical ainda são incipientes (NAVARRETE-HEREDIA & BURGOS-SOLOTIO, 2000; GUMIER-COSTA *et al.*, 2003; GRAF-PETERS *et al.*, 2011; PECCI-MADDALENA & LOPES-ANDRADE, 2017). As espécies holárticas de *Ceracis* ocorrem em quatro (*Trametes*, *Phellinus*, *Ganoderma* e *Trichaptum*) dos seis grupos de hospedeiros *sensu* ORLEDGE & REYNOLDS (2005) utilizados por ciídeos, já conhecidos e identificados para essa região. Entretanto, quatro espécies neárticas de *Ceracis* não puderam ser identificados como utilizadores de nenhum dos grupos de hospedeiros, sendo elas *Cer. curtus*, *Cer. nigropunctatus*, *Cer. pecki* Lawrence, 1971 e *Cer. thoracicornis* (OLEDGE & REYNOLDS, 2005).

Os fungos hospedeiros do grupo *Trametes*, correspondem ao grupo "*Coriolus*" de Lawrence (1973) e "*Polystictus versicolor*" de Paviour-Smith (1960), são um conjunto bem definido e extenso que compreende todos os fungos trametoides, os quais são caracterizados por basidiomas finos e coreáceos, com hifas pálidas em sistema trimítico (presença de hifas esqueletais, de ligação e generativas) (LAWRENCE, 1973). Dentre os gêneros mais comuns, vale destacar *Lenzites* (Polyporaceae), *Pycnoporus* (Polyporaceae), *Schizophyllum* (Schizophyllaceae) e *Trametes* (Polyporaceae) (LAWRENCE, 1973; ORLEDGE & REYNOLDS, 2005). As espécies desse grupo são comumente hospedeiras das seguintes espécies de *Ceracis*: *Cer. cornifer*, *Cer. dixiensis*, *Cer. minutissimus* (Mellié, 1849), *Cer. minutus* e *Cer. quadricornis* (ORLEDGE & REYNOLDS, 2005).

No grupo *Phellinus* estão espécies de Hymenochaetaceae e outras famílias relacionadas, que são caracterizadas pelos basidiomas lenhosos (perenes ou persistentes) ou fibrosos (anuais), com hifas marrons (entretanto, ficam pretas na presença de hidróxido de potássio – KOH) em sistema monomítico (presença somente de hifas generativas) ou dimítico (presença de hifas esqueletais e generativas) (LAWRENCE, 1973). Como exemplos, ressaltam-se *Cyclomyces* (Hymenochaetaceae), *Inonotus* (Hymenochaetaceae), *Phaeolus* (Laetiporaceae) e *Phellinus* (Hymenocahetaceae) (LAWRENCE, 1973; ORLEDGE & REYNOLDS, 2005). *Ceracis* que normalmente ocorrem nesse grupo de fungos hospedeiros são: *Cer. japonus* (Reitter, 1878), *Cer. laminicollis* Miyatake, 1982, *Cer. magister* Lawrence, 1971, *Cer. obrieni* Lawrence, 1967, *Cer. punctulatus*, *Cer. pullulus* e *Cer. singularis* (ORLEDGE & REYNOLDS, 2005).

As espécies pertencentes ao grupo *Ganoderma* formam um grande conjunto que é o mais deficientemente definido, correspondente aproximadamente ao grupo "*Polyporus betulinus*" de Paviour-Smith (1960), cujos representantes possuem esporóforos com características bem heterogêneas, mas os basidiomas são geralmente cortíceos à lenhosos (perenes), com hifas pálidas à marrons em sistemas monomíticos, dimíticos ou, mais usualmente, trimítico (LAWRENCE, 1973). Destacam-se nesse grupo os gêneros: *Bjerkandera* (Phanerochaetaceae), *Daedaleopsis* (Polyporaceae), *Fomes* (Polyporaceae), *Fomitopsis* (Fomitopsidaceae), *Ganoderma* (Polyporaceae) e *Heterobasidion* (Bondarzewiaceae) (LAWRENCE, 1973; ORLEDGE & REYNOLDS, 2005). As espécies de *Ceracis* que utilizam hospedeiros desse grupo são: *Cer. californicus*, *Cer. multipunctatus*, *Cer. sallei* Mellié, 1849 e *Cer. similis* (ORLEDGE & REYNOLDS, 2005).

O grupo *Trichaptum* é formado somente pelo gênero que dá nome ao grupo, pertencente à ordem Hymenochaetales, correspondente ao grupo "*Hirschioporus*" de Lawrence (1973), cujos basidiomas são finos, coriáceos ou rígidos, com hifas pálidas em sistema dimítico e himênio encrustado com cistídios (LAWRENCE, 1973). *Ceracis powelli* Lawrence, 1967 é a única espécie do gênero conhecida por ocorrer exclusivamente em espécies de *Trichaptum* (LAWRENCE, 1967; ORLEDGE & REYNOLDS, 2005).

Com relação à fauna Neotropical, há somente dois trabalhos mostrando o uso de grupos de fungos hospedeiros por ciídeos, sendo um deles focado nas espécies mexicanas (NAVARRETE-HEREDIA & BURGOS-SOLORIO, 2000) e o outro nas espécies do Sul do Brasil (GRAF-PETERS *et al.*, 2011). Navarrete-Heredia & Burgos-Solorio (2000) demonstraram padrões similares aos apresentados para as espécies que ocorrem também nos Estados Unidos (LAWRENCE, 1973; ORLEDGE-REYNOLDS, 2005), mas as espécies pertencentes exclusivamente à fauna Neotropical (*Cer. bicornis* (Mellié, 1849), *Cer. cucullatus* (Mellié, 1849), *Cer. furcifer* Mellié, 1849, *Cer. militaris* Mellié, 1849) não foram relacionadas a nenhum grupo de hospedeiros e deixadas como *incertae sedis* (NAVARRETE-HEREDIA & BURGOS-SOLORIO, 2000). Graf-Peters *et al.* (2011) incluíram somente seis espécies (três morfoespécies) de *Ceracis*: *Cer. bicornis*, *Cer. cornifer* (como *Cer. simplicicornis* (Pic, 1916a) e *Cer. limai* Lopes-Andrade *et al.*, 2002. *Ceracis bicornis* apresentou hábito polígafo, ocorrendo em vários fungos e, portanto, não pode ser colocado em nenhum dos grupos de hospedeiros identificados em trabalhos anteriores; enquanto que *Cer. cornifer* manteve o padrão já apontado em trabalhos prévios e utiliza fungos do grupo *Trametes*; já *Cer. limai* utiliza fungos do grupo *Phellinus* (GRAF-PETERS *et al.*, 2011).

Quatro espécies de *Ceracis* apresentam um grau de associação mais especializado com relação ao uso de fungos hospedeiros, compondo o grupo *Cer. furcifer*: *Cer. cornifer*, *Cer. furcifer*, *Cer. hastifer* (Mellié, 1849) e *Cer. ruficornis* Pic, 1916a (PECCI-MADDALENA & LOPES-ANDRADE, 2017). Há poucos registros dessas espécies em fungos dos gêneros *Trametes* e *Lenzites* (LAWRENCE 1967, 1973). Entretanto, a maior parte dos registros das espécies do grupo *furcifer* se dá em basidiomas de *Pycnoporus sanguineus* (L.) Murrill (Polyporaceae) (MELLIÉ, 1849; LAWRENCE, 1973; GUMIER-COSTA *et al.*, 2003; ORLEDGE & REYNOLDS, 2005; GRAF-PETERS *et al.*, 2011; PECCI-MADDALENA *et al.*, 2014; PECCI-MADDALENA & LOPES-ANDRADE, 2017). Há poucos registros de animais alimentando-se de *Pyc. sanguineus* e essa restrição no consumo pode estar relacionado ao alto grau de toxicidade dos basidiomas dessa espécie (PECCI-MADDALENA & LOPES-ANDRADE, 2017), uma vez que apresentam altas concentrações de cinabarinas e substâncias tóxicas com ação antibiótica (SMÂNIA *et al.*, 2003; GRAF-PERTERS *et al.*, 2011; PECCI-MADDALENA & LOPES_ANDRADE, 2017). Portanto, espécies do grupo *furcifer* demonstram ser os únicos animais verdadeiramente especializados no consumo de *Pyc. sanguineus* (PECCI-MADDLAENA & LOPES-ANDRADE, 2017), sendo provavelmente resistentes aos compostos tóxicos e antibióticos desse fungo (GRAF-PETERS *et al.*, 2011). O fato desses besouros utilizarem praticamente somente esse hospedeiro, que é amplamente distribuído em áreas abertas da região Neotropical, pode ter colocado as espécies do grupo numa estase evolutiva (PECCI-MADDALENA & LOPES-ANDRADE, 2017).

Uma vez que esses besouros são altamente dependentes da disponibilidade de basidiomas (ARAUJO *et al.*, 2015), estes podem disseminar consigo espécimes em seu interior levando a processos de invasão biológica (ORLEDGE *et al.*, 2010). Há poucas espécies de ciídeos conhecidas por serem invasoras, como *Cis bilamellatus* Wood, 1884 (ORLEDGE *et al.*, 2010; LOPES-ANDRADE & LÜER, 2014), *C. chinensis* Lawrence, 1991 (LOPES-ANDRADE, 2008a; LAWRENCE, 2016; SOUZA-GONÇALVES & LOPES-ANDRADE, 2018) e *C. fuscipes* Mellié, 1849 (LAWRENCE, 2016). Com relação ao gênero *Ceracis*, duas espécies já foram identificadas como invasoras (ANTUNES-CARVALHO & LOPES-ANDADE, 2013): *Cer. cucullatus* e *Cer. tabellifer*. A primeira com origem na América do Sul e introduzida em Galápagos; enquanto que a segunda é nativa da região Neotropical e foi introduzida na África, Sul e Sudeste da Ásia (ANTUNES-CARVALHO & LOPES-ANDRADE. 2013; PECCI-MADDALENA *et al.*, 2014). Entretanto, os esfeitos dessas invasões nas populações locais ainda não é conhecido (ANTUNES-CARVALHO & LOPES-ANDRADE, 2013). Porém, há evidências de que *Cer. tabellifer* não tem deslocado as espécies nativas da África do Sul de seus recursos, mas provavelmente tem usado fungos que não eram previamente utilizados e estão disponíveis nas comunidades invadidas (SOUZA-GONÇALVES, 2017).

Histórico taxonômico

Ceracis foi originalmente descrito como um subgênero dentro de *Ennearthron* Mellié (1847), para agrupar as espécies que possuíam as antenas com oito segmentos ao invés de nove, sendo elas: *Enn. (Cer.) castaneipennis*, *Enn. (Cer.) furcifer*, *Enn. (Cer.) militaris*, *Enn. (Cer.) sallei* e *Enn (Cer.) variabillis* Mellié, 1849 (MELLIÉ, 1849). Entretanto, Lacordaire (1857) elevou *Ceracis* a gênero e, após esta mudança, autores adicionaram espécies em ambos os gêneros, normalmente baseados na diferença do número de segmentos antenais (LAWRENCE, 1967). Lawrence (1967) redefiniu os limites de *Ceracis*, designando *Cer. sallei* como espécie-tipo do gênero, e transferiu 15 espécies válidas do gênero *Ennearthron*: *Cer. bicornis*, *Cer. bilamellatus* (Pic, 1916a), *Cer. californicus*, *Cer. cornifer*, *Cer. cucullatus*, *Cer. curtus*, *Cer. cylindricus* (Brèthes, 1922), *Cer. hastifer*, *Cer. japonus*, *Cer. lamellatus* (Pic, 1939), *Cer. monocerus* Lawrence, 1967 (nome substitutivo para *Enn. unicorne* Casey, 1898), *Cer. multipunctatus*, *Cer. nigricans* (Fauvel, 1904), *Cer. pullulus*, *Cer. shikokuensis* (Miyatake, 1954), *Cer. simplicicornis*, *Cer. tabellifer* e *Cer. taurulus* (Jacquelin-Duval, 1857). Algumas espécies também foram transferidas, oriundas de outros gêneros (LAWRENCE, 1967): *Cer. dixiensis*, *Cer. evansi* (Blair, 1944), *Cer. furcatus* (Bosc, 1791), *Cer. latirostris* (Gorham, 1886) e *Cer. singularis*. Lawrence (1967) também descreveu três novas espécies (*Cer. nigropunctatus*, *Cer. obrieni* e *Cer. powelli*), propôs novas sinonímias, forneceu uma revisão das espécies Neárticas, juntamente com uma chave de identificação para as espécies com ocorrência na América do Norte e proposição de afinidades morfológicas com as espécies Neotropicais e Orientais. Além disso, duas espécies foram transferidas para o gênero *Cis* (*Cer. tricornis* Gorham, 1883 e *Cer. sumatrensis* Pic, 1916b) e três deixadas como *incertae sedis* (*Cer. bifurcus* Gorham, 1898, *Cer. laticornis* Pic, 1922 e *Cer. particularis* Pic, 1922) (LAWRENCE, 1967). Lawrence (1967) ainda propôs dois grupos de espécies para aquelas que compartilhavam similaridades morfológicas: i) grupo *Cer. furcifer*, o qual incluía originalmente nove espécies – *Cer. cornifer*, *Cer. cylindricus*, *Cer. furcifer*, *Cer. hastifer*, *Cer. monocerus*, *Cer. ruficornis*, *Cer. simplicicornis* (sinonimizado com *Cer. furcifer* no mesmo trabalho), *Cer. unicornis* Gorham, 1898 e *Cer. semipallidus* Pic, 1922; e ii) grupo *Cer. cucullatus*, com cinco espécies incluídas originalmente – *Cer. cucullatus*, *Cer. bicornis*, *Cer. tabellifer*, *Cer. billamelatus* e *Cer. lamellatus*, sendo as três últimas sinonimizadas com *Cer. cucullatus* no mesmo trabalho. Poucos anos após esse extenso trabalho, Lawrence (1971), em seu estudo sobre a fauna norte americana de Ciidae, descreveu mais duas espécies (*Cer. magister* e *Cer. pecki*), forneceu chaves de identificação atualizadas das espécies e informações adicionais sobre distribuição e fungos hospedeiros daquela fauna.

Após os trabalhos de Lawrence (1967, 1971) focados principalmente na fauna Neárica, o gênero *Ceracis* ficou sem ser revisitado por quase três décadas, até que autores começaram a trabalhar com a fauna Neotropical. Lopes-Andrade (2002), discutindo os avanços no conhecimento da fauna brasileira de Ciidae, propôs um novo grupo (*Cer. furcatus*) para quatro espécies taxonomicamente problemáticas: *Cer. furcatus*, *Cer. militaris*, *Cer. variabillis* e *Cer. minutus* (indicado como *Cer. furcifer* – *lapsus calami* (ANTUNES-CARVALHO & LOPES-ANDRADE, 2011). No mesmo ano, Lopes-Andrade *et al.* (2002) propuseram um novo grupo para três espécies (uma delas nova), que dentre outras características, possuíam antenas com dez segmentos, no chamado grupo *Cer. singularis*: *Cer. furcicollis* (Blair, 1935), *Cer. limai* Lopes-Andrade *et al.*, 2002 e *Cer. singularis*. Após quase uma década, o gênero *Ceracis* voltou a ser alvo de estudo, dessa vez com a redefinição do grupo *cucullatus* para a inclusão de duas novas espécies Neotropicais (ANTUNES-CARVALHO & LOPES-ANDRADE, 2011): *Cer. cassumbensis* e *Cer. navarretei* Antunes-Carvalho & Lopes-Andrade, 2011. Passados dois anos, Antunes-Carvalho & Lopes-Andrade (2013) avaliaram populações disjuntas sob o nome *Cer. cucullatus*, comparando a morfologia de espécimes oriundas das mais variadas regiões biogeográficas. Como resultado, as sinonímias propostas por Lawrence (1967) para *Cer. cucullatus* foram revertidas, reestabelecendo *Cer. lamellatus* e *Cer. tabellifer*, e propondo *Enn. bilamellatum* Pic, 1916a como sinonímia de *Cer. tabellifer* (ANTUNES-CARVALHO & LOPES-ADNRADE, 2013). Além disso, forneceram uma chave de identificação para as espécies do grupo *cucullatus* e discutiram o sucesso de invasão de *Cer. tabellifer* no afrotrópico e outras regiões (ANTUNES-CARVALHO & LOPES-ANDRADE, 2013). Subsequentemente, Pecci-Maddalena *et al.* (2014) descreveram uma nova espécie de *Ceracis* da Mata Atlântica, *Cer. zarathustrai* Pecci-Maddalena *et al.*, 2014, discutindo as similaridades da mesma com as demais espécies já conhecidas da fauna brasileira, principalmente com as do grupo *furcifer*.

Recentemente, o gênero foi redescrito e reportado pela primeira vez para a Austrália, juntamente com a descrição de quatro espécies novas do grupo *cucullatus* (*Cer. christmasensis* Lawrence, 2016, *Cer. communis* Lawrence, 2016, *Cer. divergens* Lawrence, 2016 e *Cer. fictus* Lawrence, 2016), além, de uma chave de identificação para as espécies da região Australiana (LAWRENCE, 2016). Entretanto, *Cer. communis* e *Cer. christmasensis* são morfologiamente similares a *Cer. tabellifer* e devem ser conspecíficas (C. LOPES-ANDRADE *pers. comm.*).

Em uma continuação ao estudo das espécies de *Ceracis* Neotropicais, Pecci-Maddalena & Lopes-Andrade (2017) realizaram uma revisão do grupo *furcifer*, reduzindo o grupo à quatro espécies: *Cer. cornifer* – com quatro novas sinonímias (*Enn. cylindricum* Brèthes, 1922, *Cer. monocerus*, *Enn. simplicicorne* Pic, 1916a e *Cer. unicornis* Gorham, 1898), *Cer. furcifer*, *Cer. hastifer* e *Cer. ruficornis*. Adicionalmente, os autores forneceram uma chave de identificação para as espécies do grupo *furcifer*, compilaram dados sobre o uso de *Pyc. sanguineus* por animais e discutiram a importância das espécies do grupo como consumidores especializados desse fungo (PECCI-MADDALENA & LOPES-ANDRADE, 2017).

Portanto, considerando o conhecimento do gênero até o presente momento, estas são as espécies incluídas, com suas respectitivas sinonímias, localidade-tipo e distribuição[1]:

Ceracis Mellié 1849: 375 (como subgênero de *Ennearthron*). ET: *Ennearthron* (*Ceracis*) *sallei* Mellié 1849 (designação subsequente, Lawrence 1967).

1. *Ceracis bicornis* (Mellié 1849: 374) (*Ennearthron*); Lawrence 1967: 97. LT: Peru. D: Peru, Brasil e México.
2. *Ceracis bifurcus* Gorham 1898: 332, pl. 27, figs. 10, 10a); Lawrence 1967: 98. LT: São Vicente. [*incertae sedis*]
3. *Ceracis californicus* (Casey 1884: 36) (*Ennearthron*); Lawrence 1967: 107, fig. 15; Lawrence 1971: 497. LT: Califórnia (Estados Unidos). D: Oeste da América do Norte, incluindo México.

-*Ennearthron convergens* Casey 1898: 89; Lawrence 1967: 107 (sinonimização). LT: Los Angeles (Califórnia, Estados Unidos).

-*Ennearthron discolor* Casey 1898: 89; Lawrence 1967: 107 (sinonimização). LT: Sonoma Co. (Califórnia, Estados Unidos).

-*Ennearthron grossulum* Casey 1898: 89; Lawrence 1967: 107 (sinonimização). LT: Sul da Califórnia (Estados Unidos).

-*E. coloradense* Dury 1917: 22; Lawrence 1967: 107 (sinonimização). LT: Grand Lake (Colorado, Estados Unidos)

-*E. oregonus* Dury 1917: 22; Hatch 1962: 235 (sinonimização). LT: Corvallis (Oregon, Estados Unidos).

4. *Ceracis cassumbensis* Antunes-Carvalho & Lopes-Andrade, 2011: 53. LT: "Ilha da Cassumba" (Caravelas, Bahia, Brasil). D: Conhecido somente da localidade tipo.
5. *Ceracis castaneipennis* Mellié 1849: 376, pl. 12, fig. 21; Lawrence 1967: 97. LT: Cuba. D: Índias Ocidentais, Europa (introduzida?).

-*Cis nitidulus* Mellié 1849: 334, pl. 11, fig. 11; Reitter 1878: 28 (sinomização); Lawrence 1967: 97. LT: Lombardy (Itália).

-*Ceracis ater* Pic 1922: 2; Lawrence 1967 (sinonimização). LT: Guadalupe.

-*Ceracis rufipes* Pic 1922: 2; Lawrence 1967 (sinonimização). LT: Guadalupe.

6. *Ceracis christmasensis* Lawrence 2016: 20. LT: Ilha Christmas.
7. *Ceracis communis* Lawrence 2016: 21. LT: Ben Boyd N. P. Bittangabee (Nova Gales do Sul, Austrália). D: Leste da Austrália (Victoria ao norte de Queensland), Ilha Norfolk e Ilha Christmas.
8. *Ceracis cornifer* (Mellié 1849: 371, pl. 12, fig. 18) (*Ennearthron*); Lawrence 1967: 97; Pecci-Maddalena & Lopes-Andrade 2017: 7. LT: Brasil. D: Brasil, sudoeste do México, ilhas do Caribe, sul dos Estados Unidos e Argentina.

-*Ceracis cylindricus* (Brèthes 1922: 303) (*Ennearthron*); Lawrence 1967: 97; Pecci-Maddalena & Lopes-Andrade 2017 (sinonimização). LT: General Urquiza (Argentina).

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[1] A lista aqui apresentada, não leva em consideração as espécies novas resultantes desta tese, uma vez que estas espécies são parte dos resultados obtidos durante o desenvolvimento do trabalho. ET: espécie-tipo, LT: localidade tipo, D: distribuição.

-*Ceracis monocerus* Lawrence 1967: 115, nome substitutivo para *Ennearthron unicorne* Casey 1898: 90 (não *Ceracis unicornis* Gorham 1898); Lawrence 1967: 115, fig. 20; Lawrence 1971: 499; Pecci-Maddalena & Lopes-Andrade 2017 (sinonimização). LT: Flórida (Estados Unidos).

-*Ceracis simplicicornis* (Pic 1916a: 19) (*Ennearthron*); Lawrence 1967: 97; Pecci-Maddalena & Lopes-Andrade 2017 (sinonimização). LT: Buenos Aires (Argentina).

-*Ceracis unicornis* Gorham 1898: 332; Lawrence 1967: 98; Pecci-Maddalena & Lopes-Andrade 2017 (sinonimização). LT: São Vicente.

9. *Ceracis cucullatus* (Mellié 1849: 372, pl. 12, fig. 19) (*Ennearthron*); Scott 1926: 37, Lawrence 1967: 97; Antunes-Carvalho & Lopes-Andrade, 2013: 5 (novo senso). LT: Caiena (Guiana Francesa). D: Brasil, Colômbia, Cuba, Equador, Guiana Francesa, Guadalupe, Granada, Ilha Galápagos, México e Panamá [veja Lawrence 1967a, p. 99; Antunes-Carvalo & Lopes-Andrade 2013, p. 8–9].
10. *Ceracis curtus* (Mellié 1849: 367, pl. 12, fig. 15) (*Ennearthron*); Lawrence 1967: 110; Lawrence 1971: 497. LT: Havana (Cuba). D: Sudeste dos Estados Unidos, Bahamas e Grandes Antilhas.

-*Cis obesus* Mellié 1849: 335, pl. 11, fig. 13; Lawrence 1967 (sinonimização). LT: América do Norte.

-*Ennearthron compacta* Dury 1917: 21; Lawrence 1967 (sinonimização). LT: Key West (Flórida, Estados Unidos).

11. *Ceracis divergens* Lawrence 2016: 22. LT: Enoggera Reserve (Queensland, Austrália). D: Austrália (norte de Nova Gales do Sul ao norte de Queensland).
12. *Ceracis dixiensis* (Tanner 1934: 47) (*Octotemnus*); Lawrence 1967: 112; Lawrence 1971: 498. . LT: Zion National Park (Utah, Estados Unidos). D: Sudoeste dos Estados Unidos e México.
13. *Ceracis evansi* (Blair 1944: 126) (*Scolytocis*); Lawrence 1967: 97. LT: Taveuni (Fiji). D: Fiji.
14. *Ceracis fictus* Lawrence 2016: 23. LT: Brigalow Research Stn (Queensland, Austrália). D: Austrália (centro-oeste de Queensland).
15. *Ceracis furcatus* (Bosc 1791: 6) (*Bostrichus*); Bosc 1792: 259, pl. 38, fig.s A–C. Lawrence 1967: 97. LT: Jamaica. D: Jamaica.
16. *Ceracis furcicollis* (Blair 1935: 295, fig. 4) (*Cis*); Zimmerman 1938: 206, fig. 1h–i; Lawrence 1967: 97. LT: Kopaafaa (Hiva Oa). D: Rapa e Marquesas.
17. *Ceracis furcifer* Mellié 1849: 379, pl. 12, fig. 24; Gorham 1886: 359; Gorham 1898: 331. Lawrence 1967: 97; Pecci-Maddalena & Lopes-Andrade 2017: 16. LT: Caiena (Guiana Francesa). D: Guiana Francesa, Peru, Suriname, Guatemala (Izabal), Guadalupe, São Vicente, México e Brasil.

-*Ceracis militaris* sensu Gorham 1883: 223, pl. 10, fig. 26.

-*Ceracis semipallidus* Pic 1922: 3; Lawrence 1967 (sinonimização). LT: Guadalupe.

18. *Ceracis hastifer* (Mellié 1849: 370, pl. 12, fig. 17) (*Ennearthron*); Lawrence 1967: 97; Pecci-Maddalena & Lopes-Andrade 2017: 19. LT: Colômbia. D: Colômbia, Brasil e Peru.
19. *Ceracis japonus* (Reitter 1878: 36) (*Ennearthron*); Lawrence 1967: 97. LT: Japão. D: Japão.
20. *Ceracis lamellatus* (Pic 1939: 8) (*Ennearthron*); Lawrence 1967: 97 (sinonimização); Antunes-Carvalho & Lopes-Andrade 2013: 9 (reestabelecimento). LT: Nova Teutônia (Santa Ctarina, Brasil). D: Brasil.

21. *Ceracis laminicollis* Miyatake 1982: 77, fig. 3; Kawanabe 1994: 270 (distribuição). LT: Kenting Park (Pingtung Hsien, Taiwan). D: Taiwan, Japão (Ilha Okinawa-hontô).
22. *Ceracis laticornis* Pic 1922: 3; Lawrence 1967: 98. LT: Guadalupe. D: Guadalupe. [*incertae sedis*]
23. *Ceracis latirostris* (Gorham 1886: 355) (*Xylographus*); Lawrence 1967: 97. LT: Zapote (Guatemala). D: Guatemala.
24. *Ceracis limai* Lopes-Andrade, Madureira & Zacaro 2002: 60. LT: Viçosa, “Mata da Biologia” (Minas Gerais, Brasil). D: Sul e sudeste do Brasil, Argentina [não publicado]
25. *Ceracis magister* Lawrence 1971: 498. LT: Lignum Vitae Key (Flórida, Estados Unidos). D: Conhecido somente da localidade tipo.
26. *Ceracis militaris* Mellié 1849: 378, pl. 12, fig. 23; Gorham 1883: 223, pl. 10, fig. 26 [identificação incorreta]; Gorham 1886: 359; Gorham 1898: 331. Lawrence 1967: 97. LT: Veracruz (México). D: México e São Vicente.
27. *Ceracis minutissimus* (Mellié 1849: 334, pl. 11, fig. 12) (*Cis*); Lawrence 1967: 113, fig. 18; Lawrence 1971: 499. LT: Boston (Massachusetts, Estados Unidos). D: Leste da América do Norte.
28. *Ceracis minutus* Dury 1917: 25; Lawrence 1967, 114, fig. 19; Lawrence 1971: 499. LT: Palm Beach (Flórida, Estados Unidos). D: Sul do Texas e Flórida (Estados Unidos), Bahamas e Grandes Antilhas.
29. *Ceracis multipunctatus* (Mellié 1849: 368, pl. 12, fig. 16) (*Ennearthron*); Lawrence 1967: 116, fig. 24; Lawrence 1971: 499. LT: Cuba. D: Alabama e Flórida (Estados Unidos), México e Índias Ocidentais.
30. *Ceracis navarretei* Antunes-Carvalho & Lopes-Andrade, 2011: 57. LT: Dos Amates (Veracruz, México). D: Sul do México.
31. *Ceracis nigricans* (Fauvel 1904: 163) (*Ennearthron*); Lawrence 1967: 97. LT: Noumea (Nova Caledônia). D: Nova Caledônia.
32. *Ceracis nigropunctatus* Lawrence 1967: 118, fig. 16; Lawrence 1971: 499. LT: 4 mi. S Grosse Tete (Luisiana, Estados Unidos). D: Luisiana e Texas (Estados Unidos), México ao Panamá e Brasil (Pará, Espírito Santo).
33. *Ceracis obrieni* Lawrence 1967: 119, fig. 25; Lawrence 1971: 499. LT: 2 mi. SO Patagonia (Arizona, Estados Unidos). D: Sudeste do Arizona (Estados Unidos) ao sul de Sinaloa (México).
34. *Ceracis palaceps* Zimmerman 1942: 51, fig. 1a, b, g, h, j, pl. 1, fig. D; Lawrence 1967: 97. LT: Guam. D: Guam.
35. *Ceracis particularis* Pic 1922: 3; Lawrence 1967: 98. LT: Guadalupe. [*incertae sedis*]
36. *Ceracis pecki* Lawrence 1971: 499. LT: Florida Caverns State Park (Flórida, Estados Unidos). D: sudeste dos Estados Unidos.
37. *Ceracis powelli* Lawrence 1967: 120, fig. 23; Lawrence 1971: 501. LT: Rustler Park (Arizona, Estados Unidos). D: Sudeste do Arizona (Estados Unidos) ao sul de Durango (México).
38. *Ceracis pullulus* (Casey 1898: 90) (*Ennearthron*); Lawrence 1967: 121, fig. 22; Lawrence 1971: 501. LT: Flórida (Estados Unidos). D: Sul dos Estados Unidos e Grandes Antilhas.

39. *Ceracis punctulatus* Casey 1898: 90; Lawrence 1967: 123. LT: Flórida (Estados Unidos). D: Leste da América do Norte, Cuba e Jamaica.

-*Ceracis punctulatus rubriculus* Lawrence 1967: 124, fig. 13. LT: 10 mi. S Columbia (Missouri, Estados Unidos).

40. *Ceracis quadricornis* Gorham 1886: 359; Lawrence 1967: 127, fig. 17; Lawrence 1971: 501. LT: Tuxtla (México). D: Sul do Texas (Estados Unidos), México à Costa Rica.
41. *Ceracis quadridentatus* Pic 1922: 3; Lawrence 1967: 97. LT: Guadalupe. D: Guadalupe.
42. *Ceracis ruficornis* Pic 1916a: 20; Lawrence 1967: 97; Pecci-Maddalena & Lopes-Andrade 2017: 22. LT: Blumenau (Santa Catarina, Brasil). D: Brasil.
43. *Ceracis sallei* Mellié 1849: 377, pl. 12, fig. 22; Lawrence 1967: 128, fig. 11; Lawrence 1971: 501. LT: New Orleans (Luisiana, Estados Unidos). D: Leste da América do Norte.
44. *Ceracis schaefferi* Dury 1917: 25; Lawrence 1967: 130, fig. 14; Lawrence 1971: 502. LT: Brownsville (Texas, Estados Unidos). D: Sul do Texas (Estados Unidos) e leste do México.
45. *Ceracis shikokuensis* (Miyatake 1954: 56, figs. 3A, 7A, 7B, 7K, 10C, 10J) (*Ennearthron*); Lawrence 1967: 97. LT: Omogokei (Iyo, Shikoku, Japão). D: Conhecido somente da localidade tipo.
46. *Ceracis similis* Horn 1894: 391; Lawrence 1971: 502. LT: Coral de Piedra (Baja California, México). D: Baja California e Nayarit (México) à Costa Rica.
47. *Ceracis singularis* (Dury 1917: 14) (*Xestocis*); Lawrence 1967: 131, fig. 12; Lawrence 1971: 502. LT: Cincinnati (Oklahoma, Estados Unidos). D: Leste da América do Norte e Costa Rica.
48. *Ceracis tabellifer* (Mellié 1849: 373, pl. 12, fig. 20 (*Ennearthron*); Lawrence 1967: 97 (sinonimização); Antunes-Carvalho & Lopes-Andrade 2013: 11 (reestabelecimento). LT: Cabo da Boa Esperança (África do Sul). D: África do Sul, Maurício, Reunião, Seicheles, Aldabra, França, República Democártica do Congo, ìndia, Itáia, Quênia, Madagascar, Mayotte, Moçambique, Ruanda, Sri Lanca, Tânzania, Gâbia, Togo, Vietnã, Zâmbia (introduzido) e Brasil (terra nativa). [veja Antunes-Carvalho & Lopes-Andrade 2013: 12–15]

-*Ennearthron bilamellatum* Pic 1916a: 20; Lawrence 1967: 97 (sinonimizado com *Cer. cucullatus*); Antunes-Carvalho & Lopes-Andrade 2013: 11 (sinonimizado com *Cer. tabellifer*) LT: Madagascar.

49. *Ceracis taurulus* (Jacquelin-Duval 1857: 245, pl. 9, fig. 15) (*Ennearthron*); Lawrence 1967: 98. LT: Cuba. D: Cuba.

-*Ceracis bison* Reitter 1878: 37; Lawrence 1967: 98 (sinonimização). LT: Cuba.

50. *Ceracis thoracicornis* (Ziegler 1845: 270) (*Cis*); Lawrence 1967: 132, fig. 21; Lawrence 1971: 502. LT: “Carolina” (Estados Unidos). D: Leste da América do Norte.

-*Ennearthron mellyi* Mellié 1849: 369; Casey 1898: 88 (sinonimização). LT: América do Norte.

-*Cis pumicatus* Mellié 1849: 333, pl. 11, fig. 10; Lawrence 1967: 132 (sinonimização). TL: New Orleans (Luisiana, Estados Unidos).

-*Ennearthron unicolor* Casey 1884: 37; Casey 1898: 88 (sinonimização). LT: Willet’s Point (Nova Iorque, Estados Unidos).

-*Ennearthron laminifrons* Casey 1898: 89; Lawrence 1967: 132 (sinonimização). LT: Morgan City (Luisiana, Estados Unidos).

-*Ennearthron piceum* Casey 1898: 88; Lawrence 1967: 132 (sinonimização). LT: Columbus (Texas, Estados Unidos).

-*Enneathron oblongus* Blatchley 1910: 900; Lawrence 1967: 132 (sinonimização). LT: Marion Co. (Indiana, Estados Unidos).

-*Cis thoracicus* Dalla Torre 1911: 19. Ortografia subsequente incorreta.

-*Ceracis bifoveatus* Dury 1917: 26; Lawrence 1967: 132 (sinonimização). LT: Cincinnati (Oklahoma, Estados Unidos).

-*Cis thoracicinus* Sherborn 1931: 6493. Ortografia subsequente incorreta.

51. *Ceracis variabilis* Mellié 1849: 380, pl. 12, fig. 25; Lawrence 1967: 98. LT: Cuba. D: Cuba
52. *Ceracis zarathustrai* Pecci-Maddalena *et al.* 2014: 483, figs. 1–9. LT: “Mata da Biologia”, Viçosa (Minas Gerais, Brasil). D: Sudeste do Brasil.

Limites morfológicos atuais

O gênero *Ceracis*, como definido atualmente, pode ser reconhecido pelas seguintes características (baseado em LAWRENCE, 2016): (i) corpo oval a alongado; (ii) antena com 8 ou 9, ocasionalmente 10 segmentos; (iii) prosterno côncavo com processo prosternal laminado (exceção do grupo *furcifer*); (iv) protíbia expandida no ápice e apresentando espinhos ao longo do ângulo apical; (v) metaventrito muito convexo; (vi) discrimen curto ou ausente; e (vi) cobertura consistindo de cerdas muito curtas e finas, normalmente inconspícuas.

Entretanto, há espécies que mal se encaixam nas características diagnósticas do mesmo, constando como *incertae sedis* (*Cer. bifurcus*, *Cer. particularis* e *Cer. laticornis*), ou deixada provisioriamente (*Cer. taurulus*) (LAWRENCE, 1967). Algumas, apesar de possuírem a maior parte das características aceitas para o gênero, apresentam outras que os distinguem do mesmo (*Cer. cornifer*, *Cer. furcifer*, *Cer. hastifer* e *Cer. ruficornis*) (PECCI-MADDALENA-LOPES-ANDRADE, 2017). Lawrence (1967) deixou *Cer. bifurcus* e *Cer. laticornis* como *incertae sedis* por possuírem antenas com dez segmentos, prosterno carenado e protíbia serrada ao longo da margem externa; e *Cer. particularis* por possuir antena com oito segmentos, processo prosternal largo e ápice da protíbia com um dente. Naquele momento, *Cer. taurulus* foi deixado no gênero, mas foi reconhecido que o mesmo aparentava não estar relacionado com nenhuma outra espécie de *Ceracis* (LAWRENCE, 1967).

Pecci-Maddalena & Lopes-Andrade (2017), na revisão do grupo *furcifer*, apontaram algumas características que distinguem as espécies deste grupo das demais espécies de *Ceracis*: i) margem frontoclipeal formando um único chifre mediano, o qual é laminar em vista lateral e apresenta minúsculas cerdas esparsas ao longo dele; ii) tegmem com uma emarginação apical, formando dois lobos paralelos e com ápices arredondados ou tornando-se menos afilados; iii) pênis cilíndrico com ápice arredondado; iv) esternito VIII com uma emarginação mediana, conspícua e profunda na margem posterior; e v) processo prosternal fino, mas não laminado.

Levando-se em conta essas inconsistências morfológicas ainda existentes dentro do conjunto de espécie que compõe o gênero *Ceracis*, uma análise filogenética e revisão taxonômica mais detalhada são necessárias, numa tentativa de resolver tais problemas.

Relações filogenéticas

Até o momento, nenhuma análise filogenética do gênero *Ceracis* foi conduzida. Entretanto o resultado da única análise com base molecular e focada exclusivamente em Ciidae demonstrou que o gênero é polifilético e que o grupo *furcifer* é monofilético (LOPES-ANDRADE & GREBENNIKOV, 2015).

As espécies de *Ceracis* compartilham com alguns gêneros da família a presença de uma términália abdominal feminina reduzida e simplificada (ANTUNES-CARVALHO *et al.*, 2012). Este tipo de terminália pode ser reconhecida pelas seguintes características: i) gonóstilos ausentes ou muito curtos (geralmente <0.015 mm); ii) gonocóxitos divididos ventralmente por não mais do que dois lobos, os quais são normalmente indiscerníveis; iii) báculos dos lóbulos dos gonocóxitos basais geralmente indistintos; e iv) paraproctos curtos, normalmente tão longos quanto ou mais curtos que os gonocóxitos, com báculos dos paraproctos curvados e completamente fundidos ao respectivo báculo do proctíger (LOPES-ANDRADE, 2007b). Além de *Ceracis*, os outros gêneros que apresentam o mesmo tipo de terminália feminina são (baseado em LOPES-ANDRADE, 2007b; LAWRENCE & LOPES-ADNDRADE, 2010; ANTUNES-CARVALHO *et al.*, 2012): *Atlantocis* Israelson, *Cis* (grupo *tricornis*), *Cisarthron* Reitter, *Dichodontocis* Kawanabe, *Grossicis* Antunes-Carvalho *et al.*, *Malacocis* Gorham, *Octotemnus*, *Odontocis* Nakane & Nobuchi, *Paratrichapus* Scott, *Phellinocis* Lopes-Andrade & Lawrence, *Ropalodontus*, *Scolytocis* Blair, *Sulcacis* Dury, *Syncosmetus* Sharp, *Tropicis* Scott, *Wagaicis* Lohse, *Xylographella* Miyatake e *Xylographus*.

Apesar de existirem padrões morfológicos compartilhados entre *Ceracis* e os gêneros citados acima, ainda há uma carência de estudos filogenéticos para uma melhor compreensão da posição de *Ceracis*, suas relações sub- e supragenéricas.

Justificativa

O interesse em se trabalhar com besouros Ciidae remonta da minha dissertação de mestrado, onde trabalhei com a ecologia e taxonomia da fauna sul-africana (SOUZA-GONÇALVES, 2017). Nesta dissertação foram descritas sete novas espécies de *Cis* da África do Sul, além de terem sido avaliados os possíveis efeitos da espécie invasora *Cer. tabellifer* na estrutura da fauna sul-africana nativa. A partir do trabalho com *Cer. tabellifer*, surgiu a ideia de se trabalhar com o gênero no doutorado, uma vez que problemas taxonômicos e filogenéticos (*e. g.* espécies que não se encaixam bem nos limites atuais do gênero, polifilia do gênero apontado por filogenia molecular), já haviam sido identificados por outros autores e ainda nessecitavam de solução (LAWRENCE, 1967; LOPES-ANDRADE & GREBENNIKOV, 2015; PECCI-MADDALENA & LOPES-ANDRADE, 2017).

Como demonstrado nas seções acima, parte das espécies de *Ceracis* está organizada em quatro grupos artificias de espécies (*Cer. cucullatus*, *Cer. furcatus*, *Cer. furcifer* e *Cer. singularis*), baseados exclusivamente em similaridades na anatomia externa. Nenhuma proposição de agrupamento para as demais espécies ou classificação subgenérica foi feita até o presente momento (LAWRENCE, 1967; LOPES-ANDRADE, 2002; LOPES-ANDRADE *et al.*, 2002; PECCI-MADDALENA *et al.*, 2014). Esses grupos de espécies não podem ser considerados *a priori* como clados (LOPES-ANDRADE *et al.*, 2002) e uma análise filogenética se faz necessária para compreender as relações entre as espécies de *Ceracis* e do mesmo com os demais gêneros da família.

As espécies do grupo *Cer. cucullatus* foram examinadas e revisadas nos últimos anos (ANTUNES-CARVALHO & LOPES-ANDRADE, 2011; ANTUNES-CARVALHO & LOPES-ANDRADE, 2013; LAWRENCE, 2016), com exceção de *Cer. bicornis* (Mellié) que aparenta ser um complexo de espécies e ainda não foi revisado (C. LOPES-ANDRADE *pers. obs.*). O grupo *Cer. furcifer* foi revisado recentemente (PECCI-MADDALENA & LOPES-ANDRADE, 2017). O grupo *Cer. singularis* após sua delimitação por Lopes-Andrade *et al.* (2002) não teve nenhuma nova espécie descrita, assim como o grupo *Cer. furcatus* após sua proposição por Lopes-Andrade (2002). Vale ressaltar, que espécies deixadas como *incertae sedis* por Lawrence (1967) mal se enquadram nos limites do gênero. Além disso, *Cer. taurulus* e espécies do grupo *furcifer*, apesar de compartilharem algumas características com as demais espécies do gênero, apresentam outras que os diferenciam do mesmo (LAWRENCE, 1967; PECCI-MADDALENA & LOPES-ANDRADE, 2017). Portanto, realizar um estudo filogenético das espécies de *Ceracis* se faz necessário em uma tentativa de resolver tais problemáticas ainda presentes na classificação do gênero.

Objetivos

O objetivo geral desta tese é de compreender as relações sub- e supragenéricas de *Ceracis*, apresentando quatro capítulos com objetivos específicos. No primeiro capítulo, o objetivo foi descrever sete novos gêneros, sendo a maior parte baseda em espécies descritas como *Ceracis*, e onze novas espécies de Ciidae da região Neotropical, fornecendo dados de distribuição geográfica, fungos hospedeiros, chaves de identificação e discutindo as afinidades morfológicas destes novos gêneros dentro de Ciidae. No segundo capítulo, o objetivo foi descrever uma nova espécie de *Ceracis* da Guatemala e México, fornecendo dados de distribuição geográfica e fungos hospedeiros. No terceiro capítulo, o objetivo foi descrever uma nova espécie de *Ceracis* do Panamá, Colômbia, Costa Rica e Brasil, fornecendo também dados de distribuição geográfica e fungos hospedeiros. No quarto capítulo, o objetivo foi testar pela primeira vez a monofilia de *Ceracis* baseado em análise filogenética morfológica, bem como suas relações sub- e supragenéricas.

RESULTADOS GERAIS

Os resultados são apresentados em quatro capítulos:

Capítulo 1: Seven new genera of Ciidae (Coleoptera: Tenebrionoidea) from the Neotropical region, based mostly on species identified as *Ceracis* Mellié in collections – Neste capítulo, descrevemos sete novos gêneros: *Abebaeocis* Souza-Gonçalves & Lopes-Andrade, *Alcecis* Souza-Gonçalves & Lopes-Andrade, *Anartioscelos* Souza-Gonçalves & Lopes-Andrade, *Atomocis* Souza-Gonçalves & Lopes-Andrade, *Gyraleosomus* Souza-Gonçalves & Lopes-Andrade, *Insolitocis* Souza-Gonçalves & Lopes-Andrade e *Lipedanicis* Souza-Gonçalves & Lopes-Andrade. Descrevemos também onze novas espécies: *Abebaeocis phiaronotum* Souza-Gonçalves & Lopes-Andrade, *Anartioscelos aptenus* Souza-Gonçalves & Lopes-Andrade, *Anartioscelos almirantensis* Souza-Gonçalves & Lopes-Andrade, *Anartioscelos eurinotum* Souza-Gonçalves & Lopes-Andrade, *Anartioscelos involucris* Souza-Gonçalves & Lopes-Andrade, *Atomocis melanus* Souza-Gonçalves & Lopes-Andrade, *Gyraleosomus boliviensis* Souza-Gonçalves & Lopes-Andrade, *Insolitocis panamensis* Souza-Gonçalves & Lopes-Andrade, *Lipedanicis adelphus* Souza-Gonçalves & Lopes-Andrade, *Lipedanicis agastor* Souza-Gonçalves & Lopes-Andrade e *Lipedanicis geminus* Souza-Gonçalves & Lopes-Andrade. Propomos quatro novas combinações, todas baseadas em espécies excluídas de *Ceracis* Mellié: *Abebaeocis taurulus* (Jacquelin-Duval, 1857), *Alcecis particularis* (Pic, 1922), *Anartioscelos bifurcus* (Gorham, 1898) e *Anartioscelos laticornis* (Pic, 1922). Redescrevemos três espécies: *Abebaeocis taurulus* (Jacquelin-Duval, 1857), *Alcecis particularis* (Pic, 1922) e *Anartioscelos laticornis* (Pic, 1922). Designamos lectótipos para cinco espécies: *Ceracis bifurcus* Gorham, 1898, *Ceracis bison* Reitter, 1878, *Ceracis laticornis* Pic, 1922, *Ceracis particularis* Pic, 1922 e *Ennearthron taurulus* Jacquelin-Duval, 1857. Além disso, fornecemos chaves de indentificação para as espécies de *Abebaeocis, Anartioscelos* e *Lipedanicis,* e discutimos as afinidades morfológicas destes novos gêneros dentro de Ciidae.

Capítulo 2: *Ceracis tzotzilicus* sp. nov. (Coleoptera: Tenebrionoidea: Ciidae) from Guatemala and Mexico – Neste capítulo, descrevemos uma nova espécie de *Ceracis* Mellié: *Cer. tzotzilicus* Souza-Gonçalves & Lopes-Andrade, baseado em 200 espécimes coletados em San Cristóbal de las Casas (México) e Yepocapa (Guatemala), em altitudes acima de 2000 m. *Ceracis tzotzilicus* assemelha-se aos membros do grupo *Ceracis cucullatus* em sua fina e esparsa pontuação pronotal, mas os machos podem ser distinguidos pela ausência de uma lâmina longa na parte anterior do pronoto e fêmeas pelo ovipositor sem gonóstilos.

Capítulo 3: A peculiar new species of *Ceracis* Mellié (Coleoptera: Ciidae) from the Neotropical region – Neste capítulo, descrevemos uma nova espécie de *Ceracis* Mellié: *Cer. ascetonotum* Souza-Gonçalves & Lopes-Andrade, basedo em 54 espécimes coletados em Forth Sherman, Barro Colorado e Campana (Panamá); Vereda La Reforma e Vereda Clarete (Colômbia); Monteverde (Costa Rica); e Canarana (Centro-Oeste, Brasil). *Ceracis ascetonotum* Souza-Gonçalves & Lopes-Andrade difere das outras espécies no gênero na antena com 10 segmentos (exceto pelas espécies do grupo *Ceracis singularis*) e na morfologia muito peculiar do pronoto dos machos.

Capítulo 4: A morphology-based phylogeny of *Ceracis* Mellié (Coleoptera: Ciidae) – Neste capítulo, testamos pela primeira vez a monofilia de *Ceracis* Mellié baseado em análise filogenética morfológica, bem como suas relações sub- e supragenéricas. Um total de 22 gêneros e 57 espécies de Ciidae foram selecionados, sendo incluídos membros de todas as tribos atuais. Nossos dados foram compostos por 81 caracteres registrados da morfologia de adultos de 57 táxons terminais. Análises de parcimônia foram conduzidas sob pesagem igualitária e implícita e nossos resultados corroboraram resultados prévios baseados em dados moleculares.

CAPÍTULO 1: Seven new genera of Ciidae (Coleoptera: Tenebrionoidea) from the Neotropical region, based mostly on species identified as *Ceracis* Mellié in collections

(Anais da Academia Brasileira de Ciências. The manuscript presented here, in the form of a chapter of this thesis, is not considered valid according to the International Code of Zoological Nomenclature – ICZN)

Seven new genera of Ciidae (Coleoptera: Tenebrionoidea) from the Neotropical region, based mostly on species identified as *Ceracis* Mellié in collections

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Abstract

Ciidae is a cosmopolitan family comprising 756 species in 51 genera. The Neotropical ciid fauna encompasses 158 species in 14 genera. In this work, we describe other seven new genera, as follows: *Abebaeocis* **gen. nov.**, *Alcecis* **gen. nov.**, *Anartioscelos* **gen. nov.**, *Atomocis* **gen. nov.**, *Gyraleosomus* **gen. nov.**, *Insolitocis* **gen. nov.** and *Lipedanicis* **gen. nov.**. We also described eleven new species: *Abebaeocis phiaronotum* **sp. nov.**, *Anartioscelos aptenus* **sp. nov.**, *Anartioscelos almirantensis* **sp. nov.**, *Anartioscelos eurinotum* **sp. nov.**, *Anartioscelos involucris* **sp. nov.**, *Atomocis melanus* **sp. nov.**, *Gyraleosomus boliviensis* **sp. nov.**, *Insolitocis panamensis* **sp. nov.**, *Lipedanicis adelphus* **sp. nov.**, *Lipedanicis agastor* **sp. nov.** and *Lipedanicis geminus* **sp. nov.**. The following new combinations are proposed, all based on species excluded from *Ceracis* Mellié, 1849: *Abebaeocis taurulus* (Jacquelin-Duval, 1857) **comb. nov.**, *Alcecis particularis* (Pic, 1922) **comb. nov.**, *Anartioscelos bifurcus* (Gorham, 1898) **comb. nov.** and *Anartioscelos laticornis* (Pic, 1922) **comb. nov.**. The following species are redescribed: *Abebaeocis taurulus* (Jacquelin-Duval, 1857), *Alcecis particularis* (Pic, 1922) and *Anartioscelos laticornis* (Pic, 1922). Lectotypes are designated for *Ceracis bifurcus* Gorham, 1898, *Ceracis bison* Reitter, 1878, *Ceracis laticornis* Pic, 1922, *Ceracis particularis* Pic, 1922 and *Ennearthron taurulus* Jacquelin-Duval, 1857. We provide identification keys to species of *Abebaeocis* **gen. nov.**, *Anartioscelos* **gen. nov.** and *Lipedanicis* **gen. nov.**, and discuss the morphological affinities of these new genera within Ciidae.

Keywords. *Ceracis*, idetifications keys, minute tree-fungus beetles, new combinations, new species, taxonomy

Introduction

Ciidae is a cosmopolitan family comprising 756 species in 51 genera (Lawrence 2016, Souza-Gonçalves *et al.* 2018a, Lawrence 2019). It is divided into two subfamilies: Sphindociinae, which includes only *Sphindocis denticollis* Fall, 1917 from the northern California coasts; and Ciinae, with all other ciid species (Lawrence 1974a, Lawrence 2016). Ciinae is currently divided into three tribes: Ciini Leach, 1819, Orophiini Thomson, 1863 and Xylographellini Kawanabe & Miyatake, 1996. However, only the latter seems to be monophyletic (Lopes-Andrade & Grebennikov 2015). The suprageneric classification of the family has been controversial. Besides delimitation of Sphindociinae (Lawrence 1974a) and Xylographellini (Kawanabe & Miyatake 1996, Lopes-Andrade 2008), the other subfamily and tribes proposed until now were not defined by any exclusive combination of characters. Some authors have kept using this classification, either justifying the suprageneric taxa by a combination of characters (*e.g.* Thayer & Lawrence 2002) or assuming that they might not correspond to monophyletic clades (Lopes-Andrade 2008). Other authors have not followed the abovementioned suprageneric classification for Ciidae (*e.g.* Lawrence *et al.* 1999).

The Neotropical ciid fauna comprises 160 described species in 14 genera (number of species between parentheses): *Ceracis* Mellié, 1849 (36), *Cis* Latreille, 1796 (69), *Ennearthron* Mellié, 1847 (1), *Falsocis* Pic, 1916 (6), *Grossicis* Antunes-Carvalho *et al.*, 2012 (2), *Hadreule* Thomson, 1859 (3), *Malacocis* Gorham, 1886 (1), *Neoapterocis* Lopes-Andrade, 2007 (1), *Orthocis* Casey, 1898 (9), *Phellinocis* Lopes-Andrade & Lawrence, 2005 (3), *Porculus* Lawrence, 1987 (6), *Scolytocis* Blair, 1928 (12), *Strigocis* Dury, 1917 (4) and *Xylographus* Mellié, 1847 (8). Taxonomic and faunistics studies on Neotropical (*sensu* Morrone 2015) Ciidae has grown up in the last two decades, with emphasis on the Brazilian and Mexican faunas (*e.g.* Navarrete-Heredia & Burgios-Solorio 2000, Lopes-Andrade 2002, 2008b, Antunes-Carvalho & Lopes-Andrade 2013, Oliveira *et al.* 2013, Pecci-Maddalena & Lopes-Andrade 2017, Souza-Gonçalves *et al.* 2020).

Ceracis is an assemblage of morphologically heterogenous species, and there is evidence it does not comprise a natural group. Available molecular data, including representatives of few lineages within *Ceracis*, suggest it is polyphyletic (Lopes-Andrade & Grebennikov 2015). Furthermore, there are described and undescribed species examined by us that are considered to be *Ceracis*, but do not properly fit in the diagnosis of the genus. *Ceracis* is currently defined by the combination of the following features (based on Lawrence 1967, 2016): (i) body oval to elongate; (ii) antennae 8- or 9- segmented, occasionally 10-segmented; (iii) prosternum concave with prosternal process laminate (except for species in the *Ceracis furcifer* species-group); (iv) protibiae with outer apical angle expanded subapically to form a rounded lobe with a row of socketed spines; (v) metaventrite very convex; (vi) discrimen short or absent; and (vii) vestiture of minute setae, usually inconspicuous.

In the revision of the North American *Ceracis* (Lawrence 1967), it was redefined and several species were removed. Among these, *Ceracis bifurcus* Gorham, 1898, *Cer. laticornis* Pic, 1922 and *Cer. particularis* Pic, 1922 were left as *incertae sedis*. *Ennearthron taurulus* Jacquelin-Duval, 1857 was left in *Ceracis* by that time, but it was recognized that "(...) it does not appear to be closely related to any other *Ceracis*." (Lawrence 1967). Recently, the genus was redescribed and reported for the first time from Australia (Lawrence 2016). As it stands today, *Ceracis* includes 54 species, of which 19 are organized in four species-groups (*cucullatus*, *furcatus*, *furcifer* and *similis*) (Antunes-Carvalho & Lopes-Andrade 2011, Pecci-Maddalena *et al.* 2014, Lawrence 2016, Pecci-Maddalena & Lopes-Andrade 2017). The genus is more diverse in the Neotropical and Nearctic regions (Pecci-Maddalena *et al.* 2014), with few species in the Oriental and Palearctic regions.

We've focused on the question "what is *Ceracis*?" and the likely answer to this would exclude four species currently in the genus (*Cer. bifurcus* Gorham, 1898, *Cer. laticornis* Pic, 1922, *Cer. particularis* Pic, 1922 and *Ennearthron taurulus* Jacquelin-Duval, 1857), which barely fit its generic limits and are here transferred to three new genera. The eleven-new species described here bear part of the diagnostic features that barely could place them in *Ceracis*, but in no other ciid genus. However, instead of describing more species in *Ceracis*, enhancing its morphological heterogeneity, we decided to propose other four new genera for these species. We also designate lectotypes for *Cer. bifurcus*, *Cer. bison* Reitter, 1878, *Cer. laticornis*, *Cer. particularis* and *Enn. taurulus*, for nomenclatural stability. Additionally, we provide identification keys to species of *Anartioscelos* **gen. nov.** and *Lipedanicis* **gen. nov.**, and discuss the morphological affinities of the new genera within Ciidae.

Material and methods

Museum acronyms are as follows:

ANIC Australian National Insect Collections, CSIRO Entomology, Canberra, Australian Capital Territory, Australia (A. Ślipiński)
CAMB Coleção Ayr de Moura Bello, Rio de Janeiro, Rio de Janeiro, Brazil (A. M. Bello)
CELC Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera da Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil (C. Lopes-Andrade)
CERPE Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil (P. C. Grossi)
CEMT Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil (F. Z. Vaz-de-Mello)
CMN Canadian Museum of Nature, Ottawa, Ontario, Canada (R. Anderson)
CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada (P. Bouchard)
FMNH Field Museum of Natural History, Chicago, Illinois, U.S.A. (A. F. Newton and M. K. Thayer)
IRSNB Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (Y. Samyn)
MNHN Muséum National d’Histoire Naturelle, Paris, Île-de-France, France (T. Deuve)
NHM Natural History Museum, London, United Kingdom (M. V. L. Barclay)
SNSD Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany (K.-D. Klass)

Terms for external morphology and male terminalia of ciids follow Lawrence *et al.* (2011), Lawrence (2016) and Lopes-Andrade & Lawrence (2005, 2011), but see also Oliveira *et al.* (2013) for an explanation on the use of "tegmen" and on the description of anterocephalic horns. The following abbreviations are used for measurements (in mm) and ratios of body and exposed sclerites: BW (width of anterior edge of scutellar shield), CL (length of antennal club, which corresponds to the apical three segments in species of the genera described here), EL (elytral length along the midline), EW (greatest width of elytra), FL (length of antennal funicle, which includes the segments between the pedicel and the first segment of the club), GD (greatest depth of body measured in lateral view), GW (greatest diameter of eye), PL (pronotal length along midline), PW (greatest pronotal width), SL (length of scutellar shield), TL (total length counted as EL+PL, *i.e.* excluding head). The GD/EW and TL/EW ratios indicate the degree of body convexity and elongation, respectively. Sum and ratios of measurements of antennae are based on gross values, while measurements of each segment are based on approximate values.

Transcription of labels, dissection, photography and measurement of specimens follow the methods provided by Araujo & Lopes-Andrade (2016). Exemplar specimens of the new species from all localities were measured. The number of measured specimens depended on the number of available specimens and the observed variation in size. Differences are given in "Variation", together with standard measurements (mean and standard deviation) and ratios. Data on host fungi extracted from labels are summarized in the corresponding sections and names were updated consulting the database Index Fungorum (2019). The corresponding number of records in each fungus species were placed on the same section, indicating breeding records. The recognition of breeding records follows the criteria provided in Orledge & Reynolds (2005). The distribution maps (Figs 43–46) was created in the freeware QGIS 2.14.2-Essen.

For nomenclatural stability, lectotypes are designated for *Ceracis bifurcus*, *Ceracis bison*, *Ceracis laticornis*, *Ceracis particularis* and *Ennearthron taurulus*. The lectotypes of *Cer. bifurcus*, *Cer. bison* and *Enn. taurulus* were designated based on annotations made by PhD. John F. Lawrence, a ciid specialist who directly examined type series in 1965, and those of *Cer. laticornis* and *Cer. particularis* based on type specimens examined by us.

The abdominal terminalia of the following specimens were extracted and in some cases the specimen was completely dissected (indicated between parentheses): one male and one female paratypes of *Abe. phiaronotum* **sp. nov.** from Mount Diablo (Middlesex County, Saint Ann Parish, Jamaica); one male (completely dissected and stored in glycerin) of *Abe. taurulus* **comb. nov.** from Republic of Cuba (Greater Antilles), and two males and one female from Mexico; one male (completely dissected and stored in glycerin) and one female (completely dissected and stored in glycerin) of *Alc. particularis* **comb. nov.** from Barro Colorado Island (Canal Zone, Panama); two male paratypes of *Ana. almirantensis* **sp. nov.** from Almirante (Changuinola District, Bocas del Toro Province, Panama); one male (completely dissected and stored in glycerin) and one female (completely dissected and stored in glycerin) paratypes of *Ana. aptenus* **sp. nov.** from San Juan Bautista Valle Nacional (Oaxaca, Mexico), and one female paratype from Purulhá (Baja Verapaz Department, Guatemala); male holotype of *Ana. eurinotum* **sp. nov.** from Barro Colorado Island (Canal Zone, Panama); male holotype of *Ana. involucris* **sp. nov.** from Cerro Punta (Tierras Altas District, Chiriquí Province, Panama); two males (one completely dissected and stored in glycerin) and one female (completely dissected and stored in glycerin) paratypes of *At. melanus* **sp. nov.** from Barro Colorado Island (Canal Zone, Panama); one male (completely dissected and stored in glycerin) and one female (completely dissected and stored in glycerin) paratypes of *G. boliviensis* **sp. nov.** from Cochabamba (Cercado Province, Cochabamba Department, Bolivia); two females (one completely dissected and stored in glycerin) paratypes of *I. panamensis* **sp. nov.** from Barro Colorado Island (Canal Zone, Panama); two males and one female paratypes of *Lip. adelphus* **sp. nov.** from Parque Ecológico Quedas do Rio Bonito (Lavras, Minas Gerais, Brazil), one male paratype from Campus UFV (Viçosa, Minas Gerais, Brazil); two males and one female paratypes of *Lip. agastor* **sp. nov.** from Floresta Nacional de São Francisco de Paula (São Francisco de Paula, Rio Grande do Sul, Brazil), one male paratype from Reserva Particular do Patrimônio Nacional Bacchus (Nova Friburgo, Rio de Janeiro, Brazil), one male paratype from Estação Biológica Santa Lúcia (Santa Teresa, Espírito Santo, Brazil), one male paratype from Parque Nacional do Caparaó (Alto Caparaó, Minas

Gerais, Brazil); one male and one female paratypes from Parque Nacional do Itatiaia (Itatiaia, Rio de Janeiro, Brazil), and one male and one female paratypes from Reserva Particular do Patrimônio Nacional Vale do Moinho Brum (Santa Tereza, Rio Grande do Sul, Brazil); one male and one female paratypes of *Lip. geminus* **sp. nov.** from Reserva Biológica de Tapirapé (Marabá, Pará, Brazil), and two males (completely dissected and stored in glycerin) and two females (completely dissected and stored in glycerin) paratypes from Araguaína (Tocantins, Brazil). The female terminalia shown in Figs 3(D–E), 17(D–E), 28(D–E), 31(D–E), 34D, 37D, 42(A–B) are of paratypes from the type localities. The ovipositor shown in Fig. 25D are of a paratype from a locality rather than the type locality, because only one female is known from the type locality and we decided not to dissect it. The female terminalia shown in Figs 6(D–E), 11D are of additional material. The sclerites of aedeagi shown in Figs 2(E–G), 13(E–H), 16(E–H), 27(E–G), 33(E–H), 36(E–I), 40(E–H) are of paratypes from the type locality. The sclerites of aedeagi shown in Figs 19(A–D), 21(A–C) are of holotypes. The sclerites of aedeagi shown in Fig. 24(E–H) are of paratypes from localities rather than the respective type localities, because the only known male from each type locality is the holotype and we decided not to dissect it. The sclerites of aedeagi shown in Figs 5(E–G), 10(E–H) are of additional material identified by us as conspecific to the examined type material. In the latter case, aedeagi of type material were not extracted, because comparisons of other external features were sufficient to recognize them as conspecifics. We decided not to dissect the lectotype of *Cer. laticornis* due to its light-colored body, which indicates it may be a teneral and consequently result in a bad slide preparation. Information on the gula in the descriptions provided here is restricted to the ratio of gula width to head width. Comparisons between new and previously described genera are restricted to those which share features that can led to wrong identifications due to resemblance of general body morphology. As the suprageneric classification for Ciidae seems to not reveal monophyletic clades (except for Xylographellini), we avoid to use these comparisons throughout the text.

Taxonomy

***Abebaeocis* gen. nov.**

Fig. 1(A–E); Fig. 2(A–G); Fig. 3(A–E); Fig. 4(A–G); Fig. 5(A–G); Fig. 6(A–E); Fig. 7(A–F); Fig. 43

Type species: *Ennearhton taurulus* Jacquelin-Duval, 1857.

Etymology: The genus name derives from the Greek adjective "abebaios", which means "uncertain", "wavering", and "*Cis*", which is derived from the Greek "kis", masculine noun which means "worm that bores into wood", the last in the nominative singular and the former in the genitive singular. *Abebaeocis* is a reference to our initial hesitation concerning placement of this single species in a separate genus or within the *Lipedanicis* **gen. nov.**.

Diagnosis. This genus is distinguished by the elongate body, dual pronotal and elytral punctation, single dorsal vestiture of minute setae, each arising from one megapuncture, antennae 9-segmented, prosternum tumid, not carinate (*Abe. taurulus*) or slightly carinate, protibiae slightly enlarged at apex and outer apical angle not produced, meso- and metatibiae not enlarged at apex. Males have two anterocephalic horns or plates. It resembles *Lipedanicis* **gen. nov.**, which differs in bearing elytral vestiture arising from micropunctures, outer apical angle of protibiae produced into a tooth and female terminalia with gonocoxites not conspicuously divided in lobes ventrally, basal baculi of gonocoxites very oblique, slightly shorter or as long as outer margin of gonocoxites. *Abebaeocis* **gen. nov.** somewhat resembles species in the *Cis taurus* species-group, especially the anterocephalic projections of males, but the latter differ in the 10-segmented antennae, strongly tumid prosternum and outer apical angle of protibiae produced in a stout tooth.

Description. Body elongate, subparallel-sided (Figs 1(A–C), 3(A–C) or parallel-sided (Figs 4(A–C), 6(A–C), 7(A–C)), convex; dorsal vestiture single, consisting of minute setae, each arising from one megapuncture; dorsal micropunctures apparently glabrous. **Head** anteriormost portion visible from above; anterocephalic edge in males produced and elevated forming two horns (Figs 1D, 4D, 7D); in females, truncate (Figs 3C, 6C). **Antennae** (Figs 2A, 5A) 9-segmented; antennal club long (more than 1.7x as long as funicle), 3-segmented; apical segment subrounded, with sensillifers placed laterally in each segment; third segment at least 1.5x longer than fourth. **Labrum** longer than wide, subtruncate. **Mandibular molae** well-developed. **Apical maxillary palpomere** (Fig. 4F) pyriform. **Prementum** (Fig. 4F) short, broadly rounded at apex; ligula apparently absent. **Labial palps** (Fig. 4F) 3-segmented; apical palpomere as long as and narrower than inflated preapical palpomere. **Gular sutures** bowed. **Pronotum** (Figs 1E, 4E, 7E) lateral edges narrow, not visible for their entire lengths from above; punctation, dual; each megapuncture with one seta and micropunctures apparently glabrous; anterior edge rounded in both sexes. **Prosternum** in front of coxae as long as or slightly longer than prosternal process; tumid (Figs 1D) or tumid, slightly carinate (Figs 4D, 7D); prosternal process moderately broad, expanding to apex or subparallel-sided. **Procoxae** transverse, not projecting below plane of prosternal process (Fig. 1C, 3C, 4C, 6C, 7C). **Meso- and metacoxae** transverse. **Scutellar shield** (Figs 1E, 4E, 7E) well-developed. **Elytra** (Figs 1E, 4E, 7E) elongate, more than 1.40x as long as pronotum; punctation, dual. **Metathoracic wings** well-developed. **Mesocoxal cavities** (Fig. 4G) narrowly separated, completely closed. **Metaventrite** (Fig. 4G) slightly convex, longer than first abdominal ventrite; posterior margin, notched; discrimen, absent. **Protibiae** (Figs 2B, 5B) slightly enlarged at apex. **Meso- and metatibiae** (Figs 2(C–D), 5(C–D)) not enlarged. **First abdominal ventrite** longer than second and third ventrites combined, with sex patch in males. **Male terminalia** (Figs 2(E–G), 5(E–G)): tegmen subquadrate, outer apical edge with tiny excavations (Figs 2F, 5F, small black arrows), apex with broad V-shaped, shallow emargination, outer edges of basal portion membranous; penis subcylindrical, basal portion with truncate sclerotization (Figs 2G, 5G, red arrow). **Female terminalia** (Figs 3E, 6E): short, with paraprocts about as long as gonocoxites; gonocoxites membranous, with two conspicuous ventral lobesbasal baculi of gonocoxites oblique, much shorter than outer margins of gonocoxites; gonostyli short or long.

Included species: *Abebaeocis phiaronotum* **sp. nov.**, *Abe. taurulus* (Jacquelin-Duval, 1857) (*Ceracis*) **comb. nov.**.

Distribution: North America and Greater Antilles. Known from Republic of Cuba, Mexico, USA and Jamaica.

Key to species of *Abebaeocis*

1 TL/EW less than 1.85, sparse elytral punctures (megapunctures separated from each other by 2–3 megapuncture-widths; Fig. 1E), males with sex patch posterad of center (Fig. 1C) and ovipositor with long gonostyli (more than 3.3x as long as wide; Fig. 3E)..***Abe. phiaronotum* sp. nov.**

1’ TL/EW at least 1.95, close elytral punctation (megapunctures separated from each other by 1–2 megapuncture-widths; Figs 4E, 7E), males wit sex patch at center (Figs 4C, 7C) and ovipositor with short gonostyli (less than 1.5x as long as wide; Fig. 6E)...***Abe. taurulus* (Jacquelin-Duval)**

***Abebaeocis phiaronotum* sp. nov.**

Fig. 1(A–E); Fig. 2(A–G); Fig. 3(A–E); Fig. 43

Type locality. “Mount Diablo”, coordinates 18º13’N 77º5’W (Middlesex County, Saint Ann Parish, Jamaica).

Etymology. The species name derives from the Greek adjective “phiaros”, which means “shinning”, “bright”, and the anatomical term “notum”, both in the genitive singular. The name is a reference to the shiny dorsal surface of this species.

Diagnosis. *Abebaeocis phiaronotum* **sp. nov.** differs from *Abe. taurulus* **comb. nov.** in bearing less elongate body (TL/EW less than 1.85), sparse elytral punctation (megapunctures separated from each other by two to three megapuncture-widths), males bearing sex patch posterad of center and ovipositor with long gonostyli (more than 3.3x as long as wide).

Description, male holotype (Fig. 1(A–E)). Adult apparently not fully pigmented, lacking left antenna, left maxillary palp, both metafemurs, both metatibiae and four tarsi. Measurements in mm: TL 1.01, PL 0.35, PW 0.52, EL 0.66, EW 0.57, GD 0.47. Ratios: PL/PW 0.67, EL/EW 1.15, EL/PL 1.89, GD/EW 0.81, TL/EW 1.76. **Body** subparallel-sided, dorsum reddish dark brown; venter reddish pale brown; antenna yellowish brown; antennal club dark brown; palpi and tarsi yellowish brown; dorsal vestitureconsisting of minute suberect setae easily visible in high magnifications

(>80x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>80x). **Head** (Fig. 1D) dorsal punctation single; punctures coarse, deep, separated from each other by 2 puncture-widths, each with one minute decumbent seta (<0.01 mm); interspaces, microreticulate; anterocephalic edge produced, elevated forming two short conical, parallel horns (length 0.07 mm; basal width 0.11 mm; basal separation 0.01 mm), apices subacute. **Antenna** (Fig. 2A, left antenna in paratype) length of segments as follows (in mm, right antenna measured): 0.06, 0.04, 0.03, 0.02, 0.02, 0.02, 0.04, 0.04, 0.06 (FL 0.08 mm, CL 0.15 mm, CL/FL 1.80). **Eyes** coarsely facetted, with about 50 ommatidia; GW 0.11 mm. **Gula** 0.28x as wide as head. **Pronotum** (Fig. 1E) megapunctures coarse, shallow, about 2x as large as micropunctures, separated from each other by 1 megapuncture-width or less; interspaces, microreticulate; vestiture single, consisting of minute suberect yellowish setae (<0.01 mm); anterior edge rounded; lateral edges not crenulate, not explanate and not visible when seen from above; anterior corners rounded and posterior corners broadly rounded. **Scutellar shield** triangular, with few punctures, apparently glabrous; BW 0.07 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, shallow, about 2x as large as micropunctures, separated from each other by 2–3 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (<0.01 mm). **Metathoracic wings** apparently functional. **Hypomera** punctation coarse, shallow; almost glabrous; interspaces, microreticulate. **Prosternum** (Fig. 1D) in front of coxae tumid and slightly carinate; interspaces, microreticulate. **Prosternal process** (Fig. 1D) narrow at base and gradually expanding to apex, as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 2B, left protibia in paratype) maximum width about one-fourth its length; apical edge with spines; outer apical angle rounded; outer edge straight and smooth. **Meso- and metatibiae** (Fig. 2(C–D), left meso- and metatibia in paratype, respectively) with spines in apical edge; outer edge straight and smooth. **Metaventrite** punctation coarse, shallow; interspaces, microreticulate; posterior margin notch 0.06x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.12, 0.06, 0.05, 0.05, 0.06; first abdominal ventrite with margined, circular, setose sex patch posterad of center, transverse diameter of 0.05 mm. **Male terminalia in paratype** (Fig. 2(E–F)): **sternite VIII** (Fig. 2E) apical margin emarginate, with short setae at middle and long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 2F) 1.7x as long as wide, widest near apex, subparallel-sided and converging to base at basal third; apex shallowly emarginate at middle; outer apical edge with angulations (Fig. 2F, big black arrows) and excavations at base of each angulation (Fig. 2F, small black arrows) at laterals; medial portion with acute angulations (Fig. 2F, red arrows); basal portion subtriangular. **Penis** (Fig. 2G) as long as tegmen, 4.3x as long as wide; subparallel-sided, converging to base; apex rounded, membranous.

Females (Fig. 3A–E). Anterior edge of head truncate and anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns and abdominal sex patch. **Female terminalia in paratype** (Fig. 3(D–E)): spiculum ventrale (Fig. 3D) 1.02x as long as ovipositor (Fig. 3E); ovipositor 1.35x as long as wide; paraprocts (Fig. 3E), 0.83x as long as gonocoxites; gonocoxites (Fig. 3E) 0.71 as long as their combined widths, each with broadly rounded apex; each gonostylus (Fig. 3E) 0.21x as long as respective gonocoxite, 3.57x as long as wide.

Variation. Males, measurements in mm (n= 2, including the holotype): TL 1.01–1.03 (1.02 ± 0.01), PL 0.35–0.40 (0.38 ± 0.04), PW 0.52–0.53 (0.52 ± 0.00), EL 0.63–0.66 (0.64 ± 0.03), EW 0.57–0.58 (0.57 ± 0.00), GD 0.45–0.47 (0.46 ± 0.01), PL/PW 0.67–0.76 (0.72 ± 0.06), EL/EW 1.09–1.15 (1.12 ± 0.05), EL/PL 1.56–1.89 (1.73 ± 0.23), GD/EW 0.78–0.81 (0.80 ± 0.02), TL/EW 1.76–1.78 (1.77 ± 0.02). Female, measurements in mm: TL 1.00, PL 0.38, PW 0.48, EL 0.63, EW 0.55, GD 0.43, PL/PW 0.79, EL/EW 1.14, EL/PL 1.67, GD/EW 0.77, TL/EW 1.82.

Type material. Holotype ♂ (CMN) “Mt. Diablo, Jamaica, St. Ann Par., vi-3-68 \ J.F. Lawrence, Lot 2551 \ Peck & Fiske Collectors \ ex *Polyporus maximus* \ *Abebaeocis phiaronotum* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”. **Paratypes:** 1 ♂ (CELC, dissected) and 2 ♀♀ (1 CELC, one dissected; 1 CMN) same data as the holotype. All paratypes additionally labeled “*Abebaeocis phiaronotum* Souza-Gonçalves, Lopes-Andrade & Lawrence PARATYPUS [yellow paper]”.

Host fungus. *Polyporus maximus* (Brot.) Fr. (Polyporaceae), one record.

Distribution. Greater Antilles. Known from Saint Ann Parish (Jamaica) (Fig. 43).

Abebaeocis taurulus (Jacquelin-Duval, 1857) comb. nov.

Fig. 4(A–G); Fig. 5(A–G); Fig. 6(A–E); Fig. 7(A–F); Fig. 43

Ennearhton taurulus Jacquelin-Duval 1857a: 245, pl. 9, fig. 15; Jacquelin-Duval 1857b: 102, pl. 9, fig. 13; Lawrence 1967: 98 (placed in *Ceracis* Mellié, 1849). Type locality: Greater Antilles: Republic of Cuba (no specific locality).

Ceracis bison Reitter 1878: 37; Lawrence 1967: 98 (synonym). Type locality: Greater Antilles: Republic of Cuba (no specific locality).

Diagnosis. *Abebaeocis taurulus* **comb. nov.** differs from *Abe. phiaronotum* **sp. nov.** in bearing more elongate body (TL/EW at least 1.95), close elytral punctation (megapunctures separated from each other by one to two megapuncture-widths), males bearing sex patch at center and ovipositor with short gonostyli (less than 1.5x as long as wide).

Redescription based on male specimen from Republic of Cuba (Fig. 4A–E). Adult not fully pigmented, lacking both antennae, left metafemur, left metatibia and five tarsi. Measurements in mm: TL 0.93, PL 0.34, PW 0.42, EL 0.58, EW 0.46, GD 0.39. Ratios: PL/PW 0.82, EL/EW 1.26, EL/PL 1.71, GD/EW 0.84, TL/EW 2.00. **Body** parallel-sided, dorsum and venter yellowish brown; palpi and tarsus yellowish brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnifications (>80x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>50x). **Head** (Fig. 4D) dorsal punctation single; punctures coarse, shallow, separated from each other by 2 puncture-widths or less, each with one minute decumbent seta (<0.01 mm) in each puncture; interspaces, microreticulate; anterocephalic edge produced, elevated forming two long, parallel cylindrical horns (length 0.18 mm; basal width 0.06 mm; basal separation 0.05 mm), apices rounded. **Antennae** (Fig. 5A, left antenna in other specimen from Mexico) length of segments as follows (in mm): 0.06, 0.04, 0.03, 0.01, 0.02, 0.02, 0.04, 0.04, 0.06 (FL 0.07 mm, CL 0.13 mm, CL/FL 1.76). **Eyes** coarsely facetted, with about 50 ommatidia; GW 0.10 mm. **Gula** 0.33x as wide as head. **Pronotum** (Fig. 4E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1 puncture-width or less; interspaces, microreticulate; vestiture single, consisting of minute suberect yellowish seta (~0.01 mm); lateral edges not crenulate, not explanate and not visible when seen from above; anterior corners rounded and posterior corners broadly rounded. **Scutellar shield** triangular, with few punctures and apparently glabrous; BW 0.06 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm). **Metathoracic wings** apparently functional. **Hypomera** punctation fine, shallow; almost glabrous; interspaces, microreticulate. **Prosternum** (Fig. 4D) in front of coxae tumid; interspaces, microreticulate. **Prosternal process** (Fig. 4D) subparallel-sided, 0.9x as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 5B, left protibia in other specimen from Mexico) maximum width about one-fourth its length; apical edge with spines; outer apical angle rounded; outer edge straight, smooth. **Meso- and metatibiae** (Fig. 5(C–D), left meso- and metatibia in other specimen from Mexico) apical edge straight, smooth, with spines. **Metaventrite** (Fig. 4G, in other specimen from Republic of Cuba) punctation coarse, shallow; interspaces, microreticulate; posterior margin notch 0.07x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.10, 0.04, 0.04, 0.04, 0.05; first abdominal ventrite with margined, circular sex patch at center, transverse diameter of 0.06 mm. **Male terminalia in other specimen from Mexico** (Fig. 5(E–F)): **sternite VIII** (Fig. 5E) apical margin emarginate, with short setae at middle and long setae at subacute corners; basal portion membranous. **Tegmen** (Fig. 5F, slightly damaged during dissection) 2.0x as long as wide, widest near apex; subparallel-sided but more or less sinuous; apex shallowly emarginate at middle; outer apical edge with angulations (Fig. 5F, big black arrows) and excavations at base of each angulation (Fig. 5F, small black arrows) at laterals; basal portion truncate. **Penis** (Fig. 5G) as long as tegmen, 3.8x as long as wide; subparallel-sided, converging to base; apex with acute membranous projections (Fig. 5G, black arrows).

Females (Fig. 6(A–E)). Anterior edge of head truncate and anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns and abdominal sex patch. **Female terminalia in specimen from Republic of Cuba** (Fig. 6(D–E):

spiculum ventrale (Fig. 6D) 0.91x as long as ovipositor (Fig. 6E); ovipositor 1.54x as long as wide; paraprocts (Fig. 6E), 0.58x as long as gonocoxites (Fig. 6E); gonocoxites (Fig. 6E) 0.96x as long as their combined widths, each with broadly rounded apex; each gonostylus (Fig. 6E) 0.08x as long as respective gonocoxite, 1.43x as long as wide.

Variation. Males, measurements in mm (n= 3): TL 0.93 (0.93 ± 0.00), PL 0.34–0.38 (0.36 ± 0.02), PW 0.42–0.43 (0.42 ± 0.00), EL 0.55–0.58 (0.57 ± 0.02), EW 0.46–0.48 (0.47 ± 0.01), GD 0.35–0.39 (0.37 ± 0.02), PL/PW 0.82–0.88 (0.84 ± 0.04), EL/EW 1.16–1.26 (1.21 ± 0.05), EL/PL 1.47–1.71 (1.61 ± 0.12), GD/EW 0.74–0.84 (0.79 ± 0.05), TL/EW 1.95–2.00 (1.96 ± 0;03). Females, measurements in mm (n= 2): TL 0.90 (0.90 ± 0.00), PL 0.33–0.35 (0.34 ± 0.02), PW 0.40–0.43 (0.41 ± 0.02), EL 0.55–0.58 (0.56 ± 0.02), EW 0.45–0.48 (0.46 ± 0.02), GD 0.38 (0.38 ± 0.00), PL/PW 0.81–0.82 (0.82 ± 0.01), EL/EW 1.16–1.28 (1.22 ± 0.08), EL/PL 1.57–1.77 (1.67 ± 0.14), GD/EW 0.79–0.83 (0.81 ± 0.03), TL/EW 1.89–2.00 (1.95 ± 0.07).

Type material. Lectotype ♂, here designated (IRSNB) “Coll. Guer.-Men. [printed] \ dans le *Polyporus membranaceus*. Cuba [handwritten] \ *Ennearthron taurulus* J. du Val [handwritten] \ Type. Guerin-Men. [green paper; printed] \ Type [red paper; printed] \ LECTOTYPE *Ennearthron taurulus* Jacquelin-Duval [red paper; handwritten]”; **lectotype ♂, here designated** (MNHN, Fig. 7(A–F)) “Cuba, Taissia (or Taissia?) [handwritten] \ *Ceracis bison* m. Cuba [green label; handwritten] \ ex Coll. Reitter \ HOLOTYPE *Ceracis bison* Reitter [red paper; handwritten]”.

Additional material examined. 5 ♂♂ and 2 ♀♀ as follows: 2 ♂♂ (1 CELC, dissected and stored in glycerin; 1 CMN) and 1 ♀ (CELC) “CUBA, Mar. 1915, C. G. Lloyd, Cool. \ J.F. Lawrence, Lot 1983 \ Ex *Polyporus pargamenus* \ ex U.S.D.A. Herbaria”; 1 ♂ (CMN) “La. \ F.C. Bowditch Coll.”; 1 ♂ (CELC, dissected) “Mex. \ F.C. Bowditch Cool. \ *Ceracis variabilis* Mell. [handwritten]”; 1 ♂ (CELC, dissected) and 1 ♀ (CELC, dissected) “Mex. \ F.C. Bowditch Coll.”; 1 ♂ and 1 ♀ (SNSD) “Cuba / Coll. C. Felsche, Geschenk 1907 [green paper; pinted] / Staatl. Museum für Tierkunde Dresden”. All additionally labeled “*Abebaeocis taurulus* Souza-Gonçalves & Lopes-Andrade det.”.

Host fungi. *Trametes membranacea* (Sw.) Kreisel (Polyporaceae), one record; *Trichaptum biforme* (Fr.) Ryvarden (Hymenochaetales), one record.

Distribution. North America and Greater Antilles. Known from Louisiana (USA), Mexico and Republic of Cuba (Fig. 43).

Comments. The species was known only from the type series (Jacquelin-Duval 1857a, b, Reitter, 1878). We had access to historical material from the type locality and additional localities in Mexico and USA.

Alcecis gen. nov.

Fig. 8(A–F); Fig. 9(A–F); Fig. 10(A–H); Fig. 11(A–D); Fig. 44

Type species: *Ceracis particularis* Pic, 1922.

Etymology: The genus name derives from the Latin noun "alces", which means "moose", "elk", and "*Cis*", both in the nominative singular. The name is a reference to the male anterocephalic horns resembling moose horns.

Diagnosis. This genus is distinguished by the elongate body, dual pronotal and elytral punctation, single pronotal vestiture of short bristles arising from megapunctures, dual and subseriate elytral vestiture consisting of short bristles arising from megapunctures and minute setae arising from micropunctures, antennae 8-segmented with long club (more than 2x as long as funicle), prosternum tumid and slightly carinate,protibiae enlarged at apical one-third and outer apical angle project in a stout tooth, and meso- and metatibiae not enlarged. *Alcecis* **gen.nov.** somewhat resembles species in the *Cis bilamellatus* species-group, especially the elytral vestiture, but the latter differ in the 10-segmented antennae, males with a single plate on both anterocephalic and anterior pronotal edges, and outer apical angle of protibia expanded with several socketed spines in females.

Description. Body (Figs 8(A–C), 9(A–C), 11(A–C)) elongate, parallel-sided, convex; pronotal vestiture single, consisting of short bristles; elytral vestiture dual, consisting of short bristles and minute setae. **Head** anteriormost portion visible from above; anterocephalic edge in males produced, elevated forming two horns (Figs 8D); in females, truncate (Fig. 11C). **Antennae** (Fig. 10A) 8-segmented; antennal club long (more than 2x as long as funicle), 3-segmented; apical segment suboval, with sensillifers placed laterally in each segment; third segment at least 1.5x longer than fourth. **Labrum** longer than wide, subtruncate. **Mandibular molae** well-developed.

Apical maxillary palpomere (Fig. 9E) pyriform. **Prementum** (Fig. 9E) short, broadly rounded at apex; ligula conspicuous. **Labial palps** (Fig. 9E) 3-segmented; apical palpomere as long as and narrower than inflated preapical palpomere. **Gular sutures** bowed. **Pronotum** (Figs 8E, 9D) lateral edges narrow, not visible for their entire lengths from above; punctation, dual; each megapuncture with one bristle, micropunctures apparently glaborus; anterior edge rounded in both sexes. **Prosternum** (Fig. 8D) in front of coxae as long as prosternal process, tumid, slightly carinate; prosternal process moderately broad, subparallel-sided. **Procoxae** transverse, not projecting below plane of prosternal process (Fig. 8C, 9C, 11C). **Meso- and metacoxae** transverse. **Scutellar shield** (Figs 8E, 9D) well-developed. **Elytra** (Figs 8E, 9D) elongate and more than 1.60x as long as pronotum; punctation subseriate, dual; each megapuncture with one bristle; each micropuncture with one seta. **Metathoracic wings** well-developed. **Mesocoxal cavities** (Fig. 9F) narrowly separated, completely closed. **Metaventrite** (Fig. 9F) slightly convex, longer than first abdominal ventrite, posterior margin, notched; discrimen absent. **Protibiae** (Fig. 10B) very enlarged at apical one-third; outer apical angle projected in stout tooth. **Meso- and metatibiae** (Fig. 10(C–D)) not enlarged. **First abdominal ventrite** longer than second and third ventrites combined, with sex patch in males. **Male terminalia** (Fig. 10(E–H)): tegmen subquadrate, apical portion wider than basal portion, apex deeply emarginate; penis narrower than tegmen, apex triangular. **Female terminalia** (Fig. 11D): gonocoxites converging to apex; apical portion sclerotized; baculi of basal gonocoxites slightly oblique, much shorter than outer margin of gonocoxites; paraprocts slightly longer than gonocoxites, with pair of baculi straight, robust; gonostyli conspicuous, elongate.

Included species: *Alcecis particularis* (Pic, 1922) **comb. nov.**

Distribution: Greater and Lesser Antilles. Known from Guadeloupe and Republic of Cuba.

Alcecis particularis (Pic, 1922) comb. nov.

Fig. 8(A–F); Fig. 9(A–F); Fig. 10(A–H); Fig. 11(A–D); Fig. 44

Ceracis particularis Pic 1922: 3; Lawrence 1967: 98 (removed from *Ceracis* Mellié, 1849, but not placed in any genus). Type locality: Lesser Antilles: Guadeloupe (no specific locality).

Redescription, male lectotype, here designated (Fig. 8(A–E)). Adult apparently not fully pigmented but in good condition. Measurements in mm: TL 1.23, PL 0.47, PW 0.57, EL 0.76, EW 0.57, GD 0.49. Ratios: PL/PW 0.82, EL/EW 1.34, EL/PL 1.63, GD/EW 0.86, TL/EW 2.17. **Body** dorsum and venter reddish dark brown; antennae, palpi and tarsi yellowish brown; dorsal vestiture consisting of suberect bristles and decumbent setae, only discernible in high magnifications (>100x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>50x). **Head** (Fig. 8D) dorsal punctation dual; megapunctures coarse and deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths, apparently glabrous; interspaces, microreticulate; anterocephalic edge produced, elevated, forming two long, diverging flat horns (length 0.20 mm; basal width 0.14 mm; basal separation 0.10 mm), apices rounded, inner edge edge with one tooth. **Antennae** (Fig. 10A, left antenna in specimen from Barro Colorado Island) length of segments as follows (in mm, left antenna measured): 0.05, 0.04, 0.03, 0.02, 0.02, 0.04, 0.05, 0.07 (FL 0.06 mm, CL 0.15 mm, CL/FL 2.40). **Eyes** coarsely facetted, with about 50 ommatidia; GW 0.09 mm. **Gula** 0.43x as wide as head. **Pronotum** (Fig. 8E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1 megapuncture-width or less; interspaces, microreticulate; vestiture single, consisting of short suberect yellowish bristles (0.02–0.03 mm); lateral edges crenulate, not explanate and not visible when seen from above; anterior and posterior corners rounded. **Scutellar shield** triangular, with few punctures, apparently glabrous; BW 0.06 mm; SL 0.04 mm. **Elytra** punctation subseriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2 megapuncture-widths or less; interspaces, smooth, shiny; vestiture consisting of dense moderately short suberect yellowish bristles (0.03–0.04 mm), and very sparse minute decumbent yellowish setae (~0.02 mm). **Metathoracic wings** apparently functional. **Hypomera** punctures coarse, deep, each with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 8D) interspaces, microreticulate. **Prosternal process** (Fig. 8D) as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 10B, left protibia in specimen from Barro Colorado Island) maximum width about one-third its length; apical edge with spines; outer apical angle projected in stout tooth; outer edge straight, smooth. **Meso- and metatibiae** (Fig. 10(C–D)), left meso- and metatibia in specimen from Barro Colorado

Island) with spines in apical edge; outer edge straight, smooth. **Metaventrite** (Fig. 9F, in specimen from Barro Colorado Island) punctures coarse, deep; interspaces, microreticulate; posterior margin notch 0.10x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, deep, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.11, 0.05, 0.05, 0.05, 0.08; first abdominal ventrite with margined, circular, setose sex patch at center, transverse diameter of 0.06 mm. **Male terminalia (in specimen from Barro Colorado Island**; Fig. 10(E–H)**)**: **sternite VIII** (Fig. 10E) apical margin emarginate, with short, long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 10G, slightly damaged during dissection) 1.9x as long as wide, widest at apex; sides expanding to apex; apex shallowly emarginate at middle forming two lobes, each with one inner short expansion (Fig. 10G, small black arrows), emargination with U-shaped sclerotization (Fig. 10G, big black arrow). **Basal piece** (Fig. 10F) semicircular, 1.8x as wide as long. **Penis** (Fig. 10H) 1.2x as long as tegmen, 4.1x as long as wide; sides expanding to middle, then converging to apex; apex with conspicuous dorsal and ventral lobes, dorsal lobe with apical portion very acute and sclerotized, ventral lobe curved upwardly, sclerotized (Fig. 10H, black arrows); basal portion rounded.

Females (Fig. 11(A–D)). Anterior edge of head truncate; anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns, abdominal sex patch and each megapuncture of head with one short decumbent bristle (~0.02 mm). **Female terminalia in specimen from Barro Colorado Island** (Fig. 11D): spiculum ventrale (not shown) 1.29x as long as ovipositor (Fig. 11D); ovipositor 1.49x as long as wide; paraprocts (Fig. 11D) 1.23x as long as gonocoxites; gonocoxites (Fig. 11D) 0.70x as long as their combined widths, each with broadly rounded apex; each gonostylus (Fig. 11D) 0.23x as long as respective gonocoxite, 2.56x as long as wide.

Variation. Males, measurements in mm (n= 11, including the lectotype): TL 1.10–1.28 (1.19 ± 0.06), PL 0.38–0.47 (0.42 ± 0.03), PW 0.45–0.57 (0.52 ± 0.04), EL 0.70–0.83 (0.77 ± 0.04), EW 0.45–0.57 (0.52 ± 0.04), GD 0.40–0.49 (0.44 ± 0.03), PL/PW 0.77–0.89 (0.82 ± 0.04), EL/EW 1.34–1.61 (1.48 ± 0.07), EL/PL 1.63–1.94 (1.81 ± 0.11), GD/EW 0.76–0.89 (0.84 ± 0.04), TL/EW 2.17–2.44 (2.30 ± 0.08). Females, measurements in mm (n= 5): TL 1.15–1.23 (1.19 ± 0.03), PL 0.40–0.43 (0.42

± 0.01), PW 0.48–0.50 (0.48 ± 0.01), EL 0.75–0.80 (0.78 ± 0.03), EW 0.48–0.50 (0.48 ± 0.01), GD 0.43–0.45 (0.44 ± 0.01), PL/PW 0.80–0.89 (0.87 ± 0.04), EL/EW 1.58–1.68 (1.61 ± 0.04), EL/PL 1.76–2.00 (1.87 ± 0.09), GD/EW 0.89–0.95 (0.92 ± 0.03), TL/EW 2.40–2.58 (2.48 ± 0.07).

Type material. Lectotype ♂, here designated (MNHN, Fig. 8(A–F)) “Guadeloupe [printed] \ Ciside Nº-9 [handwritten] \ *Ceracis particularis* n. sp. [handwritten] \ LECTOTYPE *Ceracis particularis* Pic [red paper; handwritten]”. **Paralectotype** ♀ (MHNH) (previously at same card, but remount and relabeled by J.F Lawrence) same data as lectotype \ PARALECTOTYPE *Ceracis particularis* Pic [yellow paper; handwritten]”. Lectotype additionally labeled “*Alcecis particularis* (Pic, 1922) comb. nov. Souza-Gonçalves & Lopes-Andrade”

Additional material examined. 15 ♂♂ and 10 ♀♀ as follows: 10 ♂♂ (4 CELC, one dissected and stored in glycerin; 1 ANIC; 4 FMNH; 1 QMBA) and 10 ♀♀ (4 CELC, one dissected and stored in glycerin; 1 ANIC; 4 FMNH; 1 QMBA) “Barro Colorado Is., CANAL ZONE, July 14 1969 \ J.F. Lawrence, Lot 2875”; 2 ♂♂ (MNHN) “GUADELOUPE, LEO DUFAU 1904 [handwritten] \ MUS. PARIS, ENV. DE TROIS RIVIERES [handwritten]”; 1 ♂ (MNHN) “MUSEUM PARIS, GUADELOUPE, Env. de Trois Rivières, LEO DUFAU 1904 [green paper; printed] \ 2412 [handwritten] \ Vevoi [handwritten] \ Champignon lanepaul? sur le tronc de *Inga laurina* mort [handwritten]”; 2 ♂♂ (MNHN) “MUSEUM PARIS, GUADELOUPE, Env. de Trois Rivières, LEO DUFAU 1904 [green paper]”. All additionally labeled “*Alcecis particularis* (Pic, 1922) Souza-Gonçalves & Lopes-Andrade det.”.

Host fungus. Unknown.

Distribution. Greater and Lesser Antilles. Known from Guadeloupe and Republic of Cuba (Fig. 44).

Comments. The species was known only from the type series (Pic, 1922). We had access to historical material from the type locality and one additional locality (Barro Colorado Island, Panama) (Fig. 9(A–F)).

Anartioscelos gen. nov.

Fig. 12(A–E); Fig. 13(A–H); Fig. 14(A–C); Fig. 15(A–G); Fig. 16(A–H); Fig. 17(A–E); Fig. 18(A–E); Fig. 19(A–D); Fig. 20(A–E); Fig. 21(A–C) Fig. 22(A–F); Fig. 44

Type species: *Anartioscelos aptenus* **sp. nov.**.

Etymology: The genus name derives from the Greek adjective “anartios”, which means “uneven”, “odd”, and the Latinized Greek noun “skelos”, which means “leg”, both in the genitive singular. The name is a reference to odd legs of members in this genus that are both serrate and spinose.

Diagnosis. This genus is distinguished by the elongate body, dual pronotal and elytral punctation, single vestiture of minute setae, each arising from one megapuncture, antennae 10-segmented, prosternum tumid and carinate, outer edges of tibiae regularly serrate and bearing socketed spines between serration, outer angle of protibiae projected in an acute tooth, and meso- and metatibiae with outer apical angle broadly rounded. *Anartioscelos* **gen. nov.** somewhat resembles species in the *Cis taurus* species-group, especially the 10-segmented antennae, anterocephalic projections of males, and prosternum strongly tumid and carinate, but the latter differ in the outer edge of protibiae smooth, meso- and metatibiae not expanded at apical half and with outer edge smooth.

Description. Body elongate, subparallel-sided (Figs 12(A–C), 14(A–C), 18(A–C), 22(A–C)) to slightly oval (Figs 15(A–C), 17(A–C), 20(A–C)), convex; dorsal vestiture, single, consisting of minute setae. **Head** anteriormost portion visible from above; anterocephalic edge in males produced and elevated forming two horns (Figs 12D, 15D, 18D, 20D, 22D); in females, slightly produced forming two small plates (Figs 14C, 17C). **Antennae** (Figs 13A, 16A) 10-segmented; club long, 3-segmented, at least 1.4x as long as funicle; apical segment suboval, with sensillifers placed laterally in each segment; third segment as long as fourth. **Labrum** longer than wide, subtruncate. **Mandibular molae** well-developed. **Apical maxillary palpomere** (Fig. 15F) pyriform. **Prementum** (Fig. 15F) long, slightly rounded at apex; ligula apparently absent. **Labial palps** (Fig. 15F) 3-segmented; apical palpomere long and narrower than inflated and long preapical palpomere. **Gular sutures** subparallel-sided or bowed. **Pronotum** (Figs 12E, 15E, 18E, 20E, 22E) lateral edges narrow or slightly wide, visible or not visible for their entire lengths from above; punctation, dual; each megapuncture with one seta, micropunctures apparently glabrous; anterior edge rounded in both sexes or slightly emarginate in males. **Prosternum** (Figs 12D, 15D, 18D, 20D, 22D) in front of coxae slightly shorter than prosternal process, tumid, carinate; prosternal process slightly narrow or moderately broad, expanding to apex or subparallel-sided. **Procoxae** transverse, not projecting below plane of prosternal process (Fig. 12C, 14C, 15C, 17C, 18C, 20C, 22C). **Meso- and metacoxae** transverse. **Scutellar shield** (Figs 12E, 15E, 18E, 20E, 22E) well-developed (Figs 12E, 18E, 22E) or slightly reduced (Figs 15E, 20E). **Elytra** (Figs 12E, 15E, 18E, 20E, 22E) elongate and at least 1.55x as long as pronotum; punctation, dual; each megapuncture with one seta, micropunctures apparently glaborus. **Metathoracic wings** well-developed or absent (*Ana. aptenus* **sp. nov.** and *Ana. involucris* **sp. nov.**). **Mesocoxal cavities** (Fig. 15G) narrowly separated, completely closed. **Metaventrite** (Fig. 15G) slightly convex, longer than or as long as first abdominal ventrite at midline; posterior margin notched, discrimen present or not. **Protibiae** (Figs 13B, 16B) triangular; outer apical edge projected in acute tooth. **Meso- and metatibiae** (Figs 13(C–D), 16(C–D)) very enlarged; outer apical angle broadly rounded. Outer edge of all tibiae regularly serrate and with socketed spines between serration. **First abdominal ventrite** longer than second and third ventrites combined, with or without sex patch in males. **Male terminalia** (Figs 13(E–H), 16(E–H), 19(A–D), 21(A–C)): tegmen subquadrate, apex usually truncate with shallow emargination at middle (most species) or with comparatively deeper emargination forming two rounded lateral lobes (*Ana. eurinotum* **sp. nov.**), outer (Figs 13G, 16G, 21B) or inner apical edge (Fig. 19C) with angulations, with (Figs 13G, 16G, 19C) or without (Fig. 21B) excavations; penis subcylindrical, about as long and half as wide as tegmen. **Female terminalia**: females of most species are unknown, but see description of *Ana. aptenus* **sp. nov.** as example.

Included species: *Anartioscelos aptenus* **sp. nov.**, *Ana. almirantensis* **sp. nov.**, *Ana. bifurcus* (Gorham, 1898) (*Ceracis*) **comb. nov.**, *Ana. eurinotum* **sp. nov.**, *Ana. involucris* **sp. nov.** and *Ana. laticornis* (Pic, 1922) (*Ceracis*) **comb. nov.**. Another species have been seen from Loreto, Madre de Dios and Pasco (Peru), known from a short series, which will not be described here.

Distribution: North to South America and Lesser Antilles. Known from Guadeloupe, Guatemala, Mexico, Panama, Peru and Saint Vincent and the Grenadines.

Key to species of *Anartioscelos*

1 Metathoracic wings absent..**2**

1’ Metathoracic wings present...**3**

2 Elytral punctation sparse (megapunctures separated from each other by at least 3 megapuncture-widths; Fig. 15E), lateral edges of pronotum completely visible when seen from above (Fig. 15A), prosternal process narrow at base and gradually expanding to apex (Fig. 15C)...***Ana. aptenus* sp. nov.**

2’ Elytral punctation dense (megapunctures separated from each other by no more than 2 megapuncture-widths; Fig. 20E), lateral edges of pronotum not visible from above, subparallel-sided prosternal process (Fig. 20C)............................***Ana. involucris* sp. nov.**

3 (1’) TL > 1.40 mm and males with diverging anterocephalic horns...........***Ana. laticornis* (Pic)**

3’ TL < 1.40 mm and males with parallel anterocephalic horns......................................**4**

4 (3’) Lateral edge of pronotum barely explanate and completely visible from above (Fig. 12A)...***Ana. almirantensis* sp. nov.**

4’ Lateral edge of pronotum not explanate and not visible from above (Fig. 18A).............**5**

5 EL/PL ≤ 1.50. Anterocephalic horns in males long and projected forwards...***Ana. bifurcus* (Gorham)**

5’ EL/PL > 1.50. Anterocephalic horns in males short and projected upwards (Fig. 18D)...***Ana. eurinotum* sp. nov.**

***Anartioscelos almirantensis* sp. nov.**

Fig. 12(A–E); Fig. 13(A–H); Fig. 14(A–C); Fig. 44

Type locality. “Almirante”, coordinates 09º18’N 82º24’W (Changuinola District, Bocas del Toro Province, Panama).

Etymology. The species name is Latinized from “Almirante”. The name is a reference to the city where the type series was collected.

Diagnosis. *Anartioscelos almirantensis* **sp. nov.** is similar to *Ana. laticornis* **comb. nov.**, *Ana. bifurcus* **comb. nov.** and *Ana. eurinotum* **sp. nov.**, but differs from the former in the comparatively shorter body (≤1.20 mm) and discrimen about one-fifth the length of metaventrite at midline; from *Ana. bifurcus* **comb. nov.** in the trapezoidal pronotum with barely explanate lateral edges and males with anterocephalic horns short and elevated upwards. It differs from *Ana. eurinotum* **sp. nov.** in the pronotum with lateral edges visible from above, discrimen present and prosternal process narrow at base and gradually expanding to apex.

Description, male holotype (Fig. 12(A–E)). Adult apparently not fully pigmented; lacking two tarsi; elytra displaced. Measurements in mm: TL 1.19, PL 0.43, PW 0.56, EL 0.76, EW 0.58, GD 0.43. Ratios: PL/PW 0.76, EL/EW 1.32, EL/PL 1.78, GD/EW 0.74, TL/EW 2.06. **Body** subparallel-sided, dorsum and venter yellowish brown; antennae, palpi and tarsi pale yellowish brown; dorsal vestiture consisting of minute suberect setae, only discernible in high magnifications (>100x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>70x). **Head** (Fig. 12D) dorsal punctation dual, megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths, each with minute decumbent seta (<0.01 mm); interspaces, smooth and shiny; anterocephalic edge produced and elevated forming two long, broadly laminate, parallel horns (length 0.18 mm; basal width 0.13 mm; basal separation 0.09 mm), apices rounded; sides of each horn parallel. **Antennae** (Fig. 13A, left antenna in paratype) length of segments as follows (in mm, left antenna measured): 0.06, 0.04, 0.02, 0.02, 0.01, 0.02, 0.01, 0.03, 0.03, 0.06 (FL 0.07 mm, CL 0.12 mm, CL/FL 1.66). **Eyes** coarsely facetted, with about 50 ommatidia; GW 0.11 mm. **Gula** 0.58x as wide as head. **Pronotum** (Fig. 12E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (<0,01 mm); lateral edges not crenulate, barely explanate, entirely visible when seen from above; anterior corners acute; posterior corners rounded. **Scutellar shield** well developed, triangular, with few punctures; apparently glabrous; BW 0.06 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm). **Metathoracic wings** developed, apparently functional. **Hypomera** punctation coarse, deep; each puncture with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 12D) interspaces, microreticulate. **Prosternal process** (Fig. 12D) narrow at base, gradually expanding to apex, 1.4x as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 13B, left protibia in paratype) maximum width about one-third its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, serrate, with socketed spines. **Meso- and metatibiae** (Fig. 13(C–D), left meso- and metatibia in paratype, respectively) expanded at apical half; serrate, with socketed spines. **Metaventrite** punctures coarse, shallow; interspaces, microreticulate; discrimen about one-fifth the length of metaventrite at midline; posterior margin notch 0.05x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.09, 0.04, 0.04, 0.04, 0.08; first abdominal ventrite with margined, circular, setose sex patch posterad of center, transverse diameter of 0.05 mm. **Male terminalia in paratype** (Fig. 13(E–H)): **sternite VIII** (Fig. 13E) apical margin sinuous, with long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 13G) 1.7x as long as wide, widest at apex; subparallel-sided but more or less sinuous; apex shallowly emarginate at middle; outer apical edge with angulations (Fig. 13G, black arrows); apical portion almost straight; basal portion triangular. **Basal piece** (Fig. 13F) subtriangular, 1.7x as wide as long. **Penis** (Fig. 13H) as long as tegmen, 3.1x as long as wide; subparallel-sided; apex with two acute angulations (Fig. 13H, black arrows); basal portion with rounded emargination (Fig. 13H, red arrow).

Female (Fig. 14(A–C)). Anterior edge of head slightly produced forming two small subacute plates. Anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns and abdominal sex patch.

Variation. Males, measurements in mm (n= 2, including the holotype): TL 1.18–1.19 (1.18 ± 0.01), PL 0.43 (0.43 ± 0.00), PW 0.56–0.58 (0.57 ± 0.01), EL 0.75–0.76 (0.76 ± 0.01), EW 0.58–0.63 (0.60 ± 0.03), GD 0.43–0.45 (0.44 ± 0.02), PL/PW 0.74–0.76 (0.75 ± 0.01), EL/EW 1.20–1.32 (1.26 ± 0.08), EL/PL 1.76–1.78 (1.77 ± 0.01), GD/EW 0.72–0.74 (0.73 ± 0.01), TL/EW 1.88–2.06 (1.97 ± 0.12). Female, measurements in mm: TL 1.15, PL 0.40, PW 0.53, EL 0.75, EW 0.60, GD 0.45, PL/PW 0.76, EL/EW 1.25, EL/PL 1.88, GD/EW 0.75, TL/EW 1.92.

Type material. Holotype ♂ (FMNH) "PANAMA: Almirante, Boca del Toro Prov, 30 March 1959, Henry S. Dybas leg. \ CHICAGO NAT. HIST. MUSEUM, Host: *Polyporus zonalis*, FMNM (HD) #59-157, to dam on Nigua Ck. \ *Anartioscelos almirantensis* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]". **Paratypes:** 2 ♂♂ (CELC, dissected) and 1 ♀ (FMNH), same data as the holotype, additionally labeled "*Anartioscelos almirantensis* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]".

Host fungus. *Rigidoporus lineatus* (Pers.) Ryvarden (Meripilaceae), one breeding record.

Distribution. Central America. Known from Bocas del Toro Province (Panama) (Fig. 44).

Comments. We've decided not to dissect the single known female because it seems to be a teneral.

Anartioscelos aptenus sp. nov.

Fig. 15(A–G); Fig. 16(A–H); Fig. 17(A–E); Fig. 44

Type locality. "San Juan Bautista Valle Nacional", coordinates 17º46'N 96º18'W (Oaxaca, Mexico).

Etymology. The species name derives from the Latinized Greek adjective "aptenos", which means "wingless". The name is a reference to the absence of metathoracic wings on this species.

Diagnosis. *Anartioscelos aptenus* **sp. nov.** differs from all other species in the genus, except for *Ana. involucris* **sp. nov.**, in the absence of metathoracic wings. It differs from *Ana. involucris* **sp. nov.** in the comparatively sparser elytral punctation (megapunctures separated from each other by about 3 megapuncture-widths), prosternal process narrow at base and gradually expanding to apex, and males with parallel anterocephalic horns.

Description, male holotype (Fig. 15(A–E)). Adult fully pigmented and in good condition. Measurements in mm: TL 1.19, PL 0.46, PW 0.63, EL 0.73, EW 0.64, GD 0.54. Ratios: PL/PW 0.73, EL/EW 1.14, EL/PL 1.60, GD/EW 0.84, TL/EW 1.86. **Body**

slightly oval, dorsum reddish dark brown, pronotum usually darker; venter reddish dark brown; antennae yellowish brown; antennal club dark brown; palpi and tarsi yellowish brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnifications (>50x); ventral vestiture consisting of decumbent setae, easily discernible in high magnifications (>50x). **Head** (Fig. 15D) dorsal punctation single; punctures coarse, shallow, separated from each other by 2–3 puncture-widths; apparently glabrous; interspaces smooth, shiny; anterocephalic edge produced, elevated forming two long, broadly laminate, parallel horns (length 0.31 m; basal width 0.13 mm; basal separated by 0.12 mm), apices rounded; sides of each horn parallel. **Antennae** (Fig. 16A, left antenna in paratype) length of segments as follows (in mm, left antenna measured): 0.07, 0.05, 0.03, 0.03, 0.02, 0.02, 0.01, 0.04, 0.04, 0.07 (FL 0,10 mm, CL 0.14 mm, CL/FL 1.44). **Eyes** coarsely facetted, with about 30 ommatidia; GW 0.09 mm. **Gula** 0.43x as wide as head. **Pronotum** (Fig. 15E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2–3 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (<0.01 mm); anterior edge slightly emarginate forming two small angulations; lateral edges not crenulate, barely explanate, entirely visible when seen from above; anterior corners subacute; posterior corners rounded. **Scutellar shield** slightly reduced, triangular, devoid of punctures; apparently glabrous; BW 0.05 mm; SL 0.03 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 3 megapuncture-widths or less; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm). **Metathoracic wings** absent. **Hypomera** punctation coarse, shallow; each puncture with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 15D) interspaces, microreticulate. **Prosternal process** (Fig. 15D) narrow at base, gradually expanding to apex, 1.4x as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 16B, left protibia in paratype) maximum width about one-third its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, serrate, with socketed spines. **Meso- and metatibiae** (Fig. 16(C–D), left meso- and metatibia in paratype, respectively) expanded at apical half; serrate, with socketed spines. **Metaventrite** (Fig. 15G, in paratype) punctures coarse, deep; interspaces, microreticulate; discrimen absent; posterior margin notch 0.10x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.11, 0.05, 0.05, 0.05, 0.11; first abdominal ventrite with margined, circular, setose sex patch posterad of center, transverse diameter of 0.04 mm. **Male terminalia in paratype** (Fig. 16(E–H)): **sternite VIII** (Fig. 16E) apical margin sinuous, with short, long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 16G) 1.5x as long as wide, widest at apex; subparallel-sided but more or less sinuous; apex deeply emarginate at middle; outer apical edge with angulations (Fig. 16G, black arrows); apical portion almost straight; basal portion subtriangular. **Basal piece** (Fig. 16F) subtriangular, 1.6x as wide as long. **Penis** (Fig. 16H) as long as tegmen, 3.1x as long as wide; subparallel-sided; apical portion consisting of one pleated membrane; basal portion rounded.

Females (Fig. 17(A–E)). Anterior edge of head slightly produced forming two small subacute plates. Anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns, pronotal emargination and angulations, and abdominal sex patch. **Female terminalia in paratype** (Fig. 17(D–E)): short; spiculum ventrale (Fig. 17D) as long as ovipositor (Fig. 17E); ovipositor 1.28x as long as wide; paraprocts (Fig. 17E) 0.92x as long as gonocoxites; gonocoxites (Fig. 17E) subparallel, with inner sclarotizations, 0.67x as long as their combined widths, each with broadly rounded apex; basal baculi of gonocoxites oblique, about half as long as outer edge of gonocoxites; gonostyli short (Fig. 17E), 0.11x as long as respective gonocoxite, 1.33x as long as wide.

Variation. Females, measurements in mm (n= 7): TL 1.18–1.23 (1.20 ± 0.02), PL 0.43–0.48 (0.44 ± 0.02), PW 0.60–0.65 (0.61 ± 0.02), EL 0.73–0.80 (0.76 ± 0.02), EW 0.64–0.80 (0.66 ± 0.02), GD 0.48–0.55 (0.53 ± 0.03), PL/PW 0.65–0.79 (0.73 ± 0.05), EL/EW 1.12–1.20 (1.15 ± 0.03), EL/PL 1.58–1.88 (1.83 ± 0.05), GD/EW 0.76–0.85 (0.80 ± 0.03), TL/EW 1.75–1.88 (1.83 ± 0.05).

Type material. Holotype ♂ (FMNH) “MEXICO: Oaxaca, 15.1 mi S. Valle Nacional 4300’, viii.11-18.1973 \ Berl. leaf litt, cloud forest \ *Anartioscelos aptenus* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”. **Paratypes:** 1 ♂ and 8 ♀♀ as follows: 1 ♂ (CELC, dissected and stored in glycerin) and 2 ♀♀ (CELC, one dissected and stored in glycerin), same data as the holotype; 1 ♀ (FMNH) “MEXICO: Chiapas, 8 mi N Pueblo Nuevo, Solistahuacán, 6000’, viii.26-27.1973 \ Berl. leaf litt, cloud forest”; 2 ♀♀ (ANIC) “MEXICO: Chiapas, 8 mi N Pueblo Nuevo, Solistahuacán, 6000’, viii.26-27.1973 \ leaf litter, forest floor, A. Newton”; 1 ♀ (CMN, dissected) “GUAT. Baja Verapaz \ 8 km S. Purulhá, 1660 m. 29.v.1991, H & A. Howden”; 2 ♀♀ (CMN) “GUAT: BAJA VERAPAZ: 8.6 km W Chilasco., Elev. 1550 m., oak-pine-liquid amber, for. litter. R. Anderson, 91-18. 24-v-1991”. All paratypes additionally labeled “*Anartioscelos aptenus* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]”.

Host fungus. Unknown.

Distribution. North to Central America. Known from Baja Verapaz Department (Guatemala) and Oaxaca (Mexico) (Fig. 44).

Comments. The species was collected only in leaf litter, as most apterous and micropterous ciids up to date.

Anartioscelos bifurcus (Gorham, 1898) comb. nov.

Ceracis bifurcus Gorham 1898: 332, pl. 27, figs. 10–10a; Lawrence 1967: 98 (removed from *Ceracis* Mellié, 1849, but not placed in any genus). Type locality: Lesser Antilles: Saint Vincent and the Grenadines: Saint Vincent (no specific locality).

Type material. Lectotype ♂, here designated (NHM) “Type [red. marg. Disc; printed] \ Type [red paper; handwritten] \ W. Indies 98.237 [printed] \ St. Vincent, W.I. H.H. Smith 221 [printed] \ *Ceracis bifurcus* Gorh. ♂ [handwritten] \ HOLOTYPE *Ceracis bifurcus* Gorham [red paper; handwritten]”. **Paralectotype** ♂ (NHM) “W. Indies 98.237 [printed] \ St. Vincent, W.I. H.H. Smith 221 [printed] \ Sp. Figs, Type [printed] \ *Ceracis bifurcus* Go. [handwritten] \ PARATYPE *Ceracis bifurcus* Gorham [yellow paper; handwritten]”.

Host fungus. Unknown.

Distribution. Lesser Antilles. Known from Saint Vincent (Saint Vincent and the Grenadines) (Fig. 44).

Comments. The species is known only from the short type series (Gorham, 1898) and no female is known, as far as we have traced.

***Anartioscelos eurinotum* sp. nov.**

Fig. 18(A–E); Fig. 19(A–D); Fig. 44

Type locality. “Barro Colorado Island”, coordinates 09º09’N 79º51’W (Canal Zone, Panama).

Etymology. The species name derives from the Greek adjective “eurys”, which means “broad”, “wide”, and the anatomical term “notum”, both in the genitive singular. The name is a reference to the broad pronotum of the species.

Diagnosis. *Anartioscelos eurinotum* **sp. nov.** is similar to *Ana. laticornis* **comb. nov.**, *Ana. bifurcus* **comb. nov.** and *Ana. almirantensis* **sp. nov.**, but differs from the former in the comparatively shorter body (TL 1.00 mm) and converging anterocephalic horns in males; differs from *Ana. bifurcus* **comb. nov.** in the comparatively longer elytra (EL/PL > 1.50) and short anterocephalic horns in males, projected upwards; differs from *Ana. almirantensis* **sp. nov.** in the pronotum with lateral edges not visible from above, prosternal process subparallel-sided and absence of discrimen.

Description, male holotype (Fig. 18(A–E)). Adult apparently not fully pigmented but in good condition. Measurements in mm: TL 1.00, PL 0.38, PW 0.53, EL 0.62, EW 0.56, GD 0.47. Ratios: PL/PW 0.72, EL/EW 1.11, EL/PL 1.61, GD/EW 0.84, TL/EW 1.79. **Body** subparallel-sided, dorsum and venter reddish brown; antennae, palpi and tarsi yellowish brown; dorsal vestiture consisting of minute suberect setae, only discernible in high magnifications (>100x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>70x). **Head** (Fig. 18D) dorsal punctation dual; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths, each with one minute decumbent seta (<0.01 mm); interspaces smooth, shiny; anterocephalic edge produced, elevated forming two long, broadly laminate, parallel horns (length 0.19 mm; basal width 0.11 mm; basal separation of 0.09 mm), apices rounded; sides of each horn parallel. **Antennae** lengths as follows (in mm, left antenna measured): 0.06, 0.04, 0.02, 0.02, 0.01, 0.01, 0.01, 0.03, 0.03, 0.05 (FL 0.08 mm, CL 0.11 mm, CL/FL 1.47). **Eyes** coarsely facetted, with about 50 ommatidia; GW 0.10 mm. **Gula** 0.42x as wide as head. **Pronotum** (Fig. 18E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (<0,01 mm); anterior edge rounded; lateral edges not crenulate, not explanate and not visible when seen from above; anterior and posterior corners rounded. **Scutellar shield** well-developed, triangular, with few punctures and apparently glabrous; BW 0.06 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2–3 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm). **Metathoracic wings** developed, apparently functional. **Hypomera** punctures coarse, deep, each with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 18D) interspaces, microreticulate. **Prosternal process** (Fig. 18D) subparallel-sided, 1.2x as long as prosternum at midline; apex rounded. **Protibiae** maximum width about one-third its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, serrate, with socketed spines. **Meso- and metatibiae** expanded at apical half; serrate, with socketed spines. **Metaventrite** punctures coarse, shallow; interspaces, microreticulate; discrimen absent; posterior margin notch 0.06x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.16, 0.05, 0.05, 0.05, 0.06; first abdominal ventrite with margined, circular, setose sex patch posteriorly, transverse diameter of 0.04 mm. **Male terminalia in holotype** (Fig. 19(A–D)): **sternite VIII** (Fig. 19A) apical margin sinuous, with long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 19C) 1.3x as long as wide, widest at apex; subparallel-sided but more or less sinuous; apex shallowly emarginate at middle; inner apical edge with angulations (Fig. 19C, big black arrows) and excavations (Fig. 19C, small black arrows); apical portion barely emarginate; basal portion triangular with one acute angulation at middle (Fig. 19C, red arrow). **Basal piece** (Fig. 19B) subtriangular, 1.7x as wide as long. **Penis** (Fig. 19D) as long as tegmen, 3.2x as long as wide; subparallel-sided; apex with two acute angulations (Fig. 19D, black arrows); basal portion almost straight (Fig. 19D, red arrow).

Female. Unknown.

Type material. Holotype ♂ (FMNH, dissected) “Barro Colorado Is., CANAL ZONE, July 14 1969 \ J.F. Lawrence, Lot 2880 \ *Ganoderma* sp. \ *Anartioscelos eurinotum* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”.

Host fungus. *Ganoderma* sp. (Ganodermataceae), one record.

Distribution. Central America. Known from Barro Colorado Island (Panama) (Fig. 44).

Comments. This species is known only from the holotype.

Anartioscelos involucris sp. nov.

Fig. 20(A–E); Fig. 21(A–C); Fig. 44

Type locality. “Cerro Punta”, coordinates 08º51’N 82º34’W (Tierras Altas District, Chiriquí Province, Panama).

Etymology. The species derives from the Latin adjective “involucris”, which means “unable to fly”. The name is a reference to the absence of metathoracic wings in the species.

Diagnosis. *Anartioscelos involucris* **sp. nov.** differs from all other species in the genus, except for *Ana. aptenus* **sp. nov.**, in the absence of metathoracic wings. It differs from *Ana. aptenus* **sp. nov.** in the denser elytral punctation (megapunctures separated from each other by 2 megapuncture-widths), subparallel-sided prosternal process and males with converging anterocephalic horns.

Description, male holotype (Fig. 20(A–E)). Adult apparently not fully pigmented, lacking two tarsi; after dissection, body and separated elytra were glued on cardboard. Measurements in mm: TL 1.27, PL 0.48, PW 0.67, EL 0.79, EW 0.69, GD 0.57. Ratios: PL/PW 0.73, EL/EW 1.14, EL/PL 1.62, GD/EW 0.83, TL/EW 1.85. **Body** slightly oval, dorsum and venter yellowish dark brown; antennae yellowish brown, antennal club yellowish dark brown, palpi and tarsi yellowish brown; dorsal vestiture consisting of minute suberect setae, only discernible in high magnifications (>100x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>70x). **Head** (Fig. 20D) dorsal punctation dual; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths, each with one minute decumbent seta (<0.01 mm); interspaces smooth, shiny; anterocephalic edge produced, elevated forming two long, narrowly laminate converging horns (length 0.37 mm; basal width 0.12 mm; basal separation 0.14 mm), apices rounded; sides of each horn parallel. **Antennae** lengths as follows (in mm, left antenna measured): 0.06, 0.04, 0.03, 0.02, 0.02, 0.02, 0.02, 0.04, 0.04, 0.07 (FL 0.11 mm, CL 0.15 mm, CL/FL 1.34). **Eyes** coarsely facetted, with about 40 ommatidia; GW 0.10 mm. **Gula** 0.32x as wide as head. **Pronotum** (Fig. 20E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (<0,01 mm); anterior edge rounded; lateral edges not crenulate, not explanate, not visible when seen from above; anterior and posterior corners rounded. **Scutellar shield** slightly reduced, triangular, with few punctures; apparently glabrous; BW 0.05 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm). **Metathoracic wings** absent. **Hypomera** punctures coarse, deep, each with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 20D) interspaces, microreticulate. **Prosternal process** (Fig. 20D) subparallel-sided, 1.2x as long as prosternum at midline; apex rounded. **Protibiae** maximum width about one-third its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, serrate, with socketed spines. **Meso- and metatibiae** expanded at apical half; outer edge serrate, with socketed spines. **Metaventrite** punctures coarse, shallow; interspaces, microreticulate; discrimen absent; posterior margin notch 0.08x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.17, 0.06, 0.05, 0.05, 0.08; first abdominal ventrite with margined, circular, setose sex patch posterad of center, transverse diameter of 0.03 mm. **Male terminalia in holotype** (Fig. 21(A–C)): **sternite VIII** (not shown) apical margin sinuous, with short long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 21B) 1.5x as long as wide, widest at apex; subparallel-sided but more or less sinuous; apex shallowly emarginate at middle; outer apical edge with angulations (Fig. 20B, black arrows); apical portion almost straight; basal portion triangular. **Basal**

piece (Fig. 21A) subtriangular, 1.8x as wide as long. **Penis** (Fig. 21C) 1.1x as long as tegmen, 3.9x as long as wide; subparallel-sided; apex rounded (Fig. 21C, black arrow); basal portion rounded (Fig. 21C, red arrow).

Female. Unknown.

Type material. Holotype ♂ (CNC, dissected) "PAN: Chiri, 2600m, 5KmESE Cerro Punta, 28.v.77, S & J. Peck, Ber376, oak-bamboo \ *Anartioscelos involucris* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]".

Host fungus. Unknown.

Distribution. Central America. Known from Chiriquí Province (Panama) (Fig. 44).

Comments. This species was collected in leaf litter, as most apterous and micropterous ciids up to date.

Anartioscelos laticornis (Pic, 1922) comb. nov.

Fig. 22(A–F); Fig. 44

Ceracis laticornis Pic 1922: 3; Lawrence 1967: 98 (removed from *Ceracis* Mellié, 1849, but not placed in any genus). Type locality: Lesser Antilles: Guadeloupe (no specific locality).

Diagnosis. *Anartioscelos laticornis* **comb. nov.** differs from all other species in the long body (TL > 1.40 mm) and males with diverging anterocephalic horns. It is similar to *Ana. almirantensis* **sp. nov.**, *Ana. bifurcus* **comb. nov.** and *Ana. eurinotum* **sp. nov.**, but differs from the former in the absence of discrimen and of sex patch in males; from *Ana. bifurcus* **comb. nov.** in the trapezoidal pronotum with lateral edges barely explanate; and from *Ana. eurinotum* **sp. nov.** in the lateral edges of pronotum barely explanate and barely visible from above, and prosternal process narrow at apex and gradually expanding to apex.

Redescription, male lectotype, here designated (Fig. 22(A–E)). Adult apparently not fully pigmented, lacking most part of right antenna, left mesofemur, left mesotibia and all tarsi; part of left antenna mounted in cardboard. Measurements in mm: TL 1.46, PL 0.56, PW 0.63, EL 0.90, EW 0.71, GD 0.60. Ratios: PL/PW 0.81, EL/EW 1.26, EL/PL 1.60, GD/EW 0.85, TL/EW 2.05. **Body** subparallel-sided, dorsum and venter yellowish brown; antenna and palpi yellowish brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnifications (>70x); ventral vesture of decumbent setae, easily discernible in high magnifications (<50x). **Head** (Fig. 22D) dorsal punctation single; punctures coarse, shallow, separated from each other by 1 puncture-width or less; apparently glabrous; interspaces, microreticulate; anterocephalic edge produced, elevated forming two long, broadly laminate diverging horns (length 0.36 mm; basal width 0.15 mm; basal separation 0.14 mm), apices rounded; sides of each horn parallel. **Antennae** lengths as follows (in mm, left antenna measured): 0.07, 0.03, 0.02, 0.02, 0.02, 0.02, 0.02, 0.04, 0.04, 0.06 (FL 0.09 mm, CL 0.14 mm, CL/FL 1.60). **Eyes** coarsely facetted, with about 50 ommatidia; GW 0.11 mm. **Gula** 0.38x as wide as head. **Pronotum** (Fig. 22E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm); anterior edge rounded; lateral edges not crenulate, barely explanate, barely visible when seen from above; anterior corners acute; posterior corners rounded. **Scutellar shield** well-developed, pentagonal, with few punctures; apparently glabrous; BW 0.08 mm; SL 0.05 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1 megapuncture-width or less; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm). **Metathoracic wings** developed, apparently functional. **Hypomera** punctures coarse, shallow, each puncture with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 22D) interspaces, microreticulate. **Prosternal process** (Fig. 22D) narrow at apex, gradually expanding to apex, 1.3x as long as prosternum at midline; apex rounded. **Protibiae** maximum width about one-third its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, serrate, with socketed spines. **Meso- and metatibiae** expanded at apical half; outer edge serrate, with socketed spines. **Metaventrite** punctures coarse, deep; interspaces, microreticulate; discrimen absent; posterior margin notch 0.07x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, deep, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.17, 0.06, 0.06, 0.05, 0.10; first abdominal ventrite devoid of sex patch.

Females. Unknown.

Type material. Lectotype ♂, here designated (MNHN, Fig. 22(A–F)) “Guadeloupe [printed] \ Ciside Nº 17 [handwritten] \ *Ceracis* pres *bifurcus* Gorh. [handwritten] \ *Ceracis grandicollis* n. sp. [handwritten] \ *Ceracis laticornis* n. sp. [handwritten] \ LECTOTYPE *Ceracis laticornis* Pic [red paper; handwritten]”. Additionally labeled “*Anartioscelos laticornis* (Pic, 1922) comb. nov. Souza-Gonçalves & Lopes-Andrade”

Host fungus. Unknown.

Distribution. Lesser Antilles. Known from Guadeloupe (Fig. 44).

Comments. The species is known only from the type series (Pic, 1922), as far as we have traced.

Atomocis gen. nov.

Fig. 23(A–G); Fig. 24(A–H); Fig. 25(A–D); Fig. 45

Type species: *Atomocis melanus* **sp. nov.**.

Etymology: The genus name derives from the Latin noun “atomus”, which means “a small particle”, “atom”, and “*Cis*”, both in the nominative singular. The name is a reference to the small size of the body.

Diagnosis. This genus is distinguished by the short, oblong-ovate body, single pronotal and elytral punctation, single vestiture of minute setae, antennae 10-segmented with short club (less than 1.3x as long as funicle), the club with basal segment reduced, prosternum carinate, all tibiae enlarged at apical half and with broadly rounded outer apical angle. Body shape resembles that of apterous and micropterous Ciidae (*e.g. Atlantocis* Israelson, 1985, *Apterocis* Perkins, 1900, *Lipopterocis* Miyatake, 1954, *Neoapterocis* Lopes-Andrade, 2007, *Nipponapterocis* Miyatake, 1954, *Notapterocis* Lawrence, 2016 and *Polynesicis* Zimmerman, 1938), but species of *Atomocis* **gen. nov.** differ in the metaventrite long at midline, and well-developed scutellar shield and metathoracic wings.

Description. Body (Figs 23(A–C), 25(A–C)) short, oblong-ovate, convex; dorsal vestiture, single, consisting of minute setae. **Head** anteriormost portion visible from above; anterocephalic edge in males produced, elevated forming two short plates

(Fig. 23D); in females, produced forming two plates shorter than in males (Fig. 25C). **Antennae** (Fig. 24A) 10-segmented; antennal club short (less than 1.3x as long as funicle), 3-segmented; apical segment pentagonal and basal segment reduced, with sensillifers at apical border; third segment as long as fourth. **Labrum** longer than wide, truncate. **Mandibular molae** well-developed. **Apical maxillary palpomere** (Fig. 23F) pyriform. **Prementum** (Fig. 23F) short, broadly rounded at apex; ligula conspicuous. **Labial palps** (Fig. 23F) 3-segmented; apical palpomere shorter and narrower than inflated longer preapical palpomere. **Gular sutures** bowed. **Pronotum** (Fig. 23E) lateral edges slightly expanded, visible for their entire lengths from above; punctation, single; each puncture with one minute seta; anterior edge rounded in both sexes. **Prosternum** (Fig. 23D) in front of coxae slightly longer than prosternal process; carinate; prosternal process moderately broad, subparallel-sided. **Procoxae** transverse, not projecting below plane of prosternal process (Fig. 23C, 25C). **Meso- and metacoxae** transverse. **Scutellar shield** (Fig. 23E) well-developed. **Elytra** (Fig. 23E) slightly elongate, more than 1.60x as long as pronotum; punctation, single; each puncture with one minute seta. **Metathoracic wings** well-developed. **Mesocoxal cavities** (Fig. 23G) widely separated, completely closed. **Metaventrite** (Fig. 23G) strongly convex, longer than first abdominal ventrite at midline; posterior margin not notched; discrimen, absent. **Pro- meso- and metatibiae** (Fig. 24(B–D)) similar in shape, enlarged at apical half; outer apical angle roudned. **First abdominal ventrite** as long as second and third ventrites combined, with sex patch in males. **Male terminalia** (Fig. 24(E–H)): tegmen elongate, spear-shaped with lateral angulations (Fig. 24G, small black arrows); apex rounded; penis about as long and as wide as tegmen, enlarged and membranous at apex. **Female terminalia** (Fig. 25D): elongate; gonostyli slender; gonocoxites converging to apex; basal baculi of gonocoxites transverse; paraprocts shorter than gonocoxites.

Included species: *Atomocis melanus* **sp. nov.**. There are other two species, one from Zapata Department (Guatemala) and another from Barro Colorado Island (Panama), the former known from a short series with only one male in poor conditions, and the latter only from tenerals, thus we prefer not to describe them here.

Distribution: Central America. Know from Guatemala and Panama.

Atomocis melanus sp. nov.

Fig. 23(A–G); Fig. 24(A–H); Fig. 25(A–D); Fig. 45

Type locality. “Campana”, coordinates 08º43’N 79º54’ W (Capira District, Panamá Oeste Province, Panama).

Etymology. The species name derives from the Latinized Greek noun “melanos”, which means “black”, “dark”. The name is a reference to the dark dorsum of the species.

Description, male holotype (Fig. 23(A–E)). Adult fully pigmented, lacking two tarsi. Measurements in mm: TL 0.99, PL 0.33, PW 0.53, EL 0.66, EW 0.62, GD 0.47. Ratios: PL/PW 0.63, EL/EW 1.06, EL/PL 1.98, GD/EW 0.76, TL/EW 1.60. **Body** dorsum reddish black; venter reddish dark brown; antennae yellowish brown; antennal club dark brown; palpi and tarsi yellowish brown; dorsal vestiture consisting of minute suberect setae, only visible in high magnifications (>100x); ventral vestiture of minute decumbent setae, only visible in high magnifications (>100x). **Head** (Fig. 23D) dorsal punctation single; punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one minute decumbent seta (<0.01 mm); interspaces smooth, shiny; anterocephalic edge produced, elevated forming two small, converging triangular plates (length 0.08 mm; basal width 0.09 mm; basal separation 0.09 mm), apices subacute. **Antennae** (Fig. 24A, left antenna in paratype from Barro Colorado Island) lengths as follows (in mm, left antenna measured): 0.06, 0.04, 0.03, 0.03, 0.01, 0.01, 0.01, 0.02, 0.03, 0.06 (FL 0.08 mm, CL 0.10 mm, CL/FL 1.22). **Eyes** coarsely facetted, with about 20 ommatidia; GW 0.08 mm. **Gula** 0.41x as wide as head. **Pronotum** (Fig. 23E) punctures fine, shallow, separated from each other by 3–4 puncture-widths; interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (<0.01 mm); lateral edges not crenulate, barely explanate, entirely visible when seen from above; anterior and posterior corners subacute. **Scutellar shield** triangular, with few punctures; apparently glabrous; BW 0.04 mm; SL 0.03 mm. **Elytra** punctation non-seriate; punctures fine, shallow, separated from each other by 2 puncture-widths or less; interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (~0.01 mm). **Metathoracic wings** apparently functional. **Hypomera** punctures fine, shallow; almost glabrous; interspaces, microreticulate. **Prosternum**

(Fig. 23D) interspaces, microreticulate. **Prosternal process** (Fig. 23D) 0.9x as long as prosternum at midline; apex truncate. **Protibiae** (Fig. 24B, left protibia in paratype from Barro Colorado Island) maximum width about one-third its length; apical edge with spines; outer apical angle rounded; outer edge enlarged at apical half, smooth. **Meso- and metatibiae** (Fig. 24(C–D), left meso- and metatibia in paratype from Barro Colorado Island, respectively) apical edge with spines; outer edge enlarged at apical half, smooth. **Metaventrite** (Fig. 23G, in paratype from Barro Colorado Island) punctures coarse, deep; interspaces, microreticulate; discrimen absent. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.11, 0.06, 0.05, 0.04, 0.06; first abdominal ventrite with margined, oval, setose sex patch posteriorly, transverse diameter of 0.05 mm. **Male terminalia in paratype from Barro Colorado Island** (Fig. 24(A–H)): **sternite VIII** (Fig. 24E) apical margin straight, with short long setae at acute corners; basal portion membranous. **Tegmen** (Fig. 24G) 4.4x as long as wide, widest near base; elongate, converging to apex; lateral and apical portion mostly membranous; medial portion with arrow-shaped sclerotization (Fig. 24G, big black arrow) forming lateral angulations (Fig. 24G, small black arrows); apex and basal portion rounded. **Basal piece** (Fig. 24F) subpentagonal, 1.2x as wide as long. **Penis** (Fig. 24H) as long as tegmen, 3.5x as long as wide; subparallel-sided, expanding near apex; apical portion consisting of pleated membrane; basal portion subtriangular.

Females (Fig. 25(A–D)). Anterior edge of head elevated, produced forming two rounded plates, shorter than those in males. Anterior edge of pronotum rounded. Otherwise like males, but without abdominal sex patch. **Female terminalia in paratype from Barro Colorado Island** (Fig. 25D): spiculum ventrale (not shown) 1.08x as long as ovipositor (Fig. 25D); ovipositor 2.25x as long as wide; paraprocts (Fig. 25D) 0.88x as long as gonocoxites; gonocoxites (Fig. 25D) 1.22x as long as their combined widths, each with narrowly rounded apex; each gonostylus (Fig. 25D) 0.18x as long as respective gonocoxite, 4.83x as long as wide.

Variation. Males, measurements in mm (n= 6, including the holotype): TL 0.83–0.99 (0.92 ± 0.06), PL 0.30–0.35 (0.33 ± 0.02), PW 0.45–0.58 (0.52 ± 0.04), EL 0.53–0.66 (0.59 ± 0.05), EW 0.50–0.62 (0.57 ± 0.04), GD 0.38–0.48 (0.44 ± 0.04),

PL/PW 0.61–0.67 (0.65 ± 0.02), EL/EW 0.96–1.06 (1.03 ± 0.04), EL/PL 1.64–1.98 (1.76 ± 0.12), GD/EW 0.74–0.79 (0.77 ± 0.02), TL/EW 1.52–1.68 (1.62 ± 0.06). Females, measurements in mm (n= 6): TL 0.90–0.95 (0.93 ± 0.02), PL 0.33–0.35 (0.33 ± 0.01), PW 0.48–0.58 (0.54 ± 0.03), EL 0.58–0.63 (0.60 ± 0.02), EW 0.53–0.63 (0.60 ± 0.04), GD 0.40–0.48 (0.45 ± 0.03), PL/PW 0.57–0.68 (0.62 ± 0.05), EL/EW 0.96–1.10 (1.00 ± 0.05), EL/PL 1.64–1.92 (1.79 ± 0.10), GD/EW 0.72–0.80 (0.76 ± 0.03), TL/EW 1.48–1.71 (1.55 ± 0.08).

Type material. Holotype ♂ (FMNH) "Cerro Campana, Panama, PANAMA, Ag. 9, 1969 \ J.F. Lawrence, Lot 3016 \ *Polyporus trichomallus* \ *Atomocis melanus* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]". **Paratypes:** 33 ♂♂ and 32 ♀♀ as follows: 1 ♂ (CELC), same data as holotype; 1 ♀ (CELC) "Cerro Campana, Panama, PANAMA, Ag.9, 1969 \ J.F. Lawrence, Lot 3010 \ *Ganoderma* sp."; 1 ♂ (ANIC) "Barro Colorado Is., CANAL ZONE, July 13 1969 \ J.F. Lawrence, Lot 2862 \ ex *Polyporus licnoides*"; 1 ♂ (CELC, dissected) "Barro Colorado Is., CANAL ZONE, July 14 1969 \ J.F. Lawrence, Lot 2882"; 12 ♂♂ (1 ANIC; 3 CELC, one dissected and stored in glycerin; 6 FMNH; 2 QMBA) and 10 ♀♀ (2 ANIC; 2 CELC, one dissected and stored in glycerin; 4 FMNH; 2 QMBA) "Barro Colorado Island, PANAMA, 11.vii.1969, J.F. Lawrence Lot 2850 \ ex *Trichaptum perrottetti* [sic]"; 5 ♂♂ (3 CELC; 2 FMNH) and 4 ♀♀ (2 CELC; 2 FMNH) "Barro Colorado Is., CANAL ZONE, July 11 1969 / J.F. Lawrence, Lot 2850 / *Polyporus trichomallus*"; 4 ♂♂ and 3 ♀♀ (CELC) "Barro Colorado Is., CANAL ZONE, July 27 1969 / J.F. Lawrence, Lot 2475 / *Polyporus trichomallus*"; 2 ♂♂ (CELC) "Barro Colorado Is., CANAL ZONE, July 13 1969 / J.F. Lawrence, Lot 2862 / ex *Polyporus licnoides*"; 1 ♀ (CELC) "Barro Colorado Is., CANAL ZONE, July 13 1969 / J.F. Lawrence, Lot 2864 / *Rigidoporus* sp."; 2 ♀♀ (1 CELC; 1 FMNH) "Barro Colorado Is., CANAL ZONE, Aug 13 1969 / J.F. Lawrence, Lot 3026 / ex *Polyporus iodinus*"; 2 ♂♂ (FMNH) "Barro Colorado Is., CANAL ZONE, July 8 1969 / J.F. Lawrence, Lot 2805 / *Polyporus trichomallus*"; 2 ♀♀ (1 CELC; 1 FMNH) "PANAMA: Canal Zone, Barro Colorado Is., February 6 1976 / litter under rotting logs"; 3 ♂♂ (2 CELC; 1 FMNH) and 3 ♀♀ (2 CELC; 1 FMNH) "CANAL ZONE: Is. Barro Colorado, II/19-III-9-75, Lawrence, Ewrin / J.F. Lawrence, Lot 3876 / *Nigroporus vinosus*"; 1 ♂ and 3 ♀♀ (CELC) "Barro Colorado Is., CANAL ZONE, Feb. 17, 1968 / J.F. Lawrence, Lot. 2438 / *Panus siparius* [handwritten]"; 1 ♀ (CELC) "Barro Colorado Is., CANAL ZONE, Feb. 17, 1968 / J.F. Lawrence, Lot. 2439 / *Fomes sclerodermus*"; 1 ♂ (CELC) "Barro Colorado Is., CANAL ZONE, Feb. 28, 1968 / J.F. Lawrence, Lot. 2480 / *Hexagonia papyracea*"; 1 ♀ (CELC) "Barro Colorado Is., CANAL ZONE, July 3 1969 / J.F. Lawrence, Lot 2749 / ex *Polyporus sector*"; 1 ♀ (CELC) "Barro Colorado Is., Canal Zone, Pan. II-22-68 / J.F. Lawrence, Lot 2480 / *Hexagonia variegata*". All paratypes additionally labeled "*Atomocis melanus* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]".

Host fungi. *Fomes fasciatus* (Sw.) Cooke (Polyporaceae), one record; *Ganoderma* sp. (Ganodermataceae), one record; *Hymenochaete iodina* (Mont.) Baltazar & Gibertoni (Hymenochaeteceae), one record; *Nigroporus vinosus* (Berk.) Murrill (Polyporaceae), one record; *Panus tephroleucus* (Mont.) T.W. May & A.E. Wood (Polyporaceae), one record; *Phellinus gilvus* (Schwein.) Pat. (Hymenochaetaceae), two records; *Rigidoporus* sp. (Meripilaceae), one record; *Trametes variegata* (Berk.) Zmitr., Wasser & Ezhov (Polyporaceae), two records; *Trichaptum perrottetii* (Lév.) Ryvarden (Hymenochaetales), one breeding record; *Trichaptum sector* (Ehrenb.) Kreisel (Hymenochaetales), one record; *Trichaptum trichomallum* (Berk. & Mont.) Murril (Hymenochaetales), three records.

Distribution. Central America. Known from Barro Colorado Island and Panamá Oeste Province (Panamá) (Fig. 45).

Gyraleosomus gen. nov.

Fig. 26(A–G); Fig. 27(A–G); Fig. 28(A–E); Fig. 46

Type species: *Gyraleosomus boliviensis* **sp. nov.**.

Etymology: The genus name derives from the Greek adjective "gyraleos", which means "rounded", "curved", and the Latinized Greek noun "soma", which means "body". The name is a reference to the very rounded body of members in this genus.

Diagnosis. This genus is distinguished by the short, oblong-ovate body, single vestiture of minute setae arising from megapunctures on pronotum and from micropunctures on elytra, dual pronotal and elytral punctation, metathoracic wings absent, antennae 10-segmented, carinate prosternum, and all tibiae enlarged at apical three-fourths. It resembles other flightless Ciidae (*e.g.* *Atlantocis* Israelson, 1985, *Apterocis* Perkins, 1900, *Lipopterocis* Miyatake, 1954, *Neoapterocis* Lopes-Andrade, 2007, *Nipponapterocis* Miyatake, 1954, *Notapterocis* Lawrence, 2016 and *Polynesicis* Zimmerman, 1938) in the short, oblong-ovate body, metaventrite short at midline and reduced scutellar shield, but *Gyraleosomus* differs in bearing first abdominal ventrite shorter than second and third combined, female terminalia short, with paraprocts very reduced and shorter than proctiger.

Description. Body (Figs 26(A–C), 28(A–C)) oblong-ovate, convex; dorsal vestiture, single, consisting of minute setae. **Head** anteriormost portion visible from above; anterocephalic edge in males produced, elevated forming two plates (Fig. 26D); in females, slightly produced forming two tubercles (Fig. 28C). **Antennae** (Fig. 27A) 10-segmented; antennal club long (more than 1.4x as long as funicle), 3-segmented; apical segment rounded, with sensillifers placed laterally in each segment; third segment at least 1.3x longer than fourth. **Labrum** longer than wide, subtruncate. **Mandibular molae** weakly developed. **Apical maxillary palpomere** (Fig. 26F) pyriform. **Prementum** (Fig. 26F) short, slightly rounded at apex; ligula apparently absent. **Labial palps** (Fig. 26F) 3-segmented; apical palpomere as long as and narrower than inflated preapical palpomere. **Gular sutures** bowed. **Pronotum** (Fig. 26E) lateral edges very narrow, barely visible for their entire lengths from above; punctation, dual; megapunctures with setae; micropunctures apparently glabrous; anterior edge rounded in both sexes. **Prosternum** (Fig. 26D) in front of coxae slightly shorter than prosternal process, carinate; prosternal process broad, subparallel-sided. **Procoxae** transverse, not projecting below plane of prosternal process (Fig. 26C, 28C). **Meso- and metacoxae** transverse. **Scutellar shield** (Fig. 26E) reduced. **Elytra** (Fig. 26E) fused, slightly elongate, at least 1.50x as long as pronotum; punctation, dual; micropunctures with setae, megapunctures apparently glabrous. **Metathoracic wings** absent. **Mesocoxal cavities** (Fig. 26G) narrowly separated, completely closed. **Metaventrite** (Fig. 26G) strongly convex, shorter than first abdominal ventrite at midline; posterior margin, notched; discrimen, absent. **Pro- meso- and metatibiae** (Fig. 27(B–D)) similar in shape, enlarged at apical three-fourths. **First abdominal ventrite** as long as second and third ventrites combined, with sex patch in males. **Male terminalia** (Fig. 27(E–G)): tegmen subquadrate, apex with broad, shallow emargination; penis narrower and slightly longer than tegmen. **Female terminalia** (Fig. 28(D–E)): short; gonostyli short;

gonocoxites subtriangular, converging to apex, devoid of conspicuous ventral lobes; basal baculi of gonocoxites very oblique, slightly shorter than outer edge of gonocoxites; paraprocts very reduced, shorter than proctiger.

Included species: *Gyraleosomus boliviensis* **sp. nov.**

Distribution: South America. Known from Bolivia.

Gyraleosomus boliviensis sp. nov.

Fig. 26(A–G); Fig. 27(A–G); Fig. 28(A–E); Fig. 46

Type locality. "Cochabamba", coordinates 17º23'S 66º10'W (Cercado Province, Cochabamba Department, Bolivia).

Etymology. The species name is Latinized from "Bolivia". The name is a reference to the country where the type series was collected.

Description, male holotype (Fig. 26(A–E)). Adult apparently not fully pigmented, lacking right antenna, left metafemur, left metatibia, two tarsi; being covered by dust or fungus. Measurements in mm: TL 1.31, PL 0.48, PW 0.73, EL 0.83, EW 0.87, GD 0.69. Ratios: PL/PW 0.66, EL/EW 0.95, EL/PL 1.72, GD/EW 0.79, TL/EW 1.51. **Body** dorsum dark brown, pronotum reddish brown (visible only at head and elytra due to dust-covering, but visible in paratypes); venter dark brown (visible only at prosternum and metaventrite due to dust-covering, but visible in paratypes); antenna pale brown; antennal club dark brown; palpi and tarsi pale brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnifications (>60x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>60x). **Head** (Fig. 26D) dorsal punctation single; punctures coarse, deep, separated from each other by 1 puncture-width or less, each with one minute decumbent seta (~0.01 mm); interspaces, microreticulate; anterocephalic edge produced, elevated forming two small, subtriangular converging plates (length 0.08 mm; basal width 0.11 mm; basal separation 0.11 mm), apices acute. **Antennae** (Fig. 27A, left antenna in paratype) length of segments as follows (in mm, left antenna measured): 0.07, 0.05, 0.04, 0.03, 0.02, 0.02, 0.02, 0.05, 0.05, 0.08 (FL 0.12 mm, CL 0.18 mm, CL/FL 1.48). **Eyes** coarsely facetted, with about 30 ommatidia; GW 0.12 mm. **Gula** 0.35x as wide as head. **Pronotum** (Fig. 22E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1 megapuncture-width or less; interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (~0.02 mm); lateral edges slightly crenulate, not explanate, barely visible when seen from above; anterior corners subacute; posterior corners rounded. **Scutellar shield** triangular, with few punctures; apparently glabrous; BW 0.05 mm; SL 0.05 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (~0.02 mm). **Hypomera** punctures coarse, deep, each with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 26D) interspaces, microreticulate. **Prosternal process** (Fig. 26D) 1.2x as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 27B, left protibia in paratype) maximum width about one-fourth its length; apical edge with spines; outer apical angle subrounded; outer edge expanded at apical three-fourths and smooth. **Meso- and metatibiae** (Fig. 27(C–D), left meso- and metatibia in paratype, respectively), apical edge with spines; outer edge expanded at apical three-fourths, smooth. **Metaventrite** (Fig. 26G, in paratype) punctures coarse, deep; interspaces, microreticulate; discrimen absent; posterior margin notch 0.19x as long as metaventrite at midline. **Abdominal ventrites** punctures coarse, deep, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.14, 0.07, 0.07, 0.07, 0.10; first abdominal ventrite with margined, circular, setose sex patch posterad of center, transverse diameter of 0.06 mm. **Male terminalia in paratype** (Fig. 27(E–G)): **sternite VIII** (Fig. 27E) apical margin sinuous, with short, long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 27F) 1.2x as long as wide, widest at middle; subparallel-sided, converging to base; apex shallowly emarginate at middle; inner apical edge of sides with angulations (Fig. 27F, big black arrows) and narrow excavations (Fig. 27F, small black arrows); basal portion triangular. **Penis** (Fig. 27G) 1.3x as long as tegmen, 2.6x as long as wide; sides converging to base; apex with rounded projections (Fig. 27G, black arrows), apical and lateral portions consisting of pleated membrane; basal portion rounded.

Females (Fig. 28(A–E)). Anterior edge of head slightly produced forming two small tubercles. Anterior edge of pronotum rounded. Otherwise like males, but without cephalic plates and abdominal sex patch. **Female terminalia in paratype** (Fig. 28(D–E)): spiculum ventrale (Fig. 28E) 0.93x as long as ovipositor (Fig. 28E); ovipositor 1.54x as long as wide; paraprocts (Fig. 28E) 0.71x as long as gonocoxites; gonocoxites (Fig. 28E) 1.15x as long as their combined widths, each with narrowly rounded apex; each gonostylus (Fig. 28E) 0.08x as long as gonocoxite, 1.29x as long as wide.

Variation. Females, measurements in mm (n= 4): TL 1.38–1.45 (1.44 ± 0.05), PL 0.55–0.60 (0.57 ± 0.02), PW 0.75–0.80 (0.77 ± 0.02), EL 0.83–0.90 (0.88 ± 0.04), EW 0.88–0.95 (0.91 ± 0.04), GD 0.70–0.78 (0.73 ± 0.04), PL/PW 0.73–0.75 (0.74 ± 0.01), EL/EW 0.94–1.03 (0.97 ± 0.04), EL/PL 1.50–1.64 (1.54 ± 0.07), GD/EW 0.80–0.82 (0.81 ± 0.01), TL/EW 1.58–1.66 (1.59 ± 0.04).

Type material. Holotype ♂ (MNHN) “MUSEUM PARIS, BOLIVIE, COCHABAMBA, (GERMAIN), H. DONCKIER 1907 \ *Gyraleosomus boliviensis* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”. **Paratypes:** 1 ♂ (CELC, dissected and stored in glycerin) and 5 ♀♀ (2 CELC, one dissected and stored in glycerin; 3 MNHN), same data as the holotype and additionally labeled “*Gyraleosomus boliviensis* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]”.

Host fungus. Unknown.

Distribution. South America. Known from Cochabamba Department (Bolivia) (Fig. 46).

Comments. The new species was recognized in historical material of MNHN, collected at the beginning of the 20th century.

***Insolitocis* gen. nov.**

Fig. 29(A–G); Fig. 30(A–E); Fig. 31(A–B); Fig. 45

Type species: *Insolitocis panamensis* **sp. nov.**.

Etymology: The genus name derives from the Latin adjective “insolitus”, which means “unusual”, “strange”, and “*Cis*”, the last in the nominative singular and the former in the genitive singular. The name is a reference to the strange pentagonal suturation present at the first abdominal ventrite and the unusual 11-segmented antennae, unique among Ciinae.

Diagnosis. This genus is distinguished by the elongate body, dual pronotal and elytral punctation, single pronotal vestiture of minute setae arising from megapunctures, antennae 11-segmented, antennal club with small basal segment, with sensillifers organized as continuous sensory areas at the apical portion of each club segment, prosternum carinate, all tibiae club-shaped, with outer edge serrate at apical two-thirds. *Insolitocis* **gen. nov.** somewhat resembles species of *Australocis* Lawrence, 2016 and *Nipponapterocis* Miyatake, 1954 in the club segments of antennae with sensillifers organized as continuous sensory areas at the apical portion of each club segment, but the latter differs in the 10-segmented antennae and rudimentary metathoracic wings, while the former differ in the 10-segmented antennae and outer apical angle of protibiae produced in a stout tooth.

Description. Body (Fig. 29(A–C)) elongate, subparallel-sided, convex; dorsal vestiture, single, consisting of minute setae. **Head** (Fig. 29D) anteriormost portion visible from above; anterocephalic edge slightly produced, sinuous, forming two very short, lateral plates. **Antennae** (Fig. 30B) 11-segmented; antennal club long (more than 1.5x as long as funicle), 3-segmented, with sensillifers organized as continuous sensory areas at apical portion of each segment, apical segment rounded, basal segment reduced; third segment at least 3x longer than fourth. **Labrum** (Fig. 30A) longer than wide, subrounded. **Mandibular molae** well-developed. **Apical maxillary palpomere** (Fig. 30A) pyriform. **Prementum** (Fig. 30A) long, slightly rounded at apex; ligula conspicuous. **Labial palps** (Fig. 30A) 3-segmented; apical palpomere as long as and narrower than inflated preapical palpomere; basal palpomere long. **Gular sutures** bowed. **Pronotum** (Fig. 29E) lateral edges narrow, visible for their entire lengths from above; punctation, dual; megapunctures with setae; micropunctures apparently glabrous; anterior edge rounded. **Prosternum** (Fig. 29D) in front of coxae as long as prosternal process, carinate; prosternal process moderately broad, subparallel-sided. **Procoxae** transverse, not projecting below plane of prosternal process (Fig. 29C). **Meso- and metacoxae** transverse. **Scutellar shield** (Fig. 29E) well-developed. **Elytra** (Fig. 29E) elongate, more than 1.50x as long as pronotum; punctation, dual; megapunctures with setae; micropunctures apparently glabrous. **Metathoracic wings** well-developed. **Mesocoxal cavities** (Fig. 29F) narrowly separated, open at inner side. **Metaventrite** (Fig. 29F) strongly convex, longer than first abdominal ventrite; posterior margin not notched; discrimen, present. **Pro- meso- and metatibiae** (Fig. 30(C–E)) similar to each other, club-shaped; outer edge serrate at apical two-thirds. **First abdominal ventrite** longer than second and third ventrites combined, with pentagonal suturation (Fig. 29G). **Female terminalia** (Fig. 31(A–B)): elongate; gonostyli slender; gonocoxites sclerotized, converging to apex; basal baculi of gonocoxites slightly oblique, much shorter than outer edges of gonocoxites; paraprocts shorter than gonocoxites.

Included species: *Insolitocis panamensis* **sp. nov.**.

Distribution: Central America. Known from Panama.

Insolitocis panamensis sp. nov.

Fig. 29(A–G); Fig. 30(A–E); Fig. 31(A–B); Fig. 45

Type locality. “Barro Colorado Island”, coordinates 09º09’N 79º51’W (Canal Zone, Panama).

Etymology. The species name is Latinized from “Panama”. The name is a reference to the country where the type series was collected.

Description, female holotype (Fig. 29(A–E, G)). Adult apparently not fully pigmented, lacking left metafemur, left metatibia and one tarsus. Measurements in mm: TL 1.10, PL 0.40, PW 0.51, EL 0.71, EW 0.56, GD 0.47. Ratios: PL/PW 0.78, EL/EW 1.26, EL/PL 1.79, GD/EW 0.83, TL/EW 1.96. **Body** dorsum and venter reddish brown; antennae, palpi and tarsi yellowish brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnifications (>60x); ventral vestiture consisting of minute decumbent setae, easily discernible in high magnifications (>60x). **Head** (Fig. 29D) dorsal punctation single; punctures coarse, deep, separated from each other by 1–2 puncture-widths, each with one minute decumbent seta (<0.01 mm); interspaces, microreticulate. **Antennae** (Fig. 30B, left antenna in paratype) lengths as follows (in mm, left antenna measured): 0.07, 0.04, 0.03, 0.01, 0.02, 0.01, 0.01, 0.01, 0.02, 0.05, 0.07 (FL 0.09 mm, CL 0.14 mm, CL/FL 1.54). **Eyes** coarsely facetted, with about 50 ommatidia; GW 0.10 mm. **Gula** 0.29x as wide as head. **Pronotum** (Fig. 29E) megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2 megapuncture-widths or less; interspaces, microstriated; vestiture single, consisting of one minute suberect yellowish seta (<0.01 mm) lateral edges crenulate, not explanate, entirely visible when seen from above; anterior corners acute; posterior corners broadly rounded. **Scutellar shield** triangular, with few punctures; apparently glabrous; BW 0.06 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2 megapuncture-widths or less; interspaces smooth, shiny; vestiture single, consisting of minute suberect yellowish setae (~0.01 mm). **Hypomera** puncture coarse, shallow; almost glabrous; interspaces, microreticulate. **Prosternum** (Fig. 29D) interspaces, microreticulate. **Prosternal process** (Fig. 29D) as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 30C, left protibia in paratype) with maximum width about one-third its length; apical edge with spines; outer apical angle expanded; outer edge expanded at apical two-thirds, serrate. **Meso- and metatibiae** (Fig. 30(D–E), left meso- and metatibia in paratype, respectively) with spines in apical edge; outer edge expanded at apical two-thirds, serrate. **Metaventrite** (Fig. 29F, in paratype) punctures coarse, deep; interspaces, microreticulate; discrimen about one-fifth the length of metaventrite at midline. **Abdominal ventrites** punctures coarse, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.12, 0.05, 0.05, 0.04, 0.09; first abdominal ventrite with pentagonal suturation 1.93x as long as wide, widest at posterior portion, apex acute between metacoxae (Fig. 29G). **Female terminalia in paratype** (Fig. 31(A–B)): spiculum ventrale (Fig. 31A) 0.57x as long as ovipositor (Fig. 31B); ovipositor 1.80x as long as wide, widest at base; paraprocts (Fig. 31B) 0.48x as long as gonocoxites; gonocoxites (Fig. 31B) 1.24x as long as their combined widths, each with narrowly rounded apex, with two ventral lobes, basal lobe shorter than apical lobe; each gonostylus (Fig. 31B) 0.12x as long as respective gonocoxite, 3.24x as long as wide.

Male. Unknown.

Variation. Females, measurements in mm (n= 5, including the holotype): TL 1.00–1.10 (1.06 ± 0.04), PL 0.35–0.43 (0.38 ± 0.03), PW 0.45–0.51 (0.49 ± 0.02), EL 0.65–0.71 (0.67 ± 0.02), EW 0.40–0.50 (0.45 ± 0.03), GD 0.45–0.48 (0.47 ± 0.01), PL/PW 0.74–0.85 (0.79 ± 0.04), EL/EW 1.17–1.35 (1.25 ± 0.08), EL/PL 1.53–1.93 (1.76 ± 0.16), GD/EW 0.83–0.95 (0.87 ± 0.05), TL/EW 1.87–2.05 (1.97 ± 0.07).

Type material. Holotype ♀ (FMNH) “Barro Colorado Is., CANAL ZONE, July 2 1969 \ J.F. Lawrence, Lot 2741 \ *Fomes sclerodermeus* \ *Insolitocis panamensis* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”. **Paratypes:** 6 ♀♀ as follows: 2 ♀♀ (1 CELC, dissected; 1 ANIC) same data as the holotype; 4 ♀♀ (2 CELC, one dissected and stored in glycerin; 2 FMNH) “Barro Colorado Is., CANAL ZONE, July 14 1969 \ J.F. Lawrence, Lot 2885 \ *Ganoderma* sp.”. All paratypes additionally labeled “*Insolitocis panamensis* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]”.

Host fungi. *Fomes fasciatus* (Sw.) Cooke (Polyporaceae), one record; *Ganoderma* sp. (Ganodermataceae); one record.

Distribution. Central America. Known from Barro Colorado Island (Panama) (Fig. 41).

Lipedanicis gen. nov.

Fig. 32(A–E); Fig. 33(A–H); Fig. 34(A–D); Fig. 35(A–E); Fig. 36(A–I); Fig. 37(A–D); Fig. 38(A–G); Fig. 39(A–G); Fig. 40(A–H); Fig. 41(A–E); Fig. 42(A–B); Fig. 46

Type species: *Lipedanicis geminus* **sp. nov.**.

Etymology: The new genus is named in honor of Felipe and Daniel, sons of the senior author. The name derives from their nicknames “Lipe” and “Dani”, and “*Cis*”, all in the nominative singular.

Diagnosis. This genus is distinguished by the elongate body, single elytral vestiture consisting of minute setae arising from micropunctures, prosternum tumid (*Lip. adelphus* **sp. nov.**) or tumid and carinate, outer apical angle of protibiae projected in an acute tooth, outer apical angle of meso- and metatibiae angulate. It mostly resembles *Abebaeocis* **gen. nov.**, which differs in the elytral vestiture arising from micropunctures, outer apical angle of protibiae not produced into a tooth, female terminalia with gonocoxites with two conspicuous ventral lobes, and basal baculi of gonocoxites slightly oblique, much shorter than outer edges of gonocoxites. *Lipedanicis* **gen. nov.** somewhat resembles species in the *Cis taurus* species-group, especially the anterocephalic projections of males, but the latter differ in the always 10-segmented antennae, prosternal process comparatively narrower at middle and enlarged at apex, longer dorsal vestiture and outer edge of protibiae always smooth.

Description. Body elongate, subparallel-sided (Figs 35(A–C), 37(A–C), 38(A–G), 39(A–C), 41(A–C)) or parallel-sided (Figs 32(A–C), 34(A–C)), convex; dorsal vestiture, single, consisting of minute setae. **Head** anteriormost portion visible from above; anterocephalic edge in males produced, elevated forming two horns (Figs 32D, 35D, 38(A, C–F), 39D); in females, slightly emarginate forming two plates (Figs 34C, 37C, 38(B, G)) or slightly produced forming two plates (Fig. 41C). **Antennae** (Figs 33A, 36A, 40A, 41(D–E)) 8- 9- or 10-segmented; antennal club long (from 1.6x to 2.6x as long as funicle) or short (at least 1.2x), 3-segmented; apical segment oval, with sensillifers placed laterally in each segment; third segment at least 1.3x longer than fourth. **Labrum** (Fig. 39F) longer than wide, subrounded. **Mandibular molae** well-developed. **Apical maxillary palpomere** (Fig. 39F) pyriform. **Prementum** (Fig. 39F) long, slightly rounded at apex; ligula apparently absent. **Labial palps** (Fig. 39F) 3-segmented; apical palpomere as long as and narrower than inflated preapical palpomere. **Gular sutures** bowed. **Pronotum** (Figs 32E, 35E, 39E) lateral edges narrow, visible or not visible for their entire lengths from above; punctation, single or dual; punctures or megapunctures with setae; micropunctures apparently glabrous; anterior edge rounded in both sexes. **Prosternum** (Figs 32D, 35D, 39D) in front of coxae as long as or slightly shorter than prosternal process; tumid or tumid and carinate; prosternal process moderately broad, subparallel-sided. **Procoxae** transverse, not projecting below plane of prosternal process (Fig. 32C, 34C, 35C, 37C, 39C, 41C). **Meso- and metacoxae** transverse. **Scutellar shield** (Figs 32E, 35E, 39D) well-developed. **Elytra** (Figs 32E, 35E, 39E) elongate, more than 1.50x as long as pronotum; punctation, dual; each micropunctures with one seta; megapunctures apparently glabrous. **Metathoracic wings** well-developed. **Mesocoxal cavities** (Fig. 39G) narrowly separated, completely closed. **Metaventrite** (Fig. 39G) slightly or strongly convex, longer than first abdominal ventrite at midline, with notch at posterior margin, with discrimen. **Protibiae** (Figs 33B, 36B, 40B) outer edge irregularly serrate or smooth; outer apical angle projected in acute tooth. **Mesotibiae** (Figs 33C, 36C, 40C) outer edge with setae, irregularly serrate between setae or smooth; angulated from apical edge to outer edge. **Metatibiae** (Figs 33D, 36D, 40D) outer edge smooth; angulated from apical edge to outer edge. **First**

abdominal ventrite shorter than second and third ventrites combined, with or without sex patch in males. **Male terminalia** (Figs 33(E–H), 36(E–I), 40(E–H)): subquadrate; apex variable in shape, slightly to conspicuously emarginate; penis slender, about as long as to much longer than tegmen. **Female terminalia** (Figs 34D, 37D, 42(A–B)): short; gonocoxites converging to apex; basal baculi of gonocoxites very oblique, almost as long as as outer edges of gonocoxites; paraprocts short, as long as proctiger; gonostyli short.

Included species: *Lipedanicis adelphus* **sp. nov.**, *Lip. agastor* **sp. nov.** and *Lip. geminus* **sp. nov.**. A short series of a fourth species from Rio de Janeiro (Brazil) have been seen, but we've decided not to described it now because only one male in poor conditions was available.

Distribution: South America. Known from Brazil.

Key to species of *Lipedanicis*

1 Pronotal punctation single (Fig. 32E). Antennae 8-segmented (Fig. 33A); antennal club more than 2.5x as long as funicle. All tibiae with smooth outer edge............***Lip. adelphus* sp. nov.**

1' Pronotal punctation dual (Figs 35E, 39E). Antennae 9- or 10-segmented (Figs 36A, 40A, 41(D–E)); antennal club less than 2.0x as long as funicle. Outer edge of pro- and mesotibiae serrate (Figs 36(B–C), 40(B–C)), and of metatibiae smooth (Figs 36D, 40D)...**2**

2 (1') Metaventrite without discrimen (Figs 35C, 37C). Males without abdominal sex patch (Fig. 35C). Penis less than 1.5x as long as tegmen (Fig. 36(H–I))..***Lip. agastor* sp. nov.**

2' Metaventrite with discrimen (Figs 39(C, G), 41C). Males with abdominal sex patch (Fig. 39C). Penis more than 3.0x as long as tegmen (Fig. 40(H–I))...........***Lip. geminus* sp. nov.**

Lipedanicis adelphus sp. nov.

Fig. 32(A–E); Fig. 33(A–H); Fig. 34(A–D); Fig. 46

Type locality. “Parque Ecológico Quedas do Rio Bonito”, coordinates 21º19’S 44º58’W (Lavras, Minas Gerais, Brazil).

Etymology. The species name derives from the Latinized Greek noun “adelphos”, which means “twin”, “brother”, in the genitive singular. The name is a reference to the sons of the senior author.

Diagnosis. *Lipedanicis adelphus* **sp. nov.** differs from all other species in bearing antennae 8-segmented, single and comparatively coarser pronotal punctation, antennal club more than 2.5x as long as funicle and outer edge of tibiae smooth.

Description, male holotype (Fig. 32(A–E)). Adult apparently not fully pigmented, lacking one tarsus. Measurements in mm: TL 1.14, PL 0.41, PW 0.52, EL 0.74, EW 0.58, GD 0.48. Ratios: PL/PW 0.79, EL/EW 1.27, EL/PL 1.81, GD/EW 0.83, TL/EW 1.97. **Body** parallel-sided, dorsum and venter reddish dark brown; antennae yellowish brown; antennal club dark brown; palpi and tarsi yellowish brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnifications (>80x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>50x). **Head** (Fig. 32D) dorsal punctation single; punctures coarse, deep, separated from each other by 1 puncture-width or less, each with one minute decumbent seta (<0.01 mm; interspaces smooth, shiny; anterocephalic edge produced elevated forming two long, broadly laminate, converging horns (length 0.11 mm; basal width 0.11 mm; basal separation 0.06 mm), apices subacute; each horn tapering to apex. **Antennae** (Fig. 33A, left antenna in paratype) 8-segmented, lengths as follows (in mm, left antenna measured): 0.06, 0.04, 0.04, 0.02, 0.01, 0.05, 0.05, 0.07 (FL 0.07 mm, CL 0.17 mm, CL/FL 2.57). **Eyes** coarsely facetted, with about 70 ommatidia; GW 0.13 mm. **Gula** 0.54x as wide as head. **Pronotum** (Fig. 32E) punctation single; punctures deep, coarse, separated from each other by 1–2 puncture-widths (very small punctures visible in magnification ≥300x, about 0.2x as large as megapunctures); interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (<0.01 mm); lateral edges slightly crenulate, not explanate, barely visible when seen from above; anterior corners rounded; posterior corners broadly rounded. **Scutellar shield** triangular, with few punctures; apparently glabrous; BW 0.07 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths (very small punctures visible in magnification ≥300x, about 0.2x as large as megapunctures); interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (~0.01 mm). **Metathoracic wings** apparently functional. **Hypomera** punctures coarse, deep, each with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 32D) in front of coxae tumid; interspaces, microreticulate. **Prosternal process** (Fig. 32D) as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 33B, left protibia in paratype) maximum width about one-fourth its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, smooth. **Meso- and metatibiae** (Fig. 33(C–D), left meso- and metatibia in paratype, respectively) apical edge with spines; outer edge straight, smooth. **Metaventrite** punctures coarse, shallow; interspaces, microreticulate; discrimen about one-fifth the length of metaventrite at midline; posterior margin notch 0.06x as long as metaventrite at midline. **Abdominal ventrites** punctures fine, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.09, 0.07, 0.07, 0.06, 0.08; first abdominal ventrite devoid of sex patch. **Male terminalia in paratype** (Fig. 33(E–H)): **sternite VIII** (Fig. 33E) apical margin emarginate, with long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 33G) 1.6x as long as wide, widest near apex; subparallel-sided but more or less sinuous; apex deeply emarginate at middle, with angulations at inner apical edge (Fig. 33G, black arrows); basal portion rounded. **Basal piece** (Fig. 33F) subpentagonal, 1.6x as wide as long. **Penis** (Fig. 33H) 1.2x as long as tegmen, 3.9x as long as wide; subparallel-sided; apex rounded; basal portion with rounded emargination (Fig. 33H, red arrow).

Females (Fig. 34(A–D)). Anterior edge of head slightly emarginate forming two small tubercles. Anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns. **Female terminalia in paratype** (Fig. 34D): spiculum ventrale (Fig. 34D) 0.99x as long as ovipositor (Fig. 34D; ovipositor 1.39x as long as wide; paraprocts (Fig. 34D) 0.83x as long as gonocoxites; gonocoxites (Fig. 34D) 0.83x as long as their combined widths, each with narrowly subrounded apex; each gonostylus (Fig. 34D) 0.11x as long as respective gonocoxite, 1.56x as long as wide.

Variation. Males, measurements in mm (n= 5, including the holotype): TL 1.14–1.25 (1.20 ± 0.05), PL 0.38–0.45 (0.41 ± 0.03), PW 0.52–0.60 (0.56 ± 0.04), EL 0.74–0.85 (0.79 ± 0.04), EW 0.58–0.65 (0.61 ± 0.03), GD 0.48–0.53 (0.50 ± 0.02), PL/PW 0.67–0.79 (0.74 ± 0.05), EL/EW 1.24–1.35 (1.29 ± 0.04), EL/PL 1.78–2.13 (1.92 ± 0.16), GD/EW 0.76–0.87 (0.81 ± 0.05), TL/EW 1.92–2.00 (1.96 ± 0.04). Females, measurements in mm (n= 9): TL 1.13–1.43 (1.24 ± 0.09), PL 0.38–0.48 (0.42 ± 0.04), PW 0.50–0.60 (0.54 ± 0.04), EL 0.75–0.95 (0.82 ± 0.06), EW 0.55–0.68 (0.61 ± 0.04), GD 0.45–0.55 (0.51 ± 0.03), PL/PW 0.71–0.85 (0.78 ± 0.05), EL/EW 1.19–1.46 (1.34 ± 0.08), EL/PL 1.63–2.13 (1.96 ± 0.15), GD/EW 0.78–0.91 (0.83 ± 0.04), TL/EW 1.92–2.19 (2.03 ± 0.09).

Type material. Holotype ♂ (CELC) “BRASIL: MG, Lavras, “Parque Ecológico Quedas do Rio Bonito”; vi.2003, leg. F.Z. Vaz-de-Mello \ *Lipedanicis adelphus* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”. **Paratypes:** 7 ♂♂ and 9 ♀♀ as follows: 4 ♂♂ (CELC, two dissected) and 5 ♀♀ (CELC, one dissected) same data as the holotype; 3 ♂♂ (2 CELC, one dissected; 1 FMNH) and 3 ♀♀ (2 CELC; 1 FMNH) "BR: MG, Viçosa, Campus UFV, Lagoa próx. Supermercado Escola 12.iii.2010, leg. T. Fiorillo-Mariani & V.E. Sandoval-Gómez"; 1 ♀ (CELC) “BRASIL: RJ Nova Friburgo, Sans Souci, 18-20.i.2015, 22,16ºS 42,30ºO, 1050m, manual, leg. E.J. Grossi & C. Lopes-Andrade [printed] \ ex Hymenochaetaceae [handwritten]”. All paratypes additionally labeled “*Lipedanicis adelphus* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]”.

Host fungus. Hymenochaetaceae, one record.

Distribution. Brazil. Known from Minas Gerais and Rio de Janeiro (Southeast Brazil) (Fig. 46).

Comments. The species was collected only in areas of Atlantic Forest biome.

Lipedanicis agastor sp. nov.

Fig. 35(A–E); Fig. 36(A–I); Fig. 37(A–D); Fig. 38(A–G); Fig. 46

Type locality. “Floresta Nacional de São Francisco de Paula”, coordinates 29º25’S 50º23’W (São Francisco de Paula, Rio Grande do Sul, Brazil).

Etymology. The species name derives from the Greek noun "agastor", which means "from the same womb", "twin", in the genitive singular. The name is a reference to the sons of the senior author.

Diagnosis. *Lipedanicis agastor* **sp. nov.** differs from *Lip. adelphus* **sp. nov.** in the 9-segmented antennae, outer edge of pro- and mesotibiae serrate, metaventrite devoid of discrimen, and males bearing abdominal sex patch. It differs from *Lip. geminus* **sp. nov.** in being devoid of discrimen, males with abdominal sex patch and penis less than 1.5x as long as tegmen.

Description, male holotype (Fig. 35(A–E)). Adult apparently not fully pigmented but in good condition. Measurements in mm: TL 1.17, PL 0.46, PW 0.56, EL 0.71, EW 0.65, GD 0.55. Ratios: PL/PW 0.82, EL/EW 1.09, EL/PL 1.54, GD/EW 0.85, TL/EW 1.79. **Body** subparallel-sided, dorsum and venter yellowish dark brown, antennae yellowish brown; antennal club dark brown; palpi and tarsi yellowish brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnifications (>80x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>50x). **Head** (Fig. 35D) dorsal punctation dual; megapunctures coarse, shallow, about 2x as long as micropunctures, separated from each other by 2 puncture-widths or less, each with one minute decumbent seta (<0.01 mm); interspaces, microreticulate; anterocephalic edge produced, elevated forming two short, broadly laminate, parallel horns (length 0.10 mm; basal width 0.13 mm; basal separation 0.10 mm), apices rounded; sides of each horn parallel. **Antennae** (Fig. 36A, left antenna in paratype) 9-segmented, lengths as follows (in mm, left antenna measured): 0.06, 0.04, 0.04, 0.01, 0.02, 0.02, 0.04, 0.03, 0.06 (FL 0.08 mm, CL 0.14 mm, CL/FL 1.61). **Eyes** coarsely facetted, with about 60 ommatidia; GW 0.12 mm. **Gula** 0.50x as wide as head. **Pronotum** (Fig. 35E) punctation distinctly dual; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2 megapuncture-widths or less (very small punctures visible in magnification ≥300x, about 0.2x as large as megapunctures); interspaces, microreticulate; vestiture single, consisting of one minute suberect yellowish seta (<0.01 mm); lateral edges not crenulate, not explanate, not visible when seen from above; anterior corners subacute; posterior corners rounded. **Scutellar shield** triangular, with few punctures; apparently glabrous; BW 0.05 mm; SL 0.04 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 1–2 puncture-widths (very small punctures visible in magnification ≥300x, about 0.2x as large as megapunctures); interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (~0.01 mm). **Metathoracic wings** apparently functional. **Hypomera** punctures coarse, shallow, each with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 35D) in front of coxae tumid, carinate; interspaces, microreticulate. **Prosternal process** (Fig. 35D) 1.2x as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 36B, left protibia in paratype) maximum width about one third its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, serrate. **Mesotibiae** (Fig. 36C, left mesotibia in paratype) apicel edge with spines; outer edge straight, serrate. **Metatibiae** (Fig. 36D, left metatibia in paratype) apicel edge with spines; outer edge straight, smooth. **Metaventrite** punctures coarse, shallow; interspaces, microreticulate; discrimen absent; posterior margin notch 0.04x as long as metaventrite at midline. **Abdominal ventrites** punctures fine, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.12, 0.07, 0.07, 0.06, 0.09; first abdominal ventrite with unmargined, small, oval, setose sex patch posteriorly, transverse diameter of 0.02 mm. **Male terminalia in paratype** (Fig. 36(E–I)): **sternite VIII** (Fig. 36E) apical margin subrounded, with long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 36G) 1.4x as long as wide, widest near apex; subparallel-sided but more or less sinuous; apex deeply emarginate at middle, with small excavations (Fig. 36G, black arrows) at laterals; basal portion rounded; basolateral margin narrow (Fig. 36G, small red arrows), with acute angulations (Fig. 36G, big red arrows). **Basal piece** (Fig. 36F) subtriangular, 1.3x as wide as long. **Penis** (Fig. 36(H–I)) 1.3x as long as tegmen, 7,6x as long as wide; apex bilobed (Fig. 36I, black arrows); apical portion membranous; basal portion with rounded emargination (Fig. 36H, red arrow).

Females (Fig. 37(A–D)). Anterior edge of head slightly produced forming two small subacute plates. Anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns and abdominal sex patch. **Female terminalia in paratype** (Fig. 37D): spiculum ventrale (Fig. 37D) 1.05x as long as ovipositor (Fig. 37D); ovipositor

1.43x as long as wide, widest at base; paraprocts (Fig. 37D) 0.96x as long as gonocoxites; gonocoxites (Fig. 37D) 0.74x as long as their combined widths, narrowly subrounded apex; each gonostylus (Fig. 37D) 0.12x as long as respective gonocoxite, 1.40x as long as wide.

Variation. Males, measurements in mm (n= 23, including the holotype): TL 1.10–1.35 (1.22 ± 0.07), PL 0.38–0.48 (0.43 ± 0.03), PW 0.50–0.60 (0.56 ± 0.03), EL 0.69–0.90 (0.79 ± 0.05), EW 0.55–0.78 (0.63 ± 0.05), GD 0.50–0.58 (0.53 ± 0.02), PL/PW 0.70–0.86 (0.78 ± 0.05), EL/EW 1.00–1.43 (1.27 ± 0.11), EL/PL 1.54–2.07 (1.85 ± 0.16), GD/EW 0.72–0.95 (0.84 ± 0.05), TL/EW 1.60–2.22 (1.96 ± 0.14). Females, measurements in mm (n= 21): TL 1.13–1.35 (1.24 ± 0.07), PL 0.38–0.48 (0.42 ± 0.03), PW 0.50–0.63 (0.56 ± 0.04), EL 0.75–0.90 (0.82 ± 0.05), EW 0.55–0.70 (0.62 ± 0.04), GD 0.50–0.60 (0.55 ± 0.03), PL/PW 0.71–0.83 (0.76 ± 0.03), EL/EW 1.15–1.64 (1.32 ± 0.10), EL/PL 1.63–2.19 (1.94 ± 0.13), GD/EW 0.83–1.09 (0.88 ± 0.05), TL/EW 1.84–2.45 (2.01 ± 0.13). Differences between populations are restricted to body size in both sexes and horns sizes in males (Fig. 38(A–G)).

Type material. Holotype ♂ (CELC) “BRASIL: RS, São Francisco de Paula, “FLONA SFP”; iii.2007, leg. L.V. Graf \ *Lipedanicis agastor* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”. **Paratypes:** 35 ♂♂ and 36 ♀♀ as follows: 1 ♀ (CAMB) “BRASIL: RS, São Francisco de Paula, “FLONA SFP”; xi.2006, leg. L.V. Graf”; 1 ♂ (CELC) and 1 ♀ (CELC, dissected) “BRASIL: RS, São Francisco de Paula, “FLONA SFP”; ix.2006, leg. L.V. Graf”; 4 ♂♂ (CELC, one dissected; 1 CAMB) and 1 ♀ (CAMB) “BRASIL: RS, São Francisco de Paula, “FLONA SFP”; x.2006, leg. L.V. Graf”; 2 ♂♂ (CELC) “BRASIL: RS, São Francisco de Paula, “FONA SFP”; xii.2006, L.V. Graf”; 1 ♂ (CAMB) “BRASIL: RS, São Francisco de Paula, “FLONA SFP”; ii.2007, L.V. Graf”; 1 ♂ (CELC) and 5 ♀♀ (CELC) “BRASIL: ES, Venda Nova do Imigrante, 2003, leg. F.Z. Vaz-de-Mello”; 1 ♂ (CELC, dissected) “BRASIL: RJ, Nova Friburgo, “RPPN Bacchus” 16.xi.2011, leg. L.S. Araujo \ Código:, Trans.: 1, Parcela: C, Fungo 1”; 1 ♂ (CELC, dissected) “BRASIL: ES, Santa Teresa, “Estação Biológica Santa Lúcia”, 27.xi.2011, leg. L.S. Araujo \ Código:, Trans.: 1, Parcela: A, Fungo 2”; ♀ (CELC) “BRASIL: RJ, Teresópolis, “P.N. Serra dos Órgãos”; 14.xi.2011, leg. L.S. Araujo \ Código:, Trans.: 2, Parcela: E, Fungo 1”; 1 ♀ (CELC) “BRASIL: RJ, Teresópolis, “P.N. Serra dos Órgãos”; 14.xi.2011, leg. L.S. Araujo \ Código:, Trans.: 3, Parcela: D, Fungo 12”; 1 ♂ (CELC) and 1 ♀ (CELC) “BRASIL: RJ, Itatiaia, “Parque Nacional do Itatiaia”; 09.xi.2011, leg. L.S. Araujo \ Código:, Trans.: 1, Parcela: E, Fungo 2”; 1 ♂ (CELC, dissected) and 2 ♀♀ (CELC, one dissected) “BRASIL, RJ, Itatiaia, “Parque Nacional do Itatiaia”; 09.xi.2011, leg. L.S. Araujo”; 1 ♂ (CELC) “BRASIL: MG, Tiradentes, “APA São José” 12.vi.2012, leg. E.H. Oliveira & A. Yanai-Barduche \ Código:, Trans.: 2, Parcela: A, Fungo 1”; 2 ♂♂ (CELC, one dissected) “BR: MG, Alto Caparaó, Parque Nacional do Caparaó, 29.xi.2011, leg. L.S. Araujo \ Trans.: 1, Parcela: A, Fungo: 2"; 3 ♂♂ (1 CELC; 2 CERPE) and 5 ♀♀ (3 CELC; 2 CERPE) “BRASIL: RS, Canela, “Área CEEE”, [29º22’45”S e 50º43’47”W], 08.viii.2015; A.G. Mezzomo leg. \ *Fuscoporia gilva*”; 3 ♂♂ (1 CELC; 1 ANIC; 1 QMBA) and 4 ♀♀ (2 CELC; 1 ANIC; 1 QMBA) “BRASIL: RS, Canela, “Área CEEE”, [29º22’45”S e 50º43’47”W], 22.x.2015; A.G. Mezzomo leg. \ *Fuscoporia gilva*”; 1 ♀ (CELC) “BRASIL: RS, Canela, “Área CEEE”, [29º22’45”S e 50º43’47”W], 28.xi.2015; A.G. Mezzomo leg. \ *Fuscoporia gilva*”; 3 ♂♂ (1 CELC; 2 CEMT) and 4 ♀♀ (2 CELC; 2 CEMT) “BRASIL: RS, Canela, “Área CEEE”, [29º22’45”S e 50º43’47”W], 10.ii.2016; A.G. Mezzomo leg. \ *Fuscoporia gilva*”; 1 ♂ (CELC) and 1 ♀ (CELC) “BRASIL: RS, Canela, “Área CEEE”, [29º22’45”S e 50º43’47”W], 08.viii.2015; A.G. Mezzomo leg. \ *Ganoderma australe*”; 2 ♀♀ (CELC) “BRASIL: RS, Canela, “Área CEEE”, [29º22’45”S e 50º43’47”W], 10.ii.2016; A.G. Mezzomo leg. \ *Ganoderma australe*”; 1 ♂ (CELC) and 1 ♀ (CELC) “BRASIL: RS, Canela, “Área CEEE”, [29º22’45”S e 50º43’47”W], 10.ii.2016; A.G. Mezzomo leg.”; 4 ♂♂ (CELC) and 2 ♀♀ (CELC) “BRASIL: RS, Santa Tereza, RPPN Vale do Moinho Brum, [29º09’29”S e 51º41’49”W], 03.ix.2015, A.G. Mezzomo leg. \ *Fuscoporia gilva*”; 1 ♂ (CELC) and ♀ (CELC) “BRASIL: RS, Santa Tereza, RPPN Vale do Moinho Brum, [29º09’29”S e 51º41’49”W], 12.xii.2016, A.G. Mezzomo leg. \ *Trametes membranaceae* [sic]”; 1 ♂ (CELC) “BRASIL: RS, Santa Tereza, RPPN Vale do Moinho Brum, [29º09’29”S e 51º41’49”W], 03.ix.2015, A.G. Mezzomo leg. \ *Trametes villosa*”; 2 ♂♂ (CELC) and 1 ♀ (CELC) “BRASIL: RS, Santa Tereza, RPPN Vale do Moinho Brum, [29º09’29”S e 51º41’49”W], 03.ix.2015, A.G. Mezzomo leg.”; 1 ♂ (CELC) and 1 ♀ (CELC) “BRASIL: RS, Santa Tereza, RPPN Vale do Moinho Brum, [29º09’29”S e 51º41’49”W], 12.xii.2016, A.G. Mezzomo leg. \ *Trametes membranaceae* [sic]”; 1 ♀ (CELC) “BRASIL: RS, Santa Tereza, RPPN Vale do Moinho Brum, [29º09’29”S e

51º41’49”W], 12.xii.2016, A.G. Mezzomo leg. \ *Pycnoporus sanguineus*”. All paratypes additionally labeled “*Lipedanicis agastor* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]”.

Host fungi. *Phellinus gilvus* (Schwein.) Pat. (Hymenochaetaceae), four breeding records; *Ganoderma australe* (Fr.) Pat. (Ganodermataceae), two records; *Pycnoporus sanguineus* (L.) Murril (Polyporaceae, one record; *Trametes membranacea* (Sw.) Kreisel (Polyporaceae), one record; *Trametes villosa* (Sw.) Kreisel (Polyporaceae), one record.

Distribution. Brazil. Known from the states of Espírito Santo, Minas Gerais, Rio de Janeiro and Rio Grande do Sul (Southeast and South Brazil) (Fig. 46).

Comments. This is the species of *Lipedanicis* with the largest distribution in the genus. All specimens were collected in Atlantic Forest remnants above 900m over the sea. It’s probably distributed throughout the Atlantic Forest of South and Southeast Brazil.

***Lipedanicis geminus* sp. nov.**

Fig. 39(A–G); Fig. 40(A–H); Fig. 41(A–E); Fig. 42(A–B); Fig. 46

Type locality. “Araguaína”, coordinates 07º11’S 48º12’W (Tocantins, Brazil).

Etymology. The species name derives from the Latin noun “geminus”, which means “twin-born”, “twin”, in the genitive singular. The name is a reference to the sons of the senior author.

Diagnosis. *Lipedanicis geminus* **sp. nov.** differs from all other species in bearing antennal club not more than 1.2x as long as funicle, lateral edges of pronotum not visible from above and penis more than 3x as long as tegmen.

Description, male holotype (Fig. 39(A–E)). Adult apparently not fully pigmented, lacking one tarsus. Measurements in mm: TL 1.31, PL 0.50, PW 0.68, EL 0.81, EW 0.72, GD 0.63. Ratios: PL/PW 0.74, EL/EW 1.12, EL/PL 1.61, GD/EW 0.87, TL/EW 1.82. **Body** subparallel-sided, dorsum and venter reddish dark brown; antennae, palpi and tarsi yellowish dark brown; dorsal vestiture consisting of minute suberect setae, easily discernible in high magnification (>80x); ventral vestiture of decumbent setae, easily discernible in high magnifications (>50x). **Head** (Fig. 39D) dorsal punctation dual; megapunctures coarse, shallow, about 2x as large as micropunctures, separated from each other by 1–2 megapuncture-widths, each with one minute decumbent seta (<0.01 mm); interspaces, microreticulate; anterocephalic edge produced, elevated forming two long, broadly laminate converging horns (length 0.25 mm; basal width 0.11 mm; basal separation 0.14 mm), apices rounded; sides of each horn parallel. **Antennae** (Fig. 40A, left antenna in paratype) 10-segmented, lengths as follows (in mm, left antenna measured): 0.08, 0.05, 0.04, 0.03, 0.02, 0.02, 0.02, 0.04, 0.04, 0.05 (FL 0.12 mm, CL 0.14 mm, CL/FL 1.17). **Eyes** coarsely facetted, with about 70 ommatidia; GW 0.14 mm. **Gula** 0.37x as wide as head. **Pronotum** (Fig. 39E) punctation indistinctly dual; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2 megapuncture-widths or less (very small punctures visible in very magnification ≥300x, about 0.2x as large as megapunctures); interspaces, microreticulate; vestiture single, consisting of one minute suberect yellowish seta (<0.01 mm); lateral edges not crenulate, not explanate, not visible when seen from above; anterior corners rounded; posterior corners broadly rounded. **Scutellar shield** triangular, with few punctures; apparently glabrous; BW 0.07 mm; SL 0.03 mm. **Elytra** punctation non-seriate; megapunctures coarse, deep, about 2x as large as micropunctures, separated from each other by 2 megapuncture-widths or less (very small punctures visible in magnification ≥300x, about 0.2x as large as megapunctures); interspaces smooth, shiny; vestiture single, consisting of one minute suberect yellowish seta (~0.01 mm). **Metathoracic wings** apparently functional. **Hypomera** punctures fine, shallow, each with one fine decumbent seta; interspaces, microreticulate. **Prosternum** (Fig. 39D) in front of coxae tumid, carinate; interspaces, microreticulate. **Prosternal process** (Fig. 39D) 1.5x as long as prosternum at midline; apex rounded. **Protibiae** (Fig. 40B, left protibia in paratype) maximum width about one-third its length; apical edge with spines; outer apical angle projected in acute tooth; outer edge straight, serrate. **Mesotibiae** (Fig. 40C, left mesotibia in paratype) apical edge with spines; outer edge straight, serrate. **Metatibiae** (Fig. 40D, left metatibia in paratype) apical edge with spines; outer edge straight, smooth. **Metaventrite** (Fig. 39G, in paratype) punctures coarse, shallow; interspaces, microreticulate; discrimen about one-fifth the length of metaventrite at midline; posterior margin notch 0.11x as long as metaventrite at midline. **Abdominal ventrites** punctures fine, shallow, separated from each other by 1 puncture-width or less, each with one fine decumbent yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at longitudinal midline) as follows: 0.10, 0.06, 0.07, 0.07, 0.09; first abdominal ventrite devoid of sex patch. **Male terminalia in paratype** (Fig. 40(E–H)): **sternite VIII** (Fig. 40E) apical margin emarginate, with short setae near middle and long setae at rounded corners; basal portion membranous. **Tegmen** (Fig. 40G) 1.3x as long as wide, widest near base; subparallel-sided but more or less sinuous; apex shallowly emarginate at middle, with angulations at outer apical edge (Fig. 40G, big black arrows) and excavations at base of each angulation (Fig. 40G, small black arrows) at laterals; basal portion triangular. **Basal piece** (Fig. 40F) subtriangular, as wide as long. **Penis** (Fig. 40H) 3.6x as long as tegmen, 17.1x as long as wide; very elongate, subcylindrical; apex rounded; basal portion wedge-shaped (Fig. 40H, red arrow).

Females (Figs 41(A–D), 42(A–B)). Anterior edge of head slightly produced forming two small subacute plates. Anterior edge of pronotum rounded. Otherwise like males, but without cephalic horns and some specimens with 9-segmented antennae (due to fusion of third and fourth segments) (Fig. 41(D–E)). **Female terminalia in paratype** (Fig. 42(A–B)): spiculum ventrale (Fig. 42A) 1.11x as long as ovipositor (Fig. 42B); ovipositor 1.18x as long as wide; paraprocts (Fig. 42B) 0.75x as long as gonocoxites; gonocoxites (Fig. 42B) 0.76x as long as their combined widths, each with narrowly subrounded apex; each gonostylus (Fig. 42B) 0.09x as long as respective gonocoxite, 1.25x as long as wide.

Variation. Males, measurements in mm (n= 11, including the holotype): TL 1;10–1.58 (1.26 ± 0.14), PL 0.40–0.53 (0.45 ± 0.05), PW 0.58–0.83 (0.66 ± 0.08), EL 0.70–1.05 (0.81 ± 0.10), EW 0.65–0.90 (0.73 ± 0.07), GD 0.53–0.73 (0.60 ± 0.06), PL/PW 0.62–0.74 (0.68 ± 0.04), EL/EW 0.97–1.19 (1.11 ± 0.07), EL/PL 1.61–2.00 (1.82 ± 0.14), GD/EW 0.76–0.88 (0.83 ± 0.04), TL/EW 1.52–1.82 (1.73 ± 0.09). Females, measurements in mm (n= 10): TL 1.08–1.40 (1.28 ± 0.10), PL 0.38–0.50 (0.45 ± 0.04), PW 0.53–0.73 (0.64 ± 0.06), EL 0.70–0.93 (0.84 ± 0.07), EW 0.60–0.78 (0.71 ± 0.06), GD 0.50–0.70 (0.59 ± 0.06), PL/PW 0.65–0.76 (0.70 ± 0.04), EL/EW 1.13–1.24 (1.18 ± 0.03), EL/PL 1.74–2.00 (1.87 ± 0.10), GD/EW 0.80–0.90 (0.84 ± 0.03), TL/EW 1.70–1.93 (1.82 ± 0.07). Females can bear 9- or 10-segmented antennae (Fig. 41(D–E)).

Type material. Holotype ♂ (CELC) “BR: TO, Araguaína, UFT-MZV, “Mata”, iii.2015, V.E. Sandoval leg. \ *Lipedanicis geminus* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]”. **Paratypes:** 69 ♂♂ and 56 ♀♀ as follows: 12 ♂♂ (4 CELC, two dissected and stored in glycerin; 2 CAMB; 2 CERPE; 2 CEMT; 2 ANIC) and 11 ♀♀ (3 CELC, two dissected and stored in glycerin; 2 CAMB; 2 CERPE; 2 CEMT; 2 ANIC) same data as the holotype; 6 ♂♂ (CELC) and 4 ♀♀ (CELC) “BR: TO, Araguaína, UFT-MZV, 19.iv.2016; “cerrado”; leg. W.H. Brandão & E.S. Morais \ ex *Inonotus* sp.”; 10 ♂♂ (8 CELC; 2 FMNH) and 9 ♀♀ (7 CELC; 2 FMNH) “BR: TO, Araguaína; UFT-MVZ, “Perto do Córrego da Vaca”, 16.vi.2015; V.E. Sandoval leg.”; 21 ♂♂ (17 CELC; 4 QMBA) and 17 ♀♀ (13 CELC; 4 QMBA) “BR: TO, Araguaína, Campus UFT-EMVZ, iii.2015 leg. V.E. Sandoval”; 6 ♂♂ (CELC, one dissected) and 3 ♀♀ (CELC, one dissected) “BRASIL: PA, Marabá, “Reserva Biológica de Tapirapé; Amazônia Legal”, 20.xi.2003, leg. F, Gumier-Costa \ AMOSTRA Nº 29, Mata 2ª; Divino, 20.xi.2003”; 2 ♂♂ (CELC) and 4 ♀♀ (CELC) “BRASIL: PA, Marabá, “Reserva Biológica de Tapirapé; Amazônia Legal”, 20.xi.2003, leg. F, Gumier-Costa \ AMOSTRA Nº 27, Mata 2ª; Divino, 20.xi.2003”; 2 ♂♂ (CELC) and 7 ♀♀ (CELC) “BRASIL: PA, Marabá, “Reserva Biológica de Tapirapé; Amazônia Legal”, 27.xi.2003, leg. F, Gumier-Costa \ AMOSTRA Nº 56, Mata 1ª; REBIO, 27.xi.2003”; 1 ♀ (CELC) “BRASIL: PA, Marabá, “Reserva Biológica de Tapirapé; Amazônia Legal”, 27.xi.2003, leg. F, Gumier-Costa \ AMOSTRA Nº 46, Mata 1ª; REBIO, 27.xi.2003”. All paratypes additionally labeled “*Lipedanicis geminus* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]”.

Host fungus. *Inonotus* sp. (Hymenochaetaceae), one breeding record.

Distribution. South America. Known from Pará and Tocantins (North Brazil) (Fig. 46).

Comments. The species was collected only in areas of Amazon Forest.

Discussion

The suprageneric classification of Ciidae, as currently established, has been controversial, with just Sphindociinae and Xylographellini delimited by the combination of exclusive characters. The available molecular-based phylogenetic analysis (which does not include Sphindociinae) has shown only Xylographellini as a clade (Lopes-Andrade & Grebennikov 2015). We are conducting the first morphology-based phylogenetic analysis of Ciidae to understand "what is *Ceracis*" and its relationships within the family (Souza-Gonçalves & Lopes-Andrade in prep.[2]). Throughout the conduction of the present work and the phylogentic analysis of *Ceracis*, morphological characteristics observed in the antennae, tibiae, female terminalia, male ornaments so on have gave insights to draft suprageneric relationships within the family. These features will be used on the comparisons presented below. After the description of new genera proposed here, they may be formally included in a future robust phylogenetic analysis of Ciidae, contributing for a better comprehension of internal relationships in the family.

Anartioscelos bifurcus, *Ana. laticornis*, *Alc. particularis* and *Abe. taurulus*, previously included in *Ceracis* and here transferred to new genera, were known to not completely fit the diagnosis of *Ceracis* (Lawrence 1967, Pecci-Maddalena & Lopes-Andrade 2017). The exclusions of *Anartioscelos bifurcus* and *Ana. laticornis* are justified by the following features: (i) prosternum tumid and carinate; (ii) all tibiae with edges regularly serrate and bearing socketed spines between serration; (iii) outer angle of protibiae projected in an acute tooth; and (iv) meso- and metatibiae with outer apical angle broadly rounded. *Alcecis particularis* was removed due to its: (i) dual and subseriate elytral vestiture; (ii) very long antennal club (more than 2x as long as funicle); (iii) tumid and slightly carinate prosternum; and (iv) apical third of protibiae enlarged, with outer apical angle project in a stout tooth. *Abebaeocis taurulus* was removed due to its: (i) tumid prosternum; (ii) protibiae, slightly enlarged at apex and with simple outer apical angle, without any ornament.

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[2] Souza-Gonçalves, I. & Lopes-Andrade, C.. A morphology-based phylogeny of *Ceracis* Mellié (Coleoptera: Ciidae). (in prep.) – Chapter 4.

The seven genera described here are temporally included in Ciini, once they not fit in any other tribe as established up to date. In four of them (*Abebaeocis*, *Anartioscelos*, *Gyraleosomus* and *Lipedanicis*) the species bear reduced and simplified female terminalia as in several other genera (Lopes-Andrade 2007, Lopes-Andrade 2008, Antunes-Carvalho *et al.* 2012). The reduced and simplified female terminalia can be recognized by the following features: (i) gonostyli absent or very small (<0.015 mm); (ii) gonocoxites ventrally divided into no more than two lobes, usually indiscernible; (iii) baculi of basal gonocoxital lobes usually indistinct; (iv) paraprocts short, usually as long as or shorter than gonocoxites, with baculi of paraprocts bowed and completely fused to the respective proctigeral baculus. Among the species with reduced and simplified female terminalia, *Octotemnus* Mellié, 1847, *Paratrichapus* Scott, 1926, *Ropalodontus* Mellié, 1847 and *Xylographus* differ from *Abebaeocis*, *Anartioscelos*, *Gyraleosomus* and *Lipedanicis* in the strongly projecting procoxae and outer edge of each meso- and metatibiae bearing spines at least at the apical two-thirds (except for *Anartioscelos*, in which outer edges of tibiae are regularly serrate and bearing socketed spines between serration) (Lawrence 1974b, Lawrence 2016, Souza-Gonçalves *et al.* 2018b). Whereas Xylographelini genera (*Scolytocis*, *Syncosmetus* Sharp, 1891, *Tropicis* Scott, 1926 and *Xylographella* Miyatake, 1985) differs from *Abebaeocis*, *Anartioscelos*, *Gyraleosomus* and *Lipedanicis* in the compact antennal club with at least five sensillifers in each segment (Lopes-Andrade 2008).

Abebaeocis, *Anartioscelos* and *Lipedanicis* differ from *Atlantocis*, *Ceracis*, *Cisarthron* Reitter, 1885, *Dichodontocis* Kawanabe, 1994, *Malacocis*, *Odontocis* Nakane & Nobuchi, 1955, *Phellinocis*, *Sulcacis* Dury, 1917 and *Wagaicis* Lohse, 1964 in the broad prosternal process, and meso- and metatibiae being devoid of spines at the outer apical angle. It differs from *Australocis* Lawrence, 2016 in bearing well-defined sensillifers in the antennal club (Lawrence 2016); from *Ctenocis* Lawrence, 2016 in possessing single dorsal vestiture of body and meso- and metatibiae devoid of spines at the outer apical angle (Lawrence 2016); and from *Grossicis* Antunes-Carvalho *et al.* 2012 in bearing apical maxillary palpomere pyriform and procoxae not projecting below the plane of prosternal process (Antunes-Carvalho *et al.* 2012). *Anartioscelos* differs from all other described genera here in the regularly serrate outer edges of tibiae with socketed spines between serration, and meso- and metatibiae with outer apical angle broadly rounded. This latter feature is also usually found in Xylographellina Kawanabe & Miyatake, 1996 (Lopes-Andrade 2008), but the outer edges of their tibiae bear only spines, being devoid of serration. *Abebaeocis* and *Lipedanicis* resembles each other, but in the former the elytral vestiture arises from megapunctures, the protibiae is slightly enlarged at apex and devoid of tooth at the outer apical angle, and female terminalia have gonocoxites ventrally divided into two lobes, baculi of basal gonocoxites very oblique and shorter than side of respective gonocoxites. Whereas, in *Lipedanicis* the elytral vestiture arises from micropunctures, the outer edge of protibiae is projected in a tooth, the meso- and metatibiae are angulated from apical to outer edge, and the female terminalia is devoid of ventral lobes at gonocoxites, and has baculi of gonocoxites very oblique and as long as side of respective gonocoxites. In *Lipedanicis geminus* antennae are ever 10-segmented in males, but females have 9- or 10-segmented antennae. Within Ciidae, variation in antennal segmentation is known to occur only in *Phellinocis romualdoi* Lopes-Andrade & Lawrence, 2005, in which the antennae may be 8- or 9-segmented in both sexes (Lopes-Andrade & Lawrence 2005).

The monospecific *Alcecis* and *Lip. adelphus* bear 8-segmented antennae, which also occurs in *Octotemnus*, *Pseudeuxestocis* Lawrence, 2016, and some species of *Ceracis* and *Phellinocis*. *Alcecis* differs from all these four previously mentioned genera in possessing dual and subseriate elytral vestiture and broad prosternal process. *Lipedanicis adelphus* bears broad prosternal process, but the dorsal vestiture is single, consisting of minute setae, and its meso- and metatibiae are angulated from apical to outer edge.

Apterous and micropterous ciids were barely known and studied up to date, but they constitute a hidden diversity, especially in tropical and subtropical areas. Two facts have delayed broader studies on these ciids: (i) they usually occur in leaflitter and other debris, rather than in basidiomes; (ii) the reduction or loss of wings affect the morphology of their structures, making it difficult to recognize morphological affinities of micro- or apterous ciids with macropterous species in the family. There are ten Ciidae genera of exclusively apterous or micropterous ciids known up to date: *Atlantocis* (Macaronesian Islands); *Apterocis* (Hawaiian Islands); *Dimerapterocis* Scott, 1926 (Seychelles Island); *Lipopterocis* (Japan); *Neoapterocis* (Chile and Mexico); *Nipponapterocis* (Japan); *Notapterocis* (Australia; undescribed species from Republic of South Africa and Taiwan, pers. obs.); *Polynesicis* (French Polynesia) and *Syncosmetus* (Japan and China) (Lopes-Andrade 2007, Lopes-Andrade 2008, Lawrence 2016, Souza-Gonçalves *et al.* 2018a). Aside from these, there are a few micropterous Hawaiian species of *Cis*, but these are exceptions within the genus (Lopes-Andrade 2007). Before the present work, the only described apterous ciid species in the Neotropical region was *Neoapterocis mexicanus* Lopes-Andrade, 2007. Here we have described an additional Neotropical apterous ciid, *Gyr. boliviensis*, which differs from most apterous or micropterous ciids in possessing first abdominal ventrite shorter than next two together and reduced female terminalia. Species of *Atlantocis* also bear reduced female terminalia, but *Gyraleosomus* differs in possessing paraprocts shorter than proctiger.

Species of *Atomocis* resemble apterous and micropterous Ciidae in the short, oblong-ovate body shape, but differs from all of them in bearing long metaventrite, well-developed scutellar shield and metathoracic wings, and reduced basal segment of the antennal club. The latter feature also occurs in some species of *Cis*, as *C. eremicus* Lawrence, 2016 and *C. camberrae* Lawrence, 2016 (Lawrence 2016), and in *Insolitocis*, but these species of *Cis* do not have short and oblong-ovate body shape, sensillifers of antennal club are not located at the apical border, and all tibiae are not enlarged at apical half and do not have rounded outer apical angle; while the monospecific *Insolitocis* has 11-segmented antennae, sensillifers of the antennal club organized as continuous sensory areas at the apical portion of each segment, club-shaped tibiae and female terminalia with paraprocts shorter than gonocoxites.

Among all described ciid genera, *Insolitocis* is the first Ciinae with 11-segmented antennae and antennal club lacking well-defined sensillifers, which are organized as continuous sensory areas at the apical portion of each segment of the club. Within Ciidae, 11-segmented antennae occur only in *Sphindocis denticollis*, of the monospecific Sphindociinae (Lawrence 1971). However, *Insolitocis* does not share other features that characterize Sphindociinae, as (based on Lawrence 1971): (i) maxilla with two well-developed lobes; (ii) visible mesotrochantin; (iii) metendoesternite with median stalk; (iv) first two abdominal ventrites connate; (v) trochanters of heteromeroid type; and (vi) presence of tibial spurs. Additionally, the female terminalia in *Insolitocis* has paraprocts shorter than the gonocoxites and bears gonostyli, and all tibiae are club-shaped; whereas in *Sphindocis* the female terminalia has paraprocts longer than the gonocoxites and is devoid of gonostyli, and all tibiae are elongate. *Australocis*, *Insolitocis* and *Nipponapterocis* share an antennal club devoid of well-defined sensillifers, but with sensillifers of the club organized as continuous sensory areas at the apical portion of each segment of the club (Miyatake 1954, Kawanabe 1995, Lawrence 2016), but *Insolitocis* differs in possessing 11-segmented antennae, club-shaped tibiae, metaventrite with conspicuous discrimen, metacoxal cavities open at inner side and female genitalia not reduced, with paraprocts shorter than gonocoxites.

Conclusion

The Neotropical ciid fauna, now encompass 167 species in 21 genera: *Abebaeocis* (2 species), *Alcecis* (1), *Anartioscelos* (6), *Atomocis* (1), *Ceracis* (30), *Cis* (68), *Ennearthron* (1), *Falsocis* (6), *Gyraleosomus* (1), *Grossicis* (2), *Hadreule* (1), *Insolitocis* (1), *Lipedanicis* (3), *Malacocis* (1), *Neoapterocis* (1), *Orthocis* (9), *Phellinocis* (3), *Porculus* (6), *Scolytocis* (12), *Strigocis* (4) and *Xylographus* (8). A robust phylogenetic analysis of Ciidae is necessary to clarify relationships between genera and propose a better suprageneric classification for the family. In a world scenario, the present changes leave the genus *Ceracis* with 48 described species, and we expect our ongoing morphology-based phylogenetic analysis of the genus (Souza-Gonçalves & Lopes-Andrade in prep.) will shed light on its internal relationships and help us delimit further species-groups or even subgenera.

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FIGURES AND FIGURE CAPTIONS

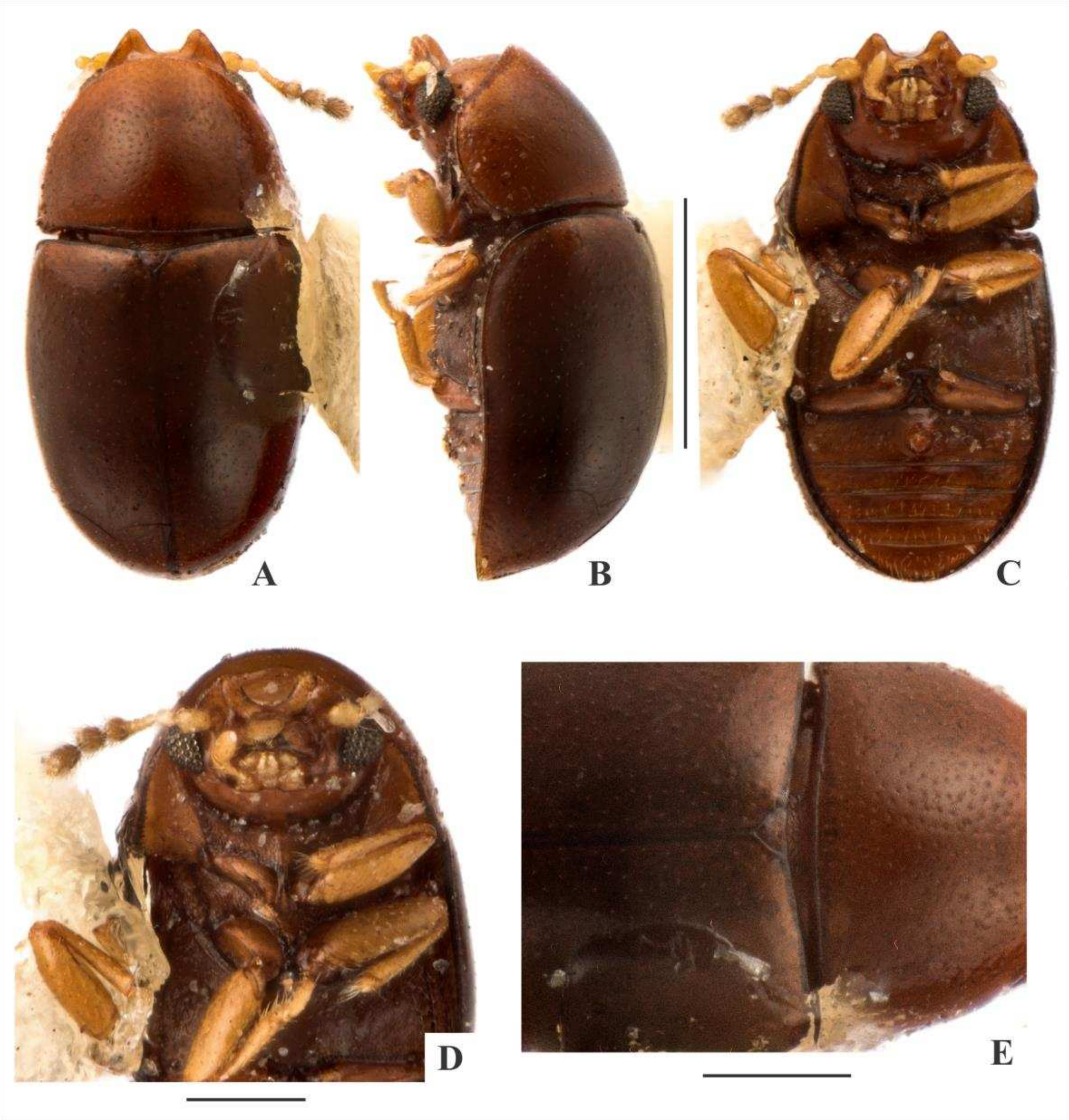

Figure 1. *Abebaeocis phiaronotum* **sp. nov.**, male holotype (A–E) from Mount Diablo (Jamaica): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

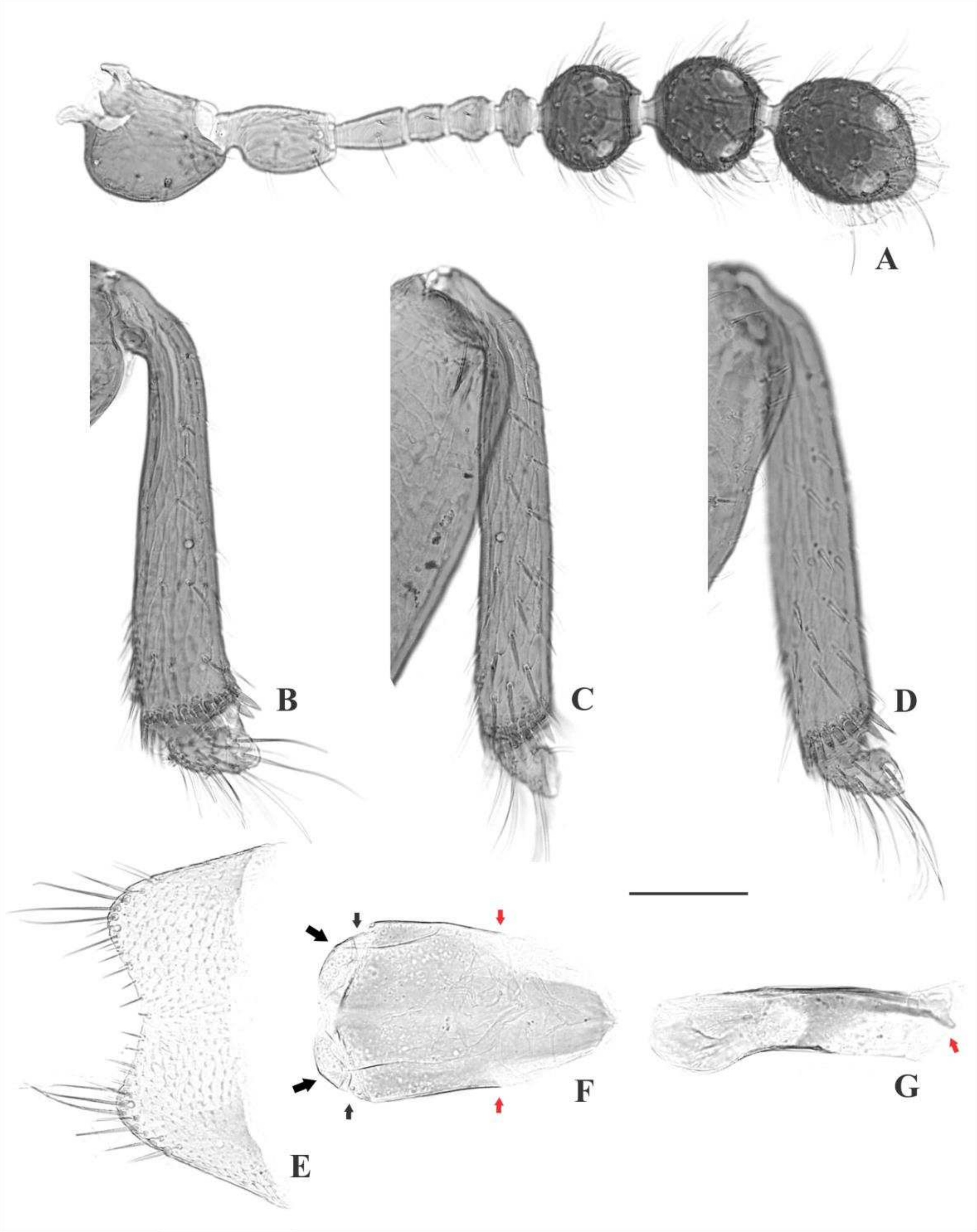

Figure 2. *Abebaeocis phiaronotum* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–G) from Mount Diablo (Jamaica): **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Tegmen, note angulations at outer apical edge (big black arrows), excavations at base of each angulation (small black

arrows) and medial acute angulations (red arrows). **G.** Dorsolateral view of penis, note truncate sclerotization at anterior portion (red arrow). Scale bar: 0.05 mm (A–G).

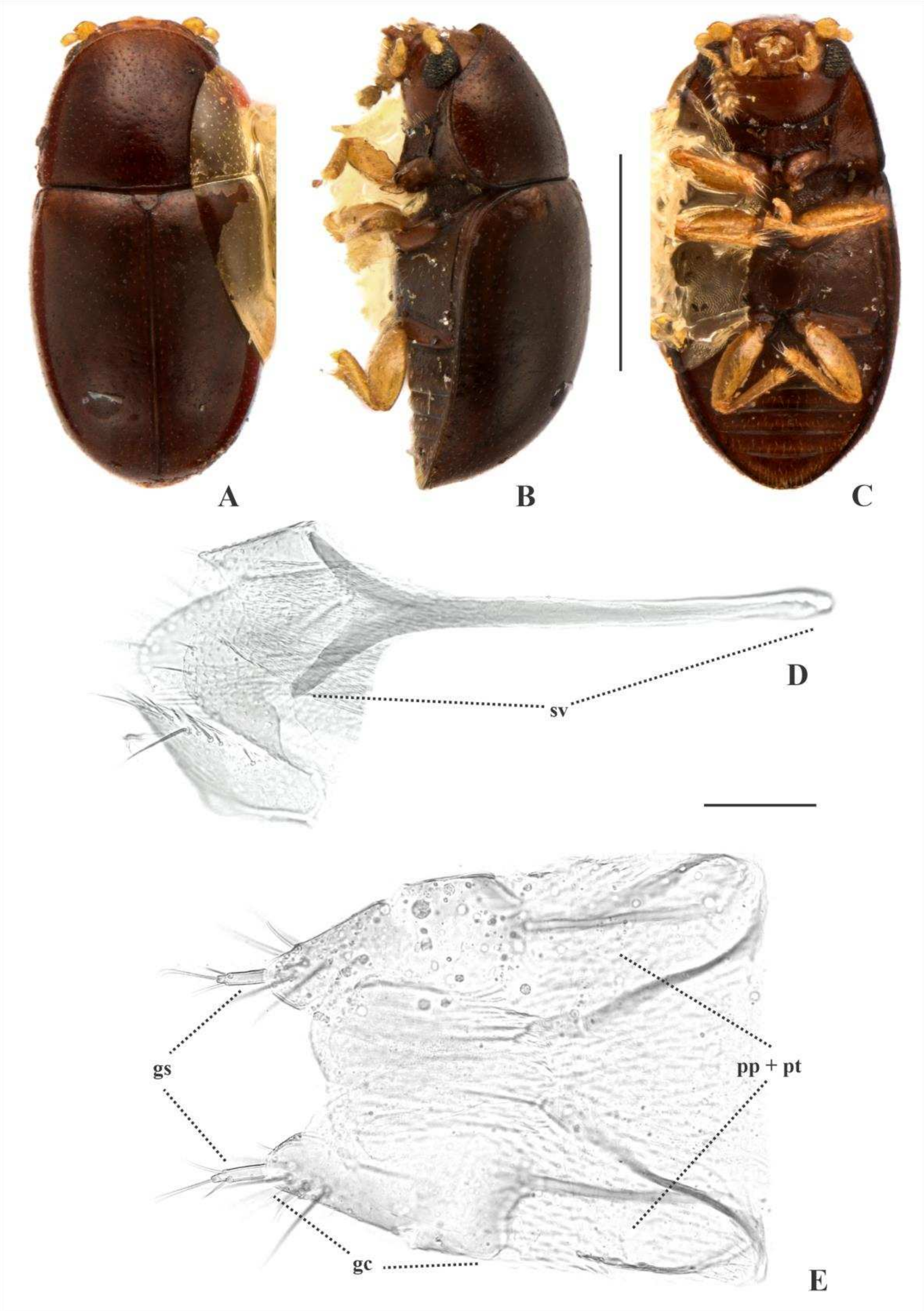

Figure 3. *Abebaeocis phiaronotum* **sp. nov.**, female paratype (A–C) from Mount Diablo (Jamaica), and female terminalia of paratype (D–E) from same locality: **A.** Dorsal view.

B. Lateral view. **C.** Ventral view. **D.** Spiculum ventrale (sv) at anterior portion of sternite VIII. **E.** Ovipositor, showing gonostyli (gs), gonocoxites (gc) and paraprocts plus proctiger (pp + pt). Scale bars: 0.5 mm (A–C); 0.05 mm (D–E).

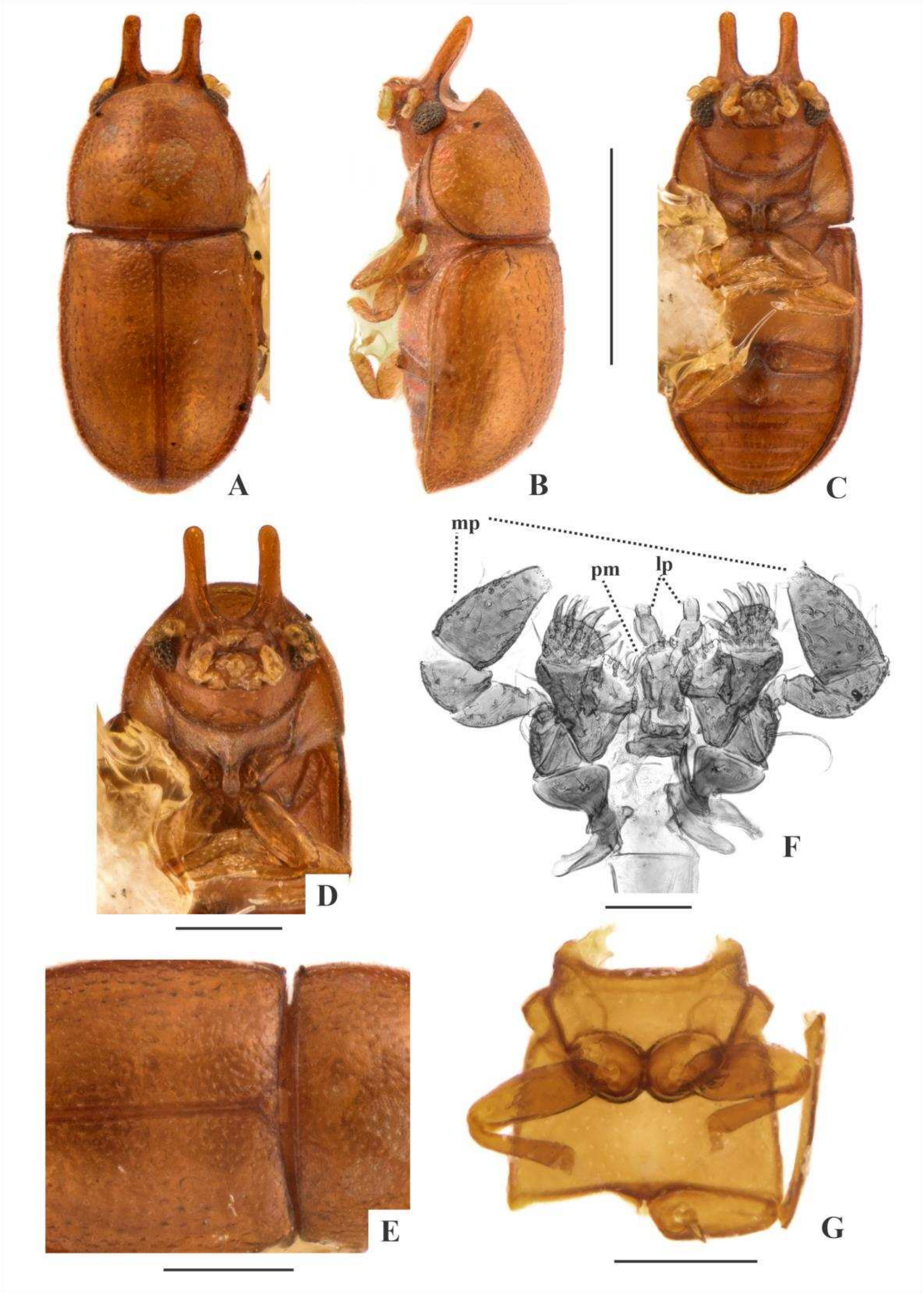

Figure 4. *Abebaeocis taurulus* (Jacquelin-Duval, 1857) **comb. nov.**, male specimen (A–E) from Republic of Cuba, mouth parts of male additional specimen (F) from Mexico and metaventrite of male additional specimen (G) from Republic of Cuba: **A.** Dorsal

view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **F.** Mouth parts, showing labial palps (lb), maxillary palps (mp) and prementum (pm). Scale bars: 0.5 mm (A–C); 0.2 mm (D–E, G); 0.05 mm (F).

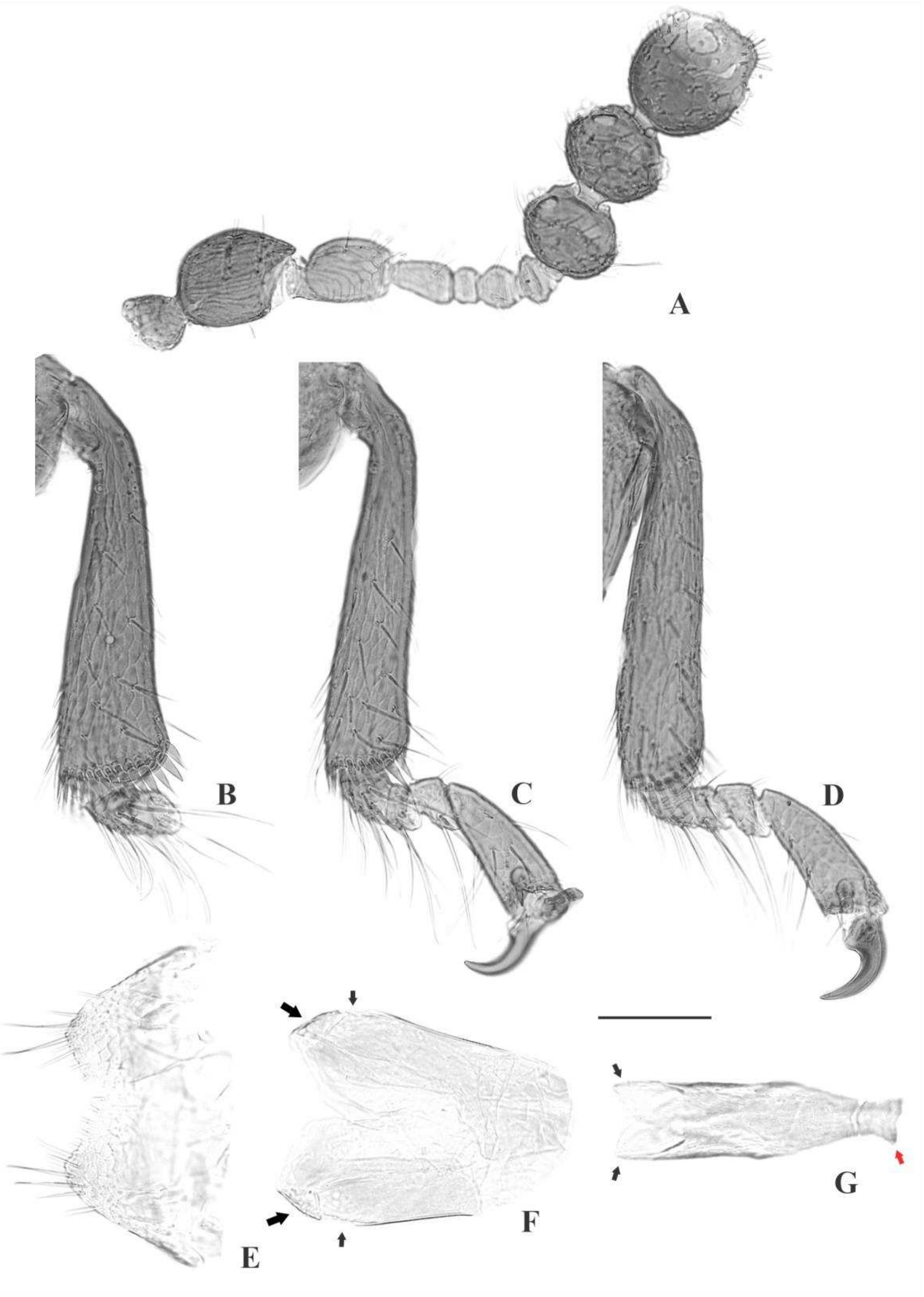

Figure 5. *Abebaeocis taurulus* (Jacquelin-Duval, 1857) **comb. nov.**, antenna, tibiae and aedeagus of specimen (A–E) from Mexico: **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Tegmen, note angulations at outer

apical edge (big black arrows) and excavations at base of each angulation (small black arrows). **G.** Penis, note apical acute and membranous projections (black arrows) and truncate sclerotization at anterior portion (red arrow). Scale bar: 0.05 mm (A–G).

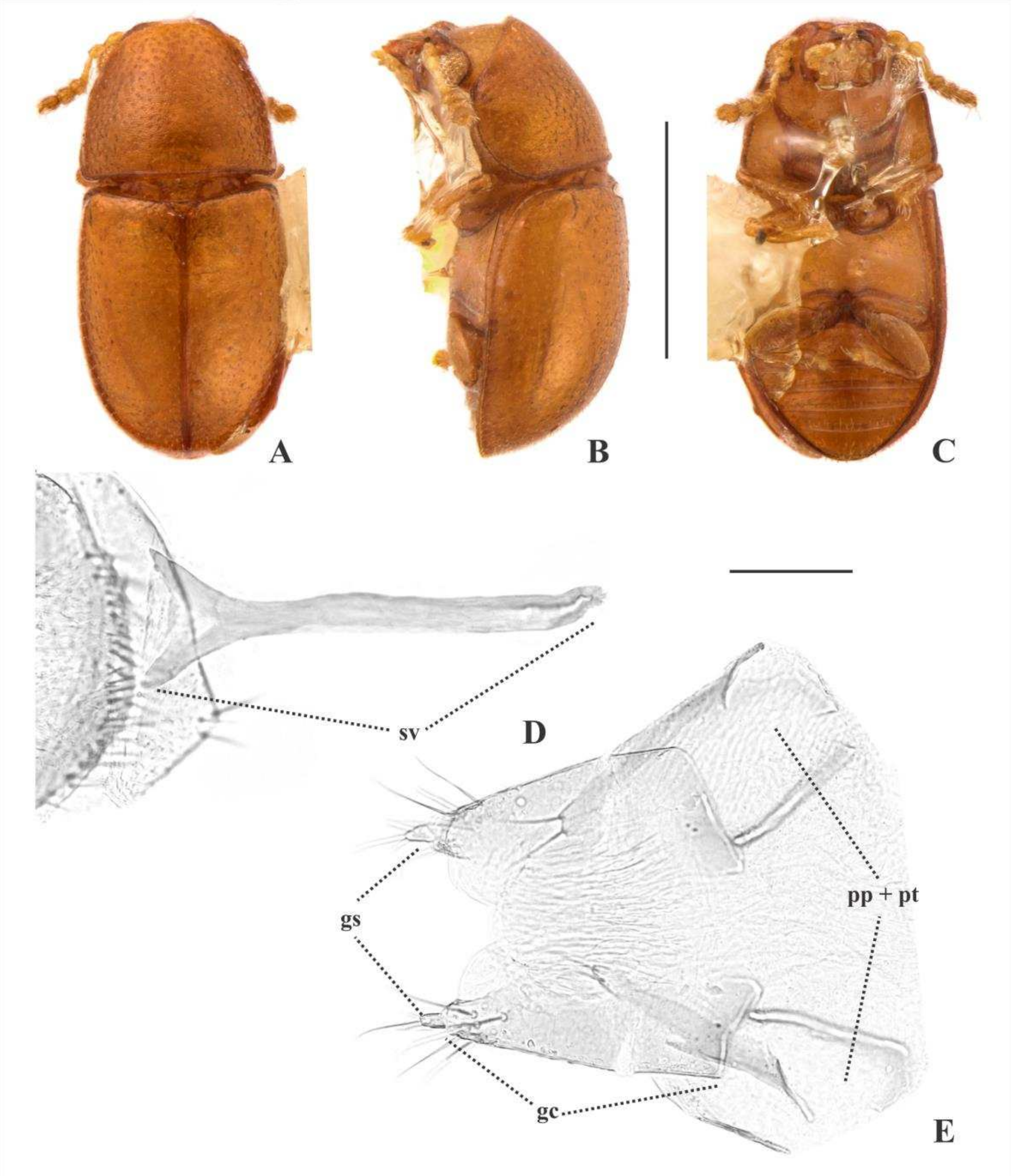

Fig. 6. *Abebaeocis taurulus* (Jacquelin-Duval, 1857) **sp. nov.**, female specimen (A–C) from Republic of Cuba, and female terminalia of specimen (D–E) from Mexico: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Spiculum ventrale (sv) at anterior

portion of sternite VIII. **E.** Ovipositor, showing gonostyli (gs), gonocoxites (gc) and paraprocts plus proctiger (pp + pt). Scale bars: 0.5 mm (A–C); 0.05 mm (D–E).

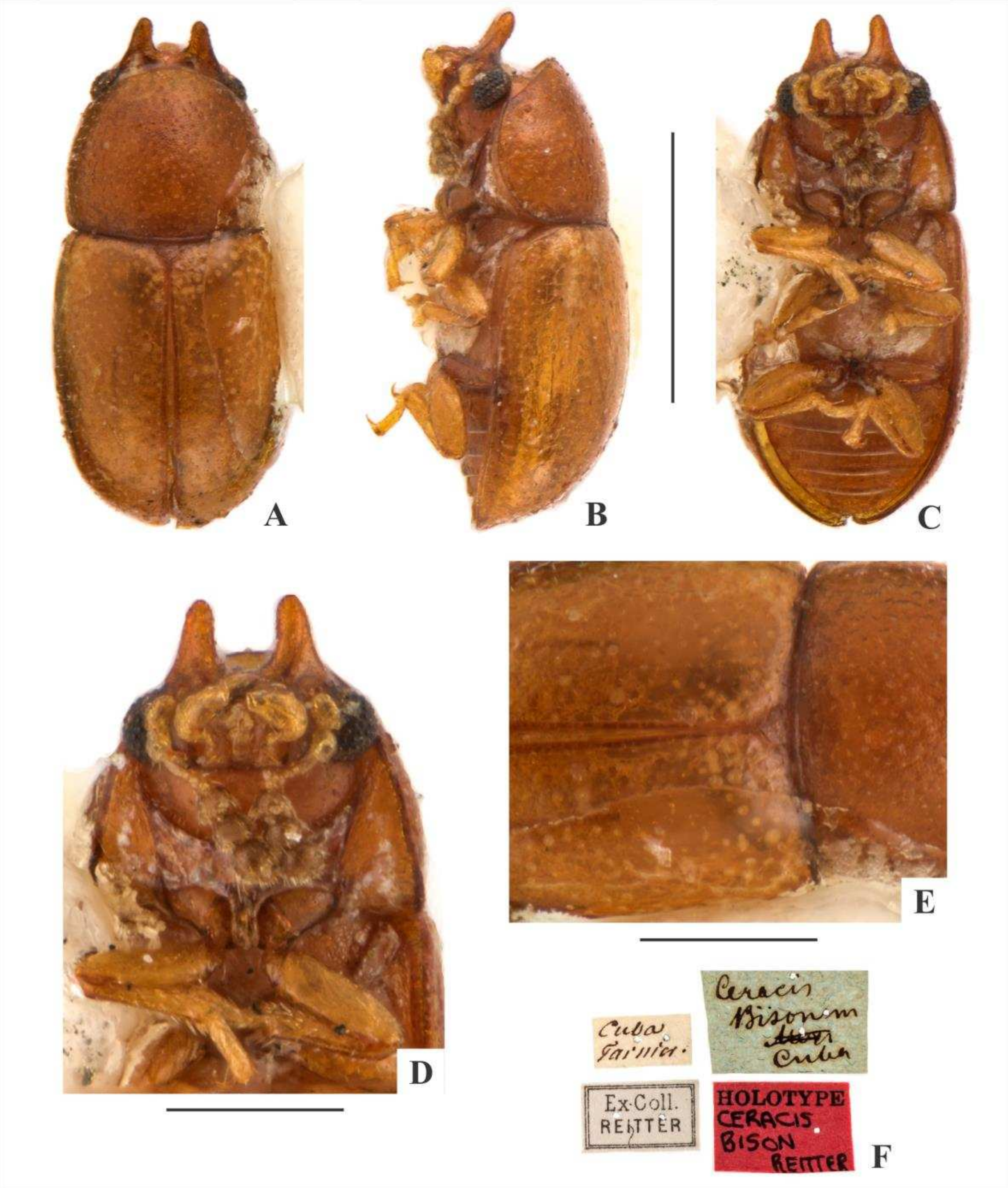

Fig. 7. *Ceracis bison* Reitter 1878, junior synonym of *Abebaeocis taurulus* (Jacquelin-Duval, 1857), male lectotype (A–E) from Republic of Cuba: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar

shield and part of the pronotum and elytra. **F.** Labels. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

Fig. 8. *Alcecis particularis* (Pic, 1922) **comb. nov.**, male lectotype (A–E) from Guadeloupe: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **F.** Labels. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

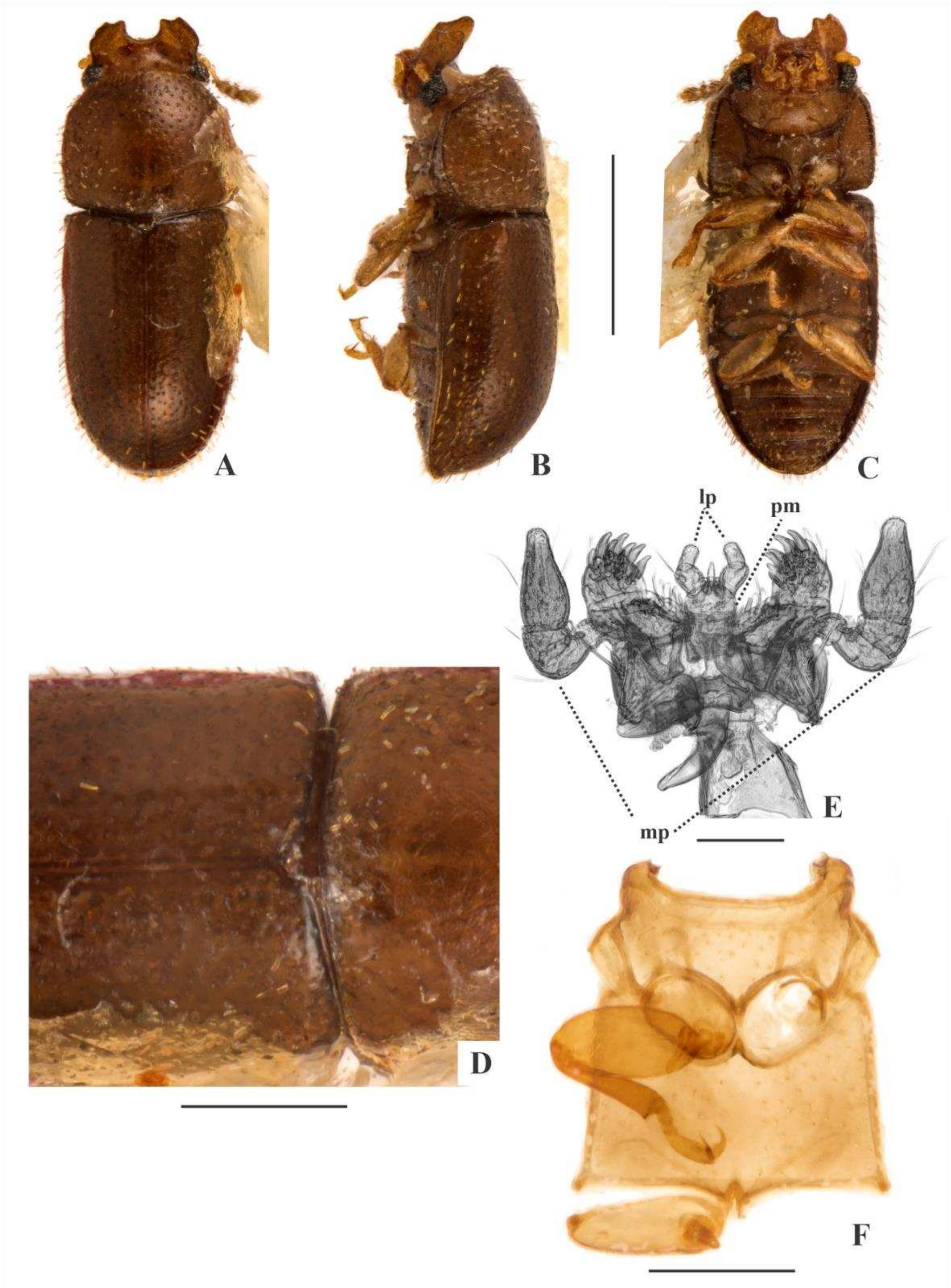

Fig. 9. *Alcecis particularis* (Pic, 1922) **comb. nov.** from Barro Colorado (Panama), showing male specimen (A–D) mouth parts of female (E) and metaventrite of male (F): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Scutellar shield and part of the

pronotum and elytra. **E.** Mouth parts, showing labial palps (lp), maxillary palps (mp) and prementum (pm). Scale bars: 0.5 mm (A–C); 0.2 mm (D, F); 0.05 mm (E).

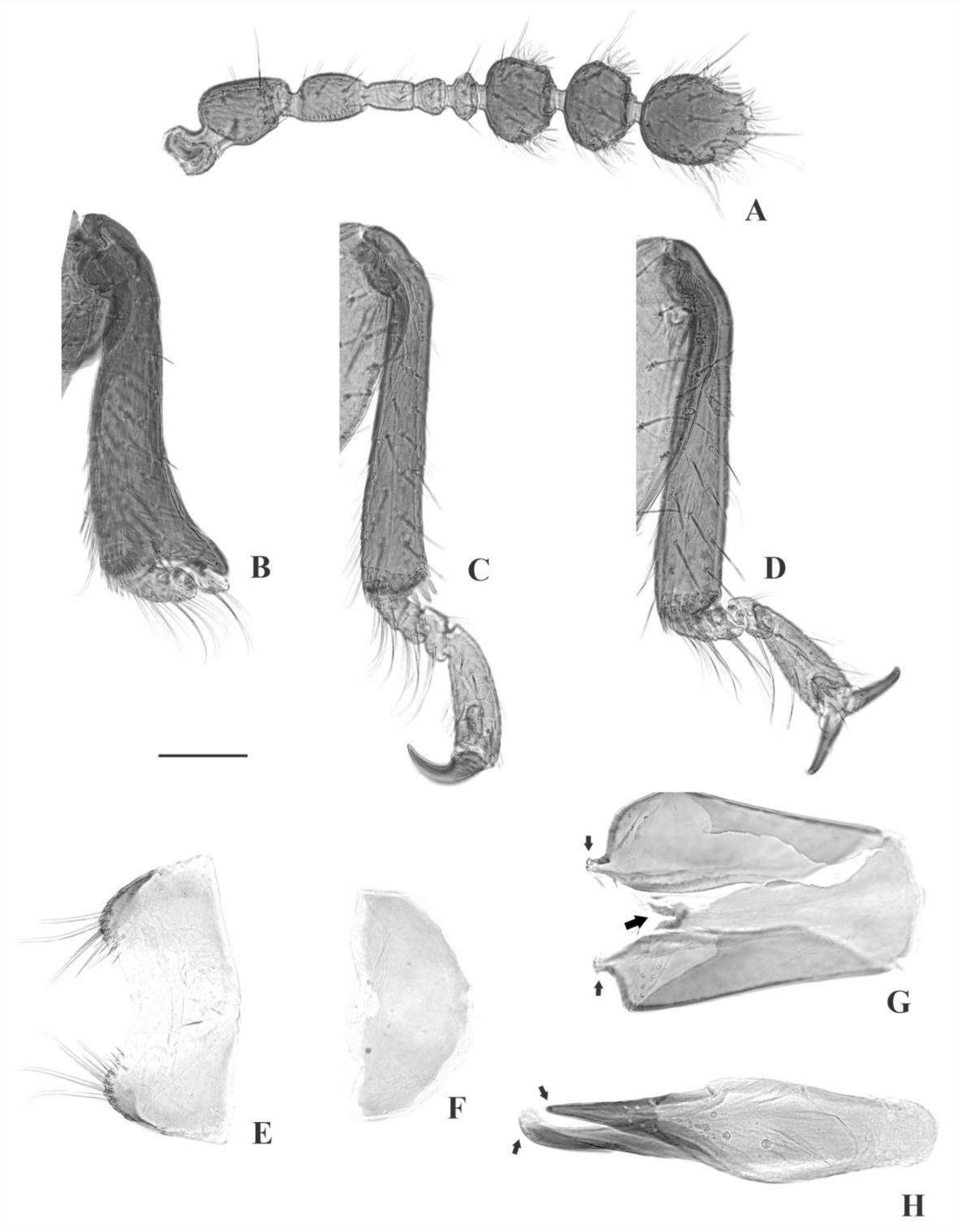

Fig. 10. *Alcecis particularis* (Pic, 1922) **comb. nov.**, antenna, tibiae and aedeagus of specimen (A–H) from Barro Colorado (Panama): **A.** Left antenna. **B.** Left protibia. **C.**

Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Basal piece. **G.** Tegmen, note U-shaped sclerotization at middle of apical emargination (big black arrows) and apical subtruncate sclerotizations (small black arrows). **H.** Penis, note bilobed apex (black arrows). Scale bar: 0.05 mm (A–H).

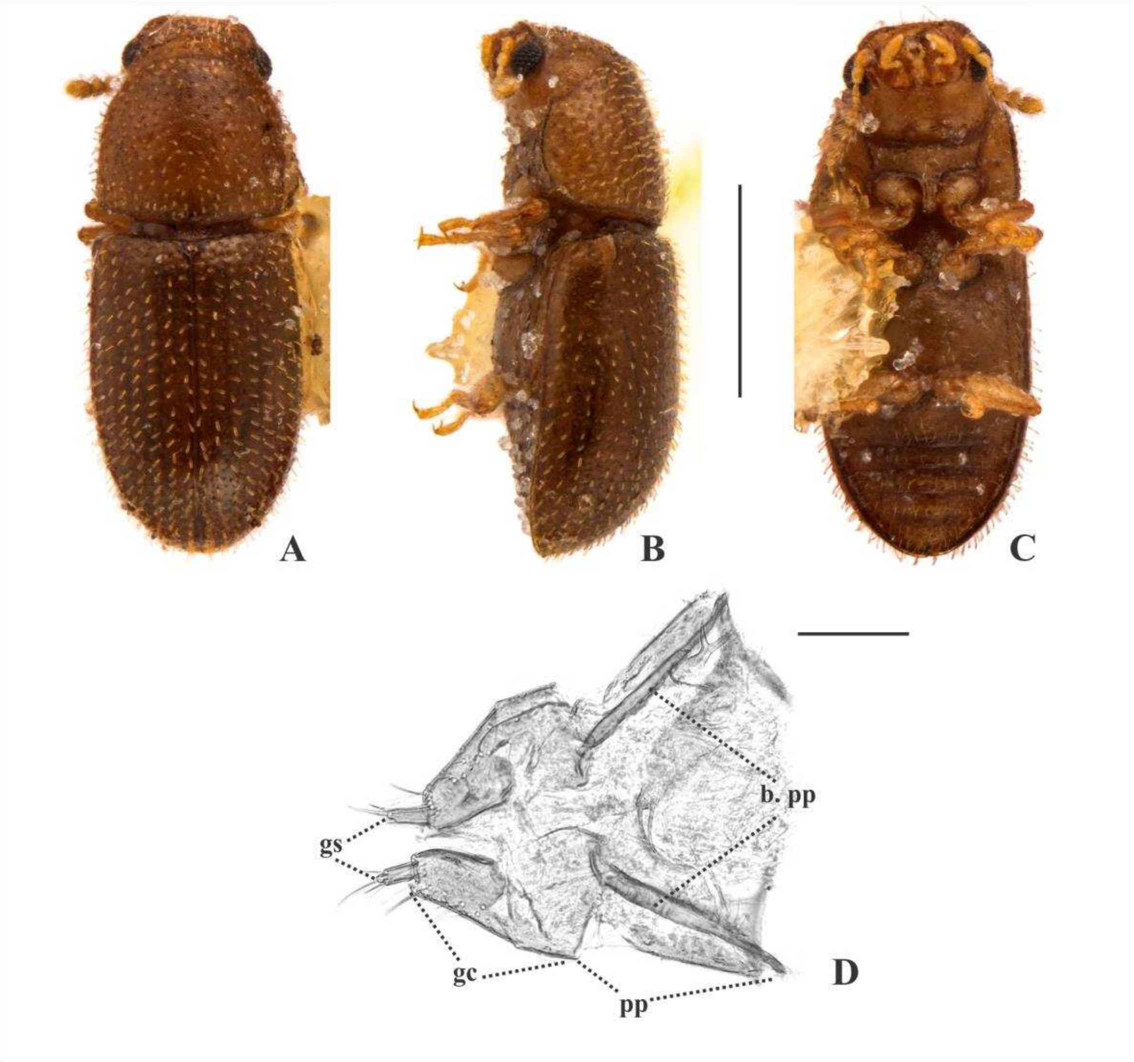

Fig. 11. *Alcecis particularis* (Pic, 1922) **comb. nov.**, female (A–C), and terminalia of another female (D) from Barro Colorado (Panama): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Ovipositor, showing gonostyli (gs), gonocoxites (gc), paraprocts (pp) and baculi of paraprocts (b. pp). Scale bars: 0.5 mm (A–C); 0.05 mm (D).

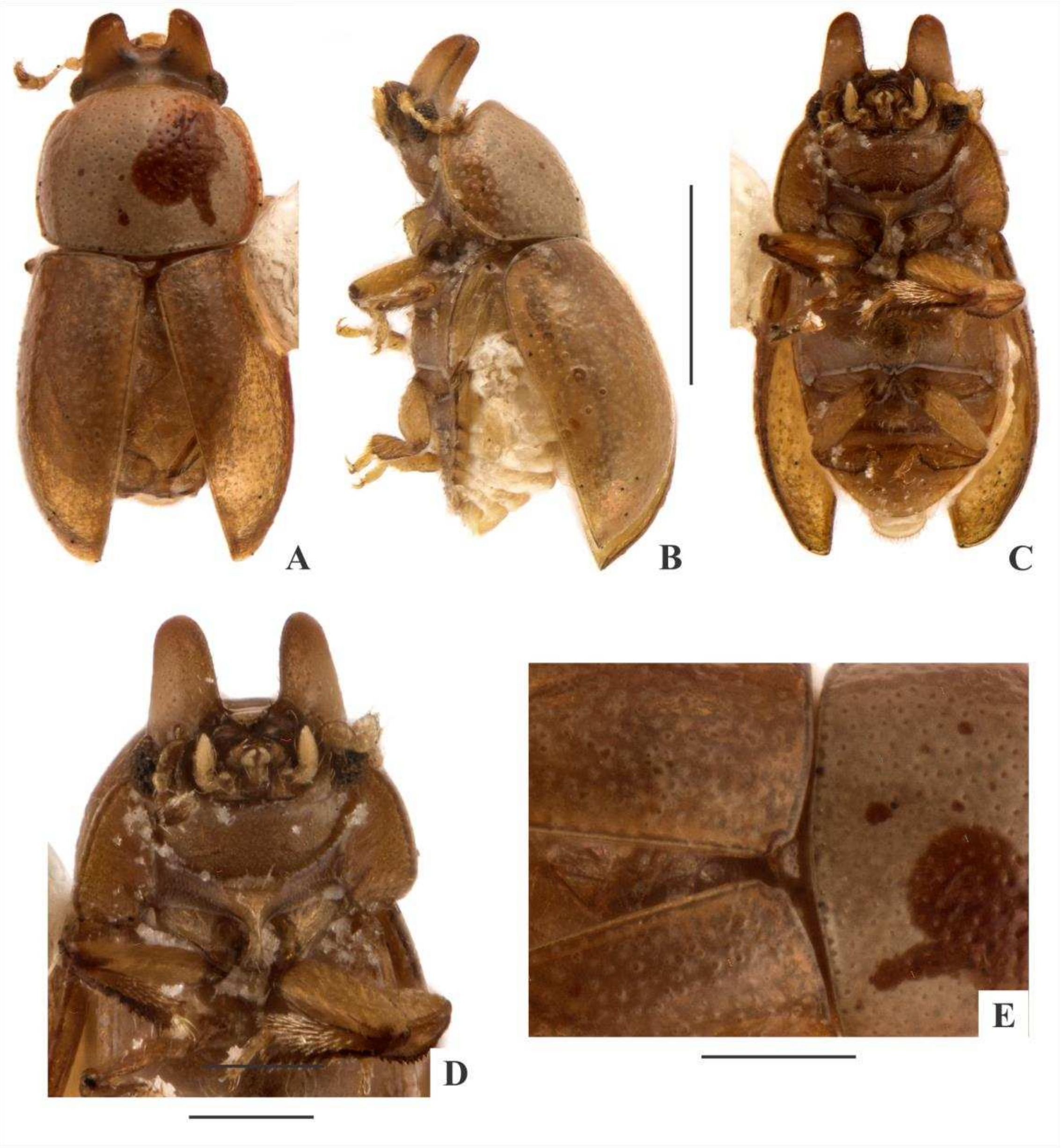

Fig. 12. *Anartioscelos almirantensis* **sp. nov.**, male holotype (A–E) from Almirante (Panama): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

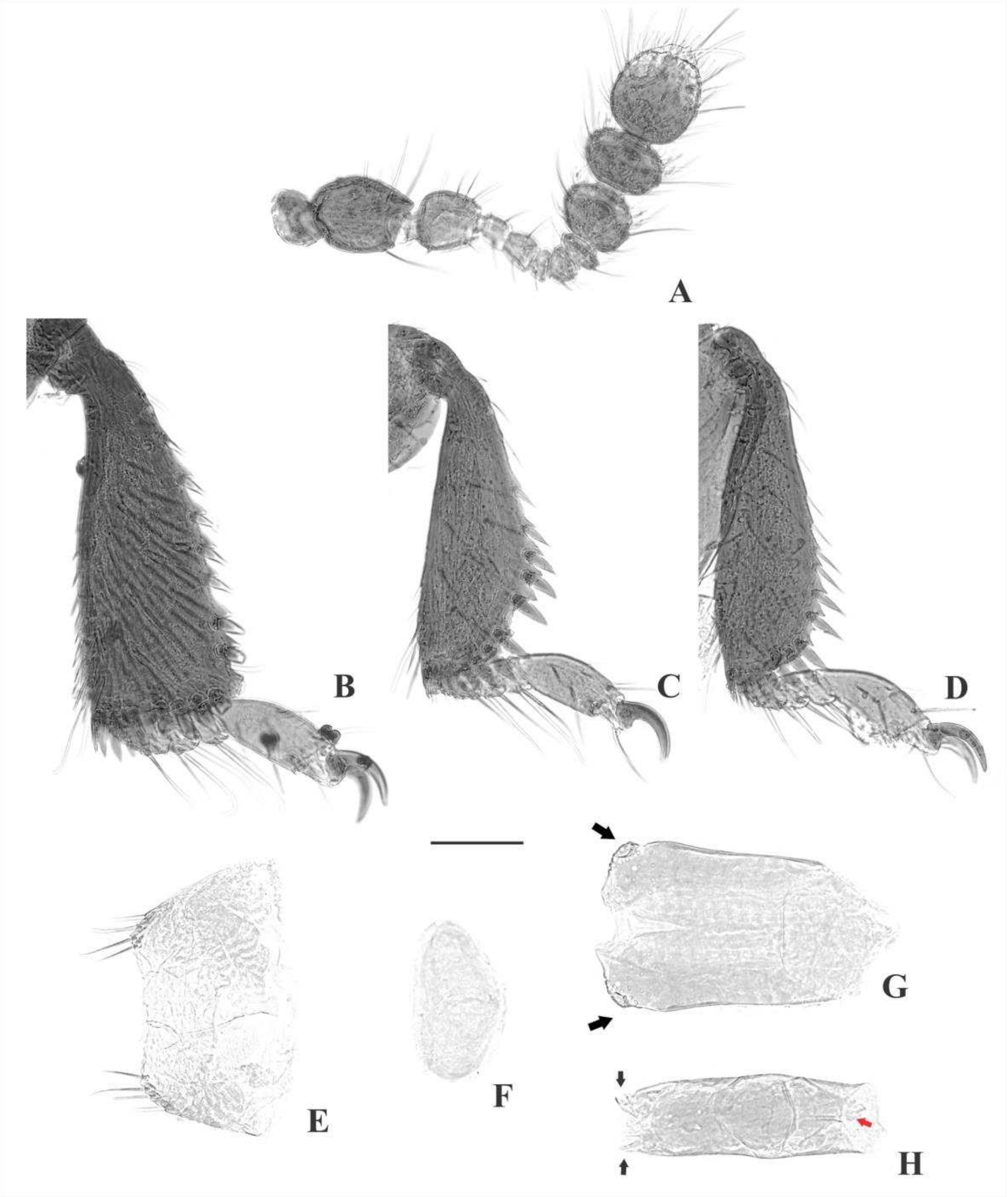

Fig. 13. *Anartioscelos almirantensis* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–H) from Almirante (Panama): **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Basal piece. **G.** Tegmen, note angulations at outer apical edge (black arrows). **H.** Penis, note apical acute angulations (black arrows) and rounded emargination at anterior portion (red arrow). Scale bar: 0.05 mm (A–H).

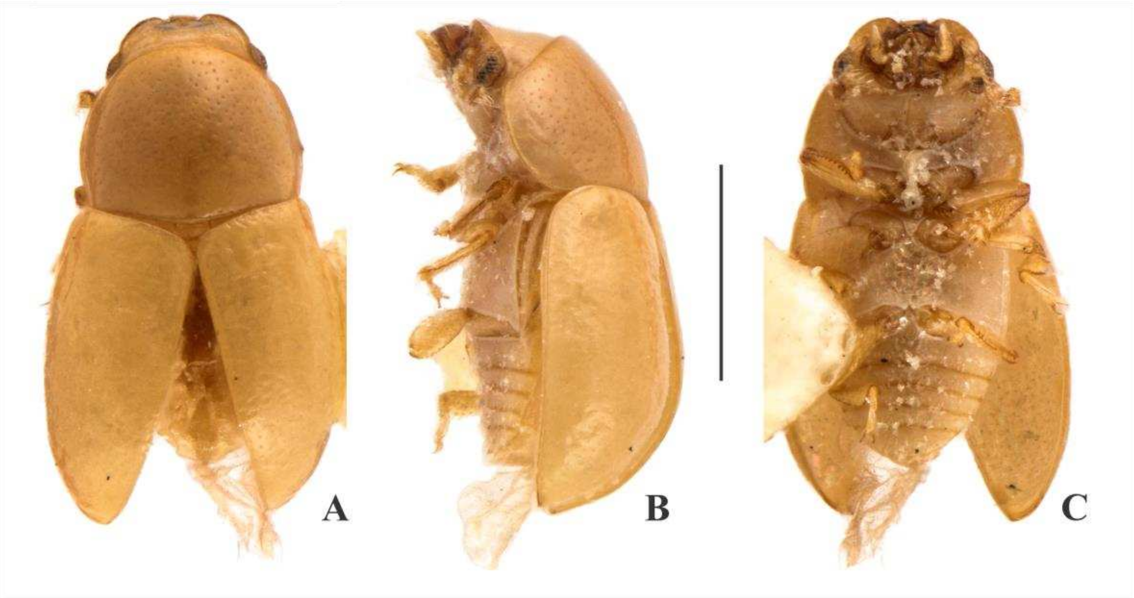

Fig. 14. *Anartioscelos almirantensis* **sp. nov.**, female paratype (A–C) from Almirante (Panama): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. Scale bar: 0.5 mm (A–C).

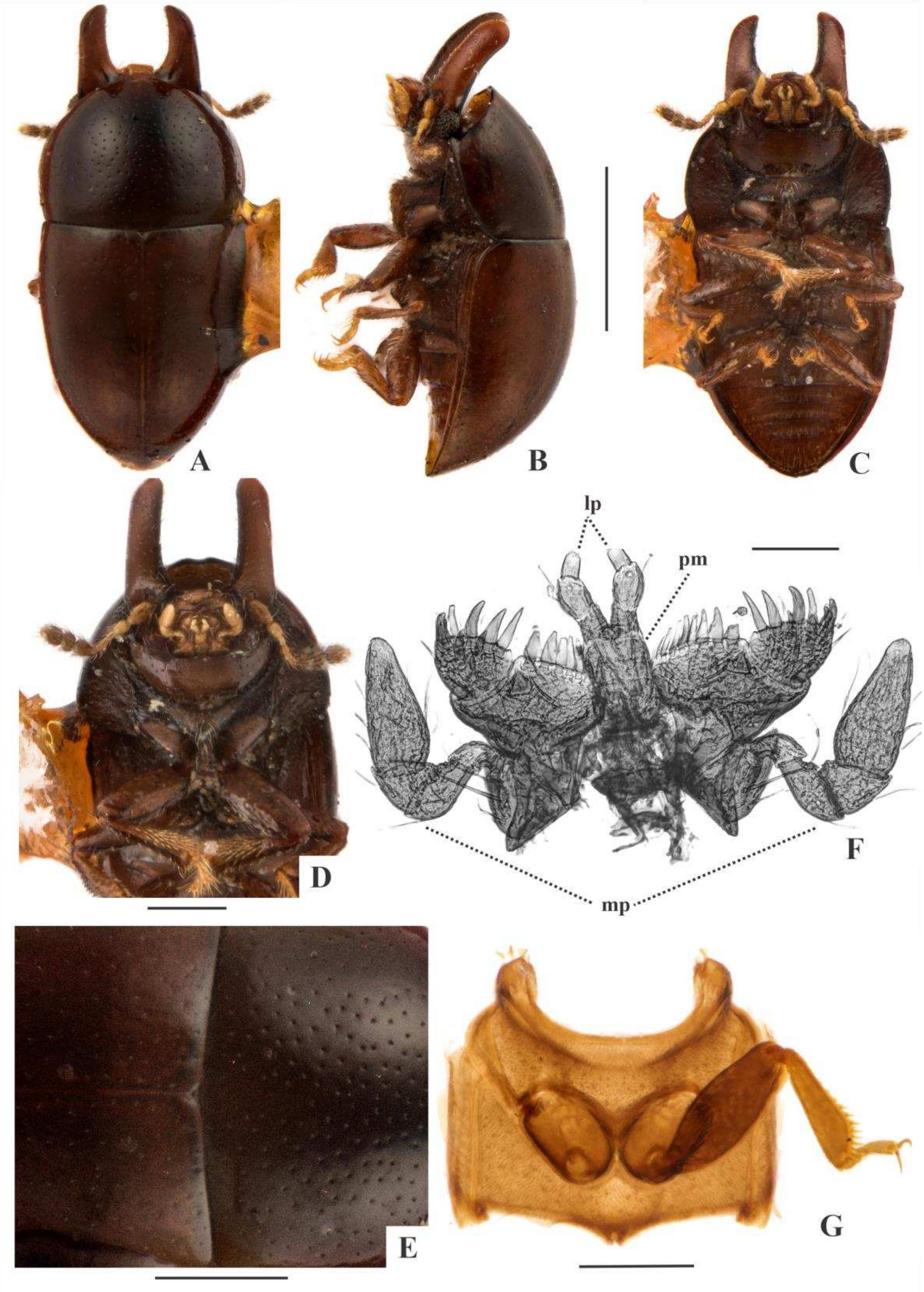

Fig. 15. *Anartioscelos aptenus* **sp. nov.**, male holotype (A–E) from San Juan Bautista Valle Nacional (Mexico), mouth parts of male paratype (F) and metaventrite of male

paratype (G) from same locality: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **F.** Mouth parts, showing labial palps (lp), maxillary palps (mp) and prementum (pm). Scale bars: 0.5 mm (A–C); 0.2 mm (D–E, G); 0.05 mm (F).

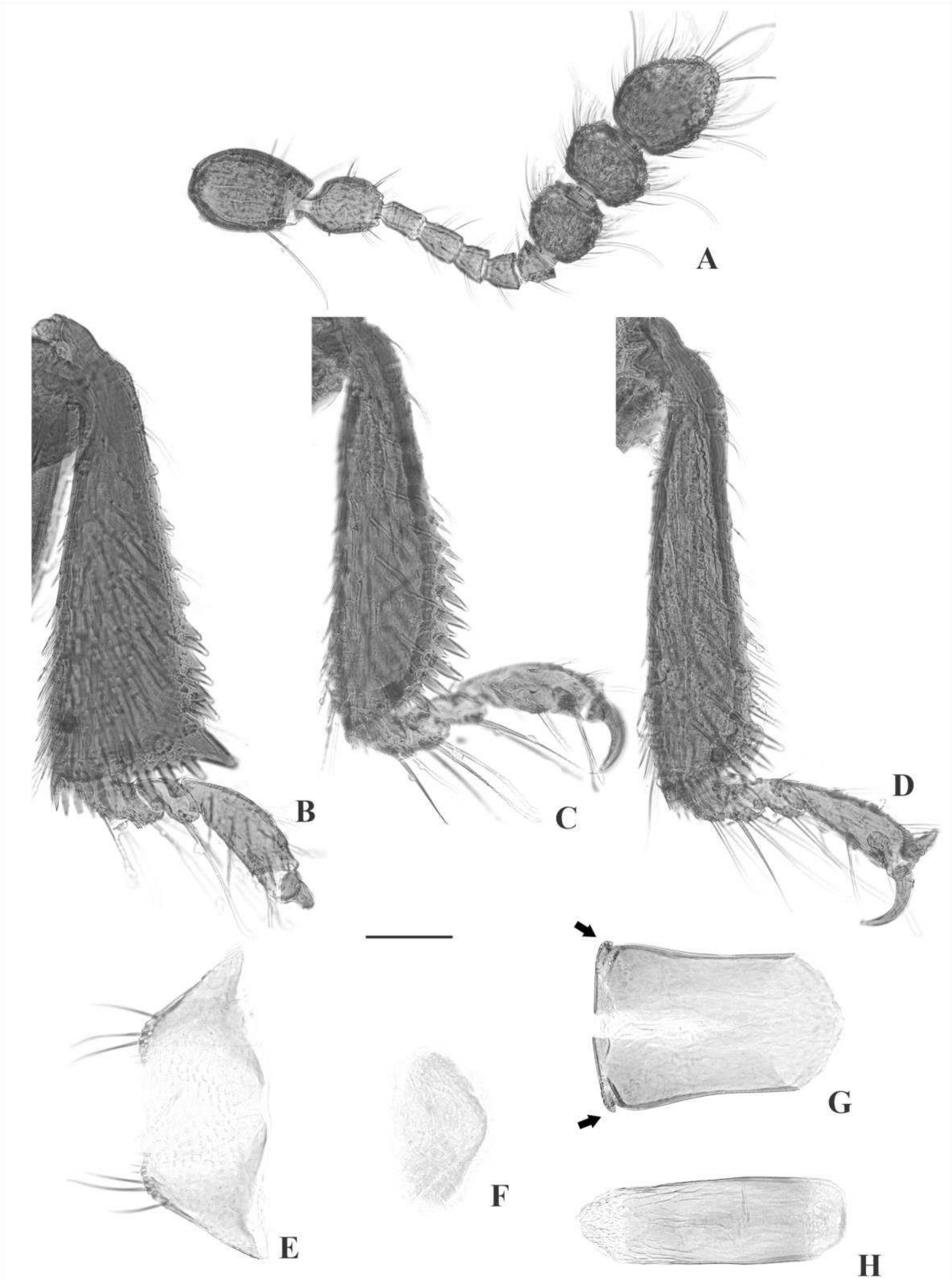

Fig. 16. *Anartioscelos aptenus* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–H) from San Juan Bautista Valle Nacional (Mexico): **A.** Left antenna. **B.** Left protibia. **C.**

Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Basal piece. **G.** Tegmen, note angulations at outer apical edge (black arrows). **H.** Penis. Scale bar: 0.05 mm (A–H).

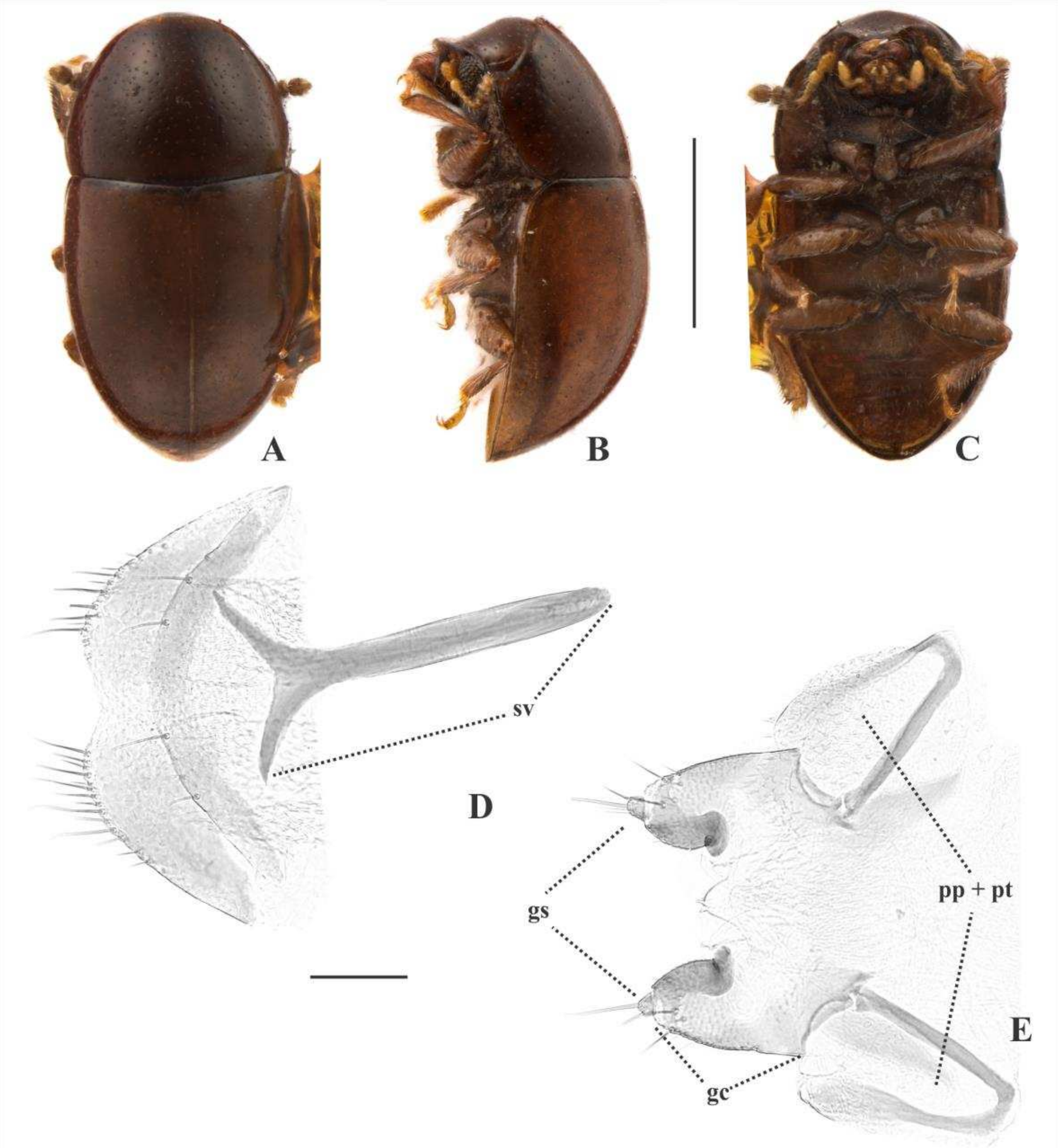

Fig. 17. *Anartioscelos aptenus* **sp. nov.**, female paratype (A–C) from San Juan Bautista Valle Nacional (Mexico) and female terminalia of paratype (D–E) from same locality: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Spiculum ventrale (sv) at anterior portion of sternite VIII. **E.** Ovipositor, showing gonostyli (gs), gonocoxites (gc) and paraprocts plus proctiger (pp + pt). Scale bars: 0.5 mm (A–C); 0.05 mm (D–E).

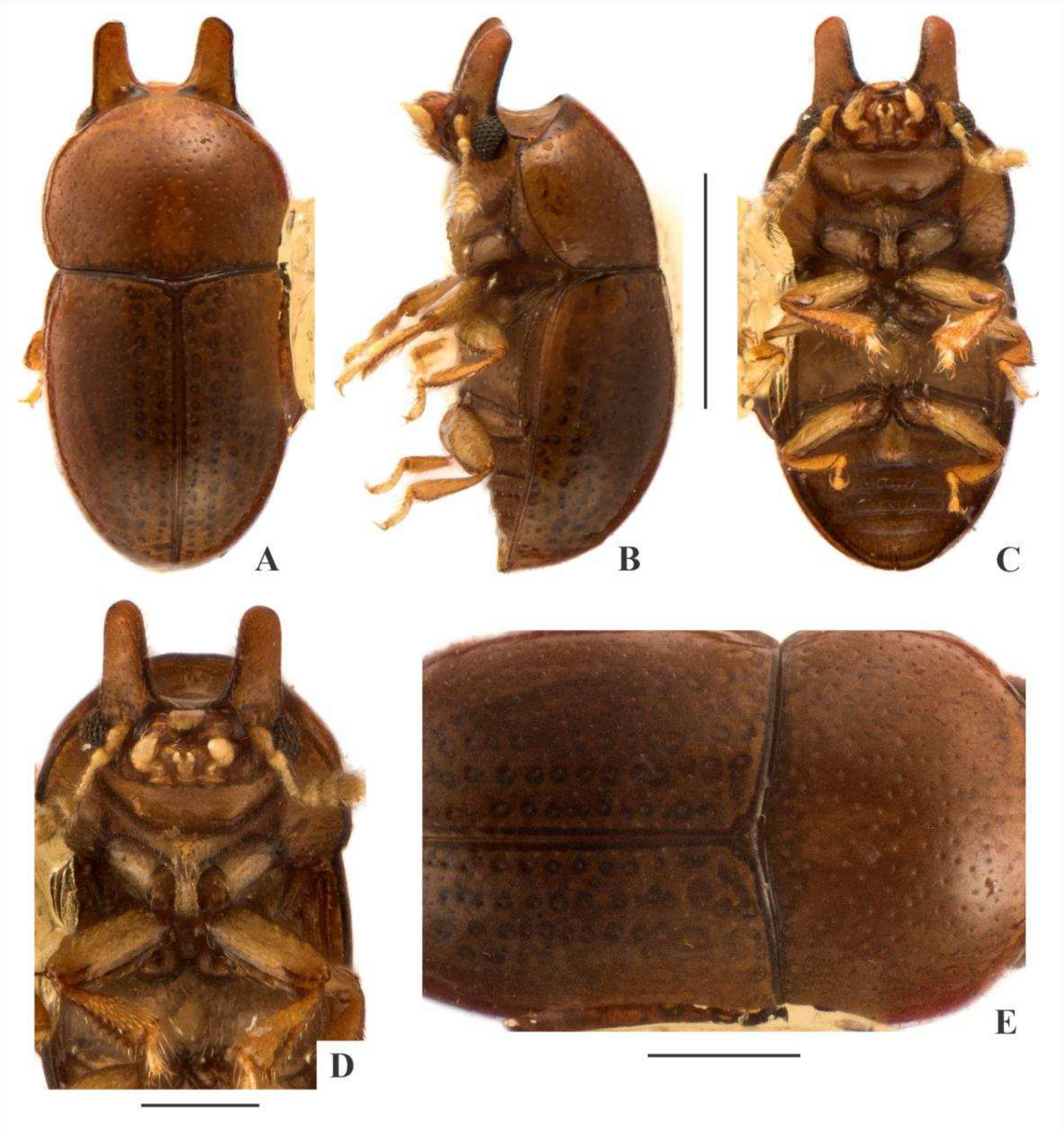

Fig. 18. *Anartioscelos eurinotum* **sp. nov.**, male holotype (A–E) from Barro Colorado Island (Panama): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

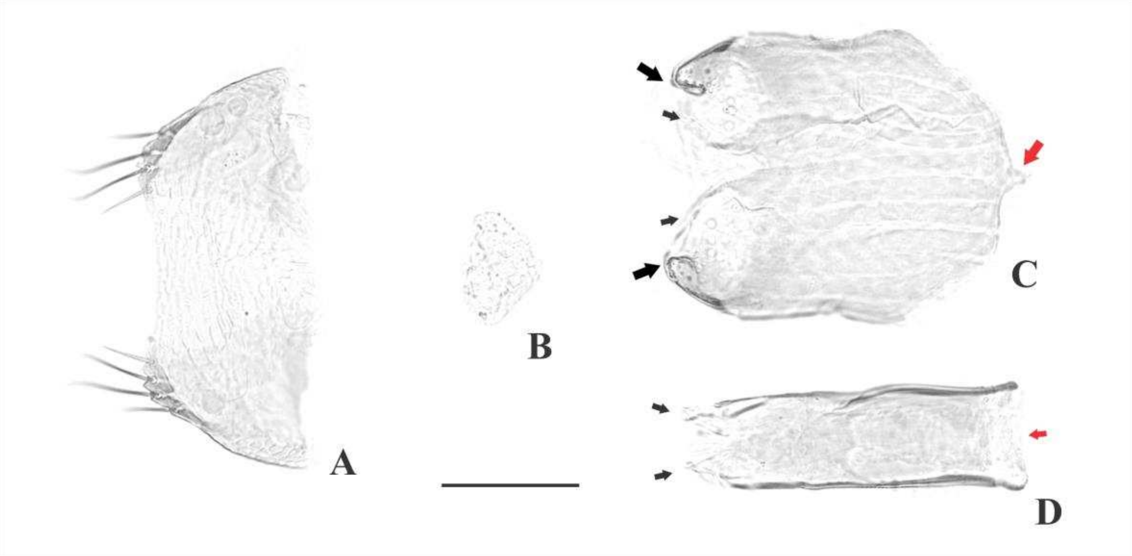

Fig. 19. *Anartioscelos eurinotum* **sp. nov.**, aedeagus of holotype (A–D) from Barro Colorado Island (Panama): **A.** Sternite VIII. **B.** Basal piece. **C.** Tegmen, note angulations at inner apical edge (big black arrows) and excavations (small black arrows), and acute angulation at anterior portion (red arrow). **D.** Penis, note apical acute angulations (black arrows) and anterior portion almost straight (red arrow). Scale bar: 0.05 mm (A–D).

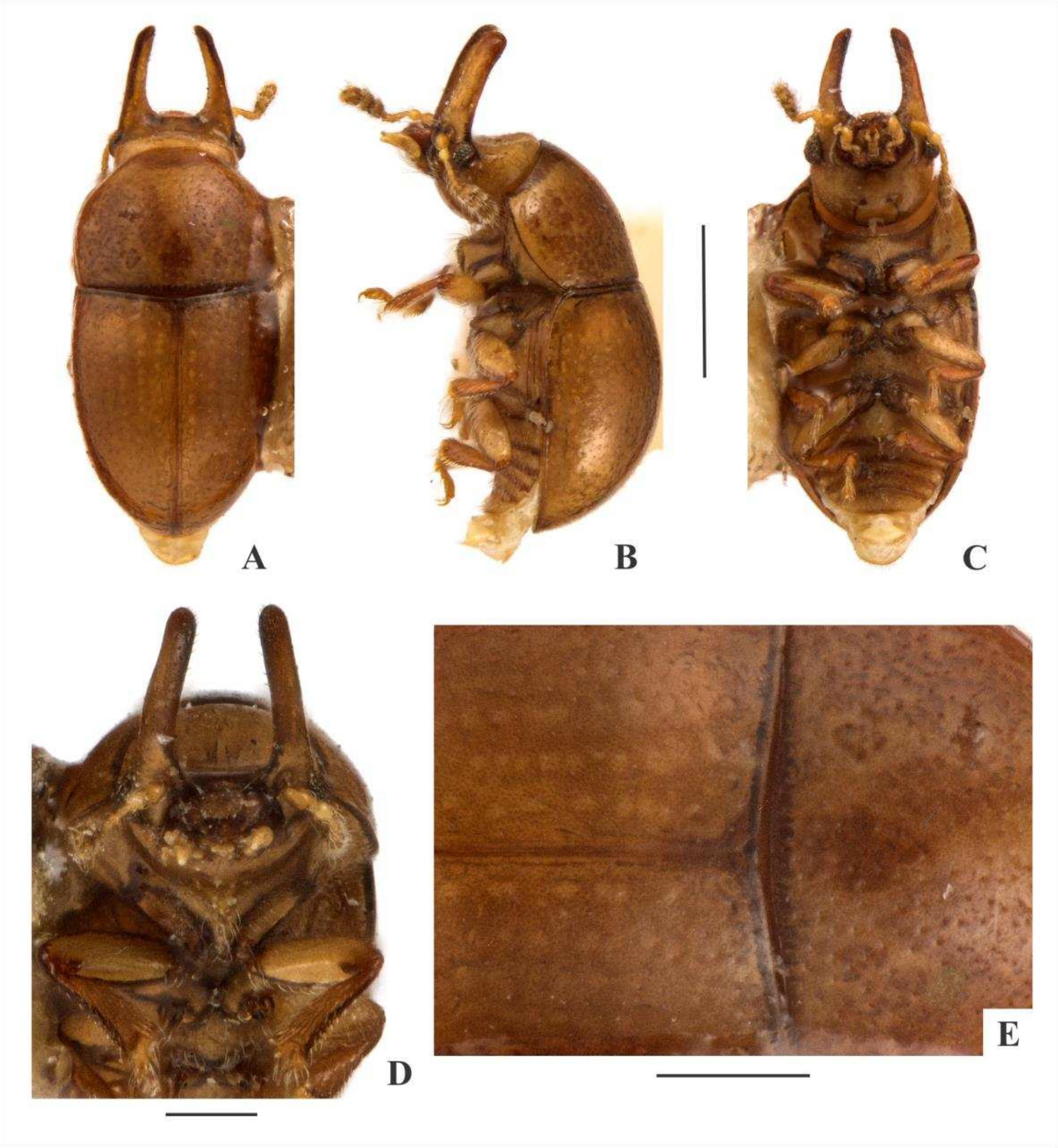

Fig. 20. *Anartioscelos involucris* **sp. nov.**, male holotype (A–E) from Cerro Punta (Panama): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

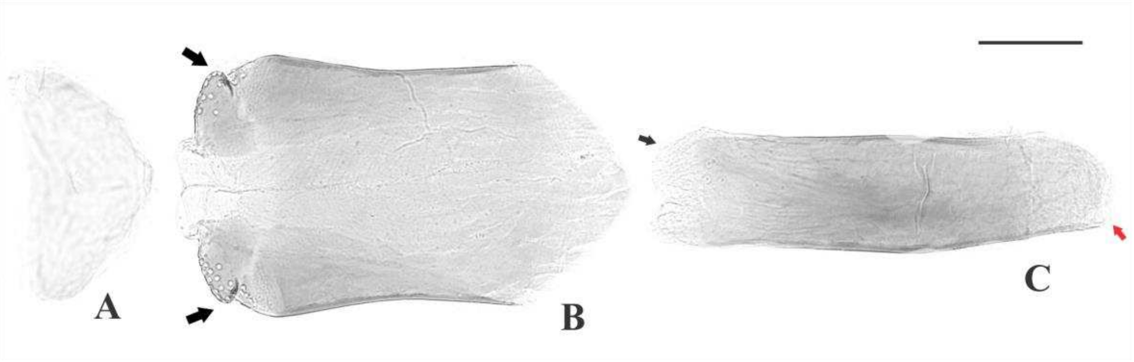

Fig. 21. *Anartioscelos involucris* **sp. nov.**, aedeagus of holotype (A–C) from Cerro Punta (Panama): **A.** Basal piece. **B.** Tegmen, note angulations at outer apical edge (black arrows). **C.** Penis, note rounded apex (black arrow) and anterior portion rounded (red arrow). Scale bar: 0.05 mm (A–C).

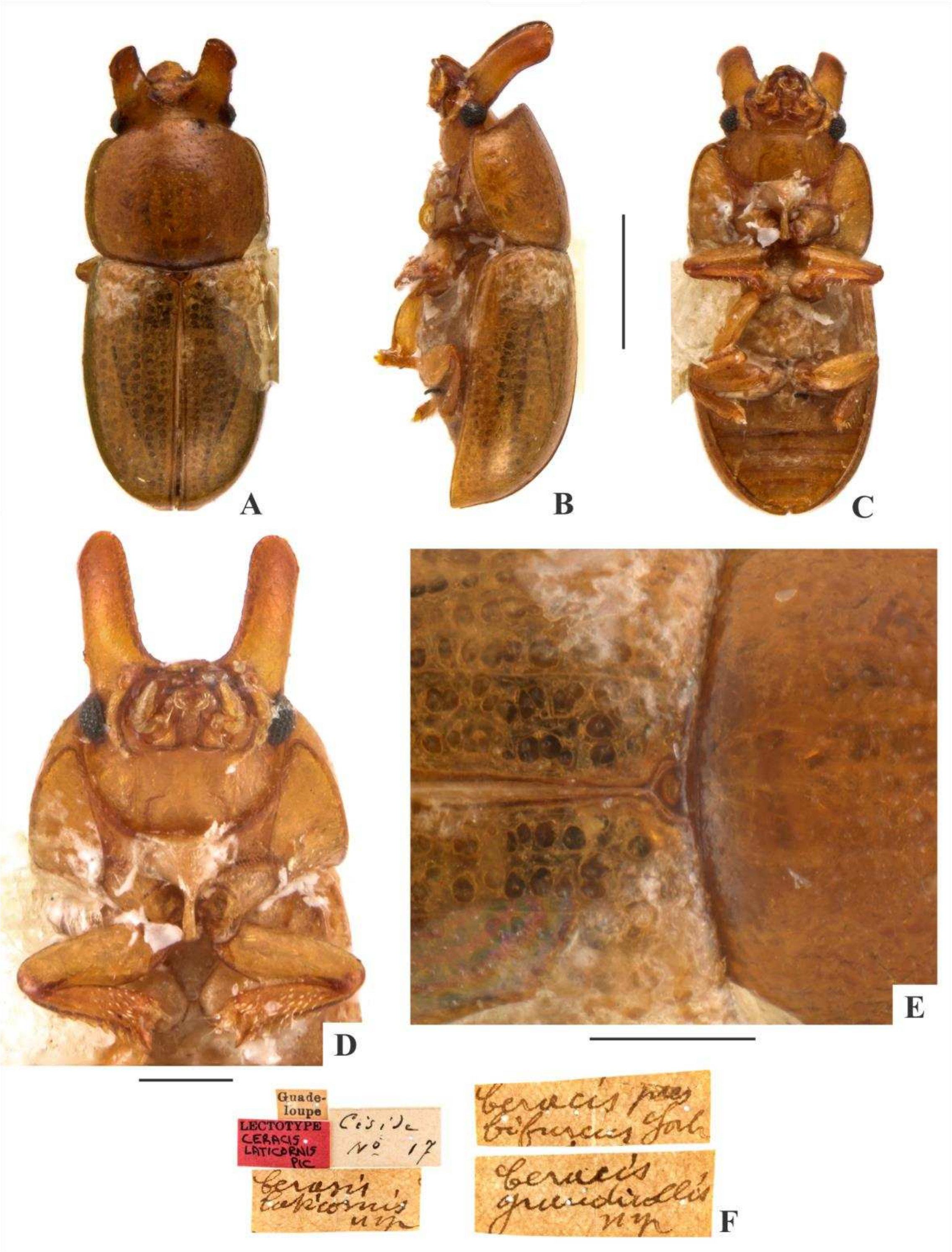

Fig. 22. *Anartioscelos laticornis* (Pic, 1922) **comb. nov.**, male lectotype (A–E) from Guadeloupe: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **F.** Labels. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

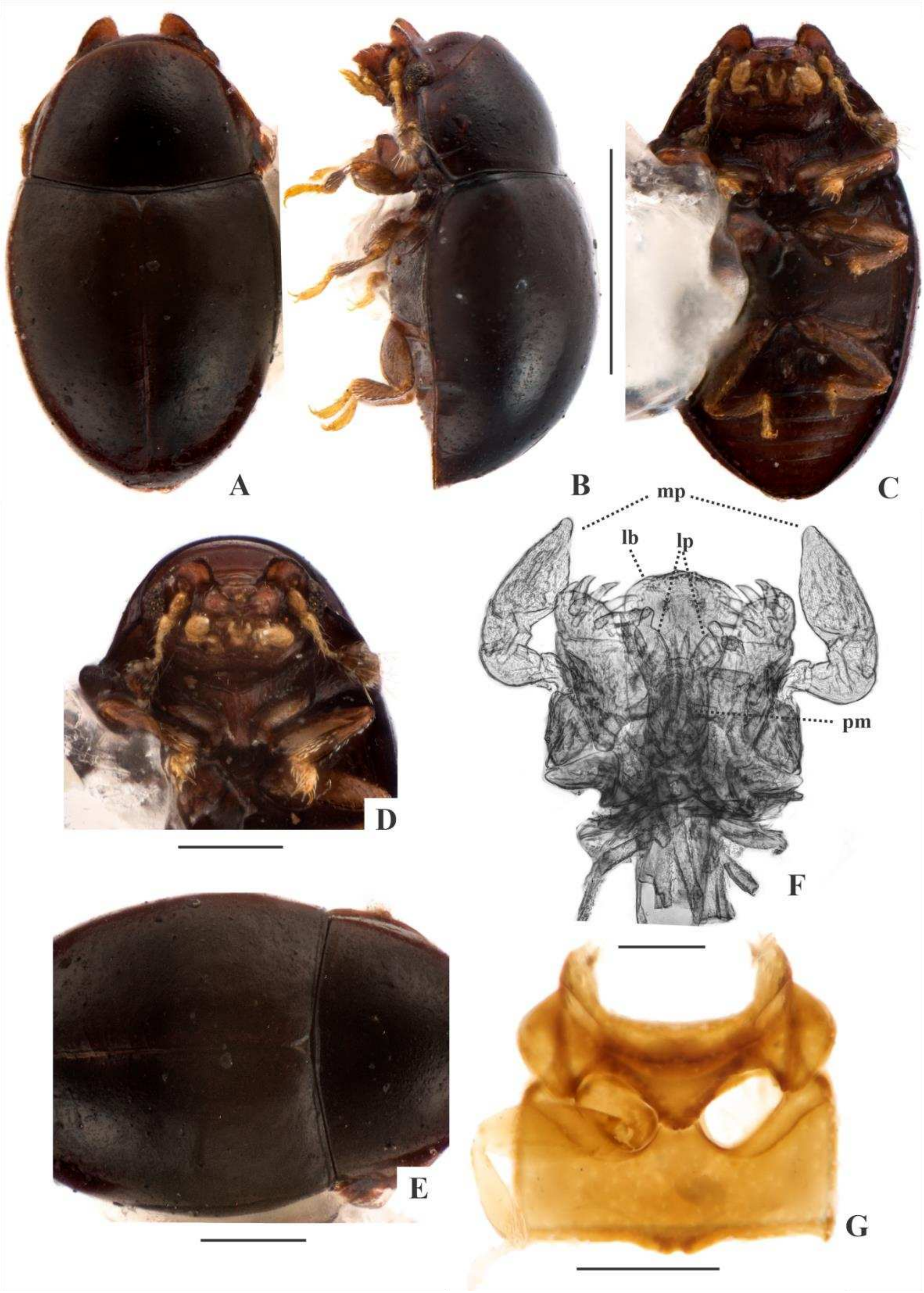

Fig. 23. *Atomocis melanus* **sp. nov.**, male holotype (A–E) from Campana (Panama), mouth parts of female paratype (F) and metaventrite of male paratype (G) from Barro

Colorado Island (Panama): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **F.** Mouth parts, showing labial palps (lp), labrum (lb), maxillary palps (mp) and prementum (pm). Scale bars: 0.5 mm (A–C); 0.2 mm (D–E, G); 0.05 mm (F).

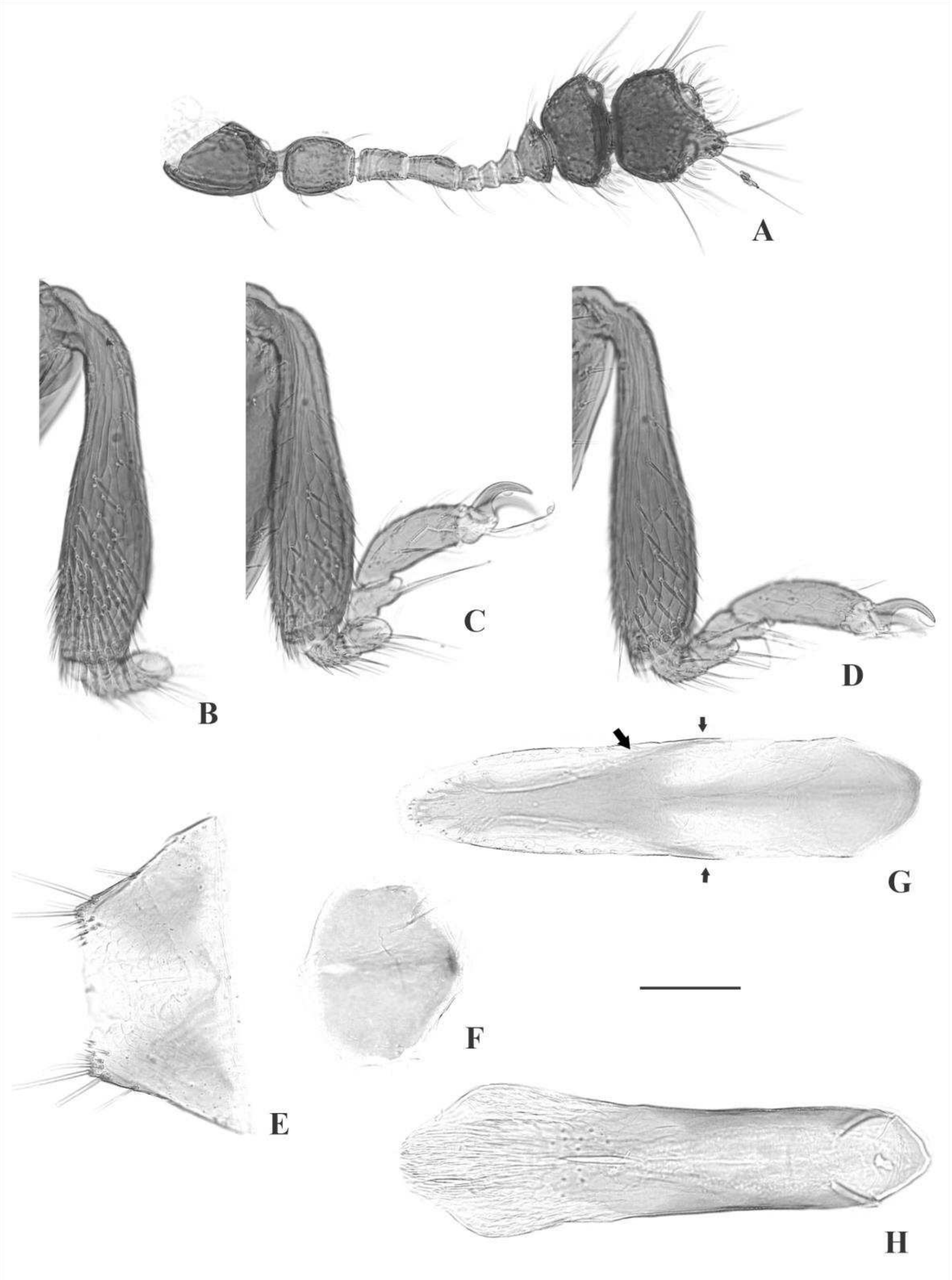

Fig. 24. *Atomocis melanus* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–H) from Barro Colorado Island (Panama): **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Basal piece. **G.** Tegmen, note arrow-

shaped sclerotization at medial portion (big black arrows) and lateral angulations (small black arrows). **H.** Penis. Scale bar: 0.05 mm (A–H).

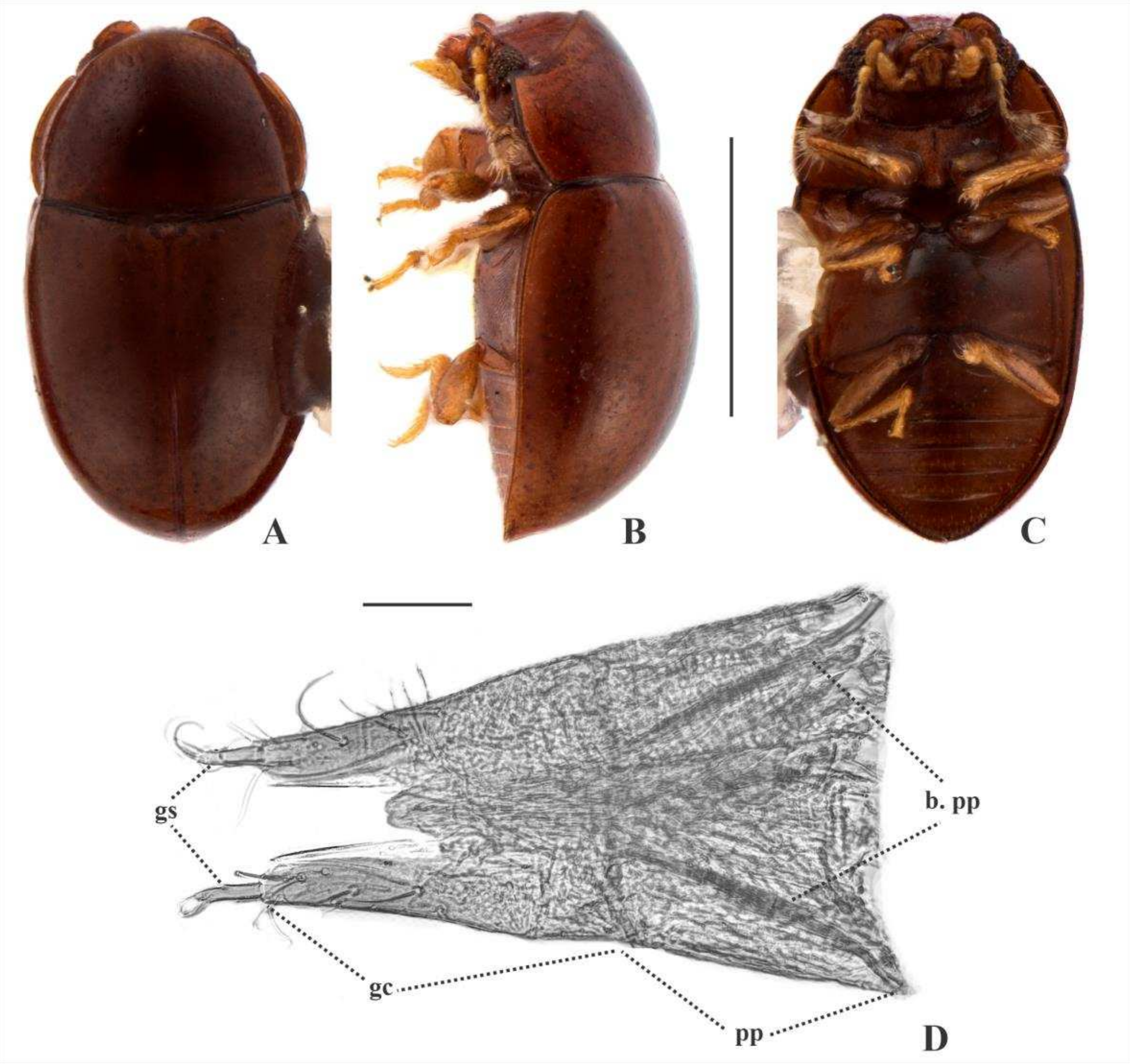

Fig. 25. *Atomocis melanus* **sp. nov.**, female paratype (A–C) from Campana (Panama), and female terminalia of paratype (D) from Barro Colorado Island (Panama): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Ovipositor, showing gonostyli (gs), gonocoxites (gc), paraprocts (pp) and baculi of paraprocts (b. pp). Scale bars: 0.5 mm (A–C); 0.05 mm (D).

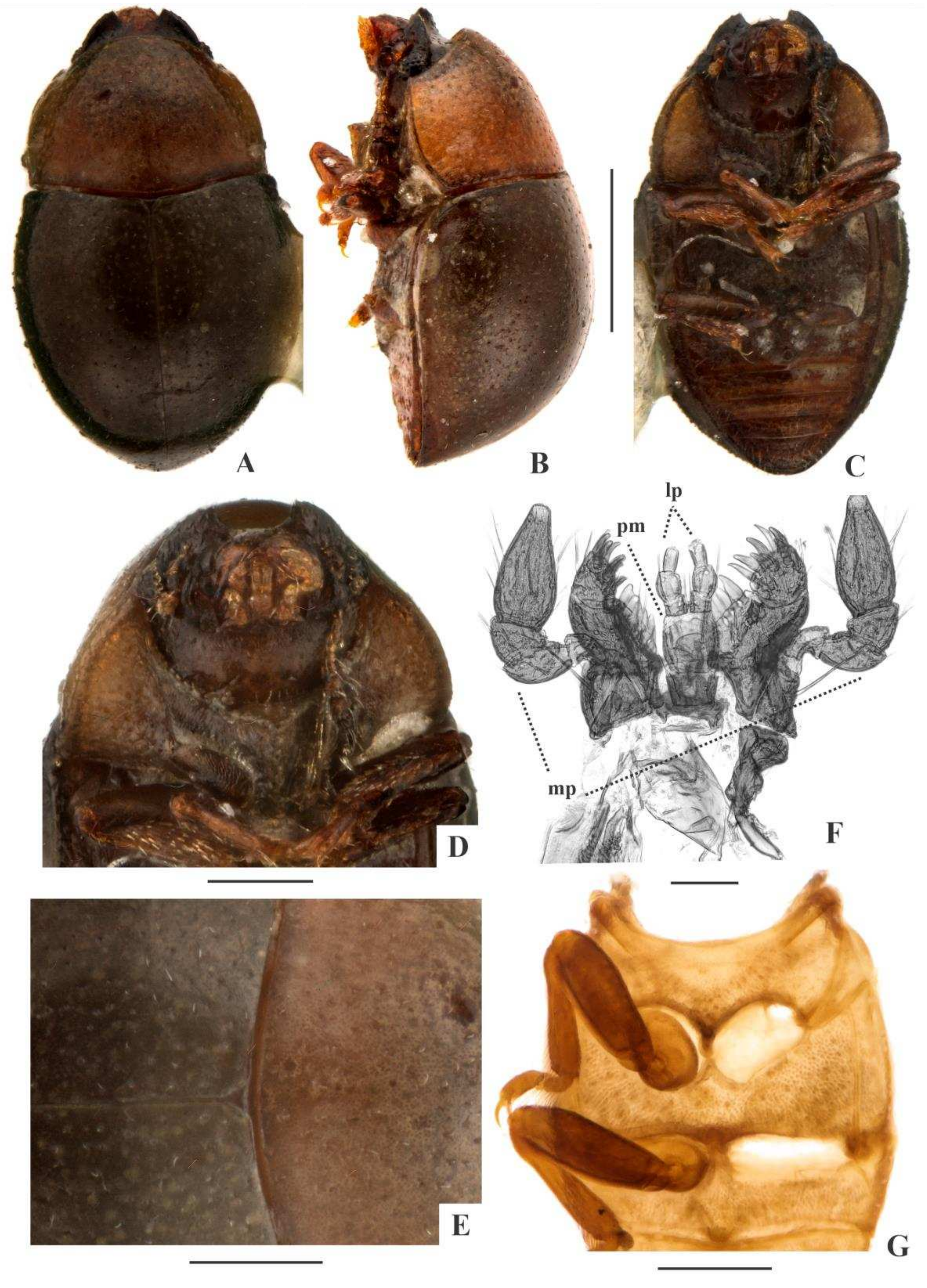

Fig. 26. *Gyraleosomus boliviensis* **sp. nov.**, male holotype (A–E) from Cochabamba (Bolivia), mouth parts of female paratype (F) and metaventrite of male paratype (G) from same locality: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique

ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **F.** Mouth parts, showing labial palps (lp), maxillary palps (mp) and prementum (pm). Scale bars: 0.5 mm (A–C); 0.2 mm (D–E, G); 0.05 mm (F).

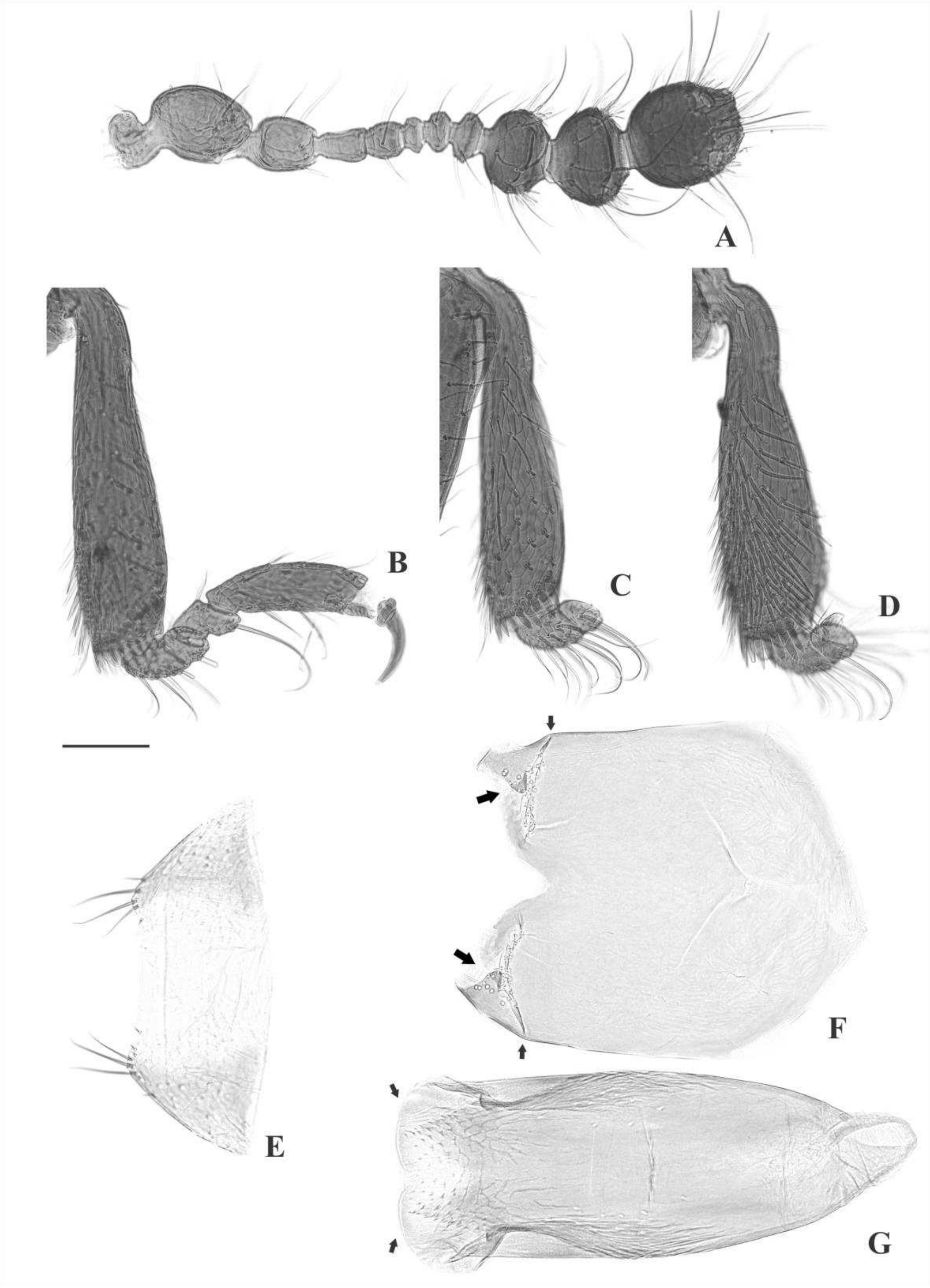

Fig. 27. *Gyraleosomus boliviensis* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–G) from Cochabamba (Bolivia): **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Tegmen, note angulations at inner apical edge

(big black arrows) and excavations at base of each angulation (small black arrows). **G.** Penis, note apical rounded projections (black arrows). Scale bar: 0.05 mm (A–G).

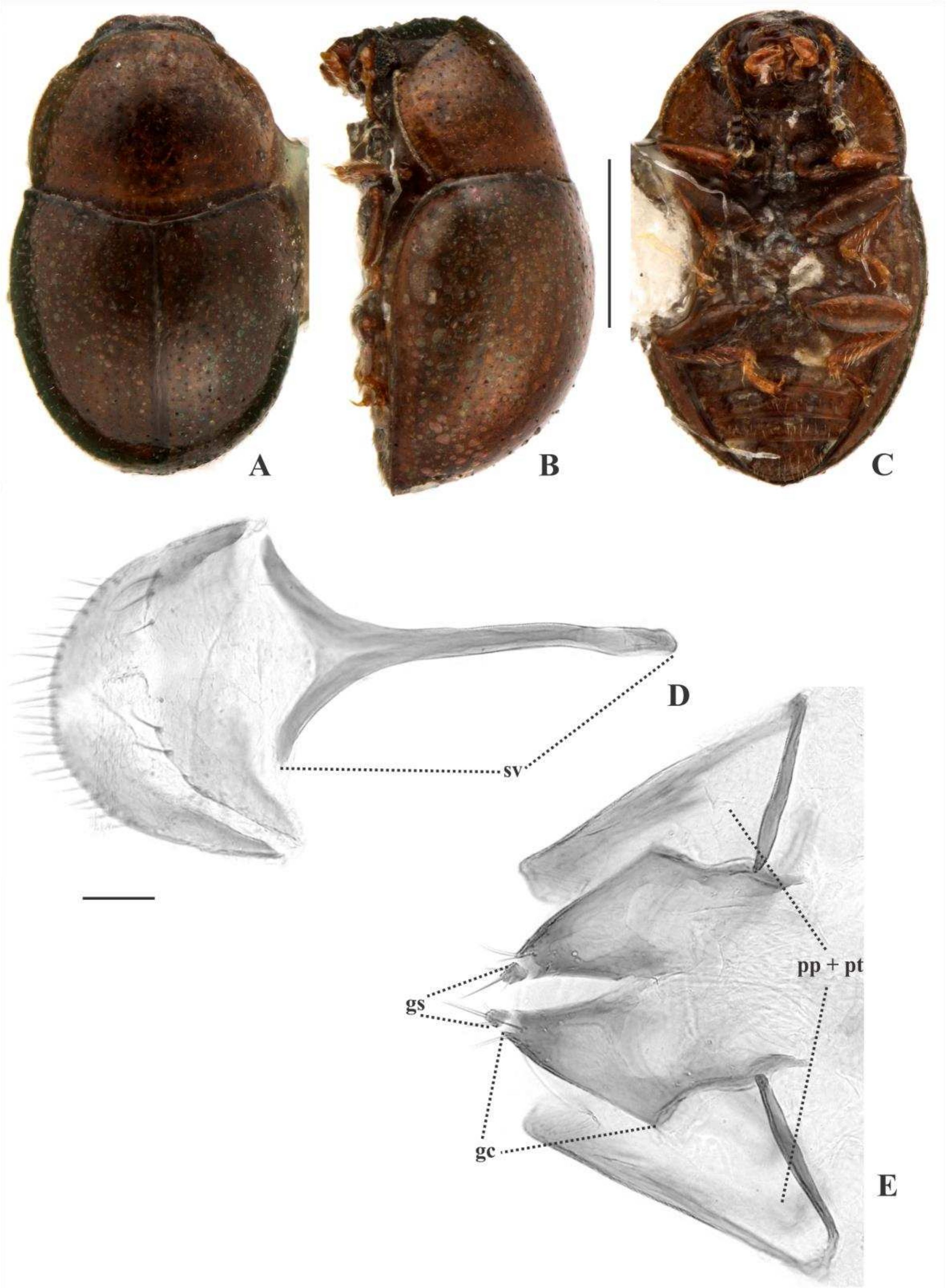

Fig. 28. *Gyraleosomus boliviensis* **sp. nov.**, female paratype (A–C) from Cochabamba (Bolivia), and female terminalia of paratype (D–E) from same locality: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Spiculum ventrale (sv) at anterior portion of sternite VIII. **E.** Ovipositor, showing gonostyli (gs), gonocoxites (gc) and paraprocts plus proctiger (pp + pt). Scale bars: 0.5 mm (A–C); 0.05 mm (D–E).

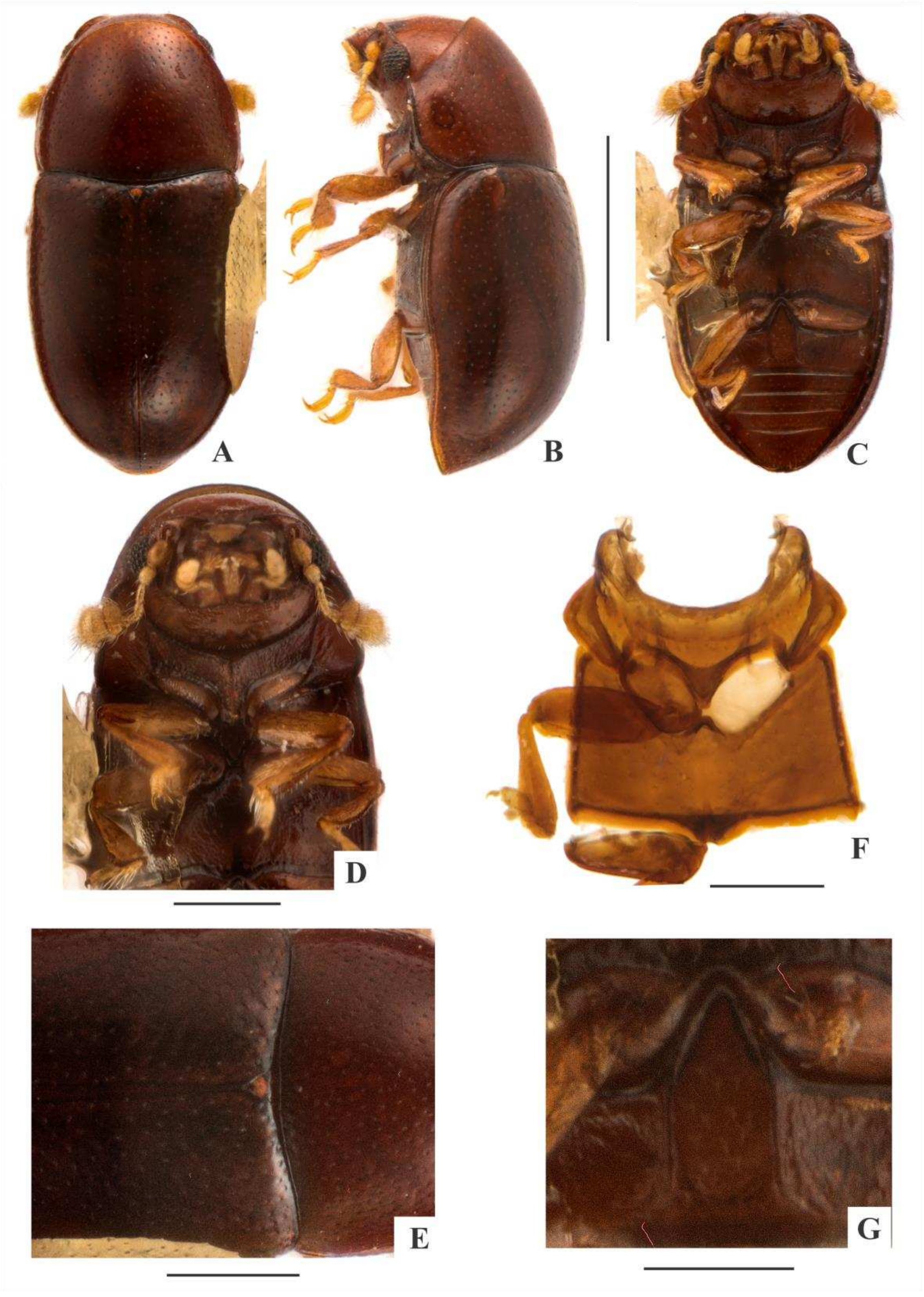

Fig. 29. *Insolitocis panamensis* **sp. nov.**, female holotype (A–E, G) from Barro Colorado Island (Panama)and metaventrite of female paratype from same locality (F): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and

prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **G.** Pentagonal suturation of first abdominal ventrite. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E); 0.1 mm (G); 0.05 mm (F).

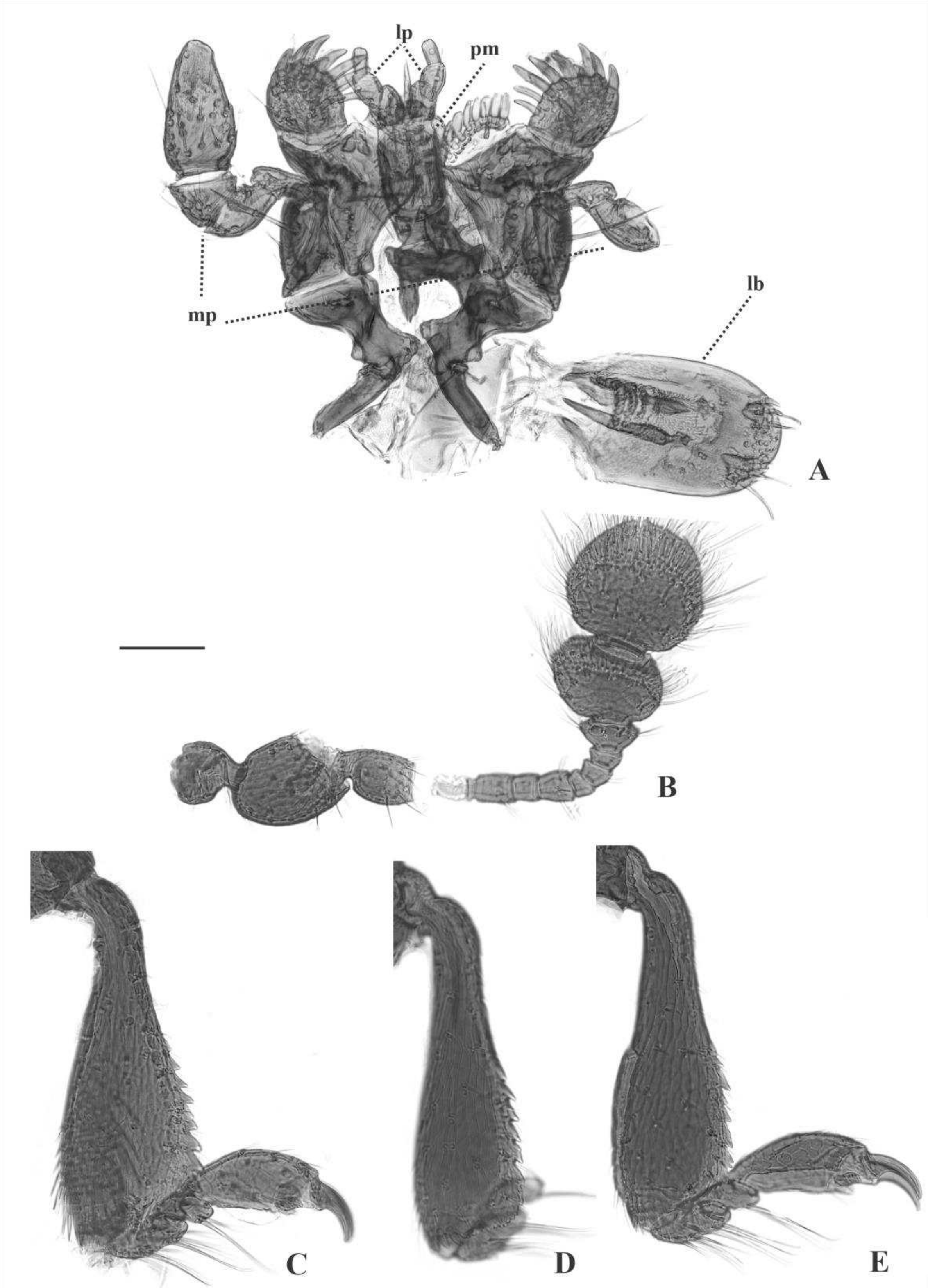

Fig. 30. *Insolitocis panamensis* **sp. nov.**, mouth parts (A), antenna and tibiae of female paratype (B–E) from Barro Colorado Island (Panama): **A.** Mouth parts, showing labial

palps (lp), labrum (lb), maxillary palps (mp) and prementum (pm). **B.** Left antenna. **C.** Left protibia. **D.** Left mesotibia. **E.** Left metatibia. Scale bar: 0.05 mm (A–E).

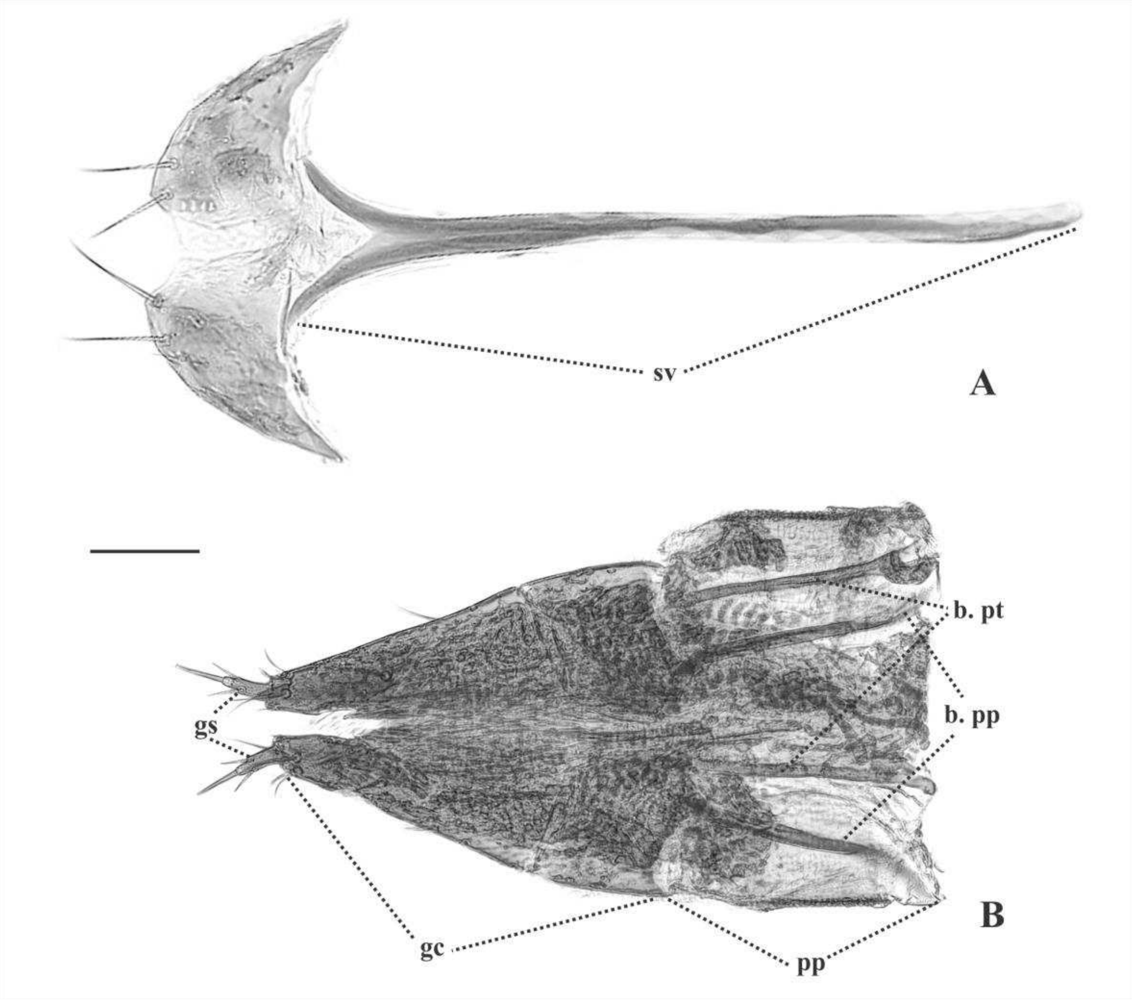

Fig. 31. *Insolitocis panamensis* **sp. nov.**, female terminalia of paratype (A–C) from Barro Colorado Island (Panama): **A.** Spiculum ventrale (sv) at anterior portion of sternite VIII. **B.** Ovipositor, showing gonostyli (gs), gonocoxites (gc), paraprocts (pp), baculi of paraprocts (b. pp), baculi of proctiger (b. pt). Scale bar: 0.05 mm (A–B).

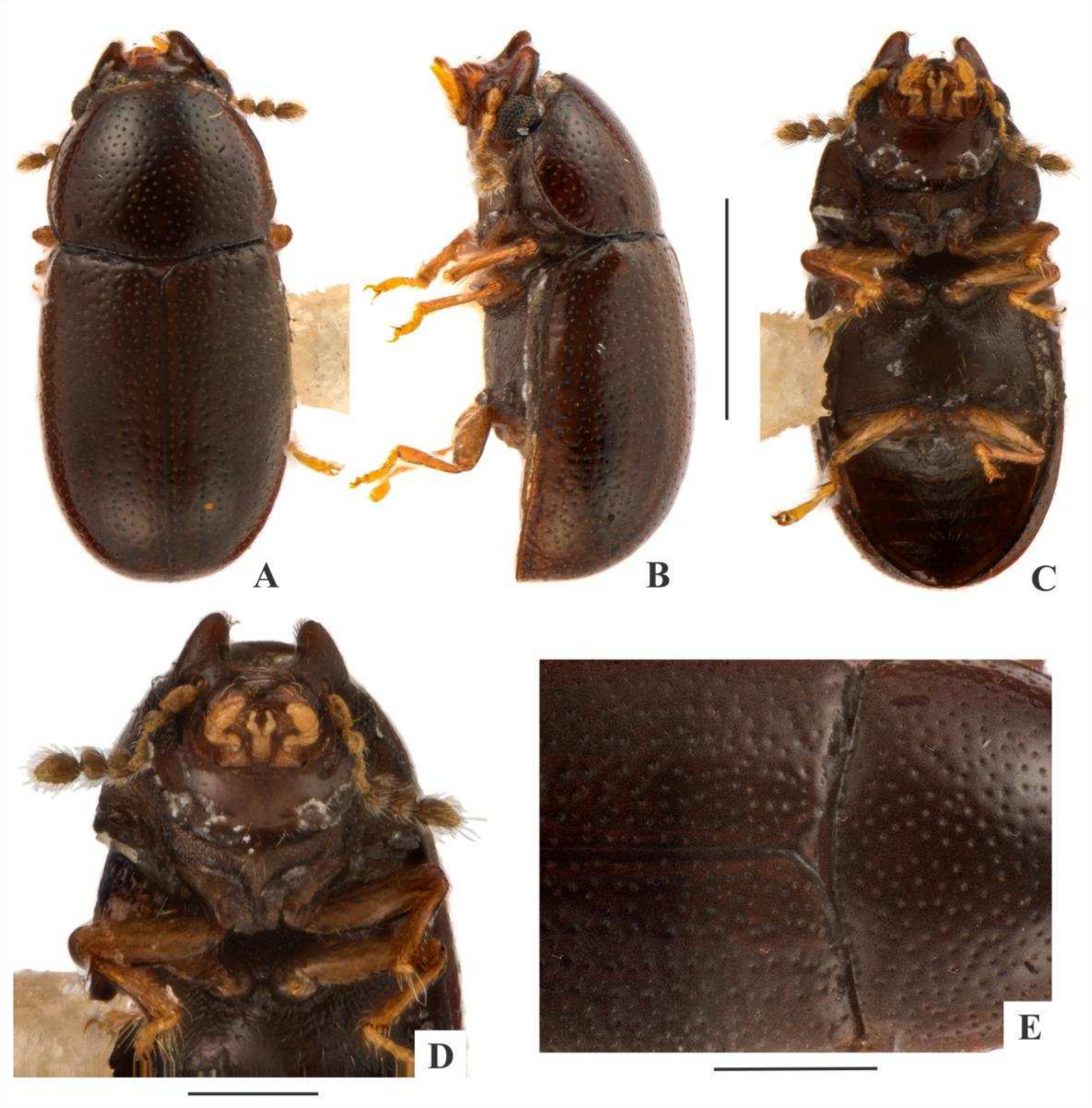

Fig. 32. *Lipedanicis adelphus* **sp. nov.**, male holotype (A–E) from Parque Ecológico Quedas do Rio Bonito (Minas Gerais, Southeast Brazil): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

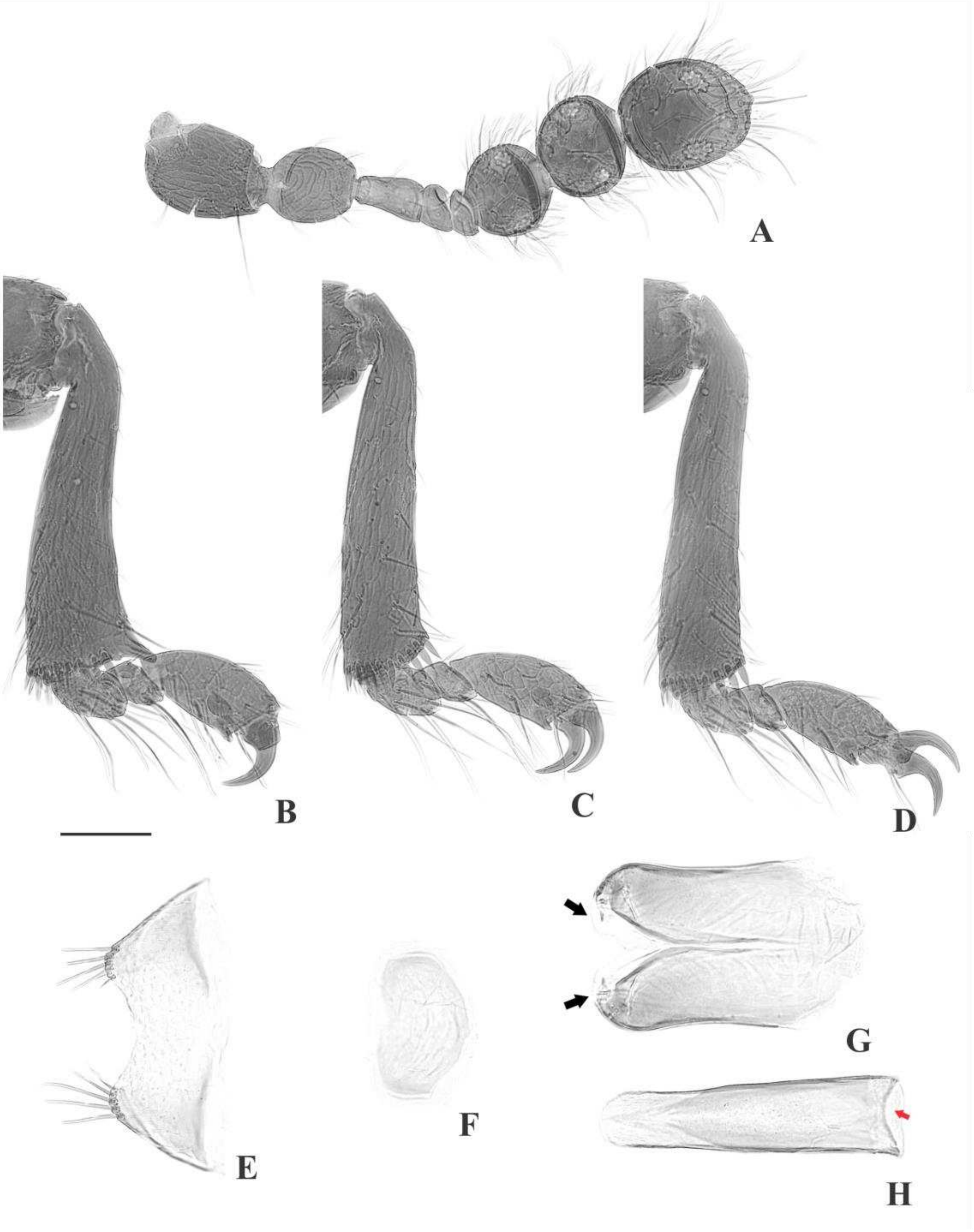

Fig. 33. *Lipedanicis adelphus* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–H) from Parque Ecológico Quedas do Rio Bonito (Minas Gerais, Southeast Brazil): **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Basal piece. **G.** Tegmen, note angulations at inner apical edge (big black arrows). **H.** Penis, note rounded emargination at anterior portion (red arrow). Scale bar: 0.05 mm (A–H).

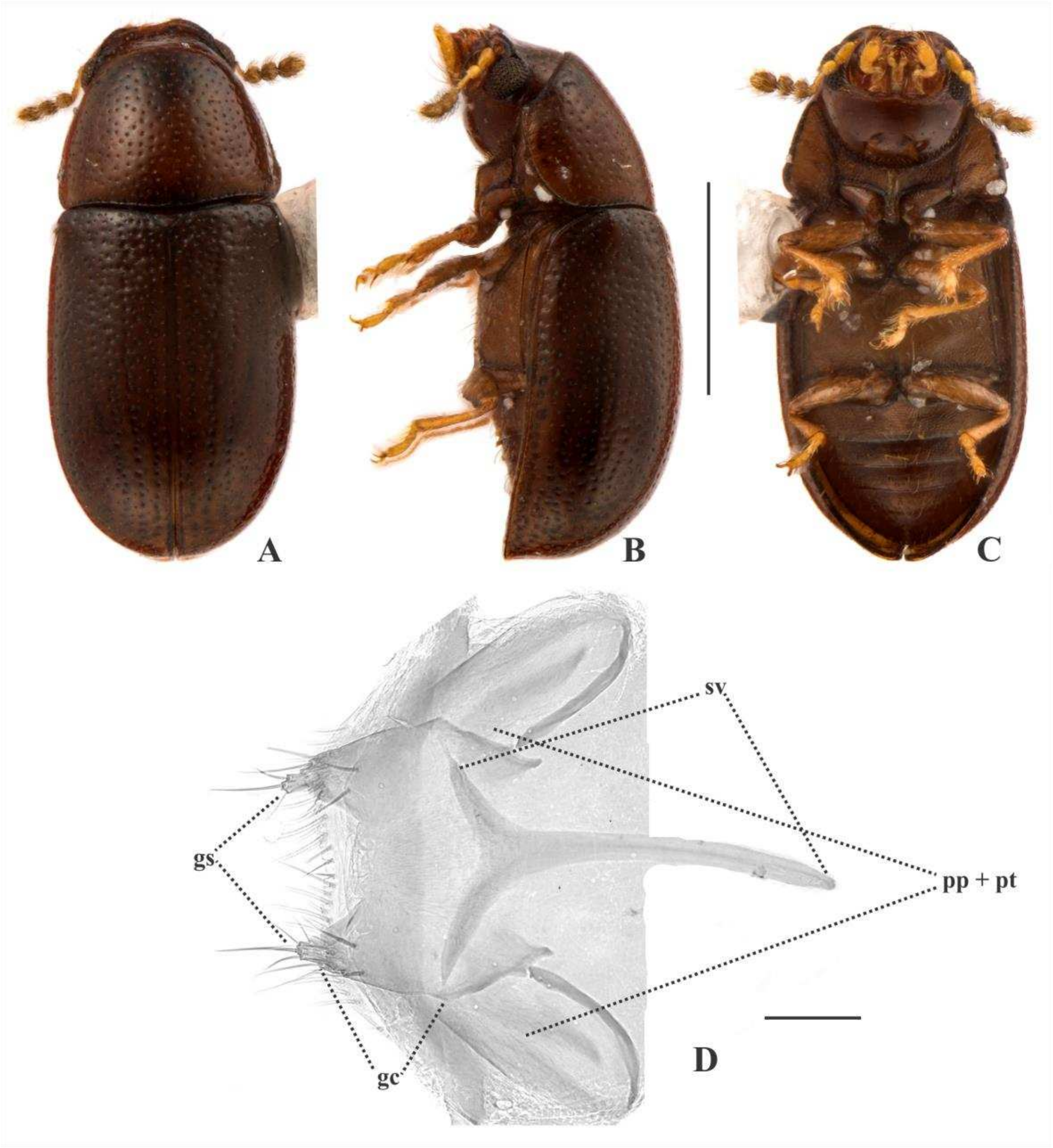

Fig. 34. *Lipedanicis adelphus* **sp. nov.**, female paratype (A–C) from Parque Ecológico Quedas do Rio Bonito (Minas Gerais, Southeast Brazil), and female terminalia of paratype (D) from same locality: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Female terminalia, showing spiculum ventrale (sv) at anterior portion of sternite VIII and ovipositor, showing gonostyli (gs), gonocoxites (gc) and paraprocts plus proctiger (pp + pt). Scale bars: 0.5 mm (A–C); 0.05 mm (D).

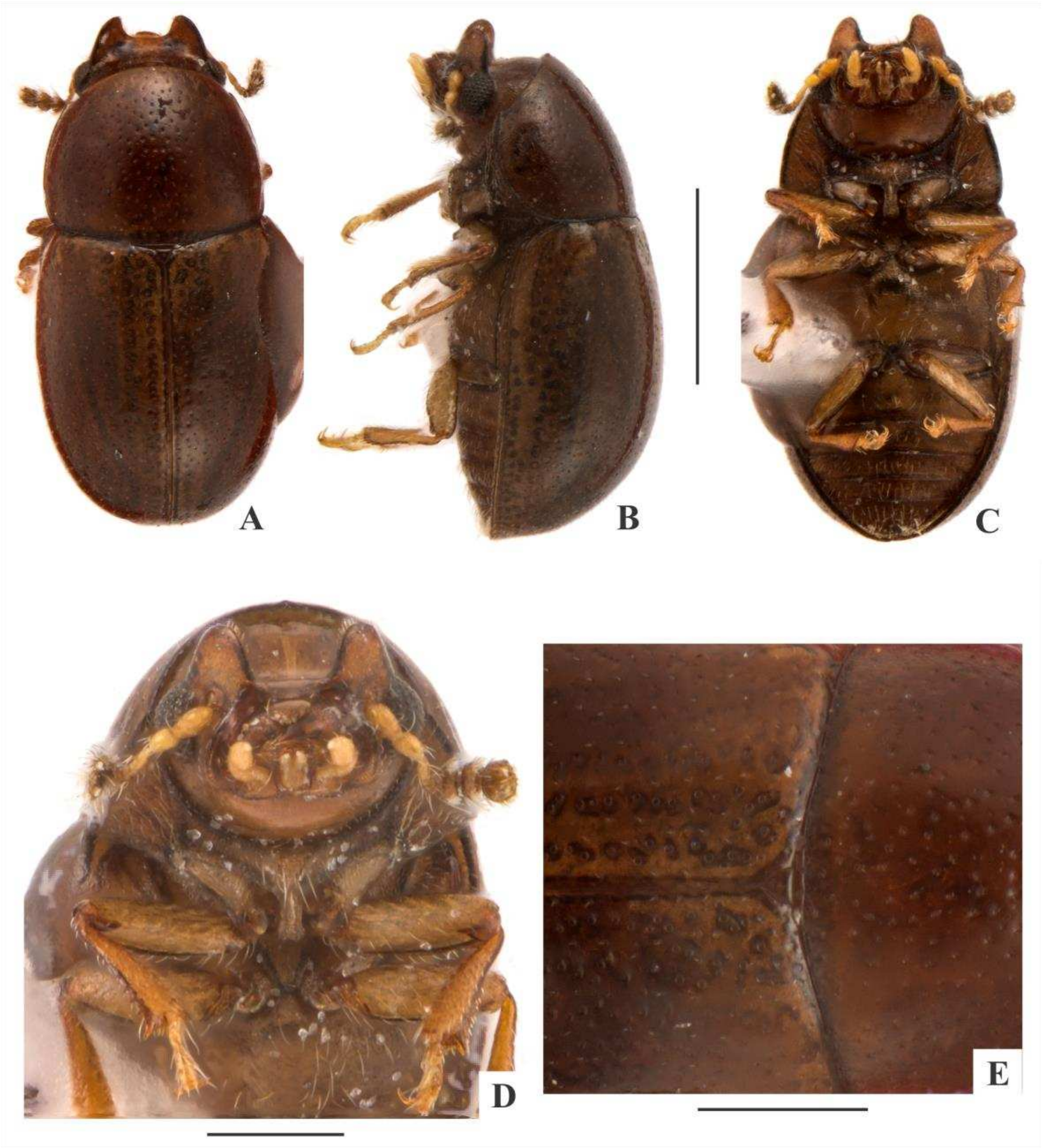

Fig. 35. *Lipedanicis agastor* **sp. nov.**, male holotype (A–E) from Floresta Nacional de São Francisco de Paula (Rio Grande do Sul, South Brazil): **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. Scale bars: 0.5 mm (A–C); 0.2 mm (D–E).

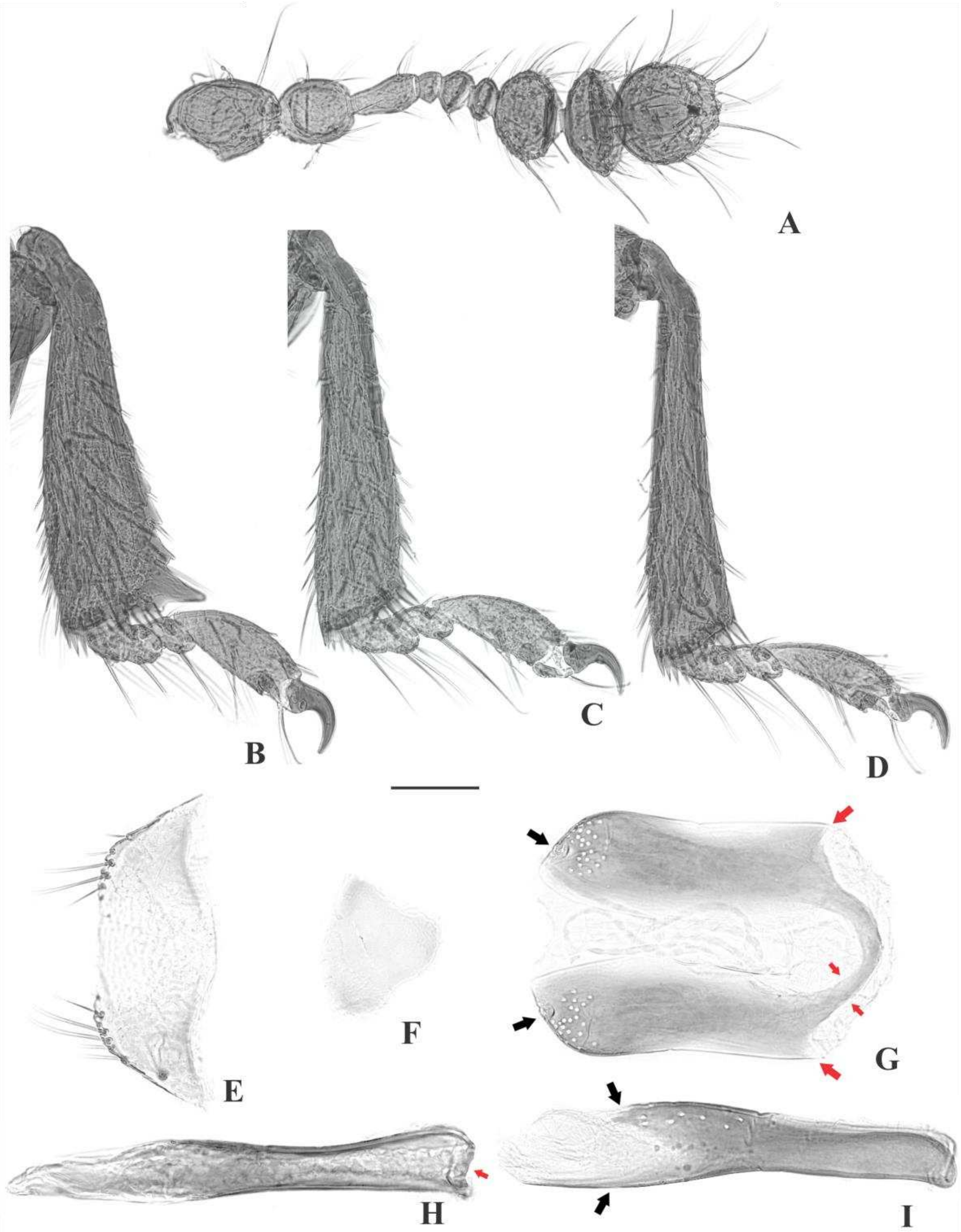

Fig. 36. *Lipedanicis agastor* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–I) Floresta Nacional de São Francisco de Paula (Rio Grande do Sul, South Brazil): **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Basal piece. **G.** Tegmen, note apical excavations (black arrows), narrow basolateral margin at anterior portion (small red arrows) and acute angulations (bog red arrows). **H.** Dorsal

view of penis, note rounded emargination at anterior portion (red arrow) and bilobed apex (black arrows). Scale bar: 0.05 mm (A–I).

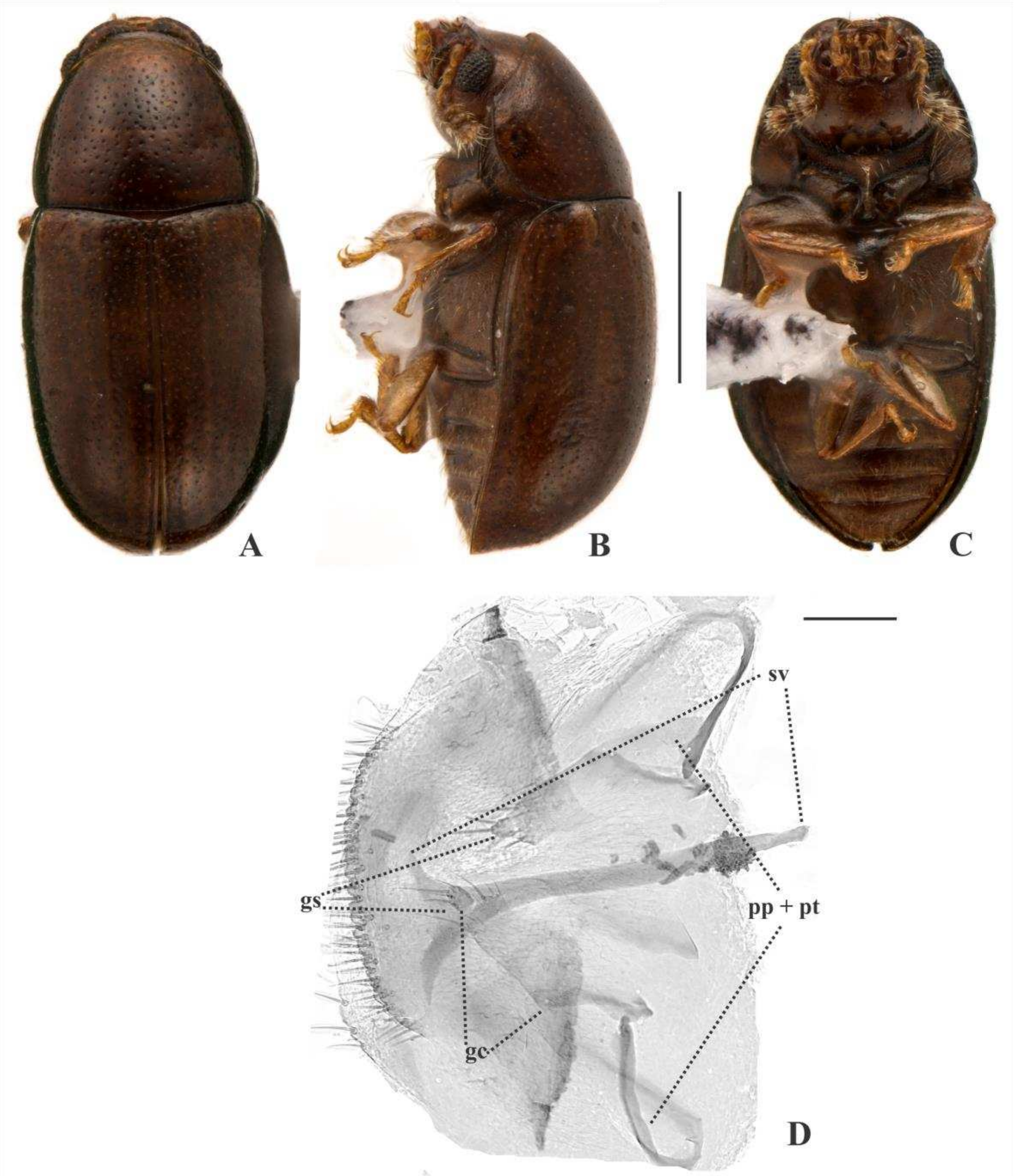

Fig. 37. *Lipedanicis agastor* **sp. nov.**, female paratype (A–C) from Floresta Nacional de São Francisco de Paula (Rio Grande do Sul, South Brazil), and female terminalia of paratype (D) from same locality: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** Female terminalia, showing spiculum ventrale (sv) at anterior portion of sternite VIII

and ovipositor, showing gonostyli (gs), gonocoxites (gc) and paraprocts plus proctiger (pp + pt). Scale bars: 0.5 mm (A–C); 0.05 mm (D).

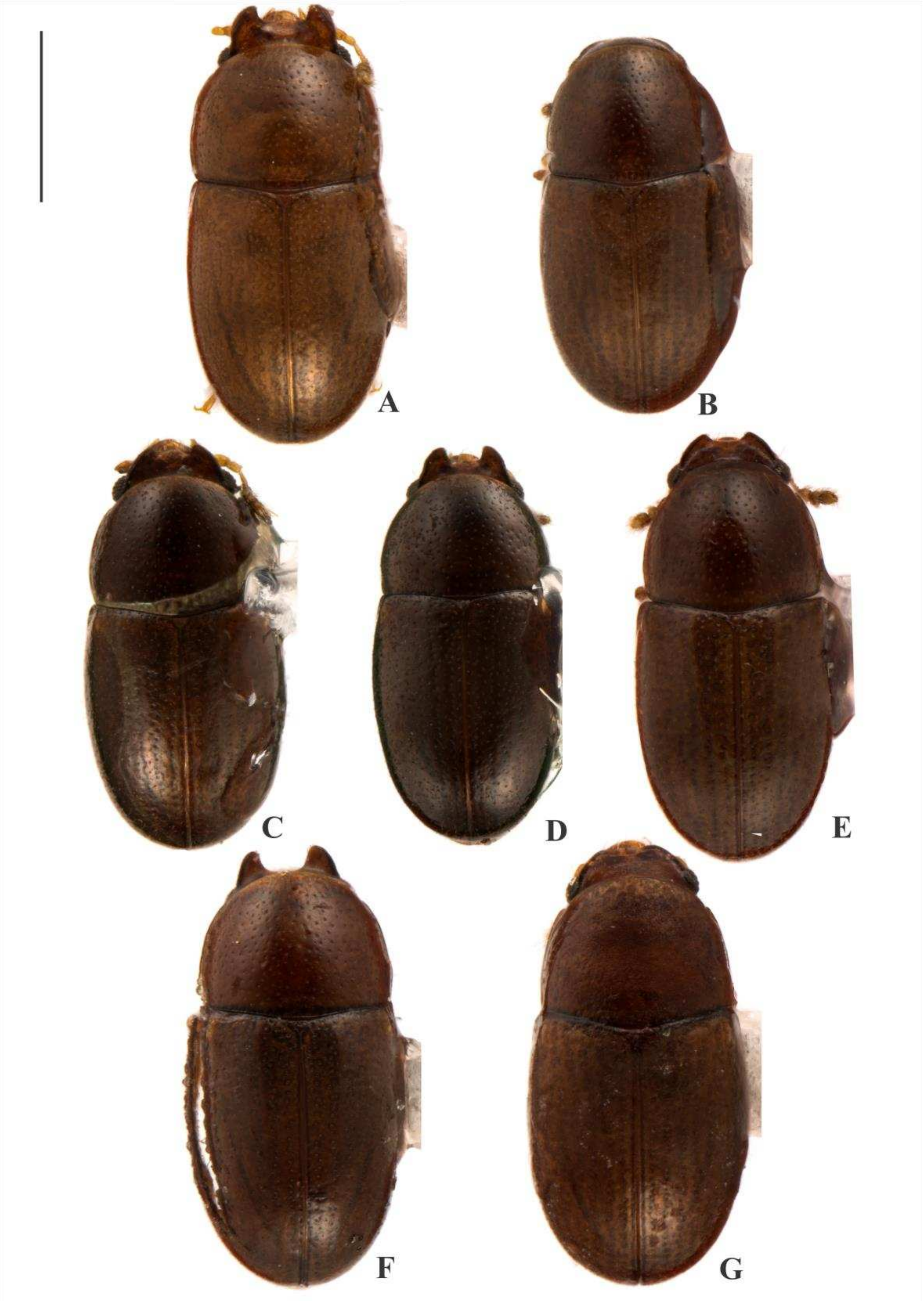

Fig. 38. Variation of *Lipedanicis agastor* **sp. nov.**: **A.** Male paratype from Parque Nacional do Itatiaia (Rio de Janeiro, Southeast Brazil). **B.** Female paratype from Parque

Nacional do Itatiaia (Rio de Janeiro, Southeast Brazil). **C.** Male paratype from Estação Biológica Santa Lúcia (Espírito Santo, Southeast Brazil). **D.** Male paratype from Área de Proteção Ambiental Serra São José (Minas Gerais, Southeast Brazil). **E.** Male paratype from Reserva Particular do Patrimônio Nacional Bacchus (Rio de Janeiro, Southeast Brazil). **F.** Male paratype from Venda Nova do Imigrante (Espírito Santo, Southeast Brazil). **G.** Female paratype from Venda Nova do Imigrante (Espírito Santo, Southeast Brazil). Scale bar: 0.5 mm (A–G).

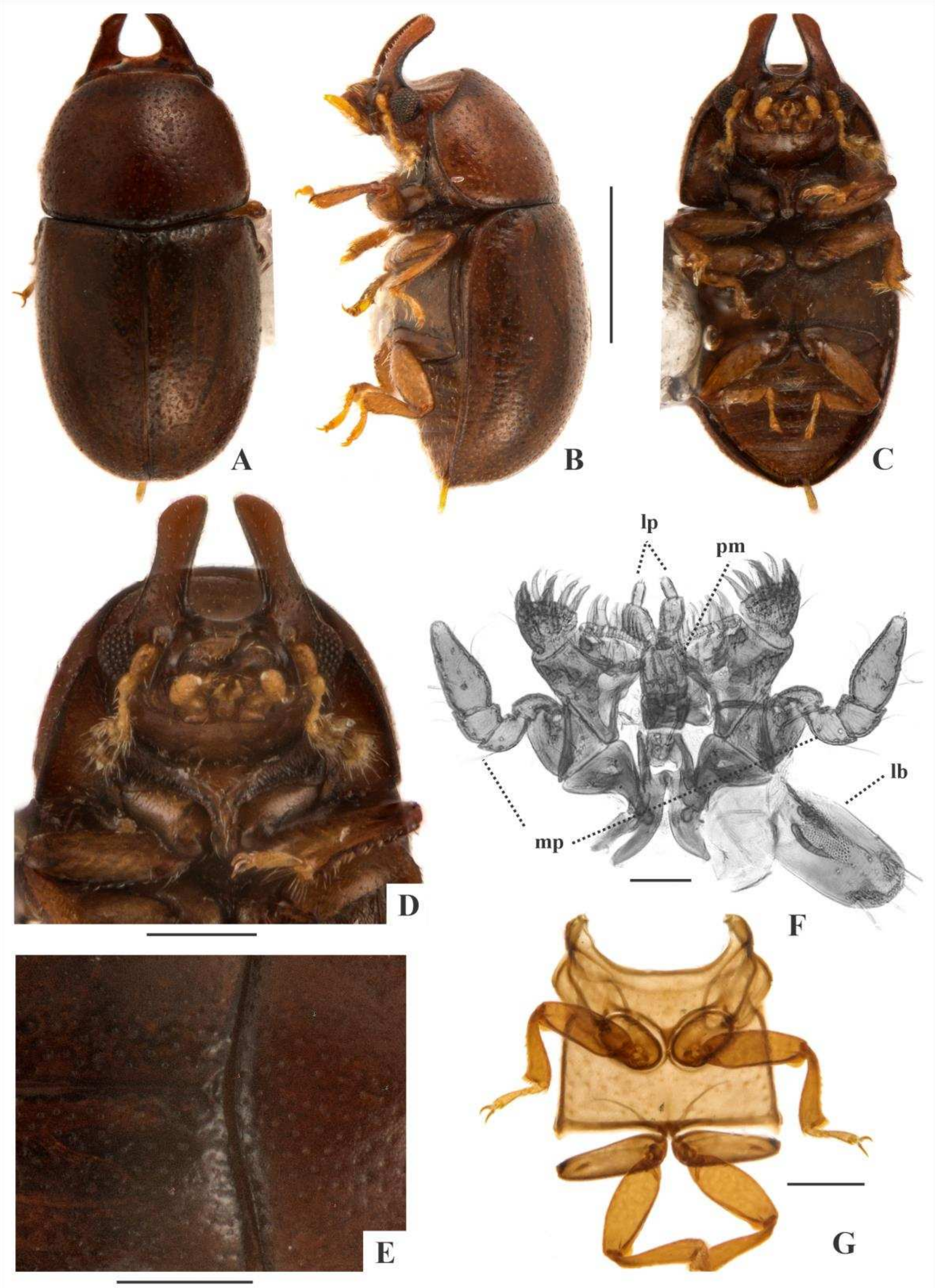

Fig. 39. *Lipedanicis geminus* **sp. nov.**, male holotype (A–E) from Araguaína (Tocantins, North Brazil), mouth parts of female paratype (F) and metaventrite of male paratype (G) from same locality: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. **D.**

Oblique ventral view of head and prosternum. **E.** Scutellar shield and part of the pronotum and elytra. **F.** Mouth parts, showing labial palps (lp), labrum (lb), maxillary palps (mp) and prementum (pm). Scale bars: 0.5 mm (A–C); 0.2 mm (D–E, G); 0.05 mm (F).

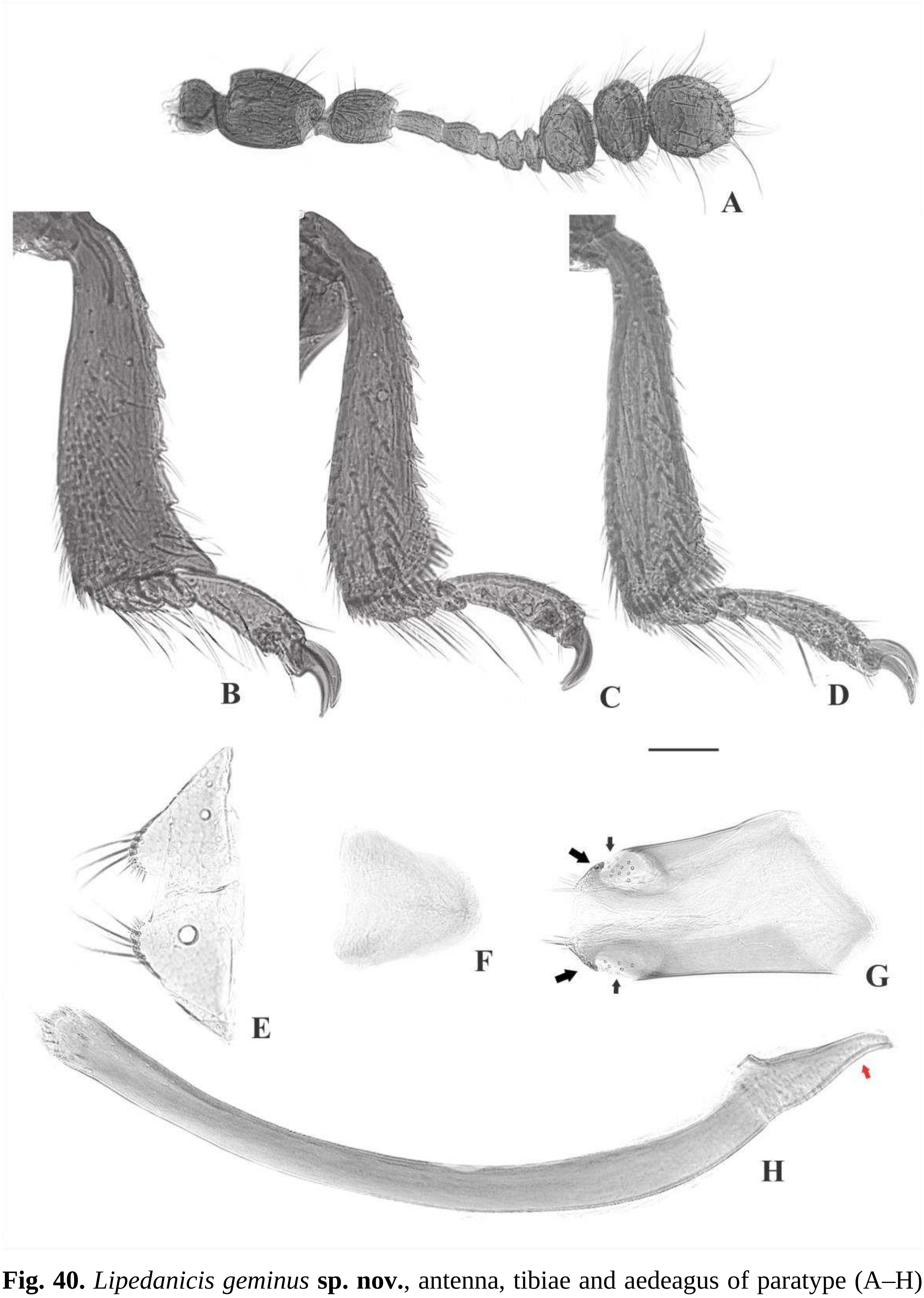

Fig. 40. *Lipedanicis geminus* **sp. nov.**, antenna, tibiae and aedeagus of paratype (A–H) from Araguaína (Tocantins, North Brazil): **A.** Left antenna. **B.** Left protibia. **C.** Left mesotibia. **D.** Left metatibia. **E.** Sternite VIII. **F.** Basal piece. **G.** Tegmen, note

angulations at outer apical edge (big black arrows) and excavations at base of each angulation (small black arrows). **H.** Lateral view of penis, note wedge-shaped anterior portion (red arrow). Scale bar: 0.05 mm (A–H).

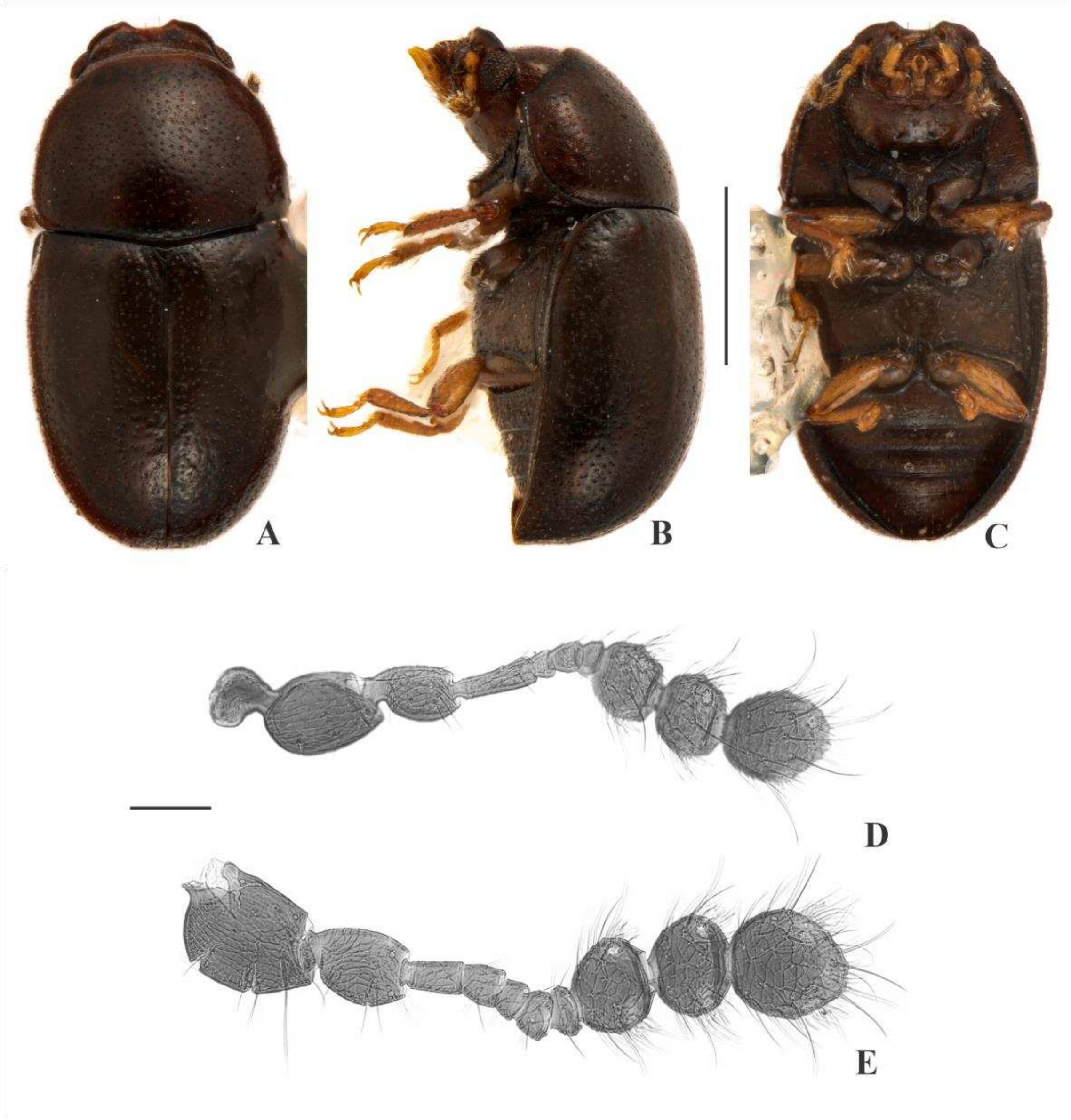

Fig. 41. *Lipedanicis geminus* **sp. nov.**, female paratype (A–C) from Araguaína (Tocantins, North Brazil), and female antennae of paratypes (D–E) from same locality, showing variation in the segment number: **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. Scale bars: 0.5 mm (A–C); 0.05 mm (D–E).

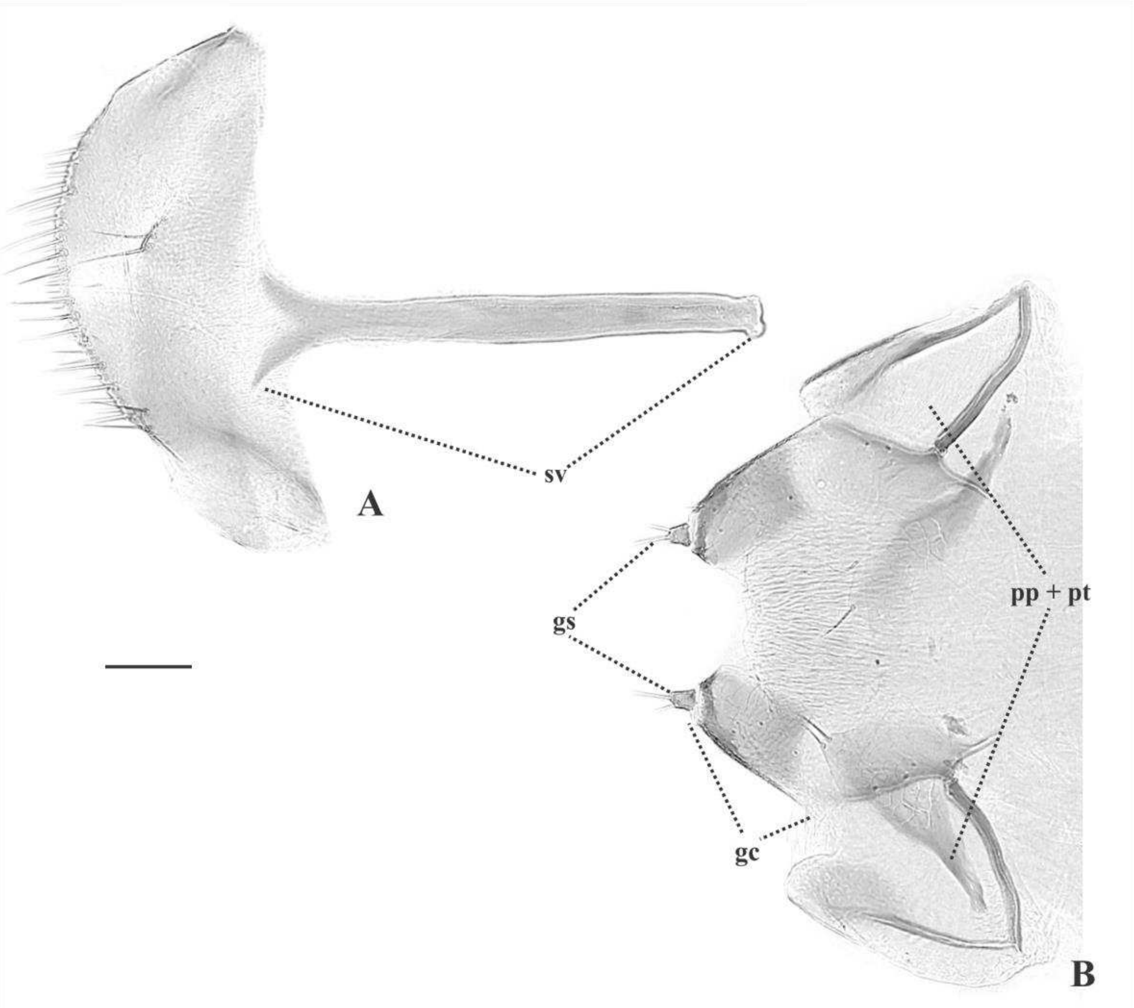

Fig. 42. *Lipedanicis geminus* **sp. nov.**, female terminalia of paratype (A–B) from Araguaína (Tocantins, North Brazil): **A.** Spiculum ventrale (sv) at anterior portion of sternite VIII. **B.** Ovipositor, showing gonostyli (gs), gonocoxites (gc) and paraprocts plus proctiger (pp + pt). Scale bars: 0.05 mm (A–B).

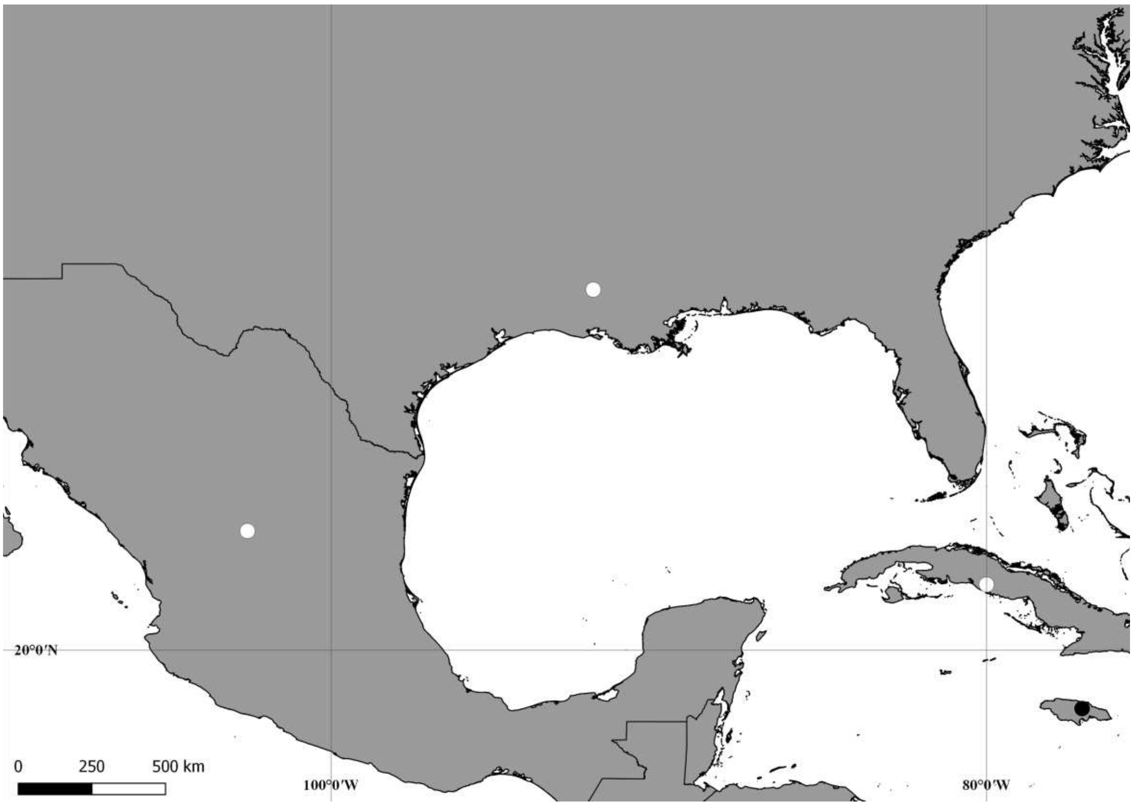

Fig. 43. Known distribution of *Abebaeocis taurulus* (Jacquelin-Duval, 1857) **comb. nov.** (white circle) and *Abebaeocis phiaronotum* **sp. nov.** (black circle).

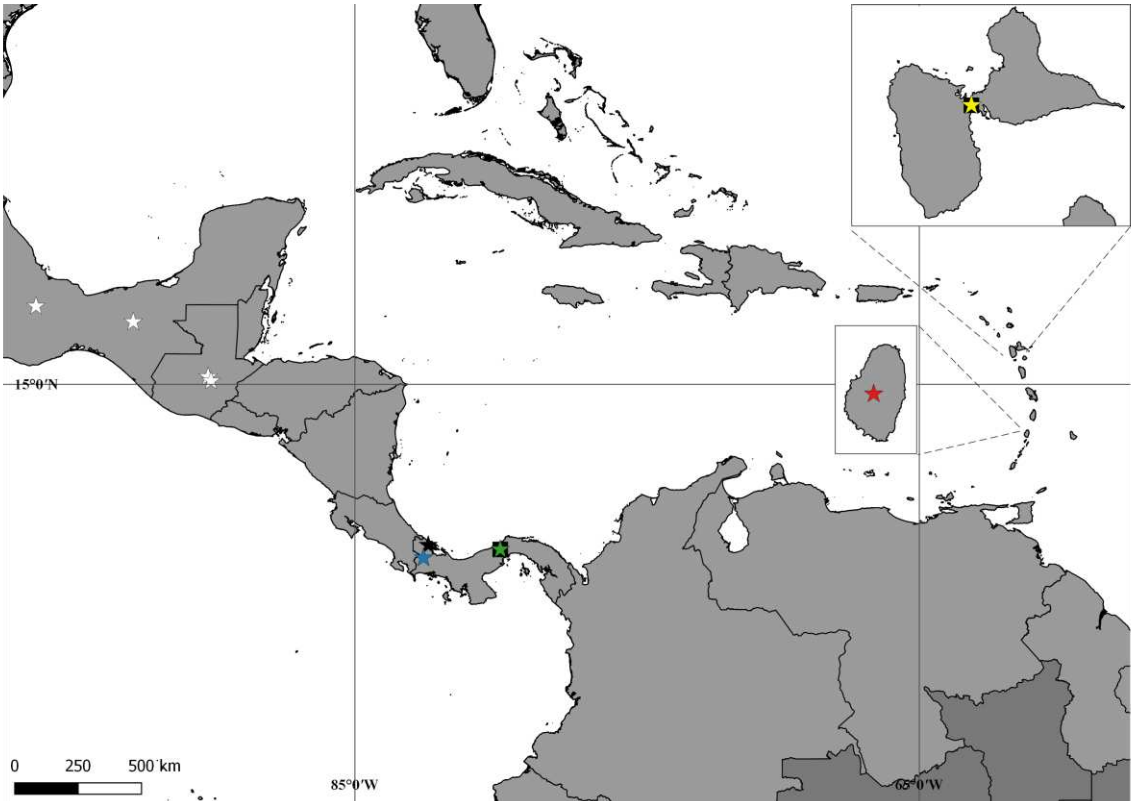

Fig. 44. Known distribution of *Alcecis particularis* (Pic, 1922) **comb. nov.** (black square), *Anartioscelos almirantensis* **sp. nov.** (black star), *Anartioscelos aptenus* **sp. nov.** (white star), *Anartioscelos bifurcus* (Gorham, 1898) **comb. nov.** (red star), *Anartioscelos eurinotum* **sp. nov.** (green star), *Anartioscelos involucris* **sp. nov.** (blue star) and *Anartioscelos laticornis* (Pic, 1922) **comb. nov.** (yellow star).

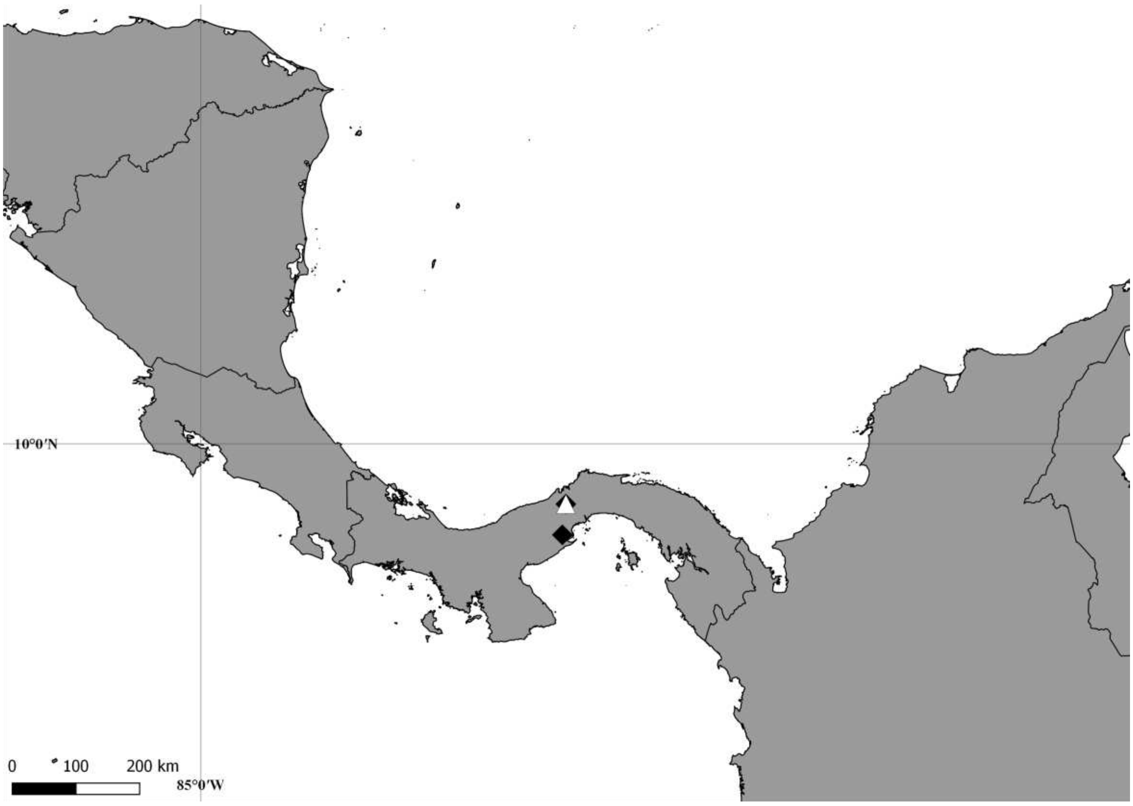

Fig. 45. Known distribution of *Atomocis melanus* **sp. nov.** (black diamond) and *Insolitocis panamensis* **sp. nov.** (white triangle).

Fig. 46. Known distribution of *Gyraleosomus boliviensis* **sp. nov.** (black triangle), *Lipedanicis adelphus* **sp. nov.** (white circle), *Lipedanicis agastor* **sp. nov.** (black circle) and *Lipedanicis geminus* **sp. nov.** (red circle).

CAPÍTULO 2: *Ceracis tzotzilicus* sp. nov. (Coleoptera: Tenebrionoidea: Ciidae) from Guatemala and Mexico

Igor Souza-Gonçalves & Cristiano Lopes-Andrade, 2020
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Ceracis tzotzilicus sp. nov. (Coleoptera: Tenebrionoidea: Ciidae) from Guatemala and Mexico

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Abstract

Ceracis tzotzilicus **sp. nov.** is described on the basis of 200 specimens collected in San Cristóbal de las Casas (Mexico) and Yepocapa (Guatemala), at an altitude above 2000 m. *Ceracis tzotzilicus* resembles members of the *Ceracis cucullatus* species-group due to the fine and sparse pronotal punctation, but males can be distinguished by the absence of a long anterior pronotal lamina and females by the ovipositor lacking gonostyli.

Keywords. Ciinae, Ciini, minute tree-fungus beetles, Neotropical

Introduction

Ciidae is a cosmopolitan family of small to minute beetles that feed, as larvae and adults on the mycelia and basidiomes of Ganodermataceae, Hymenochaetaceae, Polyporaceae and other bracket fungi (Lawrence 1971; Lawrence & Lopes-Andrade 2010). Ciidae include more than 750 species in 51 genera (Souza-Gonçalves *et al.* 2018), and is divided into two subfamilies: Sphindociinae, which includes only *Sphindocis denticollis* Fall, 1917 from the northern California coast; and Ciinae, with all other ciid species (Lawrence 1974; Lawrence 2016). Ciinae is currently divided into three tribes: Ciini Leach, 1819, Orophiini Thomson, 1863 and Xylographellini Kawanabe & Miyatake, 1996. However, only the latter seems to be monophyletic (Lopes-Andrade & Grebennikov 2015).

Faunistic and taxonomic studies on Ciidae from the Neotropical region (*sensu* Morrone 2015) have increased in the last decades, but only the Brazilian and Mexican faunas have been extensively studied (*pers. obs.*). Nine genera occur in Mexico, including 50 species (number of species between parentheses): *Cis* Latreille (22); *Ceracis* Mellié (15); *Scolytocis* Blair (4); *Strigocis* Dury (3); and *Hadreule* Thomson, *Neoapterocis* Lopes-Andrade, *Orthocis* Casey, *Porculus* Lawrence, *Sulcacis* Dury and *Xylographus* Mellié, each with one species (Navarrete-Heredia & Burgios-Solorio, 2000, Lopes-Andrade 2007, Lopes-Andrade 2008, Antunes-Carvalho & Lopes-Andrade 2011, Oliveira *et al.* 2013, Pecci-Maddalena & Lopes-Andrade 2017). In Guatemala five ciid genera are reported, with 12 species: *Cis* (6); *Scolytocis* (2); *Xylographus* (2); and *Ceracis* and *Malacocis* Gorham, including one species each (Reitter 1878, Gorham 1883, 1886, Lawrence 1967, Lopes-Andrade 2008b, Oliveira *et al.* 2013, Sandoval-Gómez *et al.* 2014).

Ceracis is the second most diverse genus of the family and encompasses 52 described species: 41 occurring in the New World, five species spread over Indo-Pacific islands (Christmas Island, Guam, Fiji, Marquesas, New Caledonia and Rapa), three in Japan and three in Australia (Abdullah 1973, Kawanabe 1994, Lawrence 1967, 1971, 2016, Lopes-Andrade *et al.* 2002, Antunes-Carvalho & Lopes-Andrade 2011, 2013, Pecci-Maddalena & Lopes-Andrade 2017). Species of *Ceracis* can be identified on the basis of the following features (after Lawrence 2016): (i) body oval to elongate; (ii) antennae 8- or 9- segmented, occasionally 10-segmented; (iii) prosternum concave

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with prosternal process laminate (except for species in the *furcifer*-group); (iv) apical outer angle of the protibiae expanded subapically, forming a rounded lobe with a row of socketed spines; (v) metaventrite convex; (vi) discrimen short or absent; and (vii) vestiture consisting of minute, usually inconspicuous setae.

Our aim in this paper is to describe the Neotropical *Ceracis tzotzilicus* **sp. nov.**, as well as to provide information about its distribution.

Material and methods

Collection acronyms are as follows:

CELC: Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera da Universidade Federal de Viçosa (Viçosa, Minas Gerais, Brazil)
CMN: Canadian Museum of Nature (Ottawa, Ontario, Canada)
CNC: Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada)
FMNH: Field Museum of Natural History (Chicago, Illinois, USA)

The terminology used in this paper for external morphology and male terminalia follows Lawrence *et al.* (2011), Lawrence (2016) and Lopes-Andrade & Lawrence (2005, 2011); see Oliveira *et al.* (2013) for an explanation on the use of "tegmen". The term "anterocephalic edge" is used in place of "frontoclypeal ridge" to refer to the anterior part of head dorsum, which constitution is not clearly known. The term "dual punctation" describes a punctation made of punctures that fall into two conspicuously different size classes and is traditionally used in the taxonomy of Ciidae. The following abbreviations are used for measurements (in mm) and ratios: BW (width of anterior edge of scutellar shield), CL (length of antennal club measured from base of the seventh to apex of the ninth segment), EL (elytral length along the midline), EW (greatest width of elytra), FL (length of antennal funicle measured from base of the third to apex of the sixth segment), GD (dorso-ventral height of body measured in lateral view, from the surface of elytra to that of the metaventrite), GW (greatest diameter of eye), PL (pronotal length along midline), PW (greatest pronotal width), SL (length of scutellar shield), TL (total length counted as EL+PL, i.e. excluding head). The GD/EW and TL/EW ratios indicate the degree of body convexity and elongation, respectively.

Transcription of labels, dissection, photography and measurement of specimens follow the methods of Araujo & Lopes-Andrade (2016). We measured specimens of the new species from all localities. Differences are indicated in "Variation", together with standard measurements (mean and standard deviation) and ratios.

The abdominal terminalia of the following specimens were extracted: four males and two females paratypes of *Cer. tzotzilicus* from San Cristóbal de las Casas (Chiapas, Mexico) and one male from Yepocapa (Chimaltenango, Guatemala). The sclerites shown in Figures 12–15, 17–18 are of paratypes from the type locality. Information on the gula in the description provided here is restricted to the ratio of gula width to head width.

The distribution map (Fig. 22) was created in the freeware QGIS 2.14.2-Essen software.

Taxonomy

Ceracis tzotzilicus sp. nov.

Figs 1–22
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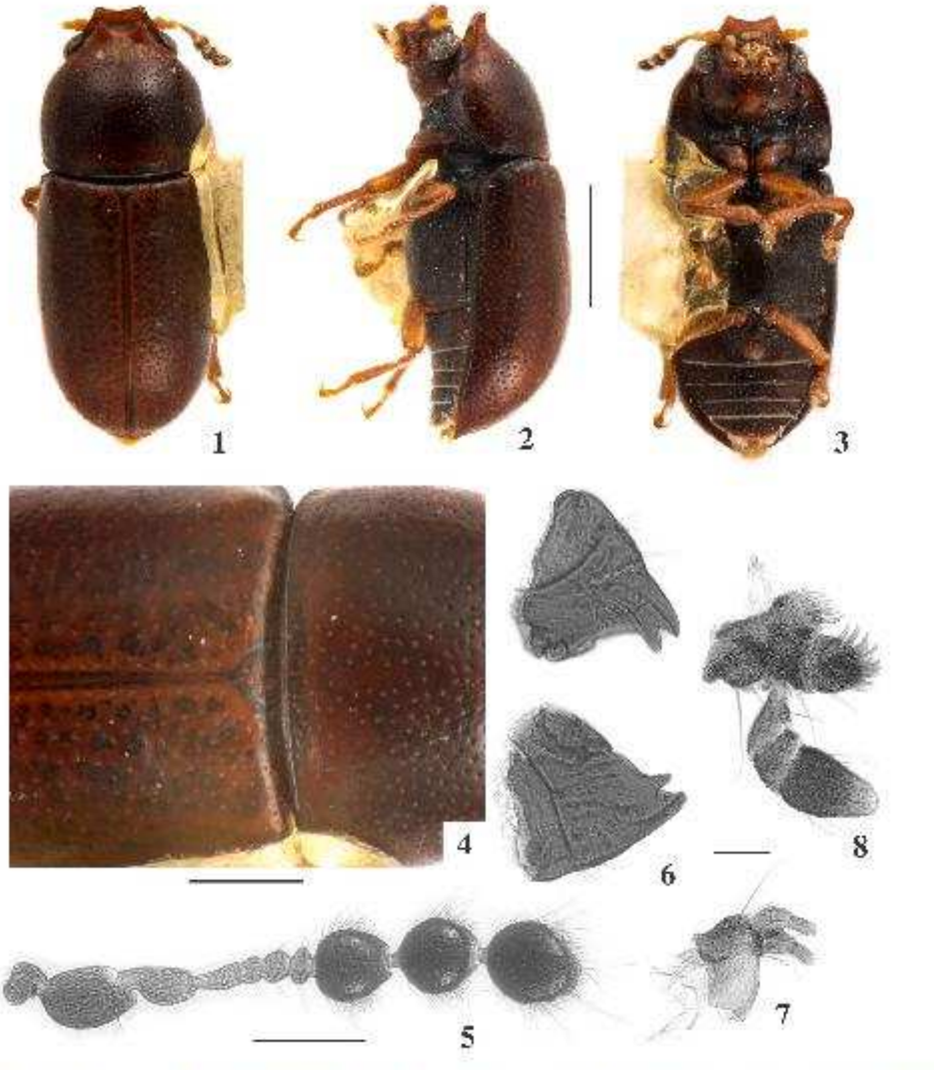
Type locality. San Cristóbal de las Casas, coordinates 16°44'N 92°38'W (Chiapas, Mexico).

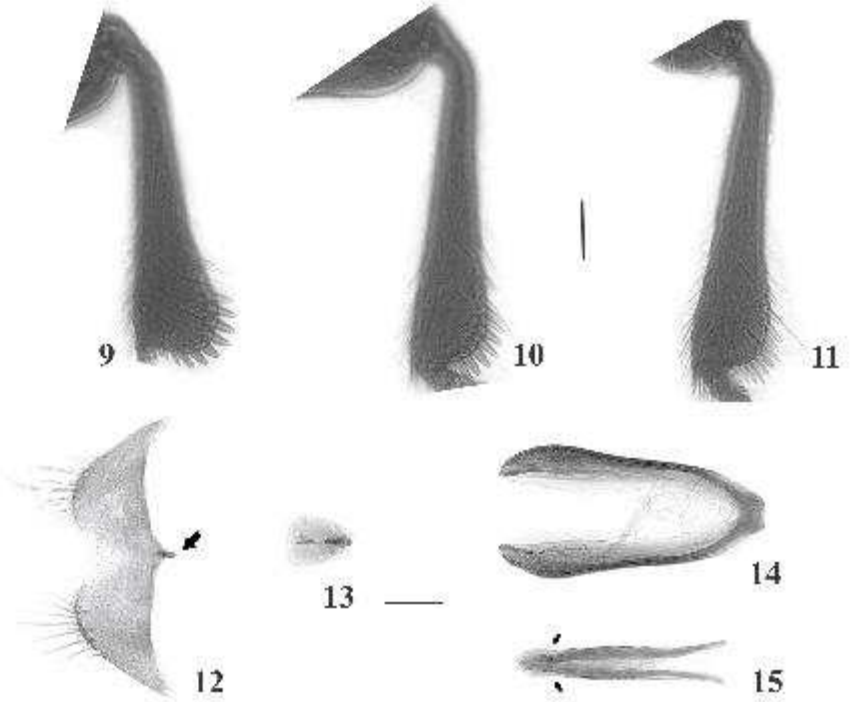
Type material. Holotype: ♂ (CNC) "MEX., HIS., 3 mi. N. S. Cristobal de las Casas 12.VI.1969 E.E. Lindquist \ Bracket fungi \ *Ceracis tzotzilicus* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]". Paratypes: 121 ♂♂ and 78 ♀♀ as follows: 105 ♂♂ (35 CELC, four dissected; 3 CMN; 67 CNC) and 69 ♀♀ (22 CELC, two dissected; 1 CMN; 46 CNC) same data as the holotype; 2 ♂♂ (1 CMN; 1 CNC) "MEX., HIS., 3 mi. N. S. Cristobal de las Casas 12.VI.1969 E.E. Lindquist \ Bracket fungi \ *Ceracis* sp. Det. J.F. Lawrence"; 15 ♂♂ (8 CELC, one dissected; 7 FMNH) and 9 ♀♀ (5 CELC; 4 FMNH) "Finca Monserat, W. slope Volcan Acatenango, Municipio Yepocapa, Chimaltenango, V:17:1948 GUAT. R.D. Mitchell leg. 214.7100 ft., ex dry polypore fungus \ CHICAGO

NAT. HIST. MuSEUM [sic], Guatemala Zool. Exped. (1948)". All paratypes additionally labeled "*Ceracis tzotzilicus* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]".

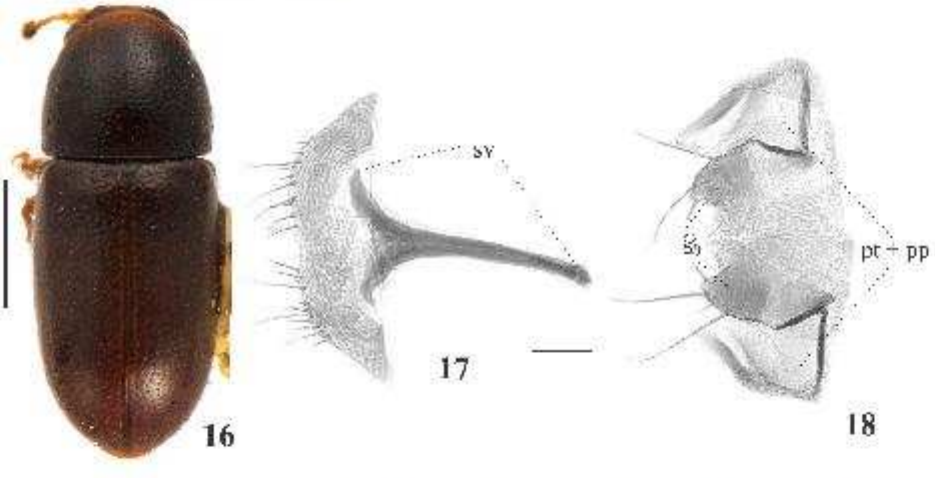
Diagnosis. *Ceracis tzotzilicus* **sp. nov.** can be distinguished from other species in the genus by the following characteristics: Antennae 9-segmented (Fig. 5). Males with anterocephalic edge produced and elevated forming a wide lamina, which is broadly emarginate apically (Figs 1, 3), and pronotum deeply emarginate forming two triangular plates (Figs 1, 3, 4). *Ceracis tzotzilicus* **sp. nov.** resembles *Ceracis bicornis* (Mellié) in the fine and sparse pronotal punctation, but in the latter species the male anterocephalic lamina is straight at apex and female ovipositor has conspicuous gonostyli.



FIGURES 1–8. *Ceracis tzotzilicus* **sp. nov.**, male holotype (1–4), antenna and mouth parts from the type locality San Cristóbal de las Casas (Mexico: Chiapas) (5–8): **1**. Dorsal view. **2**. Lateral view. **3**. Ventral view. **4**. Scutellar shield and part of pronotum and elytra. **5**. Left antenna. **6**. Mandible. **7**. Labium. **8**. Right maxilla. Scale bars: 0.5 mm (1–3); 0.2 mm (4); 0.1 mm (5) 0.05 mm (6–8).



FIGURES 9–15. *Ceracis tzotzilicus* **sp. nov.**, tibiae and aedeagus of paratype from the type locality San Cristóbal de las Casas (Mexico: Chiapas) (9–15): **9.** Left protibia. **10.** Left mesotibia. **11.** Left metatibia. **12.** Sternite VIII. **13.** Basal piece. **14.** Tegmen. **15.** Penis. Scale bars: 0.1 mm (9–11) 0.05 mm (12–15).



FIGURES 16–18. *Ceracis tzotzilicus* **sp. nov.**, dorsal view of a female (16) and terminalia of a paratype from the type locality San Cristóbal de las Casas (Mexico: Chiapas) (17–18): **16.** Dorsal view. **17.** Sternite VIII with spiculum ventrale (sv). 18. Oviposi–tor, showing gonocoxites (gc) and proctiger plus paraprocts (pt + pp). Scale bars: 0.5 mm (16); 0.05 mm (17–18).

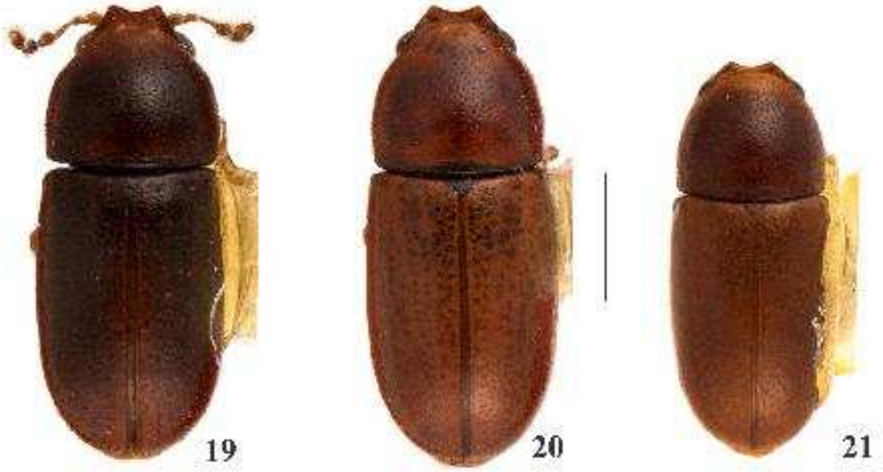
Description, male holotype (Figs 1–4). Adult, fully pigmented and in good condition, but lacking the left antenna. Measurements in mm: TL 1.67, PL 0.64, PW 0.67, EL 1.04, EW 0.72, GD 0.67. Ratios: PL/PW 0.95, EL/EW 1.44, EL/PL 1.63, GD/EW 0.93, TL/EW 2.33. **Body** elongate, convex; dorsum and venter reddish dark brown; antennae yellowish brown, club dark brown; palpi and tarsi yellowish brown; dorsal vestiture single, consisting in minute suberect setae, barely visible at high magnifications (>50x); ventral vestiture of fine decumbent setae easily discernible at high magnifications (>50x). **Head** with the anteriormost portion visible from above; dorsum concave, with a conspicuous, short protuberance on vertexal disc; punctures fine, shallow, separated from each other by two punctures-widths or less; surface glabrous; interspaces, finely microreticulate; anterocephalic edge produced and elevated, forming a wide lamina with broadly emarginate apex. **Antennae** (Fig. 5, left antenna from paratype) 9-segmented, lengths as follows (in mm, right antenna measured): 0.08, 0.04, 0.03, 0.02, 0.02, 0.01, 0.05, 0.06, 0.07 (FL 0.08 mm, CL 0.17 mm, CL/FL 2.04). Eyes coarsely facetted; each bearing about 90 ommatidia; GW 0.16 mm. **Maxillae** (Fig. 8, right maxilla in paratype) with distinctly articulated galea; lacinia more or less fused to stipes; apical maxillary palpomere pyriform, 1.5X as long as wide, widest near base and narrowly rounded at apex. **Mandibles** (Fig. 6, from paratype) as long as wide. **Labium** (Fig. 7, from paratype) with rounded contour of apical portion of prementum in lateral view; labial palpi each with three palpomeres. **Gula** 0.32x as wide as head. **Pronotum** (Fig. 4) finely, shallowly punctate; punctures of one size, with the exception of median impunctate line beginning around eight puncture-widths of base until disc; punctures scattered, separated from each other by 2–3 puncture-widths; interspaces microreticulate and shiny; vestiture single, consisting of minute, pale yellowish setae (<0.01 mm); anterior pronotal edge deeply emarginate forming two short triangular plates, slightly divergent and with acute apex; lateral edges not crenulate, not explanate and not visible when seen from above. **Scutellar shield** triangular, bearing few punctures and few minute setae; BW 0.10 mm, SL 0.07 mm. **Elytra** with non-seriate, dual punctation; megapunctures finer and closer than those on pronotum, shallow, about twice as large as micropunctures, separated from each other by 1–2 megapuncture-widths; interspaces, smooth and shiny; vestiture single, consisting of minute pale yellowish setae (~0.01 mm) arising from megapunctures. **Metathoracic wings** developed, apparently functional. **Hypomera** with fine, shallow punctation; each puncture bearing one fine decumbent seta; interspaces microreticulate. **Prosternum** in front of coxae concave; interspaces, microreticulate. **Prosternal process** laminate, as long as prosternum at midline; acute at the apex. **Protibiae** (Fig. 9, left protibia from paratype) with maximum width of about one-fourth of its length, expanded at apex. **Meso- and metatibiae** (Figs 10–11, left meso- and metatibia from paratype) each with spines in apical edge. **Metaventrite** with fine, shallow punctures; interspaces, microreticulate; discrimen indiscernible. **Abdominal ventrites** with fine, shallow punctures, separated from each other by one puncture-width or less, each bearing one fine decumbent pale yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at the longitudinal midline) as follows: 0.25, 0.08, 0.06, 0.07, 0.10; first abdominal ventrite with large circular, setose sex patch posteriorly, not margined, transverse diameter of 0.08 mm. **Male terminalia (from paratype)** (Figs 12–15): **Sternite VIII** (Fig. 12) with posterior margin slightly emarginate medially; corners broadly rounded, bearing long and short setae; lateral margins diverging; anterior margin biconcave, sub-rounded, heavily sclerotized medially forming short strut (Fig. 12, big black arrow). **Tegmen** (Fig. 14) 2X as long as wide, widest near apex, apical portion deeply and broadly emarginate; lateral edges angulate near apex; outer apical edge broadly rounded. **Basal piece** (Fig. 13) subtriangular, 1.4X as long as wide. **Penis** (Fig. 15) elongate, 0.8X as long as tegmen, 4.9X as long as wide; lateral edges sclerotized forming two struts converging near apex; lateral edges slightly angulate near apex (Fig. 15, small black arrows); apex rounded.

Females (Figs 16–18). Anterocephalic edge anteriorly truncate, barely convex; vertex convex. Anterior pronotal edge rounded. Otherwise like males, but devoid of head and pronotal ornamentations, and abdominal sex patch. **Female terminalia** (Figs 17–18) with spiculum ventrale (Fig. 17) 1.7X as long as gonocoxites; ovipositor (Fig. 18, distorted after compression between slide and cover slip) presenting reduced paraprocts, shorter than gonocoxites and barely discernible; each baculus of paraprocts bowed and completely fused to respective proctigeral baculus (Fig. 18); gonocoxites without ventral lobes and gonostyli.

Variation. Males, measurements in mm (n= 11, including the holotype): TL 1.58–1.78 (1.67 ± 0.07), PL 0.55–0.68 (0.62 ± 0.04), PW 0.63–0.70 (0.67 ± 0.02), EL 0.95–1.18 (1.05 ± 0.07), EW 0.65–0.75 (0.71 ± 0.03), GD 0.63–0.70 (0.65 ± 0.04), PL/PW 0.85–1.00 (0.93 ± 0.05), EL/EW 1.36–1.59 (1.48 ± 0.07), EL/PL 1.41–1.96 (1.70 ± 0.18), GD/EW 0.88–0.93 (0.91 ± 0.02), TL/EW 2.23–2.43 (2.36 ± 0.06). In some males, the pronotal plates are short (Fig. 19) or the plate of head is short and pronotal edge is rounded (Figs 20–21). Females, measurements in mm (n= 10): TL 1.45–1.73 (1.63 ± 0.08), PL 0.53–0.63 (0.58 ± 0.06), PW 0.55–0.70 (0.64 ± 0.05), EL 1.00–1.10 (1.05 ± 0.04), EW 0.63–0.78 (0.70 ± 0.05), GD 0.58–0.70 (0.65 ± 0.04), PL/PW 0.82–1.00 (0.91 ± 0.05), EL/EW

1.37–1.68 (1.50 ± 0.10), EL/PL 1.64–2.22 (1.82 ± 0.17), GD/EW 0.83–0.97 (0.93 ± 0.05), TL/EW 2.13–2.52 (2.32 ± 0.11). In both males and females, coloration can range from reddish brown to reddish dark brown. In specimens from Guatemala the pronotal punctation is slightly sparser than in the Mexican specimens.

Host fungi. Unknown.



FIGURES 19–21. Male variation of *Ceracis tzotzilicus* **sp. nov.** as observed in paratypes from the type locality San Cristóbal de las Casas (Mexico: Chiapas). Scale bar: 0.5 mm (19–21).

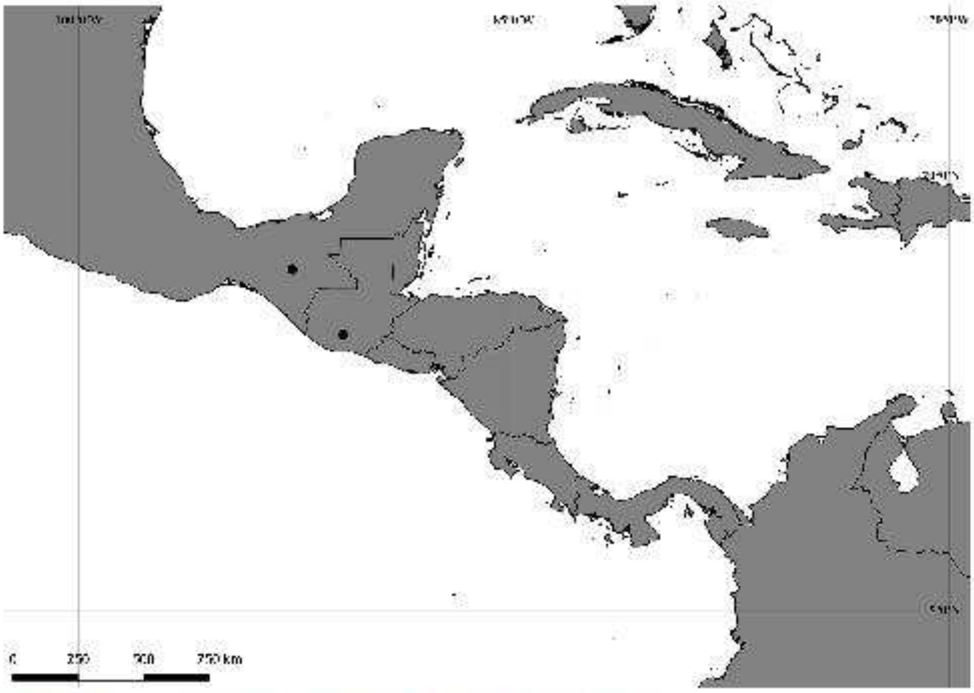


FIGURE 22. Known geographic distribution of *Ceracis tzotzilicus* **sp. nov.** in Guatemala and Mexico.

Etymology. The species epithet is a combination of the terms "tzotzil" and the Greek noun "ikos" (=belonging to), both in the genitive singular. The name is a reference to the Tzotzil, an indigenous Maya people from the central Chiapas highlands in southern Mexico, which is also the native name of the type locality.

Distribution. *Ceracis tzotzilicus* was collected in two localities over 2000 m above sea level: Central Highlands region of Chiapas (Mexico) dominated by Coniferous Forest vegetation, and in the stratovolcano Acatenango close to Antigua (Guatemala) (Fig. 22).

Comments. Currently, four species-groups are recognized within *Ceracis* (number of species between parentheses): the *cucullatus* (10), *furcatus* (4), *furcifer* (4) and *singularis* species-groups (3). This arrangement leaves 32 species (including *Cer. tzotzilicus*) without species-group assignment within the genus. The *cucullatus*-group was revised by Antunes-Carvalho & Lopes-Andrade (2011, 2013), with four new species from Australia added by Lawrence (2016). Within the *cucullatus*-group, *Cer. bicornis* (Mellié) is the unique species that was not redescribed yet and may be a species complex. The *furcatus*-group was established by Lopes-Andrade (2002) and may include possible synonyms (Lawrence 1967); it is in urge of a taxonomic revision. The *furcifer*-group was recently revised by Pecci-Maddalena & Lopes-Andrade (2017). The *singularis* group was established by Lopes-Andrade *et al.* (2002) and its species seem to be well defined. Although *Cer. tzotzilicus* resembles *Cer. bicornis* (see Diagnosis), we prefer not to assign it to either the *cucullatus* or any other species-group within *Ceracis*. We are currently conducting a phylogenetic analysis and major taxonomic propositions will be provided in forthcoming works.

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CAPÍTULO 3: A peculiar new species of *Ceracis* Mellié (Coleoptera: Ciidae) from the Neotropical region

Igor Souza-Gonçalves & Cristiano Lopes-Andrade, 2020
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A peculiar new species of *Ceracis* Mellié (Coleoptera: Ciidae) from the Neotropical region

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Abstract

Ceracis ascetonotum sp. nov. is described on the basis of 54 specimens collected in Forth Sherman, the type locality, Barro Colorado and Campana (Panama); Parque Nacional Natural Sierra de La Macarena (Meta, Colombia) and Popayán (Cauca, Colombia); Monteverde (Costa Rica); and Canarana (Central-West Brazil). *Ceracis ascetonotum* sp. nov. differs from other species in the genus in the 10-segmented antenna (except for species in the *Ceracis singularis* species-group); the very peculiar morphology of the male pronotum, which is characterized by two deep and wide impressions anteriorly, the outer borders of impressions extended forward as two lateral, elongate horns, each with an apical knob, and posterior contours of impressions joined at middle forming a thin elevation resembling a tiny horn; and the penis bearing a bilobed apex, the dorsal one with apical portion acute, and the ventral one forming two elongate and sharp struts.

Keywords: Central America, Ciinae, minute tree-fungus beetles, South America, taxonomy

Introduction

Ciidae is a cosmopolitan family of small to minute beetles, which includes more than 750 species in 51 genera (Lawrence, 2016, 2019; Souza-Gonçalves et al., 2018). These beetles feed, in both larval and adult stages, on the mycelia and basidiomes of Ganodermataceae, Hymenochaetaceae, Polyporaceae and other bracket fungi (Lawrence, 1971; Lawrence & Lopes-Andrade, 2010), being particularly diverse in tropical and subtropical regions.

Ceracis Mellié, 1849 is the second most diverse genus of the family with 53 described species of which 35 are reported from the Neotropical region (Lawrence, 1967, 1971; Antunes-Carvalho & Lopes-Andrade, 2011, 2013; Pecci-Maddalena & Lopes-Andrade, 2017; Souza-Gonçalves & Lopes-Andrade, 2020). The genus *Ceracis* can be characterized by the combination of the following features (based on Lawrence, 2016): (i) body oval to elongate; (ii) antennae 8- or 9-segmented, occasionally 10-segmented; (iii) prosternum concave with prosternal process laminate (except for species in the *Ceracis furcifer* species-group); (iv) protibiae with outer apical angle expanded subapically to form a rounded lobe with a row of socketed spines; (v) metaventrite convex; (vi) discrimen short or absent; and (vii) vestiture of minute setae, usually inconspicuous.
Here we describe the Neotropical *Ceracis ascetonotum* sp. nov., a species with broad distribution and peculiar secondary sexual features of males, based on specimens from Costa Rica, Panama, Colombia and Central-West Brazil.

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Material and Methods

Museum acronyms are as follows (name of curator between parentheses):
ANIC – Australian National Insect Collections, CSIRO Entomology, Canberra, Australian Capital Territory, Australia (A. Ślipiński)
CELC – Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera da Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil (C. Lopes-Andrade)
FMNH – Field Museum of Natural History, Chicago, Illinois, USA (A. F. Newton and M. K. Thayer).

Terms for external morphology and male terminalia of ciids follow Lawrence et al. (2011), Lawrence (2016) and Lopes-Andrade & Lawrence (2005, 2011), but see also Oliveira et al. (2013) for an explanation on the use of "tegmen". The term "anterocephalic edge" is used in place of "frontoclypeal ridge" to refer to the anterior part of head dorsum, which constitution is not clearly known. The term "single punctation" describes a punctation made of punctures that fall into one size class, while "dual punctation" describes a punctation made of punctures that fall into two conspicuously different size classes. Both terms are traditionally used in the taxonomy of Ciidae. The following abbreviations are used for measurements (in mm) and ratios: BW (width of anterior edge of scutellar shield), CL (length of antennal club measured from base of the eighth to apex of the tenth segment), EL (elytral length along the midline), EW (greatest width of elytra), FL (length of antennal funicle measured from base of the third to apex of the seventh segment), GD (dorso-ventral height of body measured in lateral view, from the surface of elytra to that of the metaventrite), GW (greatest diameter of eye), PL (pronotal length along midline), PW (greatest pronotal width), SL (length of scutellar shield), TL (total length counted as EL+PL, i.e. excluding head). The GD/EW and TL/EW ratios indicate the degree of body convexity and elongation, respectively. Sum and ratios of measurements of antennae are based on gross values, while measurements of each segment are based on approximate values.

Transcription of labels, dissection, photography and measurement of specimens followed the methods provided by Araujo & Lopes-Andrade (2016). We measured specimens of the new species from all localities. Differences are given in "Variation", together with standard measurements (mean and standard deviation) and ratios. Data on host fungus extracted from labels are summarized in the corresponding section and fungus name was updated consulting the database Index Fungorum (2020). The corresponding number of records were placed on the same section, indicating breeding records. The recognition of breeding records follows the criteria provided in Orledge & Reynolds (2005). The distribution map (Fig. 5) was created in the freeware QGIS 3.14.1-Pi.

The abdominal terminalia of the following specimens were extracted: one male and one female paratypes of *Cer. ascetonotum* sp. nov. from Barro Colorado (Canal Zone, Panama) (completely dissected and stored in glycerin); one male paratype from Canarana (Central-West Brazil) (dissected and stored in a vial containing alcohol 70%). Information on the gula in the description provided here is restricted to the ratio of gula width to head width.

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Taxonomy

Ceracis ascetonotum Souza-Gonçalves & Lopes-Andrade sp. nov.
(Figs 1–5)
Type locality. "Fort Sherman", coordinates 9º21'N 79º57'W (Canal Zone, Panama).

Type material. Holotype: ♂ (FMNH) "Fort Sherman, Canal Zone, Panama, IV-2-67 \ J.F. Lawrence, Lot. 2084 \ *Polyporus caperatus* \ *Ceracis ascetonotum* Souza-Gonçalves & Lopes-Andrade HOLOTYPUS [red paper]". PARATYPES: 24 ♂♂ and 29 ♀♀ as follows: 1 ♂ and 1 ♀ (CELC), same data as the holotype; 2 ♂♂ (1 CELC; 1 ANIC) "Barro Colorado Is., CANAL ZONE, Feb. 6, 1968 \ J.F. Lawrence, Lot. 2337 \ *Polyporus caperatus*"; 3 ♂♂ (1 CELC; 2 FMNH) and 1 ♀ (FMNH) "Barro Colorado Is., CANAL ZONE, Feb. 19, 1968 \ J.F. Lawrence, Lot. 2445 \ *Polyporus caperatus*"; 1 ♂ (ANIC) "Barro Colorado Is., CANAL ZONE, Feb. 15, 1968 \ J.F. Lawrence, Lot. 2433 \ J.F. Lawrence, Collector"; 1 ♀ (ANIC) "Barro Colorado Is., CANAL ZONE, Feb. 15, 1968 \ J.F. Lawrence, Lot. 2433"; 1 ♂ and 1 ♀ (CELC) "Barro Colorado Is., CANAL ZONE, Feb. 15, 1968 \ J.F. Lawrence, Lot. 2422 \ *Polyporus caperatus*"; 2 ♂♂ (CELC) and 1 ♀ (ANIC) "Barro Colorado Is., CANAL ZONE, Feb. 10, 1968 \ J.F. Lawrence, Lot. 2373 \ *Polyporus caperatus*"; 1 ♂ (CELC) "Barro Colorado Is., CANAL ZONE, Feb. 12, 1968 \ J.F. Lawrence, Lot. 2384 \ *Polyporus caperatus*"; 2 ♂♂ (1 CELC; 1 ANIC) and 7 ♀♀ (2 CELC; 3 ANIC; 2 FMNH) "Barro Colorado Is., CANAL ZONE, V-19-73 G. Ekis \ J.F. Lawrence, Lot. 3415 \ *Polyporus caperatus*"; 1 ♂ (CELC) "Barro Colorado Is., Canal Zone, IV-7-67 \ J.F. Lawrence, Lot. 2126 \ *Polyporus caperatus*"; 1 ♂ (FMNH) and 2 ♀♀ (1 CELC, completely dissected and stored in glycerin; 1 FMNH) "Barro Colorado Is., Canal Zone, IV-3-67 \ J.F. Lawrence, Lot. 2102 \ *Polyporus caperatus*"; 1 ♂ (CELC, completely dissected and stored in glycerin) and 1 ♀ (CELC) "Barro Colorado Is., CANAL ZONE, July 16 1969 \ J.F. Lawrence, Lot. 2895 \ *Polyporus caperatus*"; 1 ♀ (CELC) "Barro Colorado Is., CANAL ZONE, July 6 1969 \ J.F. Lawrence, Lot. 2786 \ *Polyporus caperatus*"; 1 ♂ and 1 ♀ (CELC) "MONTEVERDE, PUNTARENAS, C.R. VII-28-68 [handwritten] \ J.F. Lawrence, Lot. 2688 \ R. Andrews, Collector \ *Polyporus caperatus*"; 1 ♂ and 4 ♀♀ (CELC) "Cerro Campana, 3000', Panama., July 31, 1970, H. & A. Howden"; 4 ♂♂ and 2 ♀♀ (CELC) "COLÔMBIA: Meta, Vista Hermosa, Vda. la [sic; Vda. La] Reforma, 2-3.iv.2010, leg. J.L. Contreras \ 2º37'52.1"N [sic; 2º58'N], 75º44'10.3"W [sic; 73º54'W], 296m"; 2 ♀♀ (CELC) "COLÔMBIA: Meta, Vista Hermosa, Vereda la [sic; Vereda La] Reforma, PNN la [sic; PNN La] Macarena, 2-3.iv.2010, leg. J.L. Contreras \ 2º37'52.1"N [sic; 2º58'N], 75º44'10.3"W [sic; 73º54'W], 296m"; 1 ♀ (CELC) "COLOMBIA Cauca, Popayán Corr. Las Piedras, Vda. Clarete Fca. San Millán, 02º30'14"N, 76º33'13"W 1750m, Bosque de *Quercus* sp., 23.vii.2009, V.E. Sandoval leg.; 2 ♂♂ (CELC, one dissected and stored in 70% alcohol) and 3 ♀♀ (CELC) "BRASIL: MT; Canarana, "Faz. Sta. Marta", 23-30.xi.2007; legs [sic] CM Mews & M Pimentel". All paratypes additionally labelled "*Ceracis ascetonotum* Souza-Gonçalves & Lopes-Andrade PARATYPUS [yellow paper]".

Diagnosis. Ceracis ascetonotum sp. nov. can be distinguished from the other species in the genus (except for the members of the *Ceracis singularis* species-group; see "Comments" below) thanks to the 10-segmented antennae (Fig. 2A); males are distinguishable as follows: anterocephalic edge (Fig. 1A, C) produced and elevated, forming two blunt laminae (Fig. 1A, red arrows); pronotum (Fig. 1A–C) with two deep and wide impressions anteriorly; the outer borders of the impressions is extended forward in two lateral, elongate horns, each with an apical knob. Posterior contours of impressions joined at middle forming one thin elevation resembling a tiny horn (Fig. 1B, black arrow).

Description, male holotype (Fig. 1A–D). Adult fully pigmented and in good condition. Measurements in mm: TL 1.67, PL 0.72, PW 0.69, EL 0.95, EW 0.70, GD 0.63. Ratios: PL/PW 1.04, EL/EW 1.36, EL/PL 1.31, GD/EW 0.90, TL/EW 2.39. *Body* elongate, convex; dorsum and venter reddish dark brown; antennae yellowish brown, club dark brown; palpi and tarsi yellowish brown; dorsal vestiture single, consisting of minute suberect setae, barely visible in high magnifications (>50x); ventral vestiture of fine decumbent setae easily discernible in high magnifications (>50x). *Head* with the anteriormost portion visible from above; dorsum concave, without conspicuous protuberance on vertexal disc; punctures fine, shallow, separated from each other by two punctures-widths or less; surface glabrous; interspaces, microreticulate; anterocephalic edge produced and elevated forming two blunt laminae (Fig. 1A, red arrows) with many setae at apical edges. *Antennae* (Fig. 2A, left antenna from paratype) with ten segments, lengths as follows (in mm, left antenna measured): 0.08, 0.06, 0.03, 0.02, 0.02, 0.02, 0.02, 0.05, 0.05, 0.07 (FL 0.10 mm, CL 0.18 mm, CL/FL 1.78). *Eyes* coarsely facetted; each bearing about 90 ommatidia; GW 0.16 mm. *Maxillae* (Fig. 1E, from paratype) with distinctly articulated galea; lacinia more or less fused to stipes; apical maxillary palpomere pyriform, 1.7x as long as wide, widest near base, narrowly rounded at apex. *Mandible* 1.4x as long as wide. *Labium* (Fig. 1E, from paratype) with rounded contour of apical portion of prementum in lateral view; labial palps with three palmomeres. *Gula* 0.44x as wide as head. *Pronotum* (Fig. 1D) finely, shallowly punctate; punctures of one size; devoid of median impunctate line; punctures scattered, separated from each other by 1–2 megapuncture-widths; interspaces, microreticulate; vestiture single, consisting of minute pale yellowish setae (<0.01 mm); anterior pronotal edge with two deep and wide impressions, the outer borders of impressions extended forward as two lateral, elongate horns, each with an apical knob, and posterior contours of impressions joined at middle forming a thin elevation resembling a tiny horn (Fig. 1B, black arrow); lateral edges not crenulate, not explanate and not visible when seen from above. *Scutellar shield* triangular, bearing few punctures; apparently glabrous; BW 0.11 mm, SL 0.06 mm. *Elytra* with non-seriate, dual punctation; megapunctures finer and closer than those on pronotum, shallow, about 2x as large as micropunctures, separated from each other by one megapuncture-width or less; interspaces, smooth and shiny; vestiture single, consisting of minute pale yellowish setae (0.01–0.02 mm) arising from micropunctures; long setae more abundant than short setae at elytral apex. *Metathoracic wings* developed, apparently functional. *Hypomera* with fine, shallow punctation; each puncture bearing one fine decumbent seta; interspaces, microreticulate. *Prosternum* in front of coxae concave; interspaces, microreticulate. *Prosternal process* laminate, 1.3x as long as prosternum at midline; apex rounded. *Protibiae* (Fig. 2B, left protibia from paratype) with maximum width about one-third of its length, expanded at apex. *Meso- and metatibiae* (Fig. 2C–D, left meso- and metatibia from paratype) with spines in apical edge. *Metaventrite* with coarse, shallow punctures; interspaces, microreticulate; discrimen about one-fourth the length of metaventrite at midline. *Abdominal ventrites* with fine, shallow punctures, separated from each other by one puncture-width or less, each bearing one fine decumbent pale yellowish seta; interspaces, microreticulate; length of ventrites (in mm, from base to apex at the longitudinal midline) as follows: 0.22, 0.09, 0.09, 0.09, 0.07; first abdominal ventrite with large conspicuous, circular, margined setose sex patch posteriorly, transverse diameter 0.06 mm. *Male terminalia (from paratype)* (Fig. 2E–H): *Sternite VIII* (Fig. 2E) with posterior margin slightly emarginate medially; corners broadly rounded, bearing long and short setae; lateral margins diverging; anterior margin biconcave and sub-rounded medially. *Tegmen* (Fig. 2G) 2x as long as wide, widest near apex, apical portion deeply, broadly emarginate; lateral edges subparallel-sided, slightly angulate near apex; basolateral margins wide (Fig. 2G, red arrows); basal portion triangular.

Basal piece (Fig. 2F) subtriangular, 1.2x as wide as long. *Penis* (Fig. 2H) elongate, as long as tegmen, 4x as long as wide; lateral edges subparallel-sided, converging at middle to bilobed apex, dorsal one with apical portion acute (Fig. 2H, big black arrow), ventral one forming two elongate and sharp struts (Fig. 2H, small black arrows); basal portion rounded.

Females (Fig. 3A–E). Anterocephalic edge truncate anteriorly, barely convex; vertex convex. Anterior edge of pronotum rounded. Gula comparatively smaller than in males (0.29x as wide as head in a female from Fort Sherman, Panama). Otherwise like males, but devoid of head and pronotal ornaments, and abdominal sex patch. *Female terminalia* (Fig. 3D–E) with spiculum ventrale (Fig. 3D) 2x as long as gonocoxites; ovipositor (Fig. 18, distorted after compression between slide and cover slip) with paraprocts very reduced, shorter than gonocoxites and barely discernible; each baculus of paraprocts bowed and completely fused to respective proctigeral baculus (Fig. 3E); gonocoxites without discernible ventral lobes and without gonostyli.

Variation. Males, measurements in mm (n= 14, including the holotype): TL 1.43–2.08 (1.68 ± 0.20), PL 0.58–0.88 (0.69 ± 0.10), PW 0.55–0.80 (0.67 ± 0.07), EL 0.85–1.20 (0.99 ± 0.11), EW 0.60–0.80 (0.69 ± 0.06), GD 0.53–0.73 (0.61 ± 0.06), PL/PW 0.96–1.11 (1.03 ± 0.05), EL/EW 1.32–1.67 (1.45 ± 0.09), EL/PL 1.28–1.68 (1.45 ± 0.11), GD/EW 0.86–0.93 (0.89 ± 0.02), TL/EW 2.25–2.78 (2.45 ± 0.13). In the smallest males, pronotal impression and horns are comparatively shorter (Fig. 4A–C), while in the biggest males it is the opposite (Fig. 4D–E). Females, measurements in mm (n= 16): TL 1.20–1.78 (1.59 ± 0.13), PL 0.53–0.70 (0.61 ± 0.05), PW 0.60–0.70 (0.64 ± 0.04), EL 0.68–1.10 (0.98 ± 0.09), EW 0.60–0.78 (0.69 ± 0.05), GD 0.55–0.70 (0.63 ± 0.04), PL/PW 0.82–1.04 (0.95 ± 0.06), EL/EW 1.13–1.56 (1.43 ± 0.09), EL/PL 1.29–1.87 (1.61 ± 0.14), GD/EW 0.86–1.00 (0.91 ± 0.04), TL/EW 2.00–2.44 (2.31 ± 0.10). Pronotal punctation of specimens from Brazil are slightly finer compared to the specimens from other countries (Fig. 4B).

Host fungus. Cerrena caperata (Berk.) Zmitr., twelve records, two being breeding records.

Etymology. Species epithet is a combination of the Greek adjective "asketos" (= curiously wrought, ornamented), and the New Latin substantive "notum" derived from the Greek nōton (= the back), in the genitive singular. The name is a reference to the oddly ornamented pronotum of males.

Distribution. Ceracis ascetonotum sp. nov. has a wide distribution in the Neotropical region (Fig. 24), and mostly collected in areas dominated by Tropical and Subtropical Moist Broadleaf Forest at Colombia, Costa Rica, Panama, and at an ecotone between the Amazon Forest and Cerrado in Brazil. One specimen was collected on a *Quercus* Linn. (Fagaceae) forest in Colombia. It occurs in a wide range of altitudes, from about sea level to mountain areas 1800 m above sea level. The distributional gap in the Brazilian Amazon Forest is probably due to the low collection effort for ciid beetles in the area.

Comments. Most examined specimens were made available by John F. Lawrence (Australia) and the morphospecies was coded "*Ceracis* 660" by him. Up to date, *Cer. ascetonotum* sp. nov. cannot be placed in any previously proposed species-group and we prefer not to propose a new group for it, because we're currently conducting a phylogenetic analysis of the genus that can result in a more robust grouping of *Ceracis* species. *Ceracis ascetonotum* sp. nov. resembles members of the *Ceracis singularis* species-group in the 10-segemented antenna and the dual elytral

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punctation. However, species in the *singularis*-group have dual pronotal punctation, comparatively sparser elytral punctation, and males have anterocephalic edge with short and slightly concave lamina, and pronotum with the anterior edge forming one lamina deeply emarginate apically.

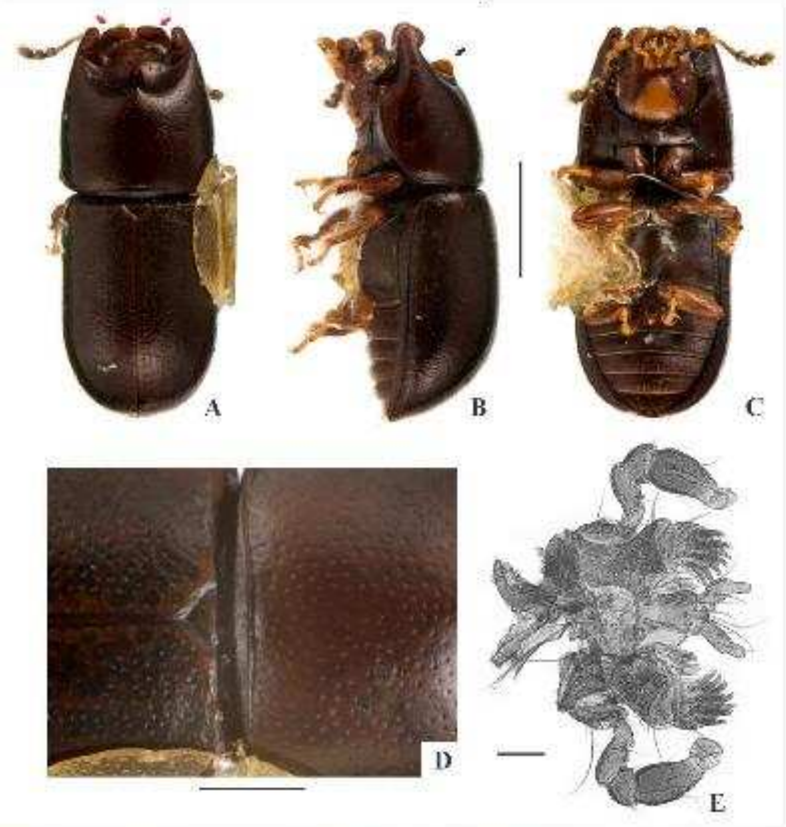

Figure 1. *Ceracis ascetonotum* sp. nov., male holotype (A–D) and mouth parts of a paratype from the type locality Fort Sherman (Canal Zone: Panama) (E): A. Dorsal view, note the anterocephalic edge with two blunt laminae (red arrows). B. Lateral view, note the pronotum with a thin elevation resembling a tiny horn (black arrow). C. Ventral view. D. Scutellar shield and part of pronotum and elytra. E. Mouth parts. Scale bars: 0.5 mm (A–C); 0.2 mm (D); 0.05 mm (E).

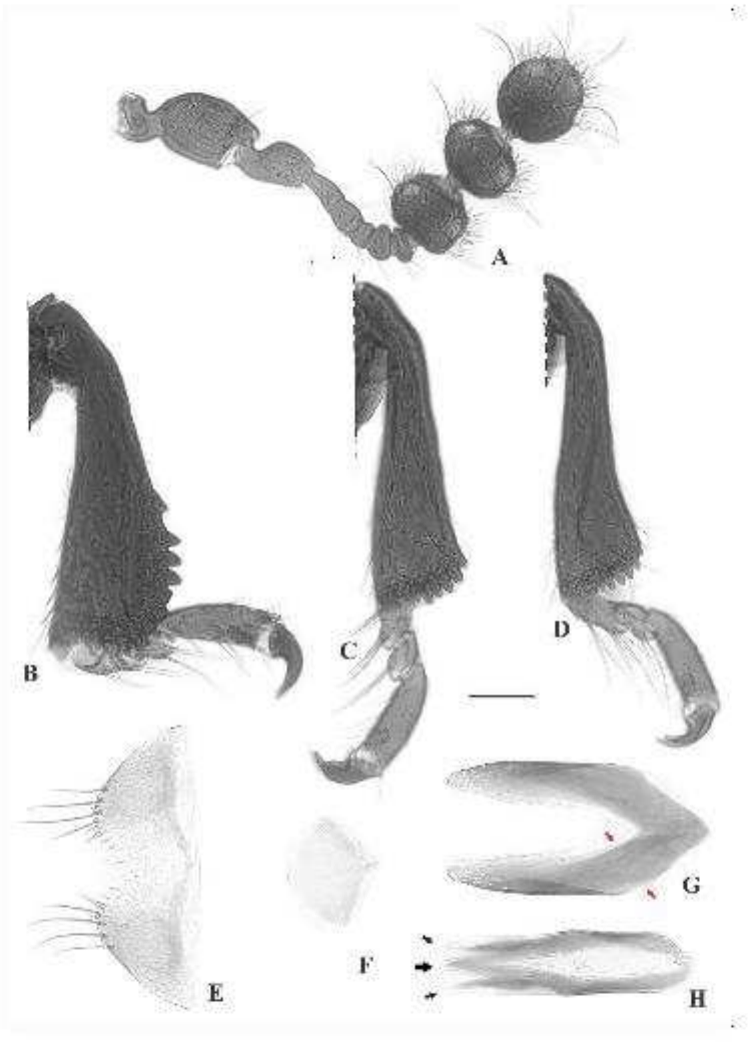

Figure 2. *Ceracis ascetonotum* sp. nov., antenna, tibiae and dissected parts of aedeagus of a paratype from the type locality Fort Sherman (Canal Zone: Panama) (A–H): A. Left antenna. B. Left protibia. C. Left mesotibia. D. Left metatibia. E. Sternite VIII. F. Basal piece. G. Tegmen, note the wide basolateral margins (red arrows). H. Penis, note bilobed apex, the dorsal one with apical portion acute (big black arrow), and the ventral one forming two elongate and sharp struts (small black arrows). Scale bar: 0.05 mm (A–H).

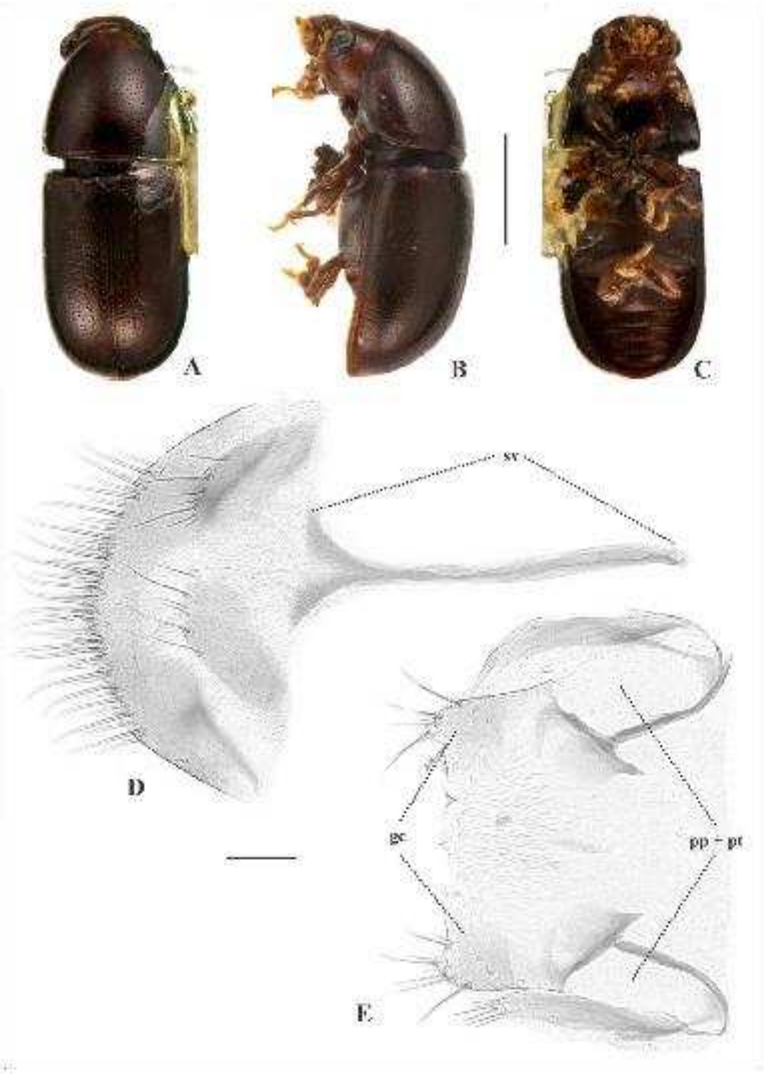

Figure 3. *Ceracis ascetonotum* sp. nov., habitus of female paratype (A–C) and female terminalia of a paratype from the type locality Fort Sherman (Canal Zone: Panama) (D–E): A. Dorsal view. B. Lateral view. C. Ventral view. D. Tergite VIII, and sternite VIII with spiculum ventrale (sv). E. Ovipositor, showing gonocoxites (gc) and proctiger plus paraprocts (pt + pp). Scale bars: 0.5 mm (A–C); 0.05 mm (D–E).

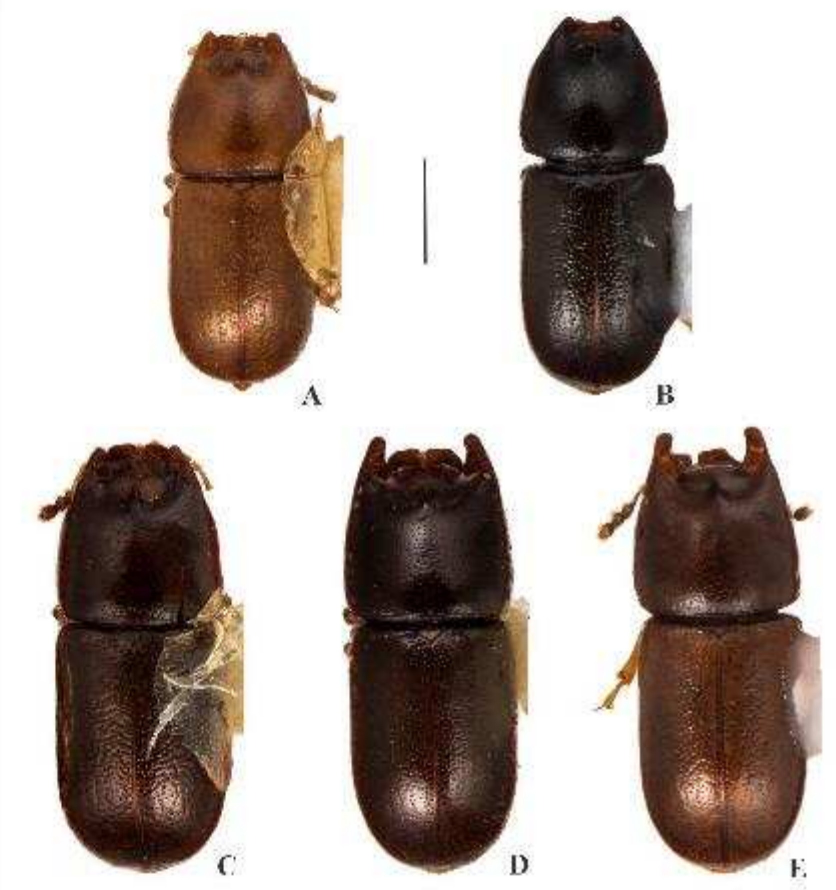

Figure 4. Variation of male *Ceracis ascetonotum* sp. nov. as observed in paratypes from: A. Barro Colorado (Panama). B. Canarana (Central-West Brazil). C. Monteverde (Costa Rica). D. Barro Colorado (Panama). E. Parque Nacional Natural Sierra de La Macarena (Colombia). Scale bar: 0.5 mm (A–E).

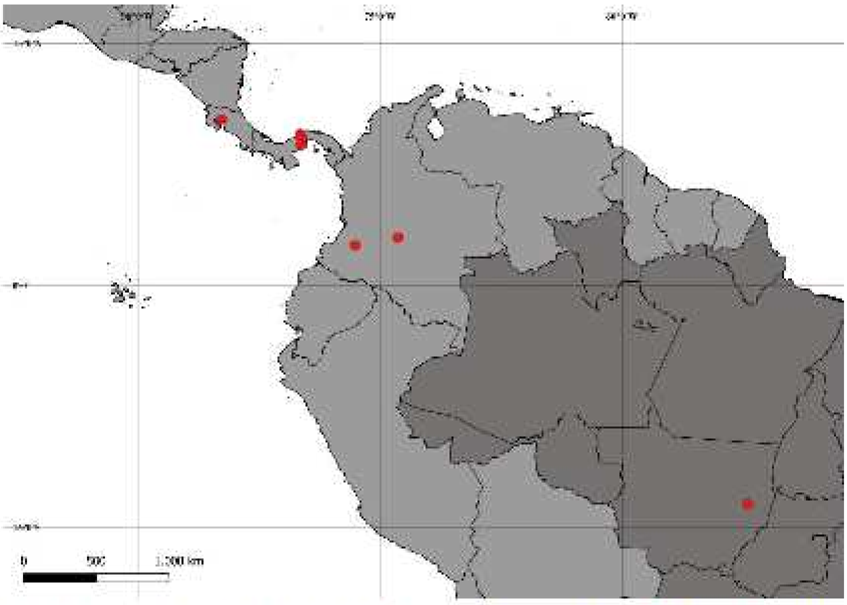

Figure 5. Known geographic distribution of *Ceracis ascetonotum* sp. nov. in Brazil, Colombia, Costa Rica and Panama. [Source: QGIS 3.14.1-Pi]

Competing interests. The authors declared that no competing interests exist in the preparation of the manuscript.

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CAPÍTULO 4: A morphology-based phylogeny of *Ceracis* Mellié (Coleoptera: Ciidae)

(Zoological Journal of the Linean Society. The manuscript presented here, in the form of a chapter of this thesis, is not considered valid according to the International Code of Zoological Nomenclature – ICZN (Ch. 03, Articles 8.2 and 8.3))

A morphology-based phylogeny of *Ceracis* Mellié (Coleoptera: Ciidae)

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Abstract

Ciidae is a family of small to minute beetles, which feed in both larval and adult stages on the mycelia and basidiomes of bracket fungi. *Ceracis* is the second most diverse genus of the family with 54 described species, most distributed at the New World. Here we tested for the first time the monophyly of *Ceracis* based on a phylogenetic analysis of morphological characters. A total of 22 genera and 57 species of Ciidae were selected as terminal taxa, including species of all recognized tribes within Ciidae. A total of 81 morphological characters were evaluated. Parsimony analyses were carried out under equal and implied weights. *Ceracis* was confirmed to be polyphyletic, with the *furcifer*-group as a well separate monophyletic group, which probably deserved genus status. *Ceracis* related genera revealed to share nonhomoplasious synapomorphies and must have its relationships more carefully and robustly investigate in future works.

Keywords. Minute tree-fungus beetles, Ciinae, phylogeny, morphology

Introduction

Ciidae is a family of small to minute beetles, with more than 750 species in 51 genera (Lawrence 2016, 2019, Souza-Gonçalves *et al.* 2018) and a cosmopolitan distribution. Ciid beetles feed in both larval and adult stages on the mycelia and badiodiomes of Ganodermataceae, Hymenochaetaceae, Polyporaceae and other bracket fungi (Lawrence 1971, Lawrence & Lopes-Andrade 2010). The family is divided into Sphindociinae, which includes only *Sphindocis denticollis* Fall, 1917 from the northern California coast, and Ciinae, with all other ciid species (Lawrence 1974a, 2016), the latter subdivided into three tribes: Ciini Leach, 1819, Orophiini Thomson, 1863 and Xylographellini Kawanabe & Miyatake, 1996.

Ceracis Mellié, 1849 is the second most diverse genus of the family and encompasses 54 described species (Antunes-Carvalho & Lopes-Andrade 2011, Pecci-

Maddalena *et al.* 2014, Lawrence 2016, Pecci-Maddalena & Lopes-Andrade 2017, Souza-Gonçalves & Lopes-Andrade 2020b, *in press*). *Ceracis* was originally described as a subgenus of *Ennearthron* Mellié,1847, but Lacordaire (1857) gave it genus level and Lawrence (1967) redefined its limits, together with the revision of Nearctic species and proposition of the affinities of these with Neotropical and Oriental species (Antunues-Carvalho & Lopes-Andrade 2011). Recently, the genus was redescribed and reported for the first time from Australia (Lawrence 2016). Among the described species, 43 occurs in the New World, five species are spread over Indo-Pacific islands (Christmas Island, Guam, Fiji, Marquesas, New Caledonia and Rapa), three occur on Japan and three on Australia (Abdullah 1973, Kawanabe 1994, Lawrence 1967, 1971, 2016, Lopes-Andrade *et al*. 2002, Antunes-Carvalho & Lopes-Andrade 2011, 2013, Pecci-Maddalena & Lopes-Andrade 2017, Souza-Gonçalves & Lopes-Andrade 2020b *in press*). The Neotropical *Cer. cucullatus* (Mellié) and *Cer. tabellifer* (Mellié) are considered to be invasive species, the former in Galapagos and the latter in Africa, South and Southeast Asia (Antunes-Carvalho & Lopes-Andrade 2013, Pecci-Maddalena *et al.* 2014).

Ceracis can be characterized by the following features (Lawrence 2016): (i) body oval to elongate; (ii) antennae 8- or 9- segmented, occasionally 10-segmented; (iii) prosternum concave with prosternal process laminate (except for species in the *furcifer*-group); (iv) protibiae with outer apical angle expanded subapically to form a rounded lobe with a row of socketed spines; (v) metaventrite convex; (vi) discrimen short or absent; and (vii) vestiture of minute setae, usually inconspicuous. None of these features are exclusive of the genus.

Currently, *Ceracis* encompass four artificial species-groups (*cucullatus*, *furcatus*, *furcifer* and *singularis*). The *cucullatus*-group was revised by Antunes-Carvalho & Lopes-Andrade (2011, 2013), with four new species from Australia added by Lawrence (2016). *Ceracis bicornis* (Mellié) is the unique species within the *cucullatus*-group that was not redescribed yet and may be a species complex (Souza-Gonçalves & Lopes-Andrade 2020a). The *furcatus*-group was established by Lopes-Andrade (2002) and encompasses very similar species that can be synonymous (Lawrence 1967). The *furcifer*-group was recently revised by Pecci-Maddalena & Lopes-Andrade (2017), who proposed four synonymies and rearranged the group in four bona species. The *singularis*-group was established by Lopes-Andrade *et al*. (2002), but without any additional information in the scientific literature.

Phylogenetic Background

The faunistic and taxonomic studies on Ciidae have grown up in the last decades, with emphasis on the Australian, Brazilian, Mexican and Southern African faunas (*e.g.* Navarrete-Heredia & Burgios-Solorio 2000, Lopes-Andrade 2002, 2008a, b, Antunes-Carvalho & Lopes-Andrade 2013, Oliveira *et al.* 2013, Lawrence 2016, Pecci-Maddalena & Lopes-Andrade 2017, Souza-Gonçalves *et al.* 2018, Lawrence 2019, Souza-Gonçalves *et al.* 2020), following the works on the North American fauna conducted by Lawrence (1967, 1971, 1974b). However, no robust phylogenetic study on Ciidae or any of their suprageneric or generic taxa have been performed up to date. Only two molecular phylogenetic studies are available: that of Buder *et al.* (2008), which tested the monophyly of the family and investigated its relationships with other cucujoid and tenebrionoid beetles, corroborating the hypothesis of monophyly and recovering the most speciose and typic genus *Cis* Latreille, 1796 as polyphyletic; and that of Lopes-Andrade & Grebennikov (2015), which recovered *Cis* and *Ceracis* as polyphyletic, with species of the *Ceracis furcifer*-group clustered outside the genus, and recognized Xylographellini as monophyletic, and Ciini and Orophiini as polyphyletic.

Doubts on the constitution of the genus Ceracis

In the absence of more evidence, besides that provided by Lopes-Andrade & Grebennikov (2015), *Ceracis* has been treated as a genus (Lawrence 2016). However, in the revision of the North American *Ceracis* (Lawrence 1967), some species were left as *incertae sedis*: *Ceracis bifurcus* Gorham, 1898, *Cer. laticornis* Pic, 1922 and *Cer. particularis* Pic, 1922. *Ennearthron taurulus* Jacquelin-Duval, 1857 was left in *Ceracis* by that time, but it was recognized that “(...) it does not appear to be closely related to any other *Ceracis*.” (Lawrence 1967). We proposed new genera to place these four previously species, because we’ve decided it was time to clear up the genus, excluding species that barely fit its generics limits (Souza-Gonçalves & Lopes-Andrade *in prep.*[3]). Nevertheless, Pecci-Maddalena & Lopes-Andrade (2017) pointed out that *furcifer*-group may be a separate genus considering some remarkable aspects distinguishing this group from other *Ceracis* (*e.g.* anterocephalic edge strongly produced forming a single median horn; tegmen with a deep apical longitudinal emargination forming two parallel lobes; penis cylindrical with rounded apex; sternite VIII with deep concave, mesal emargination at the posterior edge; prosternal process thin but not laminate). Therefore, the classification of *Ceracis* as well as its relationships within the family, and suprageneric limits remains an interesting and important area of work.

The aim of the present study is to test the monophyly of *Ceracis* and its relationship to other Ciidae genera based on a phylogenetic analysis of morphological characters.

Material and methods

Taxonomic sampling

Species were selected based on their availability, representativeness of morphological variation within Ciidae, specially within the genus *Ceracis*, and geographical distribution. A total of 22 genera and 57 species of Ciidae were selected. Most studied specimens were directly compared with primary types or historical material housed in museums. From all subfamilies and tribes, only Sphindociinae was not included, due the absence of available specimens for dissection. Members of all Ciidae tribes currently recognized were included. Information on the examined species are listed in Table 1, including authority and year of description, which are not repeated in the text.

Eighty-one characters were scored from adult morphology of 57 terminal taxa. The ingroup included 34 species of *Ceracis*, including the type species of the genus *Ceracis sallei* Mellié, representatives of all four species-groups currently adopted and new species recognized in the museum collections (Table 1). Twenty-three outgroup

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[3] Souza-Gonçalves, I. & Lopes-Andrade, C.. Seven new genera of Ciidae (Coleoptera: Tenebrionoidea) from Neotropical region, based mostly on species identified as *Ceracis* Mellié in colletions. (*in prep.*) – Chapter 1.

taxa were selected, including species of new genera under description by us and probably related to *Ceracis* (Souza-Gonçalves & Lopes-Andrade *in prep.*[4]) (Table 1).

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[4] Souza-Gonçalves, I. & Lopes-Andrade, C.. Seven new genera of Ciidae (Coleoptera: Tenebrionoidea) from Neotropical region, based mostly on species identified as *Ceracis* Mellié in colletions. (*in prep.*) – Chapter 1.

Table 1. List of examined species. Species names followed by (*) are type species from the respective genus; (#) are morphospecies delimitated by authors of this paper; (•) are morphospecies delimitated by John F. Lawrence and confirmed by authors of this paper; and (‡) species with male unknown and not examined.

Systematic assignment		**Species**	**Provenance**	**Biogeographic region (*sensu* Morrone, 2015)**
Ciidae				
Ciinae	Ciini	*Abebaeocis taurulus* (Jacquelin-Duval, 1857) i.l. *	Mexico	Neotropical
Ciinae	Ciini	*Alcecis particularis* (Pic, 1922) i.l. *	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Anartioscelos aptenus* Souza-Gonçalves & Lopes-Andrade i.l. *	San Juan Bautista Valle Nacional, Oaxaca, Mexico	Neotropical
Ciinae	Ciini	*Atomocis melanus* Souza-Gonçalves & Lopes-Andrade i.l. *	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Ceracis ascetonotum* Souza-Gonçalves & Lopes-Andrade, 2020b	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Ceracis californicus* (Casey, 1884)	Apache and Pima Counties, Arizona, USA	Nearctic and Neotropical
Ciinae	Ciini	*Ceracis cornifer* (Mellié, 1849)	Rio Paranaíba, Minas Gerais, Brazil	Nearctic and Neotropical
Ciinae	Ciini	*Ceracis cucullatus* (Mellié, 1849)	Canarana, Mato Grosso, Brazil	Neotropical
Ciinae	Ciini	*Ceracis evansi* (Blair, 1944)	Guam, Northern Mariana Islands	Oriental
Ciinae	Ciini	*Ceracis furcatus* (Bosc, 1791)	Cinnamon Bay, St. John Island, Virgin Islands	Neotropical
Ciinae	Ciini	*Ceracis furcifer* Mellié, 1849	Manaus, Amazonas, Brazil	Neotropical
Ciinae	Ciini	*Ceracis limai* Lopes-Andrade et al., 2002	São Francisco de Paula, Rio Grande do Sul, Brazil	Neotropical
Ciinae	Ciini	*Ceracis minutus* Dury, 1917	Brownsville, Texas, USA and Windsor, Jamaica	Nearctic and Neotropical
Ciinae	Ciini	*Ceracis multipunctatus* (Mellié, 1849)	Highlands Hammock State Park, Highlands County, Florida, USA and Windsor, Jamaica	Nearctic and Neotropical
Ciinae	Ciini	*Ceracis nigropunctatus* Lawrence, 1967	El Naranjo, San Luis Potosi, Mexico	Neotropical
Ciinae	Ciini	*Ceracis palaceps* Zimmerman, 1942	Tinian, Northern Mariana Islands	Oriental
Ciinae	Ciini	*Ceracis powelli* Lawrence, 1967	Tenango de Doria, Hidalgo, Mexico	Nearctic
Ciinae	Ciini	*Ceracis pullulus* (Casey, 1898)	Chipola Park, Calhoun County and Florida Caverns State Park, Jackson Conty, Florida, USA	Nearctic and Neotropical
Ciinae	Ciini	*Ceracis quadricornis* Gorham, 1886	Linares, Nuevo Léon, Mexico	Nearctic and Neotropical
Ciinae	Ciini	*Ceracis sallei* Mellié, 1849 *	Southern Pines, Moore County, North Carolina and Miami, Miami-Dade, Florida, USA	Nearctic
Ciinae	Ciini	*Ceracis similis* Horn, 1894	Malinalco, State of Mexico, Mexico	Nearctic and Neotropical
Ciinae	Ciini	*Ceracis* sp. 139 •	Córdoba, Veracruz, Mexico	Neotropical
Ciinae	Ciini	*Ceracis* sp. 224 •	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Ceracis* sp. 657 •	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Ceracis* sp. 658 •	Barro Colorado Island, Canal Zone, Panama	Neotropical

Ciinae	Ciini	*Ceracis* sp. 661 •	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Ceracis* sp. 744 •	Tamaulipas, Mexico	Neotropical
Ciinae	Ciini	*Ceracis* sp. 788 •	Campana, Capira District, Panama Oeste Province, Panama	Neotropical
Ciinae	Ciini	*Ceracis* sp. 813 •	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Ceracis* sp. A #	San Blas, Nayarit, Mexico	Neotropical
Ciinae	Ciini	*Ceracis* sp. B #	Viçosa, Minas Gerais, Brazil	Neotropical
Ciinae	Ciini	*Ceracis* sp. C #	Poconé, Mato Grosso, Brazil	Neotropical

Systematic assignment		**Species**	**Provenance**	**Biogeographic region (*sensu* Morrone, 2015)**
Ciinae	Ciini	*Ceracis* sp. D #	Licínio de Almeida, Bahia, Brazil	Neotropical
Ciinae	Ciini	*Ceracis* sp. E (aff. *punctulatus*) #	Ipatinga, Minas Gerais, Brazil	Neotropical
Ciinae	Ciini	*Ceracis tabellifer* (Mellié, 1849)	Chapada dos Guimarães, Mato Grosso, Brazil	Neotropical, Cape, Ethiopian, Palearctic and Oriental
Ciinae	Ciini	*Ceracis thoracicornis* (Ziegler, 1845)	Highlands, Macon County, North Carolina, USA	Nearctic
Ciinae	Ciini	*Ceracis tzotzilicus* Souza-Gonçalves & Lopes-Andrade 2020a	San Cristóbal de las Casas, Chiaspas, Mexico	Neotropical
Ciinae	Ciini	*Ceracis* zarathustrai Pecci-Maddalena et al., 2014	Viçosa, Minas Gerais, Brazil	Neotropical
Ciinae	Ciini	*Cis boleti* (Scopoli, 1763) *	Auckland, North Island, New Zealand	Australian, Palearctic
Ciinae	Ciini	*Cis delicatulus* (Jacquelin-Duval, 1857)	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Cis pubescens* (Friedenreich, 1881)	Viçosa, Minas Gerais, Brazil	Neotropical
Ciinae	Ciini	*Ennearthron victori* Lopes-Andrade & Zacaro, 2003	Ubá, Minas Gerais, Brazil	Neotropical
Ciinae	Ciini	*Euxestocis bicornutus* Miyatake, 1954 *	Chiba, Chiba Prefecture, Japan	Oriental
Ciinae	Ciini	*Falsocis brasiliensis* Lopes-Andrade, 2007	Viçosa, Minas Gerais, Brazil	Neotropical
Ciinae	Ciini	*Grossicis diadematus* (Mellié, 1849) *	Nova Friburgo, Rio de Janeiro, Brazil	Neotropical
Ciinae	Ciini	*Gyraleosomus boliviensis* Souza-Gonçalves & Lopes-Andrade i.l. *	Cochabamba, Cochabamba Province, Bolivia	Neotropical
Ciinae	Ciini	*Insolitocis panamensis* Souza-Gonçalves & Lopes-Andrade i.l. * ‡	Barro Colorado Island, Canal Zone, Panama	Neotropical
Ciinae	Ciini	*Lipedanicis geminus* Souza-Gonçalves & Lopes-Andrade i.l. *	Araguaína, Tocantins, Brazil	Neotropical
Ciinae	Ciini	*Malacocis farleyi* Araujo & Lopes-Andrade i.l.	Licínio de Almeida, Bahia, Brazil	Neotropical
Ciinae	Ciini	*Neoennearthron bicarinatum* Miyatake, 1954 *	Moutain Obako-dake, Nara, Japan	Oriental
Ciinae	Ciini	*Phellinocis romualdoi* Lopes-Andrade & Lawrence, 2005 *	Venda Nova do Imigrante, Espírito Santo, Brazil	Neotropical
Ciinae	Ciini	*Porculus grossus* Lawrence, 1987 *	Chapada dos Guimarães, Mato Grosso, Brazil	Neotropical
Ciinae	Ciini	*Wagaicis wagae* (Wankowicz, 1869) *	Baden-Baden, Baden-Württmberg, Germany	Palearctic
Ciinae	Orophiini	*Octotemnus glabriculus* (Gyllenhal, 1827) *	Newboro Lake, Ontario, Canada	Nearctic, Palearctic
Ciinae	Orophiini	*Paratrichapus fultoni* (Broun, 1886)	Dunedin, South Island, New Zealand	Australian
Ciinae	Orophiini	*Xylographus contractus* Mellié, 1849	Viçosa, Minas Gerais, Brazil	Neotropical
Ciinae	Xylographellini	*Scolytocis furieriae* Lopes-Andrade, 2008	Eunápolis, Bahia, Brazil	Neotropical

Morphological study and pictorial documentation

Specimens were examined under a Zeiss Stemi 508 stereomicroscope. Dissections and photographs were made under a Zeiss Discovery V20 stereomicroscope equipped with a Zeiss AxioCam 506 digital camera. Final images were the result of joining 30 to 70 images at different focal lengths using the extended focus module of Zeiss Zen 1.1.2 software. Dissected body parts were immersed in 20% KOH solution for 10–15 min to remove soft tissues, then immersed in 10 % acetic acid solution to neutralize KOH effect and washed in water. When necessary, structures were stained with a solution of 0.5% Chlorazol Black E in 85% alcohol to enhance contrast. Whole mount preparations of male and female terminalia were made using water-soluble mounting media based on polyvinyl alcohol and lactic acid. Slides were photographed under a Zeiss AxioLab compound microscope equipped with a Zeiss AxioCam MRc digital camera.

Classification system and terminology

The suprageneric classification of Ciidae is based on Lawrence (1971), Lawrence & Lopes-Andrade (2010), Lawrence (2016), Souza-Gonçalves & Lopes-Andrade (*in prep.*[5]). At the species level, we followed Lawrence (1967, 1971), Abdullah (1973), Navarrete-Heredia & Burgos-Solorio (2000), Lopes-Andrade (2002, 2008), Lopes-Andrade & Lawrence (2005, 2011), Antunes-Carvalho *et al.* (2012), Antunes-Carvalho & Lopes-Andrade (2013), Oliveira *et al.* (2013), Sandoval-Gómez *et al.* (2014), Pecci-Maddalena & Lopes-Andrade (2017), Souza-Gonçalves & Lopes-Andrade (2020a, b *in press*, *in prep.*[3]). Terms for external morphology follow McHugh *et al.* (1997), Węgrzynowicz (2002), Lopes-Andrade & Lawrence (2005, 2011), Lawrence *et al.* (2011), Oliveira *et al.* (2013) and Lawrence (2016).

Cladistic analysis

The data matrix was compiled using MESQUITE 3.10 (Maddison & Maddison 2016) and analyzed under parsimony with TNT v1.5 (Goloboff & Catalano 2016). In

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[5] Souza-Gonçalves, I. & Lopes-Andrade, C.. Seven new genera of Ciidae (Coleoptera: Tenebrionoidea) from Neotropical region, based mostly on species identified as *Ceracis* Mellié in colletions. (*in prep.*) – Chapter 1.

the cases when only females were examined, males devoid of terminalia or unknown, characters of male terminalia and/or of male were coded as '?', and those characters inapplicable were coded as '–'. Characters were defined following the logical basis proposed by Sereno (2007). The character state matrix is shown in Appendix S1. Heuristic searches were performed under equal weights (EW) and implied weights (IW) (Goloboff 1993, Goloboff *et al.* 2008a) using the Traditional search algorithms. We tested different parameters to find the best options considering the size and features of our data set. Goloboff *et al.* (2008b) suggested that the best approach is to run a number of additional sequences (RAS), each with tree bisection reconnection (TBR) branch-swapping, until the best score is hit 10 to 20 times independently for most medium-sized data sets. However, Datovo (2015) highlights that based on test with real matrices, even hit the best score 20 times is insufficient for very homoplastic matrices and that it is recommendable to hit the best score at least 50 times. Based on that information we performed the EW analysis under the following parameters (output file available in Appendix S2): Wagner trees > 'Random seed' = 0 > 1000 replications (number of additional sequences) > TBR branch-swapping > 500 trees saved per replication > 'Collapse trees after the search' (Appendix S2). The IW analysis was performed under the following parameters (output file available in Appendix S3): Wagner trees > 'Random seed' = 0 > 40000 replications (number of additional sequences) > TBR branch-swapping > 40 trees saved per replication > 'Collapse trees after the search'. The TNT implied_w script, developed for Mirande (2009), was used to identify the most appropriate K value through the formula proposed by Goloboff *et al.* (2008a). The 11 K values got by the method of Mirande (2009) resulted in three distinct trees. The final topology was got through the higher some of SPRdif and between it the best K value was used in order not to penalize too much the homoplasies. A value of 23.804 was returned and subsequently used in the IW search.

Nodes were evaluated with relative Bremer supports (Bremer 1994) for the EW analysis, following the instructions provided by Datovo (2015); and symmetric resampling (Goloboff *et al.* 2003) expressed as the difference in the GC (contradicted/present groups) frequency (5000 replications) for the IW analysis. Unsupported clades are collapsed. There are incongruencies between the topology of the trees concerning the clades in Figure 46 and Figures 47–49. These incongruencies are resultant of the analysis methods. The tree shown in figure 46 is a consensus resulted from resampling with 5000 replications and collapsing unsupported clades. On other hand, the tree shown in Figures 47–49 is the unique resultant after the IW analysis. Optimizations were performed with Winclada-ASADO 1.62 (Nixon 2002) and only unambiguous changes were mapped on the tree. We coded most characters as binary (93.8 %) and treated the multi-state characters as unordered.

Results

A total of 81 characters were scored for 23 outgroup taxa and 34 ingroup terminals of Ciidae. The complete data set comprised 14 characters from head, 42 from the thorax, six from the pregenital segments, six from the aedeagus and 13 from ovipositor. Five characters were recovered as without phylogenetic signal (RI = 0) and were removed *a posteriori* from the final analyses, but are shown at the end of the character list.

List of characters

Head.

1. Vertexal disc, protuberance: present (0) (Fig. 1); absent (1).

2. Antenna, funicle, segment IV: present (0) (Fig. 2); absent (1) (Fig. 4). In S0, segment IV can be fused or not to segment III (C3), while S1 represent the loss of segment IV.

3. Antenna, funicle, segment IV: not fused with III (0) (Fig. 2); fused with III (1) (Fig. 3). Inapplicable when C2 = S1.

4. Antenna, funicle, segment VI: present (0) (Fig. 2); absent (1) (Fig. 4). S1 represent the loss of segment VI.

5. Antenna, funicle, segment VII: present (0) (Fig. 2); absent (1) (Fig. 6). S1 represent the loss of segment VII. Among the ciid species examined here, S1 was observed only in *Octotemnus glabriculus*.

6. Antenna, club segments, articulation: loosely articulated (0) (Fig. 6); tightly articulated forming compact club (1) (Fig. 7). Corresponding to character 50 in

Lawrence *et al.* (2011). Among ciid species, S1 was observed only in Xylographellini up to date (Lopes-Andrade 2008a).

7. Antenna, apical segment of club, length relative to the width: ≥1 (0); <1 (2).

8. Antenna, club segments, organization of sensillifers on each antennomere: not organized as continuous sensory areas (0) (Fig. 3); organized as continuous sensory areas (1) (Fig. 8). Among ciid species examined here, S1 was observed only in *Insolitocis panamensis* i.l.. Among other ciid species, S1 was observed only in the monospecific *Australocis* Lawrence.

9. Antenna, club segments, delimitation of basal and apical portions: present (0) (Fig. 9); absent (1). S0 is characterized by the presence of a well delimited suture bearing long setae along it. Among the ciid species examined here, S0 was observed only in *Paratrichapus fultoni* and *Xylographus contractus*.

10. Labrum, length relative to the width: <1.5 (0); ≥1.5 (1). Labrum is measured from the base of the most sclerotized portion to the apex, not including apical setae.

11. Labial palps, apical palpomere, shape: cylindrical (0) (Fig. 10); spatula-shaped (1) (Fig. 11). Among ciid species, S1 was observed only in Xylographellini (Lopes-Andrade 2008a).

12. Labial palps, apical palpomere, length relative to the width: ≤1.5 (0); >1.5 (1).

13. Labial palps, basal palpomere, length relative to the width: ≤1 (0); >1 (1). Among ciid species, S1 is exclusive of *Xylographus* Mellié.

14. Maxilla, palps, shape of the apical palpomere: pyriform (0) (Fig. 11); abruptly expanded (1) (Fig. 10). Among ciid species, S1 occurs only in *Grossicis* Antunes-Carvalho *et al.* and species of the *Cis tricornis* group, except for *C. delicatulus*.

Thorax.

15. Pronotum, anterior edge, in males: not ornamented (0); ornamented (1). S0 is characterized by the edge rounded to slightly emarginated, while S1 is characterized by the presence of any tubercles, horns or plates.

16. Pronotum, anterior angles, whether produced or not: not produced forward (0) (Fig. 12); produced forward (1) (Fig. 13). Modified from character 102 in Lawrence *et al.* (2011). This character is equally visualized from above or from bellow.

17. Pronotum, anterior angles, apex shape: broadly rounded (0) (Fig. 13); narrowly rounded (1) (Fig. 14). Modified from character 102 in Lawrence *et al.* (2011). This character is equally visualized from above or from bellow. Inapplicable when C16 = S0.

18. Pronotum, sides, whether explanate or not: not or barely explanate (0) (Fig. 12); horizontally explanate (1) (Fig. 13). Modified from character 95 in Lawrence *et al.* (2011).

19. Pronotum, edge of lateral carina, shape: simple (0) (Fig. 12); crenulate (1) (Fig. 13). Modified from character 100 in Lawrence *et al.* (2011).

20. Pronotum, procoxal cavities, whether open or not: open (0) (Fig. 12); closed (1) (Fig. 15). Among the ciid species examined here, S1 occurs only in *Porculus grossus*.

21. Pronotum, procoxal cavities, opening at base relative to the procoxal cavity diameter: ≥1/3 (0); <1/3 (1). Inapplicable when C20 = S1.

22. Pronotum, vestiture, type: single (0); dual (1). In S1 the pronotal setae fall into two classes of length, in which the longest is at least twice as long as the shortest.

23. Pronotum, vestiture, arising from: macropunctures (0); micropunctures (1). Inapplicable when C22 = S1.

24. Pronotum, vestiture, length relative to the puncture-width: ≤1 (0); >1 (1). The puncture-widths used for comparison are from punctures in which a seta or a bristle is inserted. When C22 = S1, the most abundant vestiture class was considered for comparison.

25. Pronotum, surface between punctures: microreticulate (0); smooth to irregular (1), micostriate (2). Among the ciid species examined here, S2 was observed only in *Insolitocis panamensis* i.l..

26. Prosternum, in front of procoxae, shape: concave, flat or convex (0); slightly tumid at middle to softly biconcave (1); strongly elevated at middle (2).

27. Prosternum, in front of procoxae, at longitudinal midline: devoid of carina (0); bearing a carina (1)

28. Prosternum, prosternal process, shape: thin to broad (0) (Fig. 13); laminate (1) (Fig. 15).

29. Procoxae, position relative to the prosternum: not or slightly projecting below prosternum (0) (Fig. 16); projecting well below prosternum (1) (Fig. 17). Modified from character 127 in Lawrence *et al.* (2011).

30. Procoxae, visible portion, shape: globular or transverse and subcylindrical (0) (Fig. 16); subconical (1) (Fig. 17). Modified from character 128 in Lawrence *et al.* (2011).

31. Profemur, apex, lobe relative to the inner edge of femur: not or barely surpassing (0) (Fig. 18); conspicuously surpassing (1) (Fig. 19).

32. Protibiae, apex, shape: broadly sinuous (0) (Fig. 18); slightly sinuous (1) (Fig. 19); almost straight (2) (Fig. 20).

33. Protibiae, apex, whether bears transition of spines or not: with transition of sharp spines to socketed spines (0) (Fig. 19); without transition of sharp spines to socketed spines (1). S1 is characterized by the presence only of sharp spines at protibial apex.

34. Protibiae, outer apical angle, whether expanded forming tooth or not: not expanded (0) (Fig. 19); expanded forming one tooth (1) (Fig. 20); expanded forming two teeth (2) (Fig. 21). S0 is characterized by the outer apical angle rounded or angulate. Among ciid genera, S2 occurs only in *Phellinocis* Lopes-Andrade & Lawrence (Lopes-Andrade & Lawrence 2005).

35. Protibiae, outer apical angle, rounded lobe: present (0) (Fig. 21); absent (1). Inapplicable when C34 = S1 and S2.

36. Protibiae, outer apical angle, socketed spines: present (0); absent (1).

37. Protibiae, outer apical angle, distribution of socketed spines between sexes: similar in both sexes (0) (Fig. 22); reaching the outer edge in males (1) (Fig. 23). S1 is characterized by socketed spines reaching almost the middle length of outer edge in males. Inapplicable when C36 = S1.

38. Protibiae, outer edge, socketed spines: present (0) (Fig. 22); absent (1).

39. Protibiae, outer edge, extension of socketed spines: not reaching the middle of outer edge (0) (Fig. 22); extending to at least the middle of outer edge (1) (Fig. 23)**.** Inapplicable when C38 = S1.

40. Elytra, vestiture, type: single (0); dual (1). The S1 is characterized by presence of vestiture with two classes of width, being the longest at least twice as long as the shortest.

41. Elytra, vestiture, arising from: macropunctures (0); micropunctures (1). Inapplicable when C40 = S1.

42. Elytra, vestiture, length relative to the puncture-width: ≤1 (0); >1 (1). The puncture-widths used for comparison are from punctures in which the seta or bristle is inserted. When C41 = S1, the vestiture class with the largest length was considered for comparison.

43. Elytra, surface between punctures: microreticulated (0); smooth to irregular (1).

44. Metanotum, alar ridge of metascutellum, if touching the posterior margin of metascutum or not: touching (0) (Fig. 24); not touching (1) (Fig. 25). Modified from character 51 in Węgrzynowicz (2002).

45. Metanotum, alar ridge of metascutellum, transversal edge relative to the longitudinal edge: ≥1 (0); <1 (1).

46. Metanotum, alar ridge of metascutellum, apical margins of transversal edge: straight (0) (Fig. 24); curved (1) (Fig. 25).

47. Metanotum, alar ridge of metascutellum, width relative to the width of scutellar groove: ≥1.5 (0); <1.5 (1). Width of the alar ridge of metascutellum is measured diagonally from the inner apical angle to the outer edge. Width of scutellar groove is measured at the apical portion.

48. Mesoventral process, extension relative to the metaventrite: extending to anterior edge of metaventrite (0) (Fig. 26); extending behind middle of mesocoxae but not

reaching metaventrite (1) (Fig. 27). Modified from character 172 in Lawrence *et al.* (2011).

49. Metaventrite, length at lateral relative to the length at midline: <2 (0); >2 (1). Among the ciid species examined here, S1 was observed only in *Falsocis brasiliensis*.

50. Metaventrite, width relative to the length at midline: ≤2 (0); >2 (1).

51. Mesotibiae, outer apical angle, socketed spines: present (0) (Fig. 28); absent (1).

52. Mesotibiae, outer edge, socketed spines: not reaching the middle of outer edge (0) (Fig. 28); extending to at least two-thirds of outer edge (1) (Fig. 29). Inapplicable when C51 = S1.

53. Metatibiae, outer apical angle, socketed spines: present (0); absent (1).

54. Metatibiae, outer edge, socketed spines: not reaching the middle of outer edge (0); extending to at least two-thirds of outer edge (1). Inapplicable when C53 = S1.

55. Tibiae, shape: widened at or near apex (0) (Fig. 28); strongly widened well before apex (1) (Fig. 29). Modified from character 250 in Lawrence *et al.* (2011).

56. Tibiae, inner surface, vestiture relative to the length: reaching ≤1/3 (0); reaching >1/3 (1) (Fig. 29).

Abdomen: pregenital segments.

57. Male sternite VIII, anterior edge, median strut: present (0) (Fig. 30); absent (1). Corresponding to character 302 in Lawrence *et al.* (2011).

58. Male sternite VIII, anterior edge, shape: biconcave (0) (Fig. 31); almost straight to straight (1) (Fig. 30).

59. Male sternite VIII, posterior edge, shape: emarginate (0) (Fig. 30); rounded (1) (Fig. 32); almost straight to straight (2) (Fig. 33).

60. Male sternite VIII, posterior edge, shape of emargination: shallow (0) (Fig. 31); deep (1) (Fig. 30). Inapplicable when C59 = S1 and S2. S1 is characterized by an emargination surpassing the level of apical setae.

61. Male segment IX, anteroventral edge, sclerotized edges: forming a V- or U-shaped arc (0) (Fig. 34); forming a Y-shaped arc (spiculum gastrale) (1) (Fig. 35). This character has been called “ninth abdominal sternite” (*e,g,* Kawanabe & Miyatake 1996), “ninth-segment” (*e.g.* Lopes-Andrade & Lawrence 2005; Lopes-Andrade 2008; Lopes-Andrade *et al.* 2009), “anterior edge of sternite IX” (*e.g.* Lawrence & Lopes-Andrade 2010) or “genital ring” (*e.g.* Antunes-Carvalho *et al.* 2012). These all refers to the shape of the sclerotized edges of the anterior protusions of laterotergites of segment IX, which are fused together and to the sternite IX to form a subgenital plate (Lawrence *et al.* 2011). This structure and its parts are explained in details in character 305 of Lawrence *et al.* (2011). Among ciid species, S1 occurs only Xylographellini species (Lopes-Andrade 2008a).

62. Spiculum ventrale (= anterior strut of the female sternite VIII), length relative to the ovipositor: >1 (0); ≤1 (1). Spiculum ventrale is measured from the base to the apex, until the area which has contact with sternite VIII. Ovipositor length is the sum of length of gonostylus (not including apical setae), length of gonocoxite and length of paraproct (sometimes taken as the length of its baculum).

Abdomen: aedeagus.

63. Tegmen (= fused parameres), apical portion, emargination: present (0) (Fig. 36); absent (1).

64. Tegmen, basolateral margins, shape: narrow (0) (Fig. 36); wide (1) (Fig. 37). Inapplicable when C63 = S1 and when C63 = S0 is characterized by an emargination with length <2/3 of tegmen length.

65. Tegmen, apical portion, basiconical sensilla: restricted to the apicalmost portion of tegmen (0) (Fig. 36); spread in the apical half of tegmen (1) (Fig. 37).

66. Tegmen, base, shape: subrounded to rounded (0) (Fig. 38); subtriangular to triangular (1) (Fig. 36); truncate (2) (Fig. 39). Among the ciid species examined here, S2 was observed only in *Abebaeocis taurulus* i.l..

67. Penis, length relative to the tegmen: >1 (0); ≤1 (1).

68. Penis, lateral edges, shape: forming two struts not linked at base (0) (Fig. 40); not forming struts and linked at base (1) (Fig. 41).

Abdomen: ovipositor.

69. Proctiger (= tergite X), extension of its apex at level of: basal ventral lobe gonocoxites (0) (Fig. 42); apical ventral lobe gonocoxites (1) (Fig. 43).

70. Paraprocts, bacula: longitudinally oriented (0) (Fig. 42); bowed and completely fused to the respective proctigeral baculum (1) (Fig. 43).

71. Paraprocts, length relative to the gonocoxites: >1 (0); ≤1. Modified from character 334 in Lawrence *et al.* (2011).

72. Gonocoxites, apical long setae, length relative to the lateral length of gonocoxite: ≤1 (0); >1 (1) (Fig. 45).

73. Gonocoxites, bacula of basal gonocoxites, orientation: transverse (0) (Fig. 42); oblique (1) (Fig. 43).

74. Ventral lobe of gonocoxites, inner apical angle, shape: acute (0 (Fig. 44); rounded (1) (Fig. 45).

75. Ventral lobe of gonocoxites, medial portion, sclerotizations: present (0) (Fig. 43); absent (1).

76. Ovipositor, posterior margin, shape: slightly curved to straight (0) (Fig. 44); deeply emarginate (1) (Fig. 42).

77. Gonostyli: present (0) (Fig. 42); absent (1) (Fig. 45).

78. Gonostyli, length: ≤0.015 mm (0); >0.015 mm and ≤0.030 mm (1); >0.030 mm (2). Gonostyli are measured from the base to the apex, not including apical setae. Inapplicable when C77 = S1.

79. Gonostyli, length relative to the width: ≤2.5 (0); >2.5 (1). Gonostyli are measured from the base to the apex, not including apical setae. C77 = S1.

80. Gonostyli, shape: subparallel- to parallel-sided (0) (Fig. 44); converging to apex (1) (Fig. 42). Inapplicable when C77 = S1.

81. Gonostyli, apex, number of setae: 1 (0) (Fig. 44); >1 (1) (Fig. 42). Inapplicable when C77 = S1.

Characters excluded *a posteriori* from the analyses due to its RI = 0:

- Antenna, funicle, segment V: present (0); absent (1). S1 represents the loss of segment V. Among the ciid species examined here, S1 was observed in all *Ceracis* species with 9-segmented antennae, *Alcecis particularis* i.l., *Ennearthron victori*, *Neoennearthron bicarinatum*, *Octotemnus glabriculus* and *Phellinocis romualdoi*.

- Antenna, club segments, number of sensillifers on each antennomere: 4 (0); >4 (1). Among ciid species, S1 is known to occur only in Xylographellini species (Lopes-Andrade 2008a). Inapplicable when C9 = S1.

- Pronotum, punctation, type: single (0); dual (1). S1 is characterized by the presence of punctures with two classes of length, usually the largest is twice as large as another one. Among the ciid species examined here, S1 was observed in *Alcecis particularis* i.l., *Cis boleti*, *Cis delicatulus*, *Lipedanicis geminus* i.l. and *Xylographus contractus*.

- Elytra, punctation, type: single (0); dual (1). S1 is characterized by the presence of punctures that fall into two classes of width, in which the largest is usually twice as large as the smallest.

- Tegmen, apical portion, shape of emargination: shallow (0); deep (1). The emargination in S1 is >2/3 as long as. Inapplicable when C63 = S1.

Phylogenetic analysis

The heuristic search with EW of characters resulted in 874 most parsimonious trees of 429 steps, with a CI = 0.20 and RI = 0.57. The strict consensus tree (CI = 0.10 and RI = 0.08) with Bremer support values for each branch is shown in Appendix S4. Most nodes received low nodal support. *Ceracis* was recovered as polyphyletic and were collapsed in a single branch with most terminal taxa (Appendix S4). In this polytomy, the following clades were recovered: (i) the *furcifer*-group (*Cer. cornifer* + *Cer. furcifer*) was recovered as monophyletic and with the higher nodal support (Appendix S4, green clade); and other three clades with low nodal support, (ii) *Cer. similis* + *Cer. multipunctatus* (Appendix S4); iii) *Alc. particularis* i.l. + *C. pubescens* (Appendix S4); and (iv) (*O. glabriculus* + (*X. contractus* + *Sco. furieriae*)) (Appendix S4).

The IW analysis resulted in one most parsimonious tree. The strict consensus tree with GC frequency is shown in Figure 46, and Figures 47–49 shown the mapping of characters. The results were very similar to that from EW analysis, except for *Ceracis sensu stricto* (excluding the *furcifer*-group) in a polytomy with low nodal support. The *furcifer*-group was recovered as monophyletic (Fig. 46, green clade) and the remaining *Ceracis* in a polytomy (Fig. 46, blue clade). Some clades were recovered within the *Ceracis* polytomy, mostly with very low nodal support, except for the clade *Cer. multipunctatus* + *Cer. similis* (Fig. 46). The *furcifer*-group was supported by two homoplasious synapomorphies (character and state codes between parenthesis) (Fig. 48, green clade): “basiconical sensilla restricted to the apicalmost portion of tegmen” (65:1) and “bacula of basal gonocoxites transversally oriented (73:0). *Ceracis sensu stricto* was supported by one nonhomoplasious synapomorphy and two homoplasious synapomorphies, respectively (Fig. 49, blue clade): “vertexal disc with protuberance” (1:0), “pronotal anterior edge ornamented in males” (15:1) and “lobe in the apex of profemur conspicuously surpassing inner edge” (31:1). The clade *Cer. multipunctatus* + *Cer. similis* was also supported by one nonhomoplasious synapomorphy and two homoplasious synapomorphies, respectively (Fig. 49): “medial portion of ventral gonocoxital lobe with sclerotizations” (75:0), “metaventrite more than 2x as wide as long” (50:1) and “posterior margin of ovipositor deeply emarginate” (76:1).

Discussion

Previous molecular-based phylogenetic analysis had already shown that *Ceracis* was polyphyletic, with the *furcifer*-group forming a separate clade, while the remaining *Ceracis* were scattered in the tree (Lopes-Andrade & Grebennikov 2015). But *Ceracis* was not well-represented in that analysis. Aside from two valid species of the *furcifer*-group (*Cer. cornifer* and *Cer. furcifer*), only *Cer. thoracicornis*, *Cer. cassumbensis* Antunes-Carvalho & Lopes-Andrade and *Cer. cucullatus* (*cucullatus*-group), and *Cer. nigropunctatus* were included, as far as unidentified species (Lopes-Andrade & Grebennikov 2015). By that time, these identified *Ceracis* species represented less than 12% of the known species of the genus, species from two (*furcatus* and *singularis*) of the four species-groups and the type species of the genus, *Cer. sallei*, were not included. In that analysis, the species of the *cucullatus*-group were not recovered as a clade: *Cer. cucullatus* grouped with *Cer. nigropunctatus*, and *Cer. cassumbensis* grouped with an unidentified *Cis* species, both clades weakly supported. In the other hand, *Cer. thoracicornis* appeared together with an unidentified *Ceracis* species (Lopes-Andrade & Grebennikov 2015).

The analyses provided here independently corroborated the same view concerning the *furcifer*-group as a separate clade from the remaining *Ceracis* species. Therefore, the *furcifer*-group shall be transferred to a separate new genus to fulfill the previous molecular phylogenetic knowledge and the evidences provided here. The necessity of a separate genus for the *furcifer*-group was already pointed out by Pecci-Maddalena & Lopes-Andrade (2017), but by that time the available knowledge on the morphology of *Ceracis* species was insufficient for the proposition of a generic diagnosis for the *furcifer*-group. Unlike the analysis conducted by Lopes-Andrade & Grebennikov (2015), our results recovered *Ceracis sensu stricto* as a clade, despite the low support. Additionally, our analyses were conducted with 38% of the described *Ceracis* species, including the type species of the genus and almost all species included by Lopes-Andrade & Grebennikov (2015) (except for *Cer. cassumbensis*). Moreover, species of the other two species-groups were included in our analyses: *Cer. furcatus* and *Cer. minutus* (*furcatus*-group), and *Cer. limai* (*singularis*-group). In our analyses none of the other groups (except for the *furcifer*-group) were recovered as clades. Species of the *cucullatus*-group were recovered in two weakly supported separate clades: i) *Cer. cucullatus* grouped with *Cer. palaceps* sharing four homoplasious synapomorphies: “protibiae with almost straight apex” (32:2), “mesoventral process extending behind middle of mesocoxae but not reaching metaventrite” (48:1), “tibiae with vestiture reaching less than or 1/3 of their inner surface length" (56:0) and "tegmen with subtriangular to triangular base" (66:1); and ii) *Cer. tabellifer* grouped with *Ceracis* sp. B sharing one homoplasious synapomorphy: "male sternite VIII with posterior edge deeply emarginate" (60:1). Species of the *furcatus*-group were recovered as a weakly supported clade in IW analysis, but in the mapping of the characters they were recovered in two distinct clades: i) (*Cer. furcatus* + (*Cer. pullulus* + (*Cer. evansi* + (*Cer. multipunctatus* + *Cer. similis*)))) as sister-group of *Ceracis* sp. 224, separated by one homoplasious synapomorphy (a reversion into the genus): "vertexal disc without protuberance (1:1)"; and ii) (*Ceracis minutus* + (*Cer. nigropunctatus* + (*Cer.* sp. E (aff. *punctulatus*) + (*Ceracis* sp. C + *Caracis* sp. 744)))) as sister-group of the *Cer. tzotzilicus*, separated by three homoplasious synapomorphies: "metanotum with metascutellum alar ridge not touching the posterior margin of metascutum" (44:1), "tibiae with vestiture reaching less than or 1/3 of their inner surface length" (56:0) and "male sternite VIII with posterior edge deeply emarginate" (60:1). *Ceracis limai* (unique included species of the *singularis*-group) was not recovered with any other species in a clade, but in the mapping of the characters appeared as sister-group of all other *Ceracis sensu stricto*, bearing three homoplasious synapomorphies: "metanotum with metascutellum alar ridge wider than or 1.5x of the scutellar groove width" (47:0), "penis longer than tegmen" (67:0) and "ovipositor with slightly curved to straight posterior margin" (76:0).

The clade composed by *Cer. multipunctatus* + *Cer. similis* received intermediate nodal support, being supported by one nonhomoplasious synapomorphy (75:0) and two homoplasious synapomorphies (50:1, 76:1). Lawrence (1967) highlights that *Cer. multipunctatus* is similar to *Cer. curtus* (Mellié), *Cer. nigropunctatus* and *Cer. castaneipennis* in general form and elytral punctation, but all these three species have coarser pronotal punctation and bears ornaments in the anterocephalic edge. Additionally, *Cer. multipunctatus* is one of the few known *Ceracis* species which the pronotal and anterocephalic edge modifications are completely lacking in males. *Ceracis similis* was pointed out as closely related to the *Cer. schaefferi* Dury, but the former bears more elongate body and more prominent pronotal lamina in males (Lawrence 1967, 1971). It would be important to include *Cer. castaneipennis*, *Cer.*

curtus and *Cer. schaefferi* in subsequent analyses in order to elucidate these relationships.

Besides the low nodal support, the clade composed by (*Cer. thoracicornis* + (*Cer. cucullatus* + *Cer. palaceps*)) was supported by a unique combination (when compared with all outgroup and the remaining ingroup species) of two homoplasious synapomorphies: “outer apical angle of protibiae with socketed spines reaching almost the middle length of outer edge in males” (37:1) and “outer edge of protibiae with socketed spines extending to at least the middle of outer edge” (39:1). Beyond the abovementioned clade, the former homoplasious synamorphy is only shared with *Ceracis* sp. 661 and *Wagaicis wagae*, however, in both species the outer apical angle of protibiae has socketed spines not reaching the middle of outer edge (39:0). Lawrence (1967) already pointed out that *Cer*, *thoracicornis* would probably be closely related to the Neotropical species *Cer. cucullatus* and *Cer. bicornis* (Mellié) (another species from the *cucullatus*-group), differing from them by the comparatively coarser pronotal punctation and distinct pronotal modifications. However, in the same paper he highlights that the Oriental species *Cer. palaceps* is a distinct form and is probably not closely related to any other known species.

The type species *Cer. sallei* was recovered as a weakly supported clade with *Ceracis* sp. E (aff. *punctulatus*) in the IW analysis, but in the reconstruction of the characters it was recovered as a clade with *Ceracis* sp. 788, supported by two homoplasious synapomorphies: “metanotum with metascutellum alar ridge narrower than 1.5x of the scutellar groove width” (47:1) and “male sternite VIII with posterior edge deeply emarginate” (60:1). *Ceracis sallei* is restrict to the Nearctic region (Canada and USA) (Lawrence 1967, 1971) and belongs to the *Ganoderma* ciid host-use group (Orledge & Reynolds 2005); while *Ceracis* sp. 788 occurs in the Neotropical region (known from Panama and Jamaica) and probably belongs to the *Phellinus* ciid host-use group, since was collected only in basidiomes of *Phellinus gilvus* (Schwein.) Pat. (Hymenochaetaceae) and *Phellinus* sp..

The *furcifer*-group has distribution restricted to the Neotropical region, from southern Argentina to southern USA (Pecci-Maddalena & Lopes-Andrade 2017).

Species in this group are specialized consumers of the *Pycnoporus sanguineus* (L.) Murrill (Polyporacea), which belongs to the *Trametes* ciid host-use group (Lawrence 1973; Gumier-Costa *et al.* 2003; Orledge & Reynolds 2005; Graf-Peters *et al.* 2011). Among *Ceracis sensu stricto* species, there are two clades with species sharing some biological features: i) (*Cer. thoracicornis* + (*Cer. cucullatus* + *Cer. palaceps*)), and ii) *Cer. multipunctatus* + *Cer. similis*. In the former clade, *Ceracis thoracicornis* is restricted to the Nearctic region (Canada and USA) and is the most common widespread and polyphagous species in eastern North America (Lawrence 1967); while *Cer. cucullatus* is distributed at the Neotropical region (Mexico to Midwest Brazil and introduced at Galapagos Islands) and bears a polyphagous feed habitus too (Antunes-Carvalho & Lopes-Andrade 2013); in the other hand, *Cer. palaceps* is restricted to the Oriental region (Micronesia) but there is none information concerning it host fungi in the literature. In the latter clade, both *Cer. multipunctatus* and *Cer. similis* occur in Nearctic and Neotropical regions, the former from southeastern USA to Mexico and West Indies (Cuba, Jamaica and Montserrat), and the latter from Mexico to Costa Rica (Lawrence 1967, 1971); furthermore, both are members of the *Ganoderma* ciid host-use group (Orledge & Reynolds 2005).

In the first modern taxonomic revision of the genus *Ceracis* (Lawrence 1967), three species were left as *incertae sedis*: *Ceracis bifurcus*, *Ceracis laticornis* and *Ceracis particularis*. *Ennearthron taurulus* was left in *Ceracis*, but was pointed out as not related to any other species (Lawrence 1967). These *incertae sedis*, together with a series of odd ciid species known from museum collections and *Enn. taurulus*, were removed from *Ceracis* and placed by us in new genera (Souza-Gonçalves & Lopes-Andrade *in prep.*[6]) as follows: *Abebaeocis phiaronotum* i.l. and *Abebaeocis taurulus* i.l. in *Abebaeocis* i.l.; *Alcecis particularis* i.l. in *Alcecis* i.l.; *Anartioscelos aptenus* i.l., *Anartioscelos bifurcus* i.l., *Anartioscelos eurinotum* i.l., *Anartioscelos involucris* i.l. and *Anartioscelos laticornis* i.l. in *Anartioscelos* i.l.; *Atomocis melanus* i.l. in *Atomocis* i.l.**;** *Gyraleosomus boliviensis* in *Gyraleosomus* i.l.; *Insolitocis panamensis* in *Insolitocis* i.l.; *Lipedanicis adelphus* i.l., *Lipedanicis agastor* i.l., *Lipedanicis epamphoterus*.i.l. and

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[6] Souza-Gonçalves, I. & Lopes-Andrade, C.. Seven new genera of Ciidae (Coleoptera: Tenebrionoidea) from Neotropical region, based mostly on species identified as *Ceracis* Mellié in colletions. (*in prep.*) – Chapter 1.

Lipedanicis geminus i.l. in *Lipedanicis* i.l.. Among these, *Abebaeocis* i.l., *Anartioscelos* i.l., *Gyraleosomus* i.l. and *Lipedanicis* i.l. are recovered together with *Ceracis* related genera (*Grossicis*, *Malacocis*, *Octotemnus*, *Paratrichapus*, *Phellinocis*, *Scolytocis*, *Wagaicis* and *Xylographus*). These genera, together with the *furcifer*-group and the remaining *Ceracis* species, were grouped in a clade supported by three nonhomoplasious synapomorphies of the ovipositor: "extension of proctigeral apex at level of apical ventral lobe gonocoxites" (69:1), "bacula of paraprocts bowed and completely fused to the respective proctigeral baculum" (70:1) and "bacula of basal gonocoxites obliquely oriented" (73:1). The morphology of the ovipositor is usually stable within a ciid genus and conspicuous variations may indicate relationships at the suprageneric level. However, it shall be noted that these three abovementioned nonhomoplasious synapomorphies may be morphological convergences, due to reduction and simplification of the ovipositor as adaptations for oviposition in structurally similar host fungi (C. Lopes-Andrade, pers. obs.).

Among the taxonomically problematic species within *Ceracis*, only those in the *furcifer*-group remain to be better placed, as a new genus with the following possible diagnostic features (Pecci-Maddalena & Lopes-Andrade 2017): (i) antennal funicle with three or four segments, leading to a total or eight or nine segments; (ii) prosternal process thin, parallel-sided, but not laminate; (iii) anterocephalic edge in males strongly produced forming a single median horn, generally laminar in lateral view; (iv) sternite VIII with deep concave, mesal emargination at the posterior edge; (v) tegmen with a deep apical longitudinal emargination forming two parallel lobes; (vi) basiconical sensilla restricted to the apicalmost portion of tegmen; (vii) penis cylindrical with rounded apex; (viii) ovipositor with bacula of basal gonocoxites transversally oriented.

Our results provide insights that *Paratrichapus* Scott, *Octotemnus* Mellié and *Xylographus* Mellié (Orophiini); *Scolytocis* Blair (Xylographellini); and *Wagaicis* Lohse (Ciini) are the lineages supposedly closer to the *Ceracis sensu stricto*. These taxa composed a clade supported by four homoplasious synapomorphies, besides the low nodal support: "prosternal process laminate" (28:1), "outer edge of protibiae with socketed spines" (38:0), "tibiae with vestiture reaching more than or 1/3 of their inner surface length" (56:1) and "male sternite VIII with posterior edge shallowly emarginate” (60:0). All the clade (*Ceracis sensu stricto* + (*W. wagae* + (*P. fultoni* + (*Oc. glabriculus* + (*Sc. furieriae* + *X. contractus*))))) is a sister-group of the *furcifer*-group, being supported by an unique nonhomoplasious synapomorphy: “outer apical angle of protibiae with socketed spines” (36:0).

Among these lineages, *Paratrichapus* occurs in the Australian and Oriental regions (Souza-Gonçalves *et al.* 2019); while *Octotemnus* is distributed in the Nearctic, Palearctic, Oriental and Australian regions (Lawrence 2016); *Wagaicis* is restricted to Palearctic region (Lohse 1964; Löbl & Smetana 2008); *Scolytocis* occurs in Neotropical, Oriental and Australian regions (Lopes-Andrade 2008b; Souza-Gonçalves & Lopes-Andrade 2017); while *Xylographus* occurs in Neotropical, Ethiopian, Palearctic, Oriental and Australian regions (Sandoval-Gómez *et al* 2014; Lawrence 2016). Based on the geographical distribution of these lineages and on the *Ceracis sensu stricto*, the following biogeographical hypotheses can be proposed: i) a Tropical Gondwanan (Holotropical) origin of *Ceracis sensu stricto*; ii) a subsequent expansion of the Neotropical fauna to the Nearctic region; iii) a subsequent expansion of the Oriental fauna to the Australian region. Lawrence (1967) had already suggested that North American species had a Neotropical origin, and the Oriental species appeared not to be related to the New World species.

Our work proposed a cladistic hypothesis for *Ceracis* for the first time. The polyphyly of the genus was confirmed, corroborating previous molecular evidence. The *furcifer*-group had its monophyly corroborate, which is congruent with molecular-based reconstruction and must be elevated to a new genus. *Ceracis* related genera revealed to share nonhomoplasius synapomorphies and must be more carefully and robustly investigated in future works. The inclusion of *Ceracis* species from the Australian and Palearctic (Japanese species) regions would be very interesting in the future works in a tentative to solve the relationships between species from those regions and the remaining *Ceracis* species. The small size and the high number of homoplastic features are obstacles to be overcome in the systematics of Ciidae. Furthermore, there are structures which needs to be examined more carefully and more detailed as: epi- and hypopharynx, sclerites and alar base, elytral and pronotal punctation, endoskeleton and muscles. Study of these structures and documentation based on scanning electron microscopy (SEM) and microtomography (Micro-CT) shall be considered in future works to construct a more robust matrix and investigate the relationships within *Ceracis sensu stricto* as well as relationships of the genus within Ciidae.

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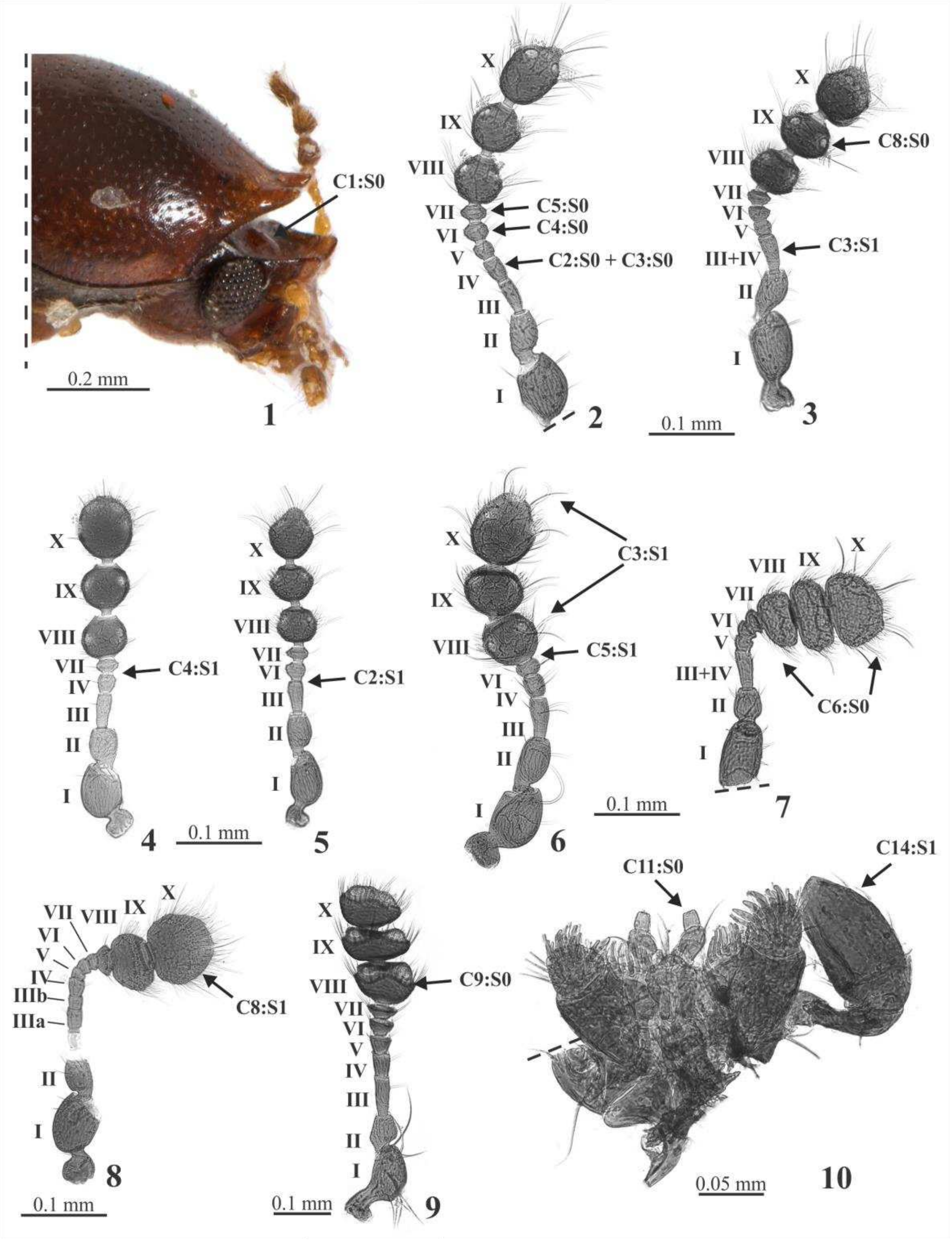
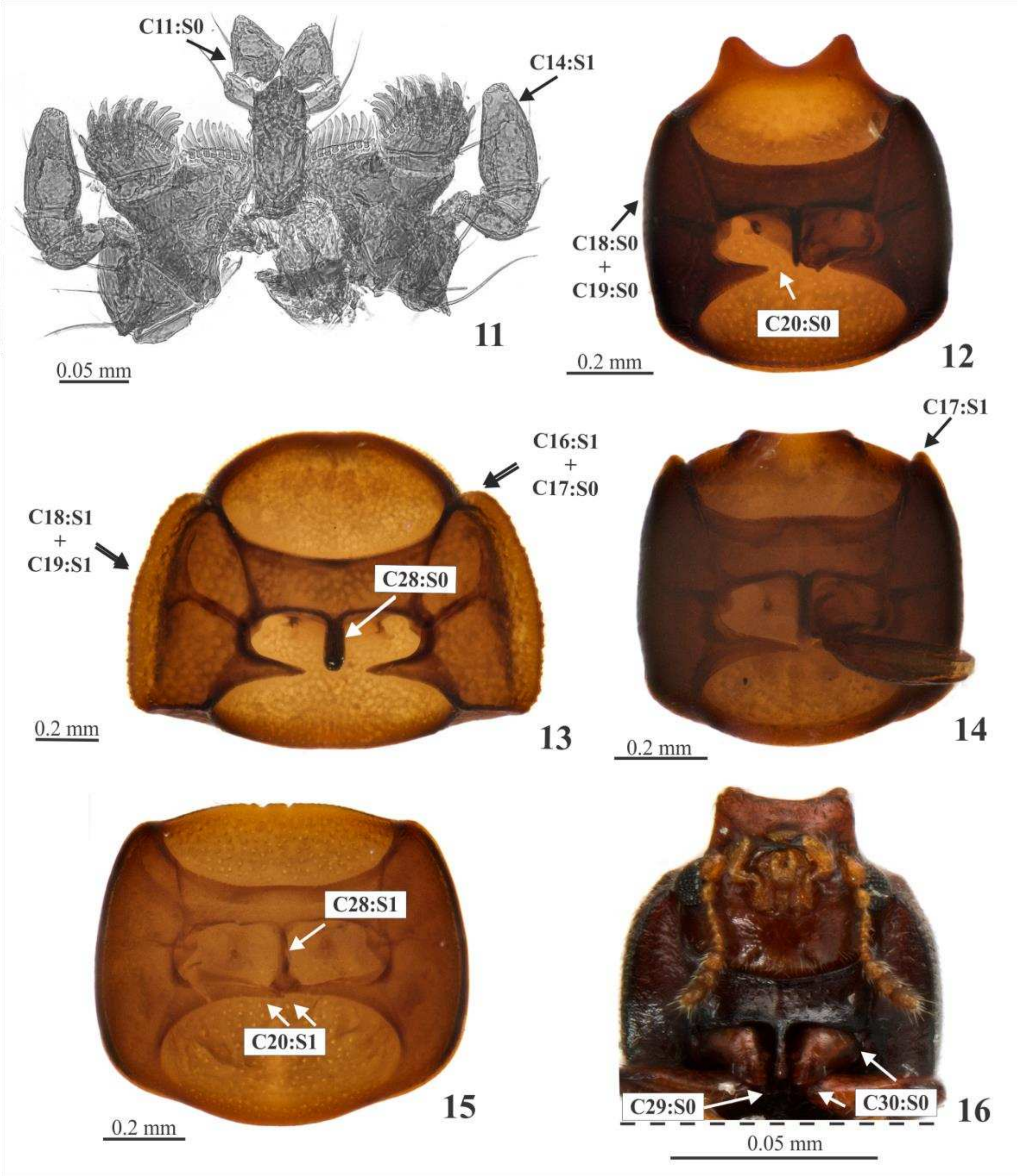
FIGURE AND FIGURE CAPTIONS

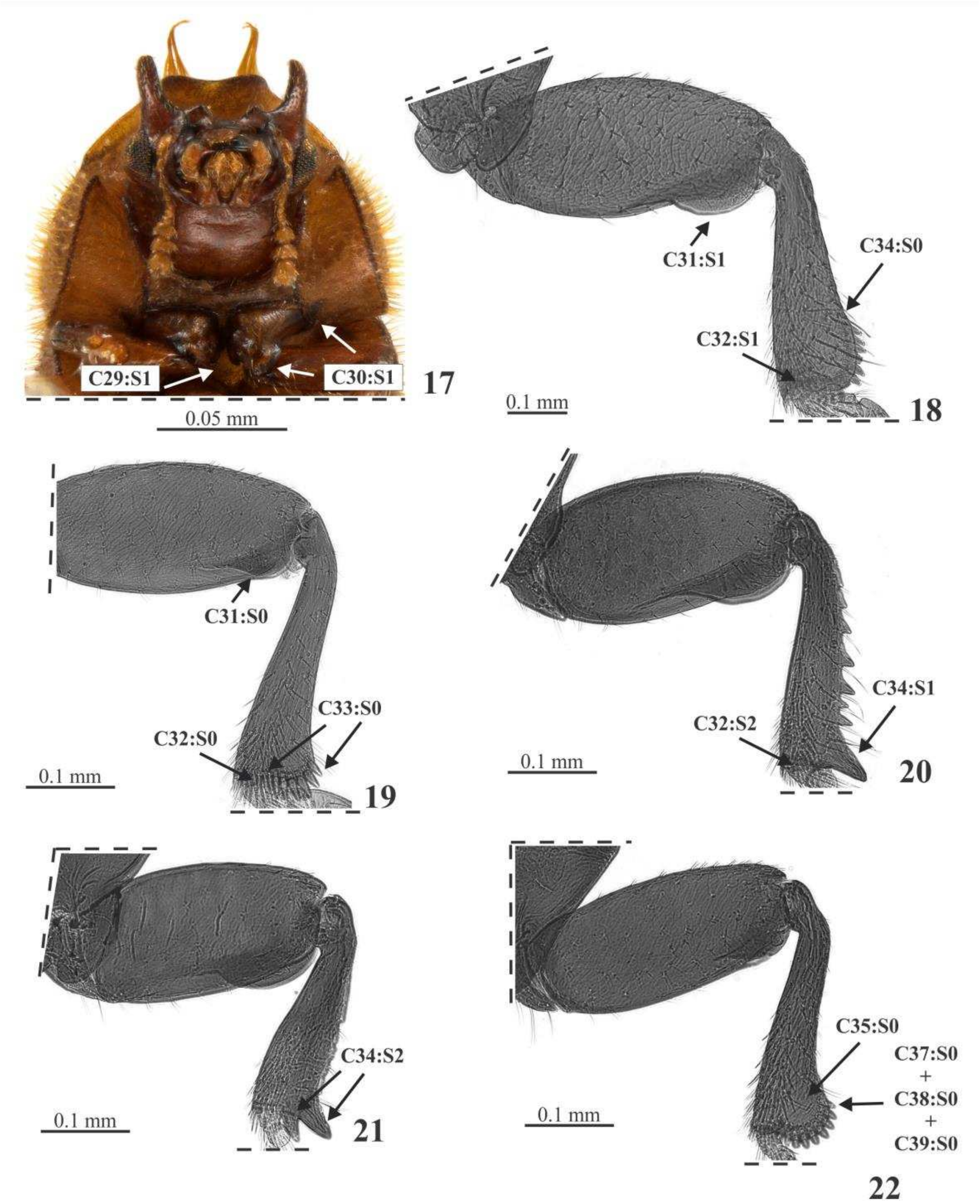


Figures 1–10. Images showing part of the morphological features included in our data matrix. “C” and “S” preceding numbers refer to character and its state, respectively. Roman numbers refer to antennal segments. **1.** *Ceracis tzotzilicus* Souza-Gonçalves &

Lopes-Andrade, lateral view of head and part of pronotum. **2.** *Ceracis limai* Lopes-Andrade *et al.*, antenna. **3.** *Ceracis multipunctatus* (Mellié), antenna. **4.** *Ceracis furcifer* Mellié, antenna. **5.** *Ceracis minutus* Dury, antenna. **6.** *Octotemnus glabriculus* (Gyllenhal), antenna. **7.** *Scolytocis furieriae* Lopes-Andrade, antenna. **8.** *Insolitocis panamensis* Souza-Gonçalves & Lopes-Andrade i.l., antenna. **9.** *Xylographus contractus* Mellié, antenna. **10.** *Grossicis diadematus* (Mellié), mouth parts.

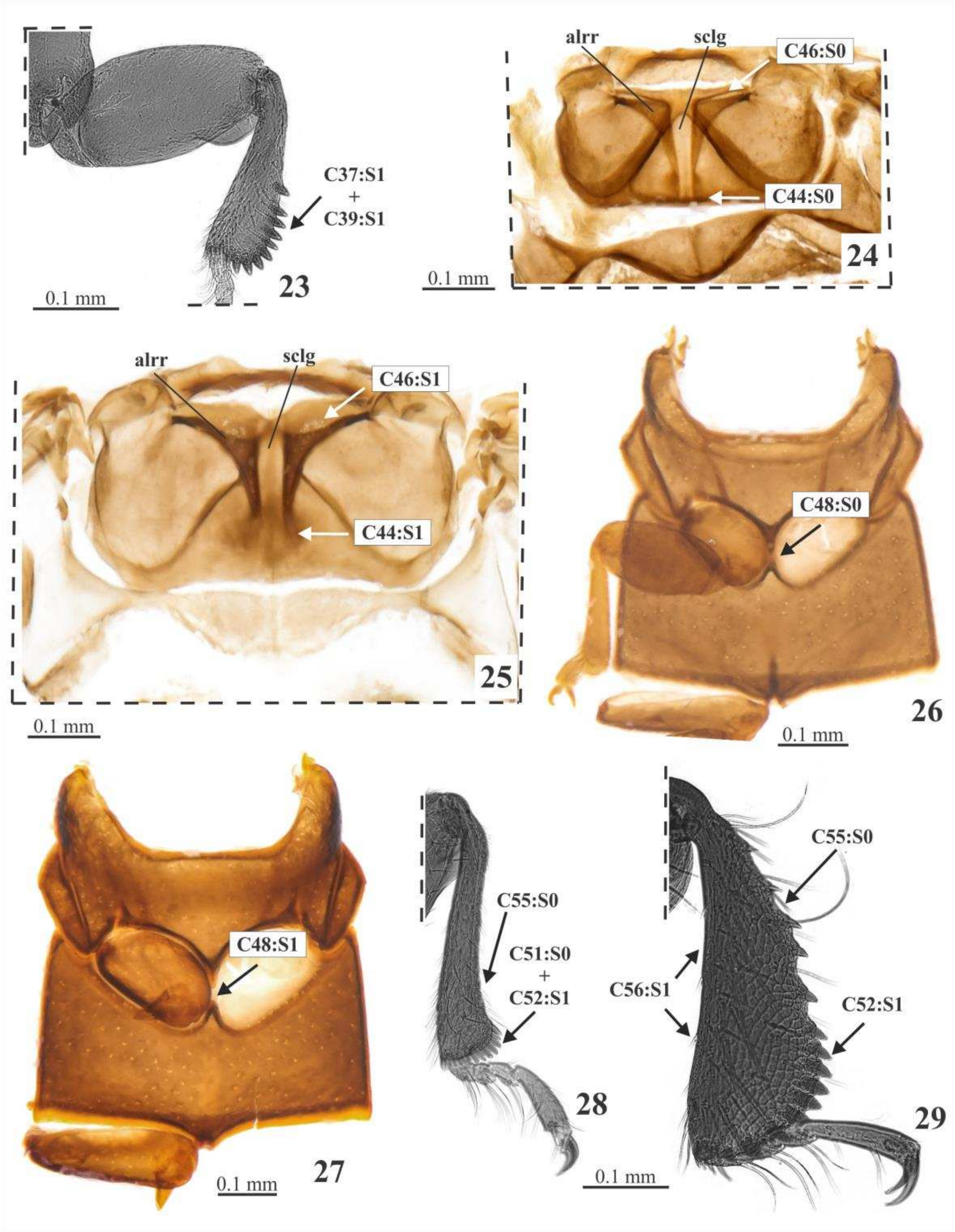


Figures 11–16. Images showing part of the morphological features included in our data matrix. “C” and “S” preceding numbers refer to character and its state, respectively. **11.** *Scolytocis furieriae* Lopes-Andrade, mouth parts. **12.** Ventral view of prothorax of *Ceracis californicus* (Casey). **13.** Ventral view of prothorax of *Cis boleti* (Scopoli). **14.** Ventral view of prothorax of *Euxestocis bicornutus* Miyatake. **15.** Ventral view of prothorax of *Porculus grossus* Lawrence. **16.** Ventral view showing pronotum, head, prosternum, procoxae and surroundings of *Cer. californicus*.



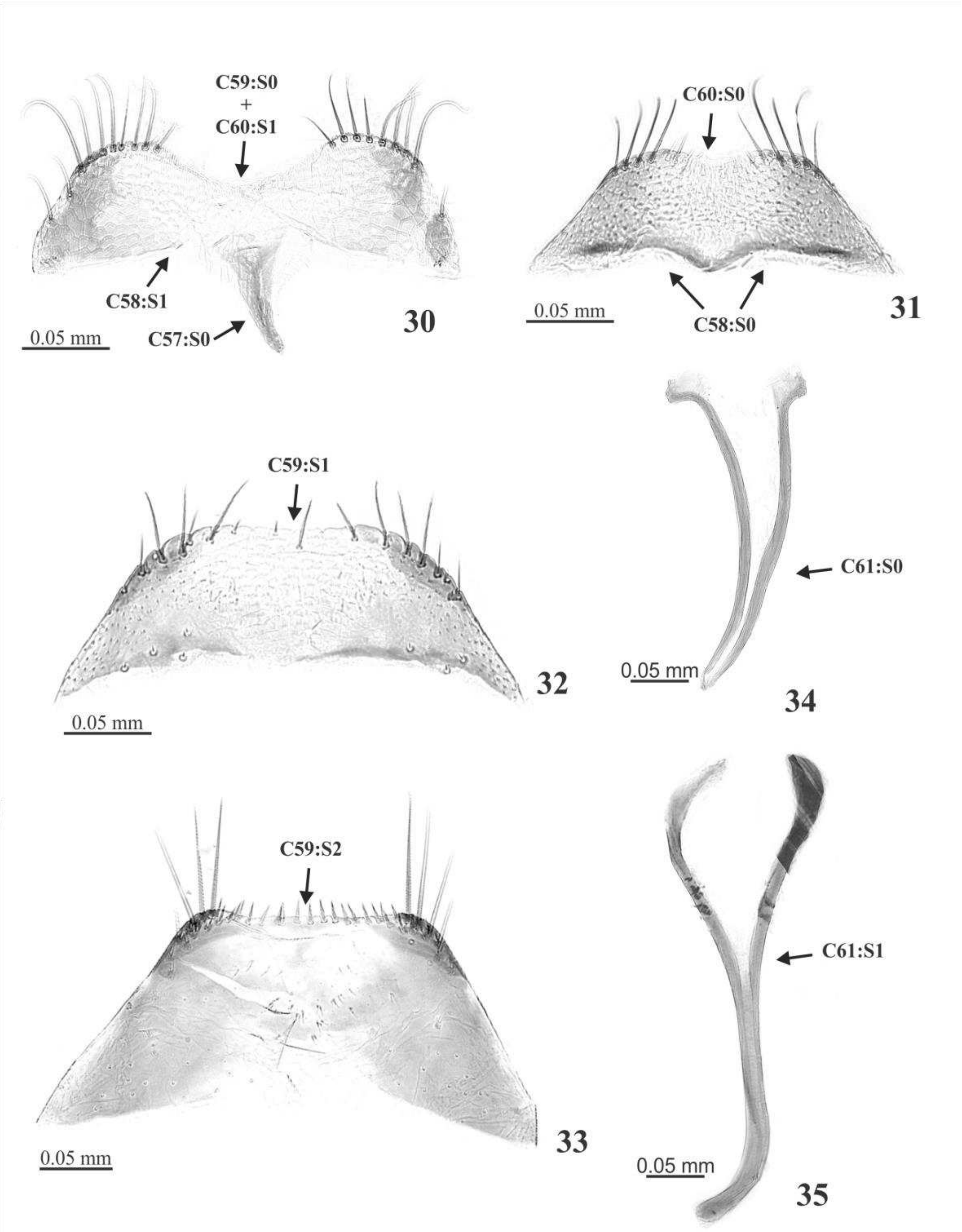
Figures 17–22. Images showing part of the morphological features included in our data matrix. “C” and “S” preceding numbers refer to character and its state, respectively. **17.** Ventral view showing pronotum, head, prosternum, procoxae and surroundings of *Falsocis brasiliensis* Lopes-Andrade. **18.** *Ceracis cornifer* (Mellié), foreleg. **19.** *Ceracis californicus* (Casey), foreleg. **20.** *Euxestocis bicornutus* Miyatake, foreleg. **21.**

Phellinocis romualdoi Lopes-Andrade & Lawrence, foreleg. **22.** *Ceracis limai* Lopes-Andrade *et al.*, foreleg.



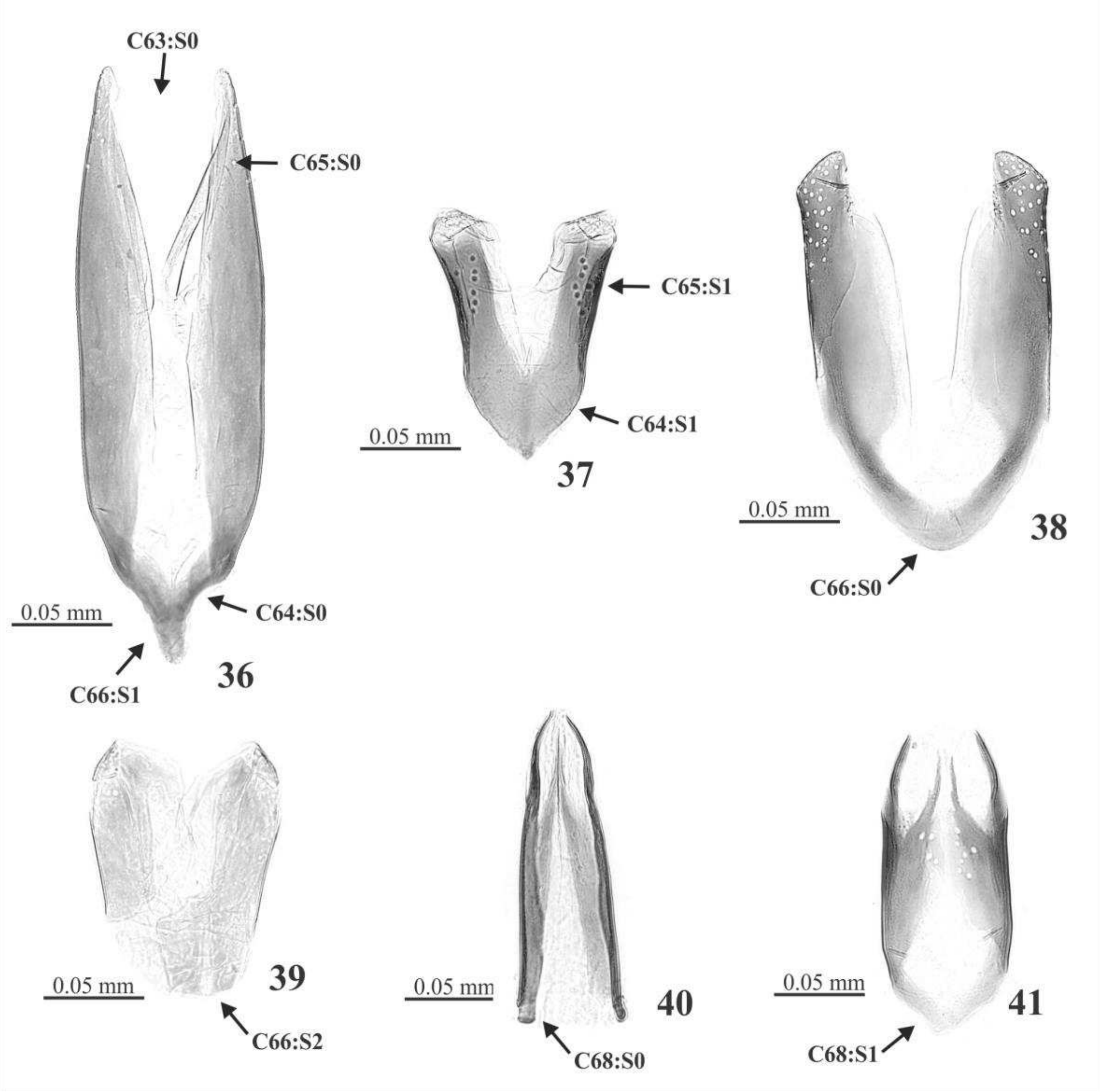
Figures 23–29. Images showing part of the morphological features included in our data matrix. "C" and "S" preceding numbers refer to character and its state, respectively. **23.**

Ceracis palaceps Zimmerman, foreleg. **24.** *Ceracis cornifer* (Mellié), metanotum (alrr = alar ridge of metascutellum, sclg = scutellar groove). **25.** *Ceracis californicus* (Casey), metanotum. **26.** *Ceracis furcifer* Mellié, metaventrite. **27.** *Ceracis multipunctatus* (Mellié), metaventrite. **28.** *Ceracis limai* Lopes-Andrade *et al.*, mesotibia. **29.** *Scolytocis furieriae* Lopes-Andrade, mesotibia.

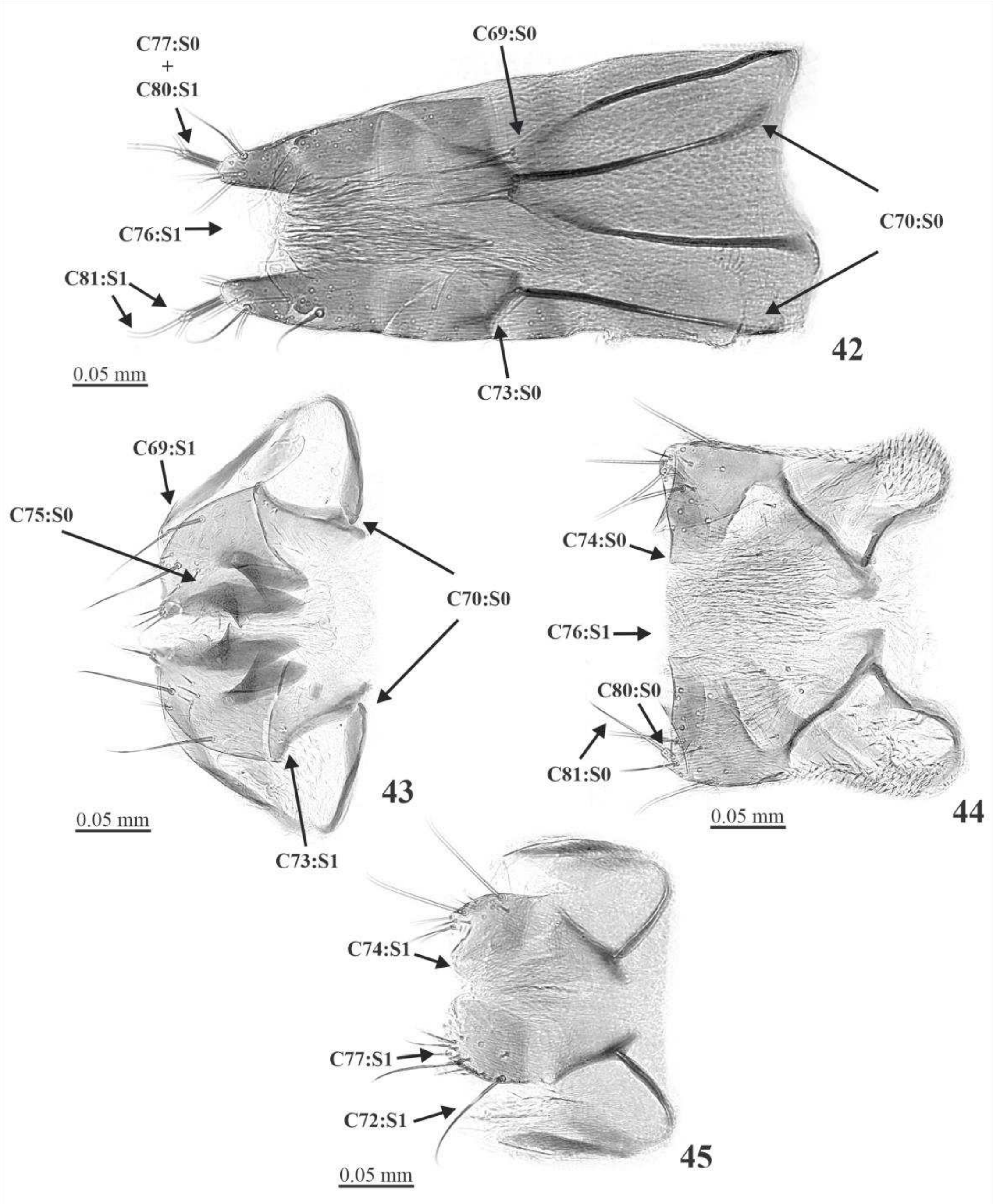


Figures 30–35. Images showing part of the morphological features included in our data matrix. “C” and “S” preceding numbers refer to character and its state, respectively. **30.** *Octotemnus glabriculus* (Gyllenhal), male sternite VIII. **31.** *Ceracis zarathustrai* Pecci-Maddalena *et al.*, male sternite VIII. **32.** *Paratrichapus fultoni,* male sternite VIII. **33.** *Falsocis brasiliensis* Lopes-Andrade, male sternite VIII. **34.** Part of male segment IX of

Malacocis farleyi Araujo & Lopes-Andrade i.l., male segment IX. **35.** Part of male segment IX of *Scolytocis furieriae* Lopes-Andrade.



Figures 36–41. Images showing part of the morphological features included in our data matrix. “C” and “S” preceding numbers refer to character and its state, respectively. **36.** *Ceracis cucullatus* (Mellié), tegmen. **37.** *Ceracis cornifer* (Mellié), tegmen. **38.** *Ceracis nigropunctatus* Lawrence, tegmen. **39.** *Alcecis particularis* (Pic) i.l., tegmen. **40.** *Ceracis californicus* (Casey), penis. **41.** *Ceracis nigropunctatus*, penis.



Figures 42–45. Images showing part of the morphological features included in our data matrix. "C" and "S" preceding numbers refer to character and its state, respectively. **42.** *Ennearthron victori* Lopes-Andrade & Zacaro, ovipositor. **43.** *Ceracis multipunctatus* (Mellié), ovipositor. **44.** *Ceracis californicus* (Casey), ovipositor. **45.** *Ceracis thoracicornis* (Ziegler), ovipositor.

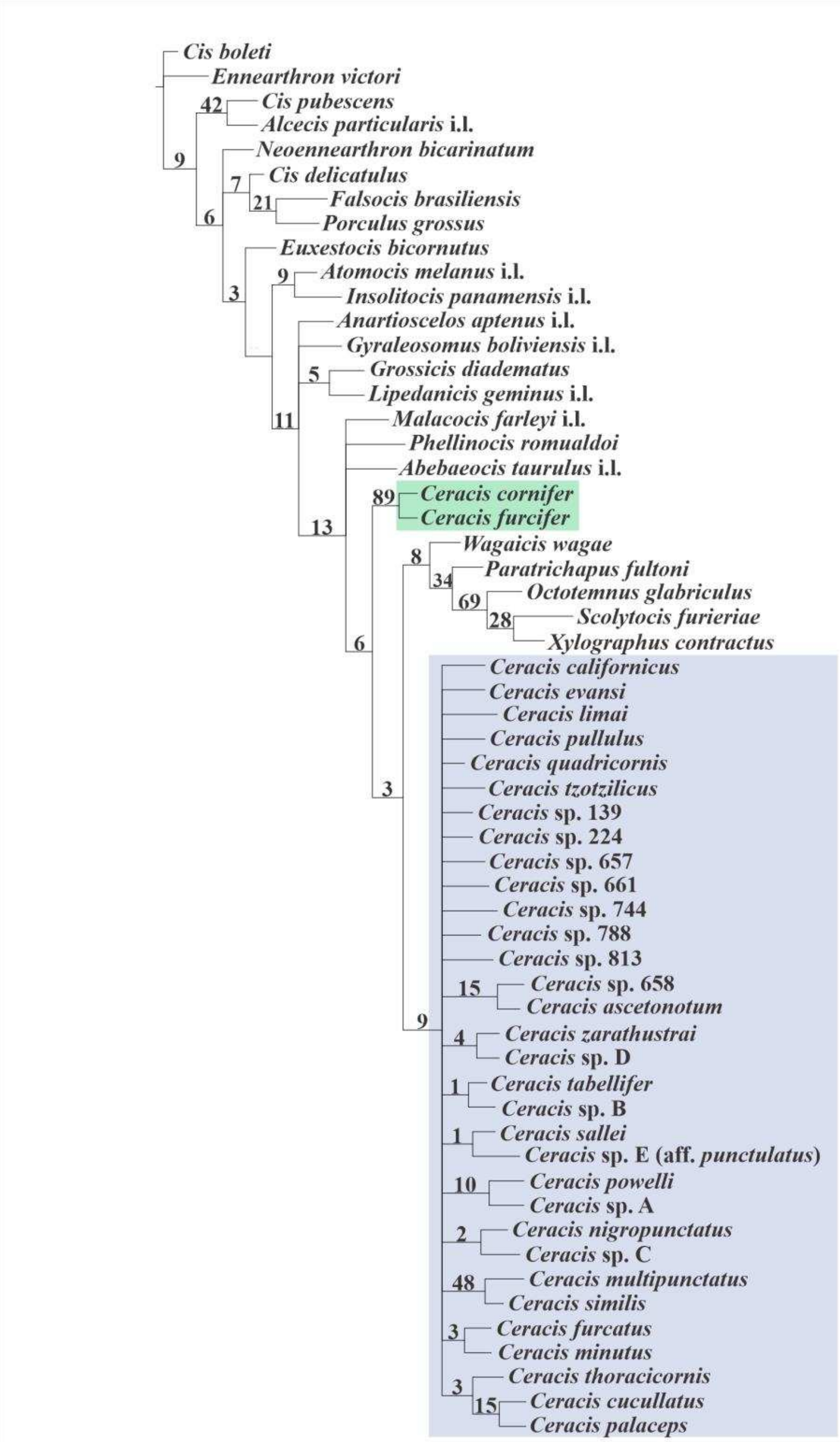


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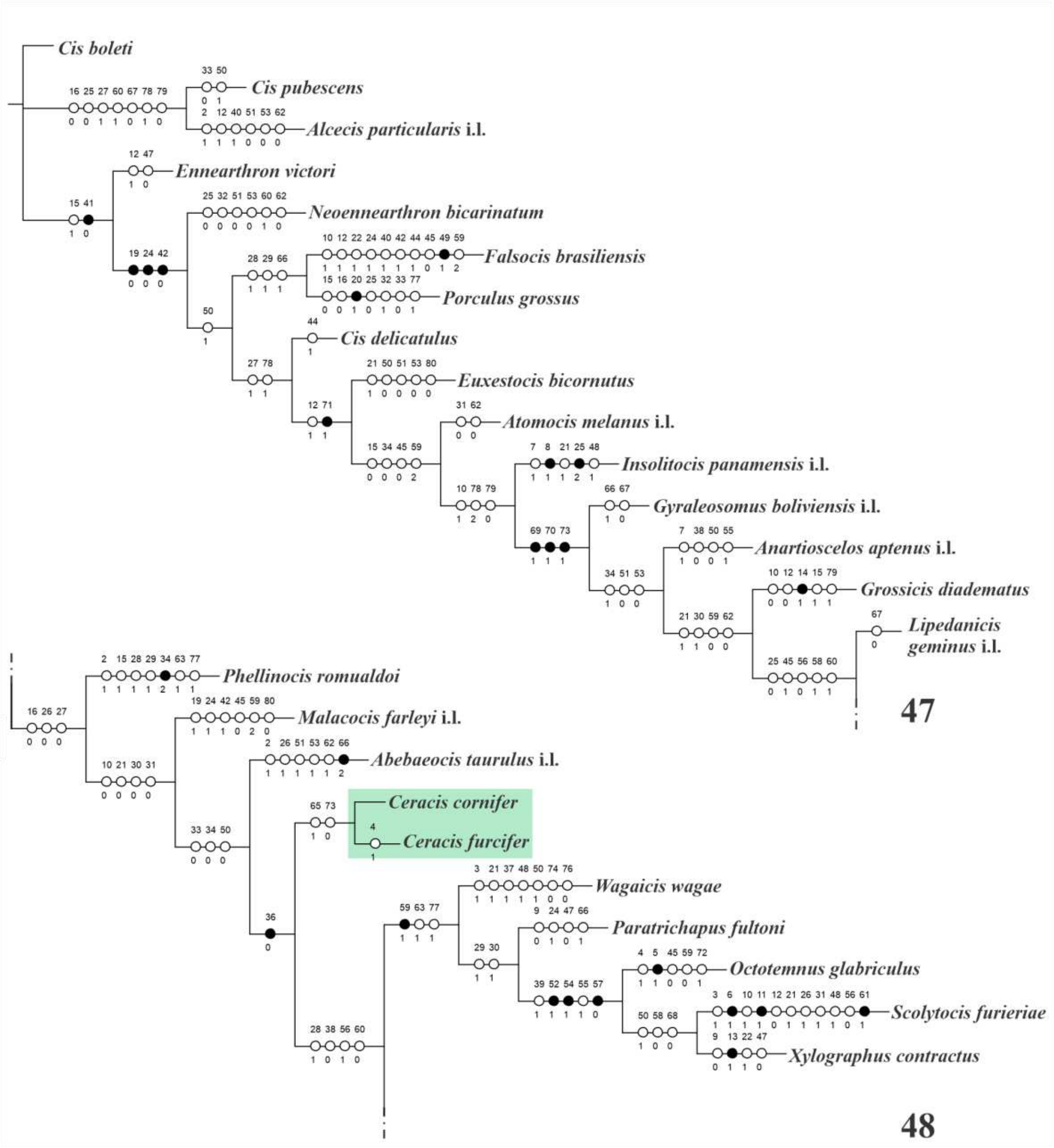
Figure 46. Strict consensus tree derived from the parsimony analysis with implied weights. Node values indicate the frequency of GC groups derived from symmetric resampling. Unsupported clades are collapsed. Colors represent important clades: green = *furcifer*-group, blue = *Ceracis* Mellié sensu stricto (excluding the *furcifer*-group).



Figures 47–48. Parts of the tree derived from the parsimony analysis with implied weights. **47.** First part. **48.** Second part. Only unambiguously characters are shown. Autapomorphies and nonhomoplasious synapomorphies are indicated by closed circles and homoplasious synapomorphies by open circles. Character number is above and the corresponding state below each circle. The *furcifer*-group is marked in green.

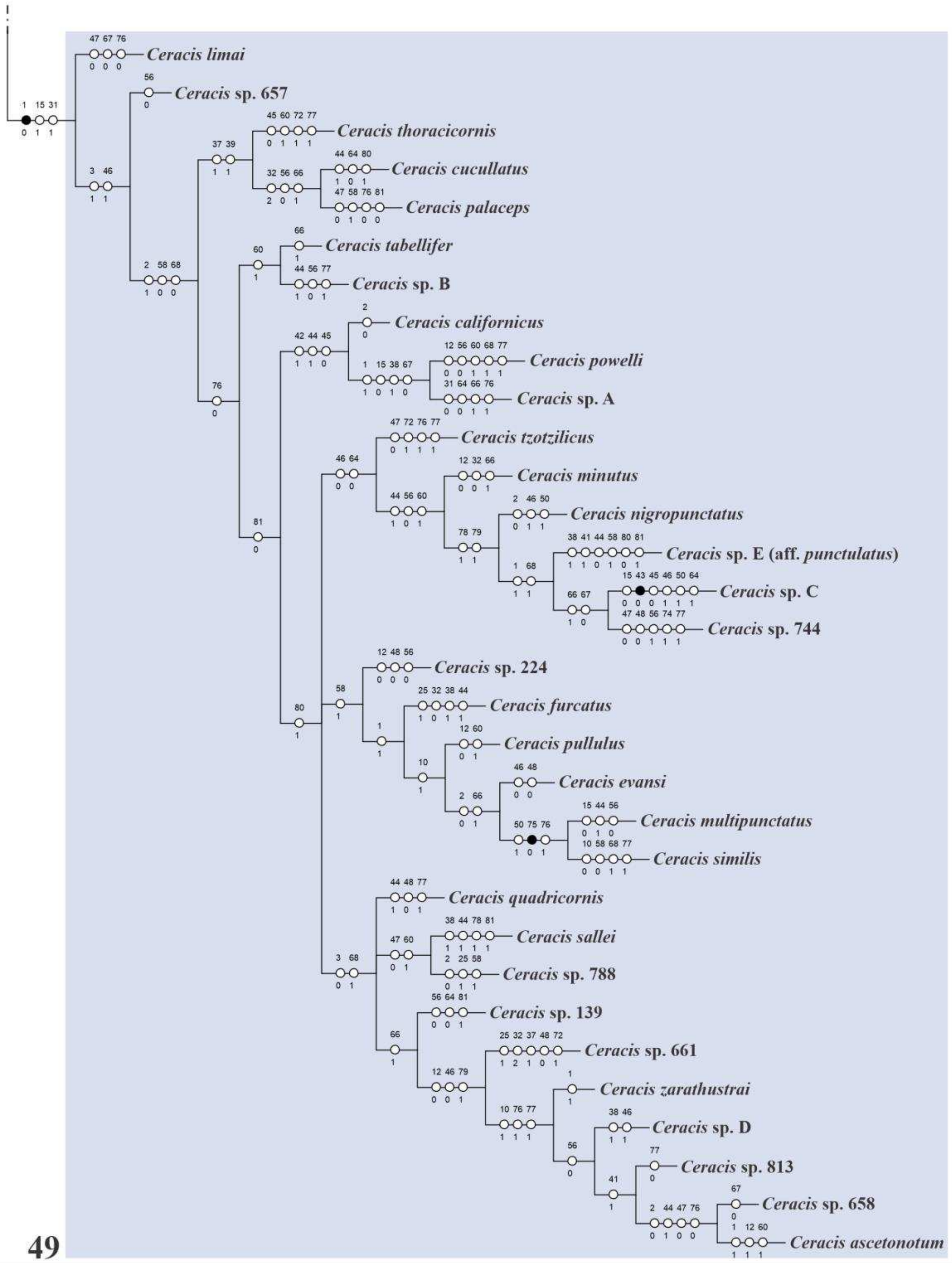


Figure 49. Last part of the tree derived from the parsimony analysis with implied weights. Only unambiguously characters are shown. Autapomorphies and nonhomoplasious synapomorphies are indicated by closed circles and homoplasious synapomorphies by open circles. Character number is above and the corresponding state

below each circle. The genus *Ceracis* Mellié stricto sensu (excluding the *furcifer*-group) is marked in blue.

SUPPORTING INFORMATION

Appendix S1. Character matrix. Inapplicable characters are indicated by "–"; missing data are indicated by "?"

Taxon / Character									1										2										3										4								
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Cis boleti	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	2	1	1	-	1	-	1	–	0	1	1	1	1	0	0	1	0
Cis delicatulus	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	2	1	0	0	1	1	2	1	1	-	1	-	1	–	0	0	0	1	1	1	0	1	1
Cis pubescens	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	1	0	0	0	0	1	0	1	1	0	0	0	1	2	0	1	-	1	-	1	–	0	1	1	1	1	1	0	1	1
Ennearthron victori	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	1	2	1	1	-	1	-	1	–	0	0	1	1	0	1	0	0	1
Euxestocis bicornutus	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	2	1	0	0	0	1	2	1	1	-	1	-	1	–	0	0	0	1	0	1	0	1	0
Falsocis brasiliensis	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	1	-	1	1	0	0	1	1	1	1	2	1	1	-	1	-	1	–	1	-	1	1	1	0	0	1	1
Grossicis diadematus	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	1	2	1	0	0	1	1	2	1	1	-	1	-	1	–	0	1	0	1	0	0	0	1	1
Malacocis farleyi i.l.	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	–	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	1	1	-	1	-	1	–	0	0	1	1	1	0	0	1	1
Neoennearthron bicarinatum	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1	-	1	-	1	–	0	0	0	1	0	1	0	1	0
Octotemnus glabriculus	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	1	1	1	0	2	0	0	1	0	0	0	1	1	-	1	1	1	0	0	1	0
Paratrichapus fultoni	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	–	0	0	0	0	0	0	1	1	0	0	1	1	1	0	2	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0
Phellinocis romualdoi	1	1	–	0	0	0	0	0	1	1	0	1	0	0	1	0	–	0	0	0	1	0	0	0	–	0	0	1	1	1	1	2	1	2	-	1	-	1	–	0	0	0	1	1	1	0	1	1
Porculus grossus	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	1	–	0	0	0	0	0	0	1	1	1	1	1	0	1	-	1	-	1	–	0	1	0	1	0	1	0	1	1
Scolytocis furieriae	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0	–	0	0	0	1	0	0	0	0	1	0	1	1	1	1	2	0	0	1	0	0	0	1	0	0	0	1	1	1	0	1	1
Wagaicis wagae	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	0	1	1
Xylographus contractus	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	–	0	0	0	0	1	-	0	0	0	0	1	1	1	0	2	0	0	1	0	0	0	1	1	-	0	1	0	1	0	0	0
Abebaeocis taurulus i.l.	1	1	–	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	-	1	–	0	0	0	1	0	1	0	1	0
Alcecis particularis i.l.	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	–	0	1	0	0	0	0	1	0	1	1	0	0	0	1	2	1	1	-	1	-	1	–	1	-	1	1	0	1	0	1	0
Anartioscelos aptenus i.l.	1	0	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	2	1	0	0	0	1	2	0	1	-	1	-	0	1	0	0	0	1	1	0	0	1	0
Atomocis melanus	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	2	1	0	0	0	0	2	0	0	1	1	-	1	–	0	0	0	1	0	0	0	0	0
Gyraleosomus boliviensis	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	–	0	1	0	0	0	0	0	1	2	1	0	0	0	1	2	1	0	1	1	-	1	–	0	1	0	1	1	0	0	1	0
Insolitocis panamensis i.l.	1	0	0	0	0	0	1	1	1	1	0	1	0	0	?	0	–	0	1	0	1	0	0	0	2	2	1	0	0	0	1	2	0	0	1	1	-	1	–	0	0	0	1	0	0	0	0	1
Lipedanicis geminus i.l.	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	2	1	0	0	1	1	2	1	1	-	1	-	1	–	0	1	0	1	0	1	0	1	0
Ceracis ascetonotum	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1
Ceracis californicus	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0
Ceracis cornifer	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	–	0	0	0	1	0	1	0	1	0
Ceracis cucullatus	0	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1	1
Ceracis evansi	1	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Ceracis furcatus	1	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	–	0	0	0	1	1	1	1	1	1

Caracis furcifer	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	–	0	0	0	1	0	1	0	1	0
Ceracis limai	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Ceracis minutus	0	1	–	0	0	0	0	0	1	0	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1
Ceracis multipunctatus	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1
Ceracis nigropunctatus	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Ceracis palaceps	0	1	–	0	0	0	0	0	1	0	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	1
Ceracis powelli	1	1	–	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	1	–	0	0	1	1	1	0	1	1	0
Ceracis pullulus	1	1	–	0	0	0	0	0	1	1	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1

Taxon / Character									1										2										3										4								
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Ceracis quadricornis	0	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
Ceracis sallei	0	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	–	0	0	0	1	1	1	1	0	1
Ceracis similis	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
Ceracis tabellifer	0	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1
Ceracis thoracicornis	0	1	–	0	0	0	0	0	1	0	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	0
Ceracis tzotzilicu	0	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1
Ceracis zarathustrai	1	1	–	0	0	0	0	0	1	1	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1
Ceracis sp. A	1	1	–	0	0	0	0	0	1	0	0	1	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	–	0	0	1	1	1	0	1	1	1
Ceracis sp. B	0	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Ceracis sp. C	1	1	–	0	0	0	0	0	1	0	0	1	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Ceracis sp. D	0	1	–	0	0	0	0	0	1	1	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	–	0	0	0	1	0	1	1	1	1
Ceracis sp. E (aff. *punctulatus*)	1	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	–	0	1	0	1	0	1	0	1	1
Ceracis sp. 139	0	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1
Ceracis sp. 224	0	1	–	0	0	0	0	0	1	0	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0
Ceracis sp. 657	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0
Ceracis sp. 658	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Ceracis sp. 661	0	1	–	0	0	0	0	0	1	0	0	0	0	0	1	0	–	0	0	0	0	0	1	0	0	0	0	1	0	0	1	2	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0
Ceracis sp. 744	1	1	–	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Caracis sp. 788	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	–	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
Ceracis sp. 813	0	1	–	0	0	0	0	0	1	1	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0

Taxon / Character	4	5										6										7										8	
	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
Cis boleti	0	0	1	–	1	–	0	1	1	0	0	0	0	1	0	–	0	0	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1
Cis delicatulus	0	1	1	–	1	–	0	0	1	1	0	0	0	1	0	–	1	0	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1
Cis pubescens	0	1	1	–	1	–	0	1	1	1	0	1	0	1	0	–	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	1	1
Ennearthron victori	0	0	1	–	1	–	0	1	1	0	0	0	0	1	0	–	0	0	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1
Euxestocis bicornutus	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	–	1	0	1	1	0	0	1	0	0	1	1	1	0	1	1	0	1
Falsocis brasiliensis	1	1	1	–	1	–	0	1	1	1	2	–	0	1	0	–	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1
Grossicis diadematus	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	–	0	0	1	1	1	1	1	0	1	1	1	1	0	2	1	1	1
Malacocis farleyi i.l.	0	1	0	0	0	0	0	0	1	1	2	–	0	0	0	–	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1
Neoennearthron bicarinatum	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	–	0	0	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1
Octotemnus glabriculus	0	0	0	1	0	1	1	1	0	1	0	0	0	0	1	–	0	0	1	1	1	1	1	1	1	1	1	1	1	–	–	–	–
Paratrichapus fultoni	0	0	0	0	0	0	0	1	1	1	1	–	0	0	1	–	0	1	1	1	1	1	1	0	1	1	1	1	1	–	–	–	–
Phellinocis romualdoi	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	–	0	0	1	1	1	1	1	0	1	1	1	1	1	–	–	–	–
Porculus grossus	0	1	1	–	1	–	0	0	1	1	0	0	0	1	0	–	1	1	1	1	0	0	0	0	0	1	1	1	1	–	–	–	–
Scolytocis furieriae	0	1	0	1	0	1	1	0	0	0	1	–	1	0	1	–	0	0	1	0	1	1	1	0	1	1	1	1	1	–	–	–	–
Wagaicis wagae	0	1	0	0	0	0	0	1	1	1	1	–	0	0	1	–	0	0	1	1	1	1	1	0	1	0	1	0	1	–	–	–	–
Xylographus contractus	0	1	0	1	0	1	1	1	0	0	1	–	0	0	1	–	0	0	1	0	1	1	1	0	1	1	1	1	1	–	–	–	–
Abebaeocis taurulus i.l.	0	0	1	–	1	–	0	0	1	1	0	1	0	1	0	–	0	2	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1
Alcecis particularis i.l.	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	–	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	1	1
Anartioscelos aptenus i.l.	0	0	0	0	0	0	1	1	1	0	2	–	0	1	0	–	0	0	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1
Atomocis melanus	0	1	1	–	1	–	0	1	1	1	2	–	0	0	1	–	0	0	1	1	0	0	1	0	0	1	1	1	0	1	1	1	1
Gyraleosomus boliviensis	0	1	1	–	1	–	0	1	1	0	2	–	0	1	0	–	0	1	0	1	1	1	1	0	1	1	1	1	0	2	0	1	1
Insolitocis panamensis i.l.	0	1	1	–	1	–	0	0	?	?	?	?	?	1	?	?	?	?	?	?	0	0	1	0	0	1	1	1	0	2	0	1	1
Lipedanicis geminus i.l.	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	–	0	1	0	1	1	1	1	0	1	1	1	1	0	0	0	1	1
Ceracis ascetonotum	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	1	1	1	1	0	1	0	1	0	1	–	–	–	–
Ceracis californicus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	1	0	0	0	0	0	0
Ceracis cornifer	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	1	1
Ceracis cucullatus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	1	1
Ceracis evansi	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	0	1	0	1	0	0	0	0	1	0
Ceracis furcatus	0	0	0	0	0	0	0	1	1	?	?	?	0	0	?	?	?	?	?	?	1	1	1	0	1	0	1	0	0	0	0	1	0
Caracis furcifer	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	1	1
Ceracis limais	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1
Ceracis minutus	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	1	0	1	0	0	0	0	1	0
Ceracis multipunctatus	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	0	1	0	0	1	0	0	0	1	1
Ceracis nigropunctatus	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1	0	0	1	1	1	0
Ceracis palaceps	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0	0

Ceracis powelli	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	0	1	–	–	–	–
Ceracis pullulus	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	1	0	1	1	1	0	1	0	1	0	0	0	0	1	0
Ceracis quadricornis	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	1	0	1	–	–	–	–
Ceracis sallei	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	1	1	0	1	0	1	0	0	1	0	1	1
Ceracis similis	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	0	1	1	–	–	–	–
Ceracis tabellifer	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0	1
Ceracis thoracicornis	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	–	–	–	–
Ceracis tzotzilicus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	1	–	–	–	–

Taxon / Character	4	5										6										7										8	
	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
Ceracis sp. C	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	1	0	1	0	0	1	1	1	0
Ceracis sp. D	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	1	1	1	–	–	–	–
Ceracis sp. E (aff. *punctulatus*)	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	1	1	0	1
Ceracis sp. 139	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1
Ceracis sp. 224	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	1	0	0	0	0	1	0
Ceracis sp. 657	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1
Ceracis sp. 658	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	1	1	0	1	0	1	0	1	–	–	–	–
Ceracis sp. 661	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0	1	1	0
Ceracis sp. 744	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0	1	–	–	–	–
Caracis sp. 788	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	1	1	1	1	1	0	1	0	?	0	0	0	0	1	0
Ceracis sp. 813	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0

Appendix S2. Output file from equal weights (EW) analysis.

```
Reading from
C:\Users\Igor\Desktop\Tese\Programs\TNT\Matriz_Ceracis_20vii2020.tnt
Matrix (81x57, 16 states). Memory required for data:   0.16 Mbytes

Space for 2000000 trees in memory
Random seed is 0
0 trees in memory
Random seed is 0
Repl. Algor.     Tree        Score       Best Score   Time       Rearrangs.
1000  TBR   130243 of 130244 ------      429         0:12:46    19,084,541,680
Completed 1000 random addition sequences.
Total rearrangements examined: 19,084,541,680.
Best score hit 177 times out of 1000.
Best score (TBR): 429.  874 trees retained.
Time 766.57 secs.

Suboptimal 1.000 x 0.000
Space for 3000 trees in memory
Start swapping from 810 trees (score 429-430)...
Repl. Algor.     Tree        Score       Best Score   Time       Rearrangs.
---   TBR       36 of 3000   ------       429         0:00:00    2,306,608
Completed TBR branch-swapping.
Total rearrangements examined: 2,306,608.
Maxtrees was reached when swapping tree 36.  Didn't swap tree(s) 37-2999.
Note: some trees of different length are identical as collapsed. Discarded.
Best score (TBR): 429-430.  2995 trees found.
Time 0.47 secs.
2995 trees condensed (when min. branch length = 0)
2982 trees retained
Time 0.41 secs.

Suboptimal 2.000 x 0.000
Space for 6000 trees in memory
 Start swapping from 2563 trees (score 429-431)...
Repl. Algor.     Tree        Score       Best Score   Time       Rearrangs.
---   TBR       13 of 6000   ------       429         0:00:00    876,413
Completed TBR branch-swapping.
Total rearrangements examined: 876,413.
Maxtrees was reached when swapping tree 13.  Didn't swap tree(s) 14-5999.
Note: some trees of different length are identical as collapsed. Discarded.
Best score (TBR): 429-431.  5973 trees found.
Time 0.66 secs.
5973 trees condensed (when min. branch length = 0)
5956 trees retained
Time 1.06 secs.
```

```
Suboptimal 3.000 x 0.000
Space for 9000 trees in memory
Start swapping from 5114 trees (score 429-432)...
Repl. Algor.     Tree        Score       Best Score   Time       Rearrangs.
---   TBR        5 of 9000   ------      429          0:00:00    358,418
Completed TBR branch-swapping.
Total rearrangements examined: 358,418.
Maxtrees was reached when swapping tree 5.  Didn't swap tree(s) 6-8999.
Note: some trees of different length are identical as collapsed. Discarded.
Best score (TBR): 429-432.  8946 trees found.
Time 1.08 secs.
8946 trees condensed (when min. branch length = 0)
8926 trees retained
Time 2.09 secs.

Suboptimal 4.000 x 0.000
Space for 12000 trees in memory
Start swapping from 7748 trees (score 429-433)...
Repl. Algor.     Tree        Score       Best Score   Time       Rearrangs.
---   TBR        2 of 12000  ------      429          0:00:00    179,501
Completed TBR branch-swapping.
Total rearrangements examined: 179,501.
Maxtrees was reached when swapping tree 2.  Didn't swap tree(s) 3-11999.
Note: some trees of different length are identical as collapsed. Discarded.
Best score (TBR): 429-433.  11870 trees found.
Time 1.87 secs.
11870 trees condensed (when min. branch length = 0)
11837 trees retained
Time 3.42 secs.

Suboptimal 5.000 x 0.000
Space for 15000 trees in memory
Start swapping from 10332 trees (score 429-434)...
Repl. Algor.     Tree        Score       Best Score   Time       Rearrangs.
---   TBR        1 of 15000  ------      429          0:00:00    120,454
Completed TBR branch-swapping.
Total rearrangements examined: 120,454.
Maxtrees was reached when swapping tree 1.  Didn't swap tree(s) 2-14999.
Note: some trees of different length are identical as collapsed. Discarded.
Best score (TBR): 429-434.  14856 trees found.
Time 2.65 secs.
14856 trees condensed (when min. branch length = 0)
14811 trees retained
Time 5.16 secs.

Note: for consensus calculation, trees will be
temporarily collapsed (when min. branch length = 0)
Note: fastest algorithm used to calculate supports (only trees within absolute support)
Copied legends: "Relative bremer supports (from 14811 trees, cut 0)"
```

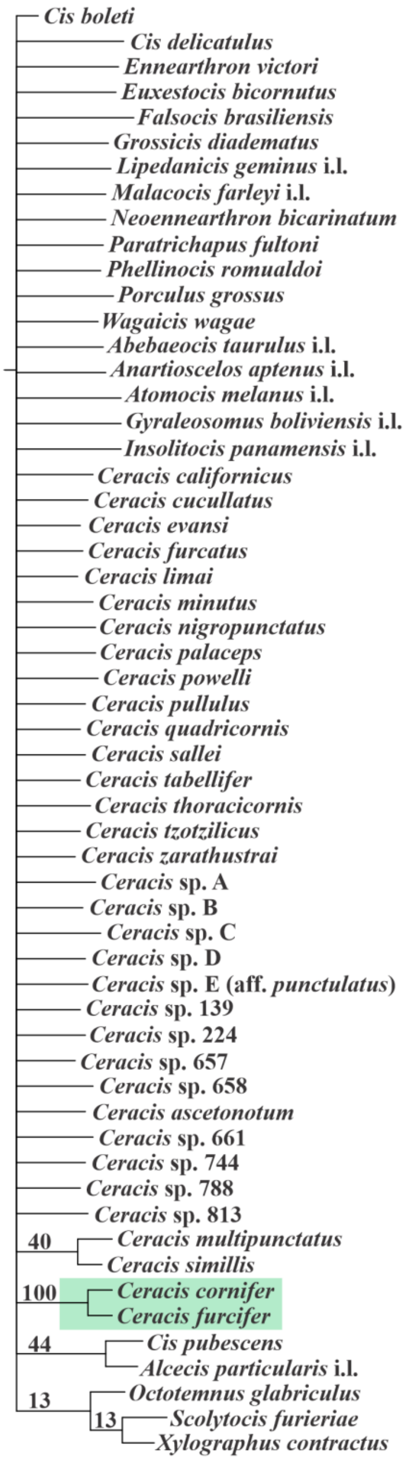
```
Time 26.04 secs.
```

Appendix S3. Output file from implied weights (IW) analysis.

```
Reading from
C:\Users\Igor\Desktop\Tese\Programs\TNT\Matriz_Ceracis_20vii2020.tnt
Matrix (81x57, 16 states). Memory required for data:   0.16 Mbytes

Random seed is 0
Implied Weighting is ON
Weighting strength is 23.80400
Space for 2000000 trees in memory
0 trees in memory
Random seed is 0
Repl. Algor.     Tree        Score       Best Score   Time       Rearrangs.
40000 TBR    55862 of 55863  ------      10.76588     0:13:40    12,399,669,324
Completed 40000 random addition sequences.
Total rearrangements examined: 12,399,669,324.
Best score hit 141 times out of 40000.
Best score (TBR): 10.76588.  1 trees retained.
Time 820.67 secs.

Space for 20000 trees in memory
Auto-collapse searches is OFF
Copied legends: "GC values, 5000 replicates, cut=1 (tree 0) - Symmetric Resampling
(P=33)"
Average group support: 10.8
368.58 secs. to complete resampling
```



S4

Appendix S4. Strict consensus tree derived from the parsimony analysis with equal weights. Node values represent Bremer support. Unsupported clades are collapsed. Colors represent important clades: green = *furcifer*-group.

CONCLUSÕES GERAIS

O atual trabalho buscou ampliar o conhecimento sobre a fauna de besouros ciídeos da região Neotropical, bem como compreender as relações sub- e supragenéricas de *Ceracis*. A partir da publicação dos resultados desta tese, a diversidade de Ciidae contará com um aumento de 13 espécies e sete gêneros novos, sendo duas as espécies de *Ceracis* já descritas e publicadas durante a elaboração da tese (*Cer. tzotzilicus* Souza-Gonçalves & Lopes-Andrade, 2020 e *Cer. ascetonotum* Souza-Gonçalves & Lopes-Andrade, 2020). Com isso, Ciidae passará a ter 58 gêneros e 770 espécies. O número de espécies em *Ceracis* após a publicação de toda tese passará para 50 espécies, sendo que: i) com a publicação do primeiro capítulo, das 52 espécies previamente incluídas no gênero, quatro serão transferidas para novos gêneros (*Cer. bifurcus* e *Cer. laticornis* para *Anartioscelos* i.l., *Cer. particularis* para *Alcecis* i.l., e *Cer. taurulus* para *Abebaeocis* i.l.); e ii) nos capítulos II e III foram descritas duas novas espécies, *Cer. tzotzilicus* e *Cer. ascetonotum*, respectivamente. Na região Neotropical, a diversidade de Ciidae passará de 158 espécies e 14 gêneros para 171 espécies e 21 gêneros. A fauna Neotropical de *Ceracis* continuará sendo a mais diversa com 32 espécies descritas, seguida pela região Neártica com 20 espécies, destacando que esta contagem não leva em conta somente as espécies exclusivas da fauna de cada região. Vale ressaltar que há ainda cerca de 40 morfoespéies de *Ceracis* da região Neotropical já reconhecidas em coleções, o que nos próximos anos irá mais do que dobrar o número de espécies do gênero conhecidas no neotrópico.

Os resultados provenientes deste trabalho fornecem evidências de que *Paratrichapus*, *Octotemnus* e *Xylographus* (Orophiini), *Scolytocis* (Xylographellini) e *Wagaicis* (Ciini) são as linhagens supostamente mais próximas à *Ceracis*. Estes táxons formaram um clado que, apesar de ter tido um baixo suporte, é sustentado por quatro sinapomorfias: processo prosternal laminado, presença de espinhos na margem externa da protíbia, cerdas alcançando mais do que 1/3 da face interna da tíbia e margem posterior do esternito VIII em machos com uma emarginação rasa. Todo esse clado, (*Ceracis* + (*Wagaicis* + (*Paratrichapus* + (*Octotemnus* + (*Scolytocis* + *Xylographus*))))), é irmão do grupo *furcifer* (o qual é monofilético e precisa ser transferido para um novo gênero), sendo sustentados por uma única sinapomorfia, a presença de espinhos no ângulo externo apical da protíbia.

Dentre as linhagens supostamente mais próximas à *Ceracis*, *Paratrichapus* está distribuído pelas regiões Australiana e Oriental (SOUZA-GONÇALVES *et al.*, 2019); já *Octotemnus* tem distribuição nas regiões Neártica, Paleártica, Oriental e Australiana (LAWRENCE, 2016); *Wagaicis* é restrito à região Paleártica (LOHSE, 1964; LÖBL & SMETANA, 2008); *Scolytocis* ocorre nas regiões Neotropical, Oriental e Australiana (LOPES-ANDRADE, 2008b; SOUZA-GONÇALVES & LOPES-ANDRADE, 2017); enquanto que *Xylographus* ocorre nas regiões Neotropical, Etíope, Paleártica, Oriental e Australiana (SANDOVAL-GÓMEZ *et al.*, 2014; LAWRENCE, 2016). Considerando a distribuição geográfica dessas linhagens supostamente mais próximas e de *Ceracis*, as seguintes hipóteses biogeográficas podem ser propostas: i) uma origem Gondwana Tropical (Holotrópica) para *Ceracis*; ii) uma subsequente expansão da fauna Neotropical para região Neártica; iii) uma subsequente expansão da fauna Oriental para a fauna Australiana. Lawrence (1967) já havia sugerido que as espécies da Ámerica do Norte tinham origem Neotropical e que as espécies da região Oriental não parecem estar relacionadas às espécies do Novo Mundo.

Neste trabalho tivemos acesso e incluímos nas análises espécies de *Ceracis* de praticamente todas as regiões biogeográficas de ocorrência do gênero, com exceção da região Australiana e das espécies da região Paleártica. Nos próximos trabalhos, seria intessante incluir espécies dessas duas regiões, preenchendo a lacuna que ainda existe nas relações das espécies dessas faunas com as demais do gênero *Ceracis*. Além disso, há estruturas que precisam ser examinadas com mais cautela e riqueza de detalhes, como por exemplo: epi- e hipofaringe; base alar e escleritos alares; pontuação pronotal e elitral, sob microscopia eletrônica; endoesqueleto e musculatura, sob microtomografia. Estas estruturas não puderam ser analisadas com maior clareza e resolução, devido ao diminuto tamanho dos espécimes e principalmente à falta de acesso a equipamentos que fornecessem imagens mais detalhadas.

A partir de um trabalho incluindo espécies das regiões biogeográficas não examinadas neste estudo, analisando mais detalhadamente as estruturas citadas acima e buscando por mais caracteres a partir das mesmas, será possível avançar na resolução das relações supra- e subgenéricas de *Ceracis*. Entretanto, esta tese cumpre com seu objetivo em contribuir para expansão do conhecimento das relações sub- e supragenéricas de *Ceracis* e também no conhecimento de Ciidae da região Neotropical.

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