CAIO ANTUNES DE CARVALHO

TAXONOMIA DE *Ceracis cucullatus* (MELLIÉ) (COLEOPTERA, CIIDAE): OCORRÊNCIA, FUNGOS HOSPEDEIROS E *STATUS* DE INVASOR

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Magister Scientiae*.

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APROVADA: 29 de fevereiro de 2012.

Adilson Ariza Zacaro

Paschoal Coelho Grossi

Cristiano Lopes Andrade
(Orientador)

Dedico este trabalho a todos aqueles que enxergam grandeza nas pequenas formas de vida animal

“Quando crianças, tememos a escuridão. O desconhecido nos perturba. Qualquer coisa pode estar lá fora. Ironicamente, é nosso destino viver no escuro. Parta da Terra na direção que quiser. E, depois de um flash inicial de azul, você está cercado pelo negrume. Pontuado aqui e ali, pelas estrelas distantes e fracas. Mesmo depois de crescidos, a escuridão ainda possui o poder de nos amedrontar. Então, há aqueles que dizem que não devemos investigar muito de perto quem mais pode estar vivendo nessa escuridão. Melhor não saber, dizem.

Há 400 bilhões de estrelas na Via Láctea, dessa imensa multidão será que nosso enfadonho Sol é a única com um planeta habitado? Talvez. Talvez a origem da vida, ou da inteligência, seja demasiadamente improvável. Ou, talvez civilizações ergam-se o tempo todo. Mas aniquilam a si mesmas assim que se tornam capazes. Ou, aqui e ali, salpicados pelo espaço, talvez haja mundos algo como o nosso. Nos quais outros seres olham para cima e se perguntam, como nós, quem mais vive na escuridão.

A vida é uma raridade em comparação. Você pode observar dúzias de mundos, e descobrir que em apenas um deles a vida surge, evolui e persiste. Se nós humanos um dia formos para esses mundos, será porque uma nação, ou um consórcio delas, acreditará ser de seu interesse, ou do interesse da espécie humana. Em nosso tempo, cruzamos o sistema solar e enviamos quatro espaçonaves às estrelas. Mas continuamos procurando por habitantes. A vida procura pela vida.”

Carl Sagan

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SUMÁRIO

RESUMO

CARVALHO, Caio Antunes de, M.Sc., Universidade Federal de Viçosa, fevereiro de 2012. **Taxonomia de *Ceracis cucullatus* (Mellié) (Coleoptera: Ciidae): ocorrência, fungos hospedeiros e *status* de invasor**. Orientador: Cristiano Lopes Andrade.

Ceracis cucullatus (Mellié, 1849) é uma espécie de Ciidae (Coleoptera: Tenebrionoidea), família cosmopolita de besouros micetobiontes que vivem associados à basidiomas de macrofungos poróides – utilizados por esses besouros como *habitat*, alimento e local de reprodução. *Ceracis cucullatus* foi descrito com base em espécimes coletados em Caiena (Guiana Francesa) e no Cabo da Boa Esperança (África do Sul). Essa espécie nomeia o grupo *cucullatus*, composto por *C. bicornis* (Mellié, 1849), *C. cucullatus*, *C. billamelatus* (Pic, 1916), *C. lamellatus* (Pic, 1939) e *C. tabellifer* (Mellié, 1849), sendo os três últimos nomes sinônimos juniores de *C. cucullatus*. Uma vez que *C. billamelatus* foi descrito de Madagascar, *C. lamellatus* do Brasil e *C. tabellifer* da África do Sul, a sinonímia dessas espécies com *C. cucullatus* fez com que esta fosse reconhecida como sendo de ampla distribuição. Os registros de ocorrência de populações nomeadas como *C. cucullatus* em áreas antes não colonizadas por essa espécie são antigos e têm crescido ao longo dos anos. Contudo, embora suas populações disjuntas venham sendo interpretadas como uma unidade taxonômica coesa, comparações prévias entre espécimes Neotropicais e Afrotropicais revelaram inconsistências na morfologia externa, incluindo a forma da terminália abdominal de machos, entre as populações, causando incerteza quanto a real unidade dessa espécie. Além disso, as sinonímias supracitadas envolvendo *C. cucullatus* desconsideraram a análise da morfologia da terminália abdominal de machos, o que torna essa junção tênue. O objetivo central deste trabalho é revisar *Ceracis cucullatus*, avaliando a conspecificidade dos biótipos que atualmente estão sob este nome. Nós comparamos a morfologia externa de populações de diversas localidades das regiões Neotropical, Afrotropical, Afrotemperada e Oriental. Como principais resultados, nós descrevemos duas espécies novas, redefinimos os limites do grupo *cucullatus* para incluí-las, revalidamos *C. lamellatus* e *C. tabellifer*, invalidamos a sinonímia de *C. bilamellatus* com *C. cucullatus*, e propomos *C. bilamellatus* como sinônimo júnior de *C. tabellifer*. Além disso, nós redescrevemos *C. cucullatus*, *C. lamellatus* e *C. tabellifer*, e fornecemos uma chave de identificação para as espécies do grupo, além de fotos da morfologia externa, em especial da terminália abdominal masculina das espécies tratadas neste estudo. Adicionalmente, e em face das mudanças taxonômicas propostas aqui, nós fornecemos um novo panorama para a distribuição das espécies e conduzimos uma ampla discussão sobre o *status* de invasor de *C. tabellifer* fora da região Neotropical e de *C. cucullatus* s. str. em Galápagos. Com base nas espécies de fungos hospedeiros e em registros históricos de *C. tabellifer* que são reunidos e apresentados nesse trabalho, nós discutimos as principais razões para o sucesso da invasão deste ciídeo na África, ilhas do Oceano Índico, Sul e Sudeste Asiático, e seu potencial impacto sobre faunas autóctones de Ciidae.

ABSTRACT

CARVALHO, Caio Antunes de, M.Sc., Universidade Federal de Viçosa, February, 2012. **Taxonomy of *Ceracis cucullatus* (Mellié) (Coleoptera: Ciidae): occurrence, host fungi and invader status**. Advisor: Cristiano Lopes Andrade.

Ceracis cucullatus (Mellié, 1849) is a species of Ciidae (Coleoptera: Tenebrionoidea), a cosmopolitan family of mycetobiont beetles that live and breed in polypore basidiomes. *Ceracis cucullatus* was described in 1849 based on specimens collected in Cayenne (French Guiana) and in Cape of Good Hope (South Africa). This species names the *cucullatus* group, which comprises *C. bicornis* (Mellié, 1849), *C. cucullatus*, *C. billamelatus* (Pic, 1916), *C. lamellatus* (Pic, 1939) e *C. tabellifer* (Mellié, 1849), the latter three names being synonymies of *C. cucullatus*. As *C. billamelatus* was described from Madagascar, *C. lamellatus* from Brazil and *C. tabellifer* from South Africa, their synonymization with *C. cucullatus* led it to be considered a widely distributed species. The records of populations named as *C. cucullatus* in areas previously not colonized by this species are old and have grown over the years. Yet, although their disjunct populations have been considered a cohesive taxonomic unit, previous comparisons between Neotropical and Afrotropical specimens shown inconsistencies in the external morphology, including male abdominal terminalia, causing uncertainty about the real unity of this species. In addition, the synonymies involving *C. cucullatus* neglected the analysis of the morphology of male abdominal terminalia, which makes this junction tenuous. The aim of this paper is to review *Ceracis cucullatus*, evaluating the conspecificity of the biotypes under this name. We compared the general external morphology and male abdominal terminalia of populations from several localities of the Neotropical, Afrotropical, Afrotemperate and Oriental region. As results, we described two new species, redefined the morphological limits of the *cucullatus* group, revalidate *C. lamellatus* and *C. tabellifer*, invalidate the synonymy of *C. bilamellatus* with *C. cucullatus*, and propose *C. bilamellatus* as a junior synonym of *C. tabellifer*. Furthermore, we redescribed *C. cucullatus*, *C. lamellatus* and *C. tabellifer*, and provided an identification key to species of the group. Additionally, in face of the taxonomic changes proposed here, we provided a new scenario for the distribution of the species and conducted a broad discussion about the invader status of *C. tabellifer*

outside the Neotropical region, and of *C. cucullatus* s. str. in Galapagos. Based on host fungi species and historical records of *C. tabellifer* gathered and presented in this paper, we discuss the main reasons for its invasion success in Africa and elsewhere, and its potential impact on native fauna.

1. Introdução

Ciídeos são besouros fungívoros obrigatórios (micetobiontes), de distribuição cosmopolita, que vivem associados a corpos-de-frutificação (basidiomas) de macrofungos poróides, os quais são utilizados como *habitat*, alimento e local de reprodução (Paviour-Smith, 1960; Lawrence, 1973; Navarrete-Heredia & Burgos-Solorio, 2000; Orledge & Reynolds, 2005; Graf-Peters *et al.*, 2011). Ciidae abrange cerca de 650 espécies descritas, agrupadas em 42 gêneros (Lawrence & Lopes-Andrade, 2010), sendo considerada uma das famílias mais abundantes e diversas de besouros micetobiontes (Graf-Peters *et al.*, 2011). Ciídeos apresentam distribuição mundial, ocorrendo em quase todos os continentes e em grande parte das terras insulares das regiões tropicais e subtropicais (Lawrence & Lopes-Andrade, 2010).

A taxonomia de Ciidae avançou muito nos últimos 10 anos. Durante esse período, e desconsiderando os resultados da presente dissertação, 49 espécies e três gêneros foram descritos, a maior parte da região Neotropical (Drogvalenko, 2002; Kawanabe, 2002; Królik, 2002; Lopes-Andrade *et al.*, 2002; Kawanabe, 2003; Lopes-Andrade & Zacaro, 2003a, 2003b; Lopes-Andrade *et al.*, 2003; Ruta, 2003; De Almeida & Lopes-Andrade, 2004; Kawanabe, 2005; Lopes-Andrade & Lawrence, 2005; Kawanabe, 2007; Lopes-Andrade, 2007a; Lopes-Andrade, 2007b; Lopes-Andrade, 2008; Lopes-Andrade *et al.*, 2009; Lopes-Andrade, 2010a, 2010b; Lopes-Andrade, 2011; Lopes-Andrade & Lawrence 2011; Antunes-Carvalho *et al.*, 2012). Entretanto, embora abrigue a maioria das espécies, o conhecimento da biodiversidade de ciídeos das terras tropicais e subtropicais ainda é parco (Graf-Peters *et al.*, 2011) e espelha a escassez histórica de estudos taxonômicos direcionados às faunas dessas regiões.

1.1. Considerações gerais sobre o gênero *Ceracis* Mellié

Ceracis Mellié está incluído na subfamília Ciinae Leach, na tribo Ciini Leach, junto com outros 31 gêneros. *Ceracis* foi originalmente proposto como subgênero de *Ennearthron* Mellié e inicialmente incluía cinco espécies (Mellié, 1849). Posteriormente, *Ceracis* foi elevado a gênero (Lacordaire, 1857). Lawrence (1967) ampliou os limites morfológicos do grupo e transferiu para *Ceracis* várias espécies formalmente descritas em *Ennearthron*, além de espécies de outros gêneros como *Cis* Latreille, *Octotemnus* Meliié, *Scolytocis* Blair e *Xylographus* Mellié. Esse foi o único estudo direcionado à *Ceracis* e deu ênfase às espécies neárticas. Desde então, esparsas descrições de espécies foram publicadas (Lawrence, 1971; Miyatake, 1982; Lopes-Andrade *et al*., 2002).

Membros de *Ceracis* podem ser diferenciados morfologicamente de outros gêneros de Ciinae por apresentarem a forma do corpo de oval a alongado e cilíndrico, revestimento consistindo de cerdas finas e diminutas (subglabro), antenas com 8 a 10 antenômeros, margens laterais do pronoto estreitas, ângulos anteriores do pronoto obtusos ou arredondados, prosterno côncavo a achatado ou ligeiramente convexo, processo prosternal laminado, protíbias expandidas na região apical e com uma fileira de espinhos margeando o ângulo apical externo, metaventrito medianamente a fortemente convexo e machos com marca sexual circular ou oval no primeiro ventrito abdominal (adaptado de Lawrence, 1967). Geralmente, além dessas características, os machos da maioria das espécies possuem a margem anterior do pronoto projetada para frente e/ou para cima, podendo assumir uma enorme variedade de formas e tamanhos.

Atualmente, *Ceracis* engloba 47 espécies descritas, sendo portanto o segundo gênero mais diversificado de Ciidae, ficando atrás apenas de *Cis* Latreille, um gênero considerado polifilético (Buder, 2008). Nesses gêneros, a organização de espécies morfologicamente similares em grupos de espécies tem se mostrado uma prática útil, principalmente por facilitar o reconhecimento de espécies novas ou de sinônimos. Em *Ceracis*, 17 espécies estão organizadas em quatro grupos. *Ceracis bicornis* e *C. cucullatus* formam o grupo *cucullatus* (*sensu* Lawrence, 1967). O grupo *furcatus* (*sensu* Lopes-Andrade, 2002) abrange *C. furcatus* (Bosc), *C. militaris* Mellié, *C. minutus* Dury e *C. variabilis* (Mellié). As espécies *C. cornifer* (Mellié), *C. cylindricus* (Brèthes), *C. furcifer* Mellié, *C. hastifer* (Mellié), *C. monocerus* Lawrence, *C. ruficornis* Pic, *C. simplicicornis* (Pic) e *C. unicornis* Gorham compõem o grupo *furcifer* (*sensu* Lawrence, 1967). O grupo *singularis* (*sensu* Lopes-Andrade *et al*. 2002) inclui *C. furcicollis* (Blair), *C. limai* Lopes-Andrade *et al.* e *C. singularis* (Dury).

Muitas das espécies descritas de *Ceracis* ocorrem nas regiões Neártica e/ou Neotropical (Lawrence, 1967). Contudo, vale salientar que não há nenhum registro de ocorrência de espécies deste gênero na região Andina (Lopes-Andrade, 2010a).

Alguns representantes ocorrem em regiões biogeográficas (*sensu* Morrone, 2002) fora das Américas, como as espécies *C. japonus* (Reitter) e *C. shikokuensis* (Miyatake) na região Paleártica (somente no Japão), *C. palaceps* Zimmerman, *C. evansi* (Blair) e *C. furcicollis* (Blair) na região Oriental, *C. nigricans* (Fauvel) na região Neoguineana, e a espécie invasora *C. cucullatus* (Mellié) nas regiões Afrotemperada e Afrotropical, incluindo ilhas no oeste do Oceano Índico.

1.2. A terminália de macho na taxonomia de Ciidae

Ciídeos são besouros muito pequenos (0,5 a 7 mm) (Lawrence & Lopes-Andrade, 2010) e *Ceracis* inclui algumas das menores espécies (0,8 a 2,2 mm) (Lawrence, 1967). O tamanho e a precariedade das descrições da maioria das espécies dificulta a identificação de membros de *Ceracis*. Este cenário, além de ofuscar a real diversidade desses organismos, trava o uso destes por pesquisadores e restringe o avanço do conhecimento de besouros micetobiontes à grupos taxonomicamente resolvidos.

A maneira mais eficaz de distinguir espécies de *Ceracis* é combinando informações clássicas da morfologia externa (*e.g.* forma da margem anterior do pronoto e cabeça em machos) e da terminália abdominal – genitália (lobo mediano e tégmen) + segmentos pré-genitais (peça basal, oitavo tergito, fusão do nono e décimo tergitos, e anel genital) – dos machos. Isso se deve principalmente à estabilidade e especificidade morfológica que a terminália masculina de ciídeos possui. Essa condição está amplamente difundida na taxonomia animal e é explicada em grande parte pela rápida divergência evolutiva da terminália entre espécies filogeneticamente próximas (Eberhard, 2010). Em Ciidae, esse quadro pode ser evidenciado pelas recentes descrições de táxons novos, fundamentadas fortemente nessas características (*e.g.* Lopes-Andrade, 2007; Lopes-Andrade, 2008; Lopes-Andrade *et al.*, 2009; Lopes-Andrade, 2010a; Lopes-Andrade, 2011). Contraditoriamente, a despeito da sua importância, a morfologia dessa estrutura está reportada na literatura apenas para duas das 47 espécies descritas no gênero, *C. limai* Lopes-Andrade *et al.* e *C. sallei* Mellié (Lawrence, 1967; Lopes-Andrade *et al.* 2002).

1.3. *Ceracis cucullatus* (Mellié): história taxonômica, distribuição e o *status* de espécie invasora

Ceracis cucullatus foi inicialmente descrita como *Ennearthron cucullatum* por Mellié (1849) e posteriormente transferida para *Ceracis* por Lawrence (1967). Juntamente com *C. bicornis* (Mellié, 1849), *C. tabellifer* (Mellié, 1849), *C. billamelatus* (Pic, 1916) e *C. lamellatus* (Pic, 1939) forma o grupo *cucullatus* (Lawrence, 1967). Entretanto, Lawrence (1967) propôs os últimos três nomes como sinônimos de *C. cucullatus*, argumentando que essas foram descritas como espécies distintas principalmente com base em diferenças no tamanho e grau de desenvolvimento das projeções pronotais dos machos. Essas características exibem uma ampla variação no tamanho e, algumas vezes, até mesmo na forma, pois apresentam crescimento alométrico. Portanto, mesmo dentro de uma população, indivíduos grandes possuem o pronoto fortemente projetado enquanto os pequenos apresentam uma projeção reduzida. Essa condição pode comprometer a delimitação e identificação das espécies, gerando casos de sinonímias.

Uma vez que *C. billamelatus* foi descrito de Madagascar, *C. tabellifer* da África do Sul e *C. lamellatus* do Brasil, a sinonímia dessas espécies com *C. cucullatus* fez com que esta fosse reconhecida como de ampla distribuição. Os registros de ocorrência de populações nomeadas como *C. cucullatus* em áreas antes não colonizadas por esta espécie são antigos e tem crescido ao longo dos anos. Registros de sua introdução já foram relatados para a Itália e França (Abeille de Perrin, 1874; Müller *et al*. 2001, Orledge *et al*. 2010). Houve um registro desse ciídeo na Grã Bretanha, embora a espécie não tenha se estabelecido no país (Orledge *et al.*, 2010). Diversos registros de *C. cucullatus* em ambientes insulares também são conhecidos, como nas ilhas Galápagos, no Oceano Pacífico, e nas ilhas Reunião, Maurício, Seychelles e Aldabra, a oeste do Oceaco Índico (Lesne, 1917; Scott, 1926; Lawrence, 1967). Considerando que a maioria das espécies de *Ceracis* se concentra na região Neotropical, e dado a ausência de espécies deste gênero no continente africano, a presença de populações de *C. cucullatus* em terras africanas vem sendo interpretada como resultado de eventos pretéritos de introdução (Scott, 1926; Lawrence, 1967). O registro de indivíduos habitando as ilhas Galápagos também sugere ser resultado de introdução da espécie, já que não há nenhuma espécie conhecida de ciídeo autóctone dessas ilhas. Embora seja notável sua eminente propagação, as razões para o sucesso da invasão desses ciídeos em novos *habitats* permanecem obscuras. O escasso conhecimento sobre a biologia desses besouros tem limitado as explicações para esse avanço e dificultado interessantes estudos sobre a ecologia dessa espécie e seu potencial impacto sobre faunas autóctones.

Alguns grupos de ciídeos podem apresentar associação com diversas espécies de fungos, enquanto outros apresentam restrição a uma ou poucas espécies de hospedeiros (Lawrence, 1973; Majka, 2007). Este comportamento pode ser constatado, também, em espécies de *Ceracis* (Lawrence, 1967). A existência de relação específica entre grupos de ciídeos e espécies de fungo hospedeiro, ou "host-use groups", já foi evidenciada por Orledge & Reynolds (2005). Dados recentes sobre a utilização de fungos por ciídeos na região Neotropical reforçam a hipótese de que uma mesma espécie ou espécies próximas de fungo são frequentemente utilizadas por espécies de ciídeos morfologicamente similares (Graf-Peters *et al*. 2011). *Ceracis bicornis*, espécie morfologicamente similar a *C. cucullatus*, possui hábito alimentar polífago (Graf-Peters *et al*. 2011), o que sugere a capacidade de explorar uma gama maior de espécies de fungos. Isso poderia indicar maior potencial de colonização de novos *habitats*. Entretanto, essas informações ainda são escassas para *C. cucullatus* e para a maioria das espécies de *Ceracis*.

Assim como *C. cucullatus*, outras espécies de Ciidae também possuem distribuição disjunta e são consideradas espécies invasoras em diversas partes do globo, como *Cis bilamellatus* Wood (Orledge *et al*. 2010), *Cis chinensis* Lawrence (Lopes-Andrade *et al*. 2008; Rose, 2009), *Cis creberrimus* Mellié, *Cis fuscipes* Mellié (Lawrence, 1971) e *Hadreule elongatula* (Gyllenhal) (Lawrence, 1971; Majka, 2007). No entanto, embora as populações neotropicais e africanas nomeadas como *C. cucullatus* têm sido interpretadas como uma unidade taxonômica coesa, comparações prévias entre espécimes dessas duas regiões biogeográficas revelaram inconsistências na morfologia externa e na forma da terminália abdominal de machos entre as populações, causando incerteza quanto a real unidade dessa espécie. As sinonímias supracitadas envolvendo *C. cucullatus* desconsideraram a análise da morfologia da terminália de machos das espécies sinonimizadas, o que torna essa junção tênue, principalmente considerando o alto grau de variação morfológica. Nesse contexto, torna-se imprescindível que a unidade de *C. cucullatus* seja testada por meio de uma análise comparativa mais precisa da morfologia externa, incluindo a morfologia da terminália de machos, de espécimes de diferentes regiões biogeográficas.

2. Objetivos

O objetivo geral do presente trabalho é revisar *Ceracis cucullatus* (Mellié) e avaliar a conspecificidade dos biótipos que atualmente estão sob este nome. Os objetivos específicos são:

- Examinar e comparar a morfologia externa, incluindo a da terminália abdominal de machos, de espécimes nomeados como *Ceracis cucullatus* oriundos das regiões Neotropical, Afrotropical Afrotemperada e Oriental;
- Elucidar os limites morfológicos de *C. cucullatus*, redescrevê-la e propondo novos táxons ou novos *status* para os espécimes que porventura não se enquadrem nos novos limites estabelecidos;
- Construir um mapa da distribuição geográfica de *C. cucullatus* e discutir o *status* de invasor desse táxon;
- Estabelecer os limites morfológicos do grupo *cucullatus* e propor uma chave de identificação para as espécies nele incluídas.

3. Material e Métodos

3.1. Material examinado

Na condução deste estudo, analisei cerca de 3000 exemplares adultos de *Ceracis* obtidos em empréstimos das instituições nacionais e internacionais listadas abaixo. Entre parênteses, cidade e respectivo país onde se encontra cada coleção, seguido do nome do curador.

ANIC – Australian National Insect Collection; CSIRO Ecosystem Sciences (Canberra, Australia: John F. Lawrence)
CMN – Canadian Museum of Nature (Ottawa, Canadá: François Génier)
CZUG – Colección Entomológica del Centro de Estudios em Zoología, Universidad de Guadalajara (Zapopan, Jalisco, Mexico: José Luis Navarrete Heredia)
KMMA – Koninklijk Museum voor Midden Afrika (Tervuren, Bélgica: Marc De Meyer)
LAPC – Cristiano Lopes-Andrade Private Collection (Viçosa, Minas Gerais, Brasil)
MFN – Museum für Naturkunde (Berlim, Alemanha: Manfred Uhlig)
MHNG – Muséum d'Histoire Naturelle (Genebra, Suíça: Giulio Cuccodoro)
MZLU – Museum of Zoology, Lund University (Lund, Suécia: Roy Danielsson)
MNHN – Muséum national d' Histoire naturelle (Paris, França: Thierry Deuve)
SANC – South African National Collection of Insects (Pretória, África do Sul: Riaan Stals)
SNSD - Senckenberg Naturhistorische Sammlungen Dresden (Dresden, Alemanha: Klauss Dieter-Klass)

3.2. Análise da morfologia externa

3.2.1. Medições

Os exemplares foram medidos em estereomicroscópio ZEISS Stemi 2000 com escala ocular de um milímetro. Foram mensuradas as seguintes estruturas (abreviações em inglês, para corresponder ao apresentado nos capítulos): comprimento total do corpo (TL), comprimento do pronoto (PL), maior largura do pronoto (PW), comprimento dos élitros (EL), maior largura dos élitros (EW) e profundidade do corpo (GD). Com essas medidas, as seguintes proporções corporais foram obtidas: EL/EW, EL/PL, GD/EW, PL/PW, TL/EW. A proporção entre GD/EW foi utilizada como parâmetro indicador do grau de convexidade do corpo, sendo TL/EW indicador do grau de alongamento corporal. Para cada espécie examinada, forneço valores de variação, média e desvio padrão para cada uma das medidas e proporções citadas acima.

3.2.2. Análise e fotografia em estereomicroscópio

Analisei a morfologia externa dos espécimes no mesmo estereomicroscópio em que foram medidos, em magnificação máxima de 100 vezes. Comparei exemplares de todas as populações disponíveis para estudo. Pelo menos um exemplar de cada espécie analisada foi fotografado. Quando se tratava de uma espécie descrita, foi fotografado o lectótipo ou paralectótipo, aqui designados. No caso de espécies novas, o holótipo foi fotografado. As fotos foram tiradas com uma câmera digital Canon EOS 1000D acoplada ao estereomicroscópio. Imagens de alta qualidade foram obtidas pela técnica de automontagem, que consiste em tirar uma sequência de fotos em diferentes planos de foco e compilá-las em uma única imagem mais informativa. Essa técnica vem sendo largamente empregada na taxonomia de Ciidae por contornar problemas de profundidade de campo em fotos onde uma grande magnificação é requerida (ver Lopes-Andrade, 2010a; Antunes-Carvalho & Lopes-Andrade, 2011; Lopes-Andrade, 2011). Em uma primeira fase do trabalho, as fotos foram compiladas no *freeware* Combine ZP (Hadley, 2010). Posteriormente passei a utilizar o *software* Zerene Stacker (versão 1.04) que apresentou imagens com melhor resolução quando o número de fotos compiladas era maior (geralmente acima de 60 fotos). Quando necessário, as imagens resultantes foram editadas com a ajuda do *software* Corel Photo-Paint X5, utilizando os filtros *Intensificação de contraste* e *Equilibrar amostra/destino*, e as ferramentas *Cortar* e *Pintura*.

3.2.3. Análise e fotografia em microscópio eletrônico de varredura

Quando pertinente, espécimes foram examinados em Microscopia Eletrônica de Varredura convencional (MEV) para visualização de estruturas taxonomicamente informativas. Em tais casos foi adotado o seguinte procedimento: (i) os espécimes foram desidratados em série alcoólica (70, 80, 95 e 100%), (ii) submetidos à secagem em aparelho de ponto crítico, (iii) montados em suportes de alumínio, (iv) cobertos com ouro e (v) fotografados em MEV (LEO VP 1430). Quando necessário, além do MEV convencional, as amostras foram fotografadas em MEV de pressão variável (MEV-PV) seguindo apenas a etapa (iii). As imagens foram obtidas em meio digital. No decorrer do trabalho, constatou-se que o custo das análises por microscopia eletrônica não compensava as informações obtidas.

3.3. Análise da morfologia da terminália de machos

3.3.1. Dissecção

Sempre que possível, pelo menos um macho de cada localidade foi dissecado para estudo da morfologia da terminália. Para tal, espécimes foram mantidos em solução de KOH + detergente + água (na proporção 2:1:18) por pelo menos 12 horas, tempo suficiente para o amolecimento dos tecidos para dissecção. Após esta etapa, os exemplares foram passados para uma lâmina escavada, umedecida com uma gota de água, onde foram cuidadosamente dissecados com ajuda de alfinetes entomológicos. As estruturas removidas do corpo do animal, em geral genitália e oitavo esternito, foram incluídas em gel de Downs (Downs, 1943) e montadas entre lâmina e lamínula. Ao fim desse processo, a lâmina foi mantida em estufa à 60° C durante uma hora para secagem. As lâminas foram etiquetadas com os mesmos dados da etiqueta original do espécime e este foi montado em triângulo.

3.3.2. Análise e fotografia em microscópio óptico

Apresento fotografias de genitália e oitavo esternito de todas as espécies analisadas neste estudo. As lâminas com escleritos foram cuidadosamente analisadas em microscópio óptico ZEISS Axiolab A1 e fotografados com uma câmera digital ZEISS Axiocam Erc5S integrada ao mesmo microscópio. Quando pertinente, foram montadas lâminas de antenas, aparelho bucal, asas e pernas, seguindo o mesmo protocolo da montagem de lâminas de escleritos da terminália. As fotografias obtidas foram posteriormente editadas utilizando o *software* Corel Photo-Paint X5. Pranchas foram montadas com as imagens finais de cada estrutura e incluídas nas descrições. A terminologia adotada para a morfologia da terminália abdominal de machos foi a de Lopes-Andrade & Lawrence (2005) e de Lawrence *et al*. (2011).

3.4. Descrição de novos táxons

Espécies consideradas novas foram cuidadosamente comparadas com síntipos (lectótipos e paralectótipos aqui designados), plesiótipos ou topótipos das espécies de *Ceracis* do grupo *cucullatus* e confrontadas com os dados da literatura. Quando comprovado que se tratava de uma espécie nova, o processo de descrição seguiu as seguintes etapas: (i) todos os espécimes desse táxon presentes na coleção foram separados, (ii) um dos espécimes machos foi selecionado para ser o holótipo e foi devidamente etiquetado; os demais foram etiquetados como parátipos, (iii) o holótipo foi fotografado em estereomicroscópio, (iv) parátipos foram fotografados em MEV ou MEV-PV (essa etapa foi realizada apenas quando necessário e possível), (v) alguns espécimes machos foram dissecados para extração da terminália abdominal e preparação de lâminas, que foram examinadas e fotografadas (o número de espécimes dissecados dependeu do tamanho da série-tipo e da necessidade de mais preparações), (vi) cerca de 20 espécimes de cada sexo, quando disponíveis, foram medidos (ver parâmetros morfométricos no tópico *Análise da morfologia externa*), (v) as características diagnósticas e (vi) a morfologia externa e a morfologia da terminália de machos foram descritas. Espécies com descrições arcaicas e pouco informativas foram redescritas. A terminologia adotada para as estruturas morfológicas do adulto foi a de Lawrence *et al*. (2011). Ao fim do estudo, elaborei uma chave de identificação para as espécies do grupo *cucullatus*.

3.5. Mapas e distribuição geográfica

Construí um mapa com registros de ocorrência de espécimes de *C. cucullatus*. Esses registros foram obtidos através da observação direta da etiqueta dos exemplares examinados e/ou por meio de informações da literatura. As coordenadas das localidades mostradas no mapa foram obtidas na base de dados geográficos GeoNames (Wick, 2010). Posteriormente usei esses dados para traçar a distribuição das espécies e construir o mapa com a ajuda do *freeware* DIVA-GIS (Hijmans *et al.* 2011) ou do *software* ArcGis 9.3.

3.6. Espécimes coletados na África do Sul e registros de fungos hospedeiros

Examinei centenas de exemplares do biótipo africano nomeado como *C. cucullatus* pertencentes à SANC. Esses espécimes foram obtidos através de extensivas coletas de orelhas-de-pau realizadas em diversas localidades da África do Sul, entre os anos de 2002 e 2010, por uma equipe de pesquisadores do Agricultural Research Council (Pretória, África do Sul). Esses pesquisadores não estavam interessados diretamente nos Ciidae, mas nos parasitóides desses organismos, principalmente as espécies de *Astichus* Foerster (Hymenoptera: Eulophidae). Quatro espécies de *Astichus* foram encontradas parasitando esses ciídeos da África do Sul e descritas recentemente (Neser, 2012). Ao longo dessas coletas, os fungos obtidos no campo foram levados ao laboratório onde os ciídeos, parasitóides e outros insetos foram posteriormente triados. Tanto os fungos como as árvores que serviam de substrato foram identificados até o menor nível taxonômico possível, a maioria até espécie. Alguns dos ciídeos foram montados em triângulos e devidamente etiquetados com informações sobre a localidade de coleta, coordenadas geográficas e espécie de fungo hospedeiro. A outra parte dos ciídeos triados foi mantida em cápsulas de gelatina. Tive acesso a todos os exemplares das populações que continham parasitóides, o que me permitiu saber o número de espécimes nomeados como *C. cucullatus* obtidos em cada coleta, quantas espécies de Ciidae estavam presentes no mesmo fungo e quais eram os fungos hospedeiros. Apresento esses dados no segundo capítulo dessa dissertação.

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4. Resultados

Apresento os resultados desta dissertação em dois capítulos, sendo o primeiro um artigo publicado e o segundo um manuscrito a ser submetido. **O manuscrito (Capítulo 2) não deve ser considerado como publicação válida para fins de nomenclatura zoológica, de acordo com as normas do Código Internacional de Nomenclatura Zoológica (Cap. 3, Art. 8.2 e Art. 8.3).**

CAPÍTULO I

Two new Neotropical species of *Ceracis* Mellié (Coleoptera, Ciidae) and redefinition of the *cucullatus* group

Caio Antunes-Carvalho & Cristiano Lopes-Andrade

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Two new Neotropical species of *Ceracis* Mellié (Coleoptera, Ciidae) and redefinition of the *cucullatus* group

Caio Antunes-Carvalho[1,†], Cristiano Lopes-Andrade[2,‡]

1 *Programa de Pós-Graduação em Entomologia, Departamento de Entomologia, Universidade Federal de Viçosa, 36570-000, Viçosa, Minas Gerais, Brazil* **2** *Departamento de Biologia Animal, Universidade Federal de Viçosa, 36570-000, Viçosa, Minas Gerais, Brazil*

† *urn:lsid:zoobank.org:author:257E8142-E3F7-4D8B-A099-1A1A5CE9B3BD*
‡ *urn:lsid:zoobank.org:author:6A3F4101-8599-44D9-9210-BCD5DD8564E9*

Corresponding author: *Caio Antunes-Carvalho* (cantunescarvalho@gmail.com)

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Abstract

Two new Neotropical species of *Ceracis* Mellié are described: *Ceracis cassumbensis* Antunes-Carvalho & Lopes-Andrade, **sp. n.** from a single locality in northeastern Brazil and *Ceracis navarretei* Antunes-Carvalho & Lopes-Andrade, **sp. n.** from a single locality in southern Mexico. Scanning Electron Microscope images of adults and photographs of holotypes and male terminalia are provided for both species, their similarities and differences with other *Ceracis* are briefly discussed, and the *cucullatus* species-group is redefined for including the new species described herein.

Keywords
Ciid, minute tree-fungus beetle, Ciinae, Brazil, Mexico

Introduction

Ceracis Mellié (Coleoptera: Ciidae: Ciinae) encompasses 47 described species, being the second most speciose genus of the family. The genus was redefined by Lawrence (1967), who dealt mostly with Nearctic *Ceracis* but briefly discussed their affinities to

Neotropical and Indo-Pacific species. He has also proposed two species-groups, the *furcifer* and the *cucullatus*, each including morphologically related species.

Ceracis cucullatus (Mellié), which names the *cucullatus* group, has drawn the attention of ciidologists due to its broad and disjunct geographic distribution. It is widespread in the Neotropical region, also occurring in several localities of the Afrotropical and Afrotemperate regions (sensu Morrone 2002), including several islands (Mellié 1849, Scott 1926, Blackwelder 1945, Lawrence 1967, Lopes-Andrade 2008, Lopes-Andrade et al. 2009, Lawrence and Lopes-Andrade 2010). There is a single record of the species from France (Abeille de Perrin 1874), but it is possibly not established there.

While conducting a survey on the morphology, life cycle and geographic distribution of *C. cucullatus*, mainly to evaluate the conspecificity of disjunct populations under this name, we found two morphologically related new species. Here we describe *Ceracis cassumbensis* sp. n., a rare record of Ciidae in a Brazilian estuarine system, and *Ceracis navarretei* sp. n. from southern Mexico. We include them in the *cucullatus* species-group, which is redefined.

Material and methods

Holotypes were neither dissected nor examined under Scanning Electron Microscope (SEM). SEM images of whole specimens (Figs 4-6, 14-16) and photographs of dissected sclerites of male terminalia (Figs 7-10, 17-20) are from topotypes (specimens collected in the type locality but not labeled as paratypes; sensu Evenhuis 2008). These figures are cited in the descriptions for the purpose of illustration.

Examination of specimens, measurements and descriptions were made under a Zeiss Stemi 2000 stereomicroscope with a scale ocular. Holotypes were photographed with a Canon EOS 1000D digital camera attached to the same stereomicroscope. Digital photographs taken from different focus were processed and enhanced in the image stacking freeware CombineZP (Hadley 2010). Permanent slide preparations of male terminalia followed the methodology detailed by Lopes-Andrade (2011) and were photographed with a Canon A640 digital camera adapted to a Zeiss Axioskop 40 compound microscope. SEM images were taken with a LEO 1430 VP. A few topotypes were dehydrated in a series of alcohol solutions, dried in a Critical Point Dryer (Balzers CPD 020), mounted on stubs and sputter-coated with gold (Balzers Sputter Module SCA 010).

The following abbreviations are used for measurements and ratios: CL, length of the antennal club; EL, elytral length (taken from the base of scutellum to the elytral apex); EW, greatest elytral width; FL, length of the antennal funicle; GD, greatest depth of the body (taken from the elytra to the metaventrite); PL, pronotal length along midline; PW, greatest pronotal width; TL, total length (EL+PL; head not included). Range, mean and standard deviation are given for the abovementioned measurements and the following ratios: EL/EW; EL/PL; GD/EW; PL/PW; TL/EW. The ratio GD/EW was adopted as an indication of degree of convexity, and TL/EW indicates degree of body elongation. These measurements and ratios were taken from the whole type series. Measurements of antennomeres, eyes, scutellum and abdominal ventrites were taken only from holotypes. Morphological variations between specimens of the type series (males and females) are given in the section on "Variation", together with measurements and ratios (accompanied by mean ± standard deviation). Specimens selected as holotypes are fully pigmented males.

We compared specimens of *C. cassumbensis* sp. n. and *C. navarretei* sp. n. with named specimens of *C. cucullatus* from Brazil, Galapagos and several localities from Africa. Dissected terminalia of males from these localities were also carefully compared. The terminology adopted for external morphology and male terminalia's sclerites are explained by Lopes-Andrade and Lawrence (2005) and Lopes-Andrade (2008). The term sensillifer is used here to designate the compound sensory structure on the ciid antennal club (see Lawrence 1971, Lopes-Andrade and Lawrence 2005, Lawrence and Lopes-Andrade 2010). For a brief explanation on the use of the terms mesoventrite and metaventrite, see Lopes-Andrade (2007).

The following acronyms are used in this paper:

ANIC	Australian National Insect Collection, CSIRO Ecosystem Sciences (Canberra, Australia)
CZUG	Colección Entomológica del Centro de Estudios en Zoología, Universidad de Guadalajara (Zapopan, Jalisco, Mexico)
LAPC	Cristiano Lopes-Andrade Private Collection (Viçosa, MG, Brazil)

Descriptions

Ceracis cassumbensis Antunes-Carvalho & Lopes-Andrade, sp. n.

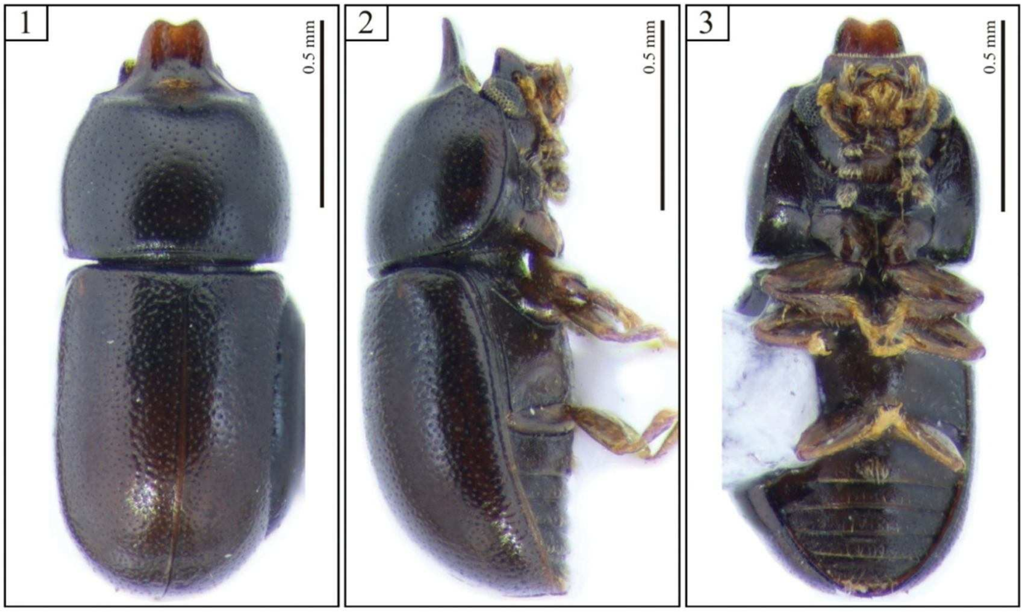
urn:lsid:zoobank.org:act:26A7C976-D6E8-44C2-AC4A-A795421CAE24
http://species-id.net/wiki/Ceracis_cassumbensis
Figs 1–10

Type-locality. "Ilha da Cassumba" (Cassumba island) in Caravelas, southern portion of the state of Bahia, northeastern Brazil (17°46'S, 39°17'W).

Etymology. The specific epithet refers to the *terra typica* of the species.

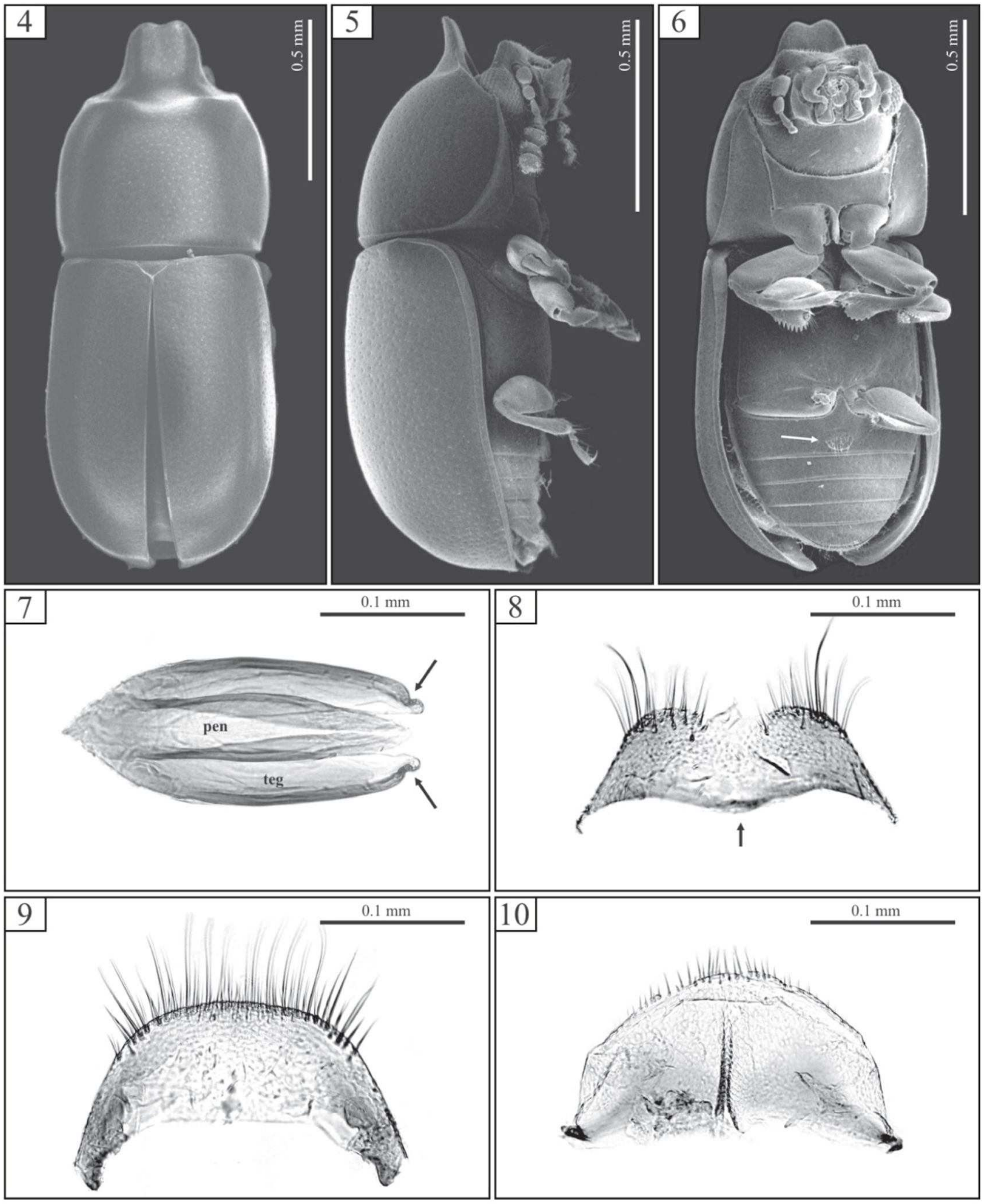
Diagnosis. Each antenna with eight antennomeres. Pronotum with relatively fine punctation; its anterior edge projected for- and upward forming a raised plate, slightly concave, with a short emargination at apex. Elytral punctation relatively dense. First abdominal ventrite with a broad transversely oval, setose sex patch (Fig. 6, arrow). Tegmen with lateral edges bearing a small excavation near apex (Fig. 7, arrows).

Description. Male holotype (Figs 1-3), measurements in mm: TL 1.56; PL 0.60; PW 0.64; EL 0.96; EW 0.64; GD 0.56. Ratios: PL/PW 0.94; EL/EW 1.50; EL/PL



Figures 1–3. Habitus of *Ceracis cassumbensis* Antunes-Carvalho & Lopes-Andrade, sp. n., holotype. **1** Dorsal view **2** Lateral view **3** Ventral view.

1.60; GD/EW 0.88; TL/EW 2.44. Body elongate, robust; dorsal and ventral surfaces dark brown, almost black; basal antennomeres and funicle, mouthparts and legs mostly yellowish brown; antennal club blackish and terminal palpomere of the maxillary palp yellowish black. Head barely visible from above; dorsal surface subglabrous, sparsely punctate, bearing a transverse impression at disc, preceded by a weak protuberance (seen in the dissected topotype); frontoclypeal ridge produced forward, transversely concave, with anterior margin emarginate at middle forming two subtriangular plates visible from below (Fig. 6), the anterior edge with a row of setae along it. Each eye with a widest diameter of 0.14 mm; some short slender yellowish setae emerging from the intersection between ommatidia. Each antenna with eight antennomeres (FL 0.09, CL 0.17, CL/FL 1.89); length of antennomeres (in mm) as follows (from base to apex): 0.07, 0.05, 0.05, 0.03, 0.02, 0.05, 0.05, 0.07; each antennomere of the club bearing several sparse slender setae, and four conspicuous sensillifers symmetrically positioned at its upper portion. Pronotum with sides reasonably rounded, widest at middle; lateral margins narrow, not visible from above, except for the most posterior corners; anterior edge projected for- and upward, forming a curved raised plate, slightly concave, with a short emargination at apex (Figs 1, 4); disc impressed in the area surrounding pronotal projection; anterolateral angles inconspicuously produced, relatively obtuse; punctation relatively fine, single, uniformly distributed, the posterior half of the median longitudinal surface devoid of punctures; distance between punctures from 1.75



Figures 4–10. *Ceracis cassumbensis* Antunes-Carvalho & Lopes-Andrade, sp. n., SEM of male topotypes (4–6) and slide preparations of male terminalia of a topotype (7–10). **4** Dorsal view **5** Lateral view **6** Ventral view, showing the transversely oval sex patch at the first abdominal ventrite (arrow) **7** Aedeagus showing penis (pen) and tegmen (teg). Note the conspicuous excavation in either side of tegmen (arrows) **8** Eighth sternite with anterior margin rounded at middle (arrow) **9** Eighth tergite **10** Fused ninth and tenth tergites.

to 2.25 puncture-widths, being greater at the anterior half of pronotum (including pronotal projection); each puncture bearing a fine yellowish decumbent minute seta; in between punctures shiny, microreticulate. Scutellum small, triangular, with few punctures, each one bearing a short, fine, decumbent bristle; basal width 0.11mm and length along the longitudinal midline 0.05 mm. Hind wings developed. Elytra with sides subparallel at the basal two-thirds, then abruptly converging toward apex; punctation single, confused, denser than pronotal punctation; punctures irregular, but ever finer than those on pronotum; vestiture similar to that of pronotum, but in between punctures smooth and shiny. Ventral sclerites microreticulate. Prosternum in front of coxae shallowly concave longitudinally, and a bit transversely convex; surface beside coxae weakly concave; prosternal process laminate, reasonably elevated, almost as long as coxae. Metaventrite moderately convex, bearing sparse slender setae; punctation shallow, consisting mostly of few punctures close to the lateral edges; median suture (discrimen) obscurely indicated posteriorly (see section on "variation"). Abdominal ventrites bearing sparse slender decumbent yellowish setae, longer than those on the dorsal surface; punctation shallow and sparse; lengths of abdominal ventrites (from base to apex, at the longitudinal midline) as follows (in mm): 0.19; 0.08; 0.08; 0.06; 0.06; length of abdominal ventrites together 0.46 mm; abdominal width (basal width of the first abdominal ventrite) 0.63 mm; first abdominal ventrite bearing a broadly transverse margined setose sex patch (Fig. 6, arrow), located postered of center, with a transverse diameter of 0.06 mm. Apex of each protibia expanded; outer apical angle rounded and bearing a row of spines.

Male terminalia. (Figs 7–10) Ninth segment (=genital ring) V-shaped. Fused ninth and tenth tergites (Fig. 10) with posterior margin rounded and bearing small suberect bristles at middle; sides slightly diverging, almost subparallel. Eighth sternite (Fig. 8) with posterior margin shallowly emarginate at middle; posterior angles rounded and bearing some bristles; lateral margins diverging; anterior margin biconcave, rounded and slightly sclerotized at middle but not forming a strut (Fig. 8, arrow). Eighth tergite (Fig. 9) with posterior margin almost straight, bearing long and short bristles along it; lateral margins diverging; anterior margin concave. Aedeagus (Fig. 7) around twice as long as wide; basal piece not observed, possibly membranous. Tegmen slightly longer than and twice as wide as penis; posterior portion subtriangular, then subparallel sided at most of its length, lateral edges slightly curved inward to apex; both sides bearing a small excavation near apex (Fig. 7, arrows). Penis elongate, subcylindrical; sides subparallel at the basal three-fourths, with apical one-fourth subtriangular and weakly sclerotized.

Females. Differing from males in the following features: frontoclypeal ridge rounded, not produced. Lateral margins of pronotum rounded; anterior margin rounded, not produced, bearing small yellowish setae along it; pronotal and elytral punctation slightly finer than in males. Abdominal sex patch absent.

Variation. Males, measurements in mm (n=21, including holotype): TL 1.12–1.80 (1.46 ± 0.18); PL 0.44–0.84 (0.66 ± 0.11); PW 0.48–0.76 (0.63 ± 0.07); EL 0.68–0.96 (0.80 ± 0.07); EW 0.52–0.76 (0.64 ± 0.07); GD 0.44–0.68 (0.55 ± 0.06).

Ratios: PL/PW 0.92–1.19 (1.04 ± 0.07); EL/EW 1.12–1.33 (1.25 ± 0.06); EL/PL 1–1.55 (1.23 ± 0.14); GD/EW 0.76–0.92 (0.86 ± 0.04); TL/EW 2.15–2.50 (2.28 ± 0.09). Body varying from dark reddish brown to dark brown (almost black). Frontoclypeal ridge and apex of pronotum weakly developed in the smallest males and strongly projected in the largest ones. Discrimen indiscernible to barely discernible in most individuals.

Females, measurements in mm (n=10): TL 1.32–1.56 (1.45 ± 0.09); PL 0.56–0.68 (0.62 ± 0.05); PW 0.56–0.68 (0.61 ± 0.05); EL 0.76–0.92 (0.84 ± 0.05); EW 0.6–0.72 (0.66 ± 0.04); GD 0.52–0.6 (0.56 ± 0.04). Ratios: PL/PW 1–1.07 (1.01 ± 0.02); EL/EW 1.17–1.44 (1.28 ± 0.09); EL/PL 1.24–1.44 (1.36 ± 0.08); GD/EW 0.81–0.94 (0.85 ± 0.05); TL/EW 2.06–2.44 (2.22 ± 0.12).

Type series. Male holotype (LAPC) "BRASIL: BA Caravelas; Ilha da Cassumba 30.ii.2006 *leg.* K.S. Furieri, F.C.C. Barreto, E.S. Rediguieri" "*Ceracis cassumbensis* Antunes-Carvalho & Lopes-Andrade HOLOTYPUS" [printed on red paper]. Paratypes: 20 males, 10 females (LAPC), same data as holotype. All paratypes distinguished labeled "*Ceracis cassumbensis* Antunes-Carvalho & Lopes-Andrade PARATYPUS" [printed on yellow paper].

Natural history. Cassumba is a continental island at the Caravelas-Peruípe estuarine system, with around 120Km^2. It is located at the northern portion of the Atlantic Forest and encompasses forest remnants and large mangrove areas mixed in a landscape apparently well preserved. It is the first record of Ciidae from the island and a rare record of the family from a Brazilian estuarine system. However, we do not know either the host-fungus of this single collection of *C. cassumbensis* sp. n. or whether it was caught close to a mangrove or a forest remnant at the island.

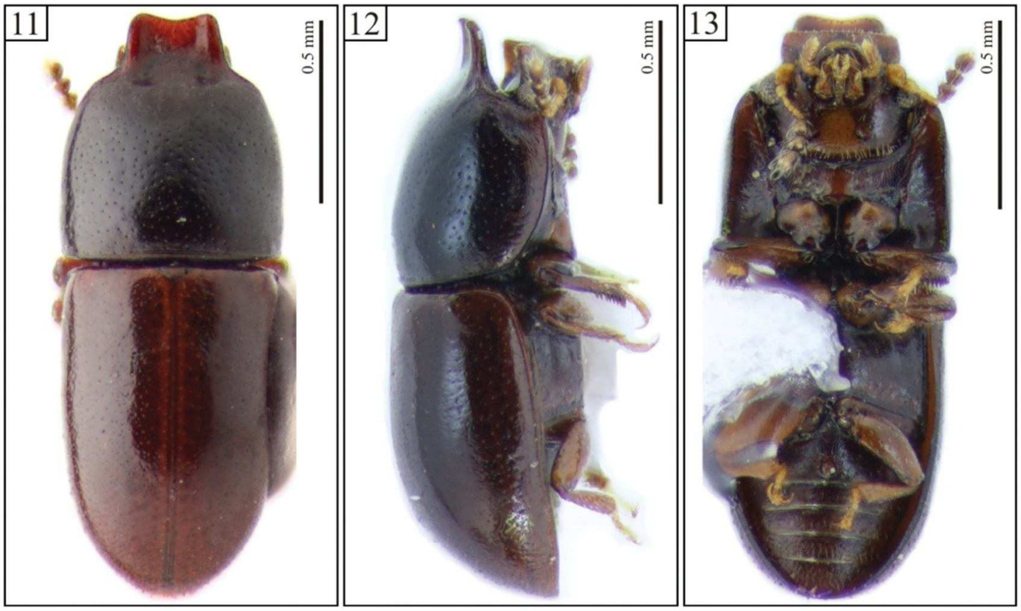
Ceracis navarretei Antunes-Carvalho & Lopes-Andrade, sp. n.

urn:lsid:zoobank.org:act:63754F8E-972F-418F-988A-FA24504AFAA9
http://species-id.net/wiki/Ceracis_navarretei
Figs 11–20

Type-locality. Dos Amates, southern portion of the state of Veracruz, southern Mexico (17°24'N, 94°35'W).

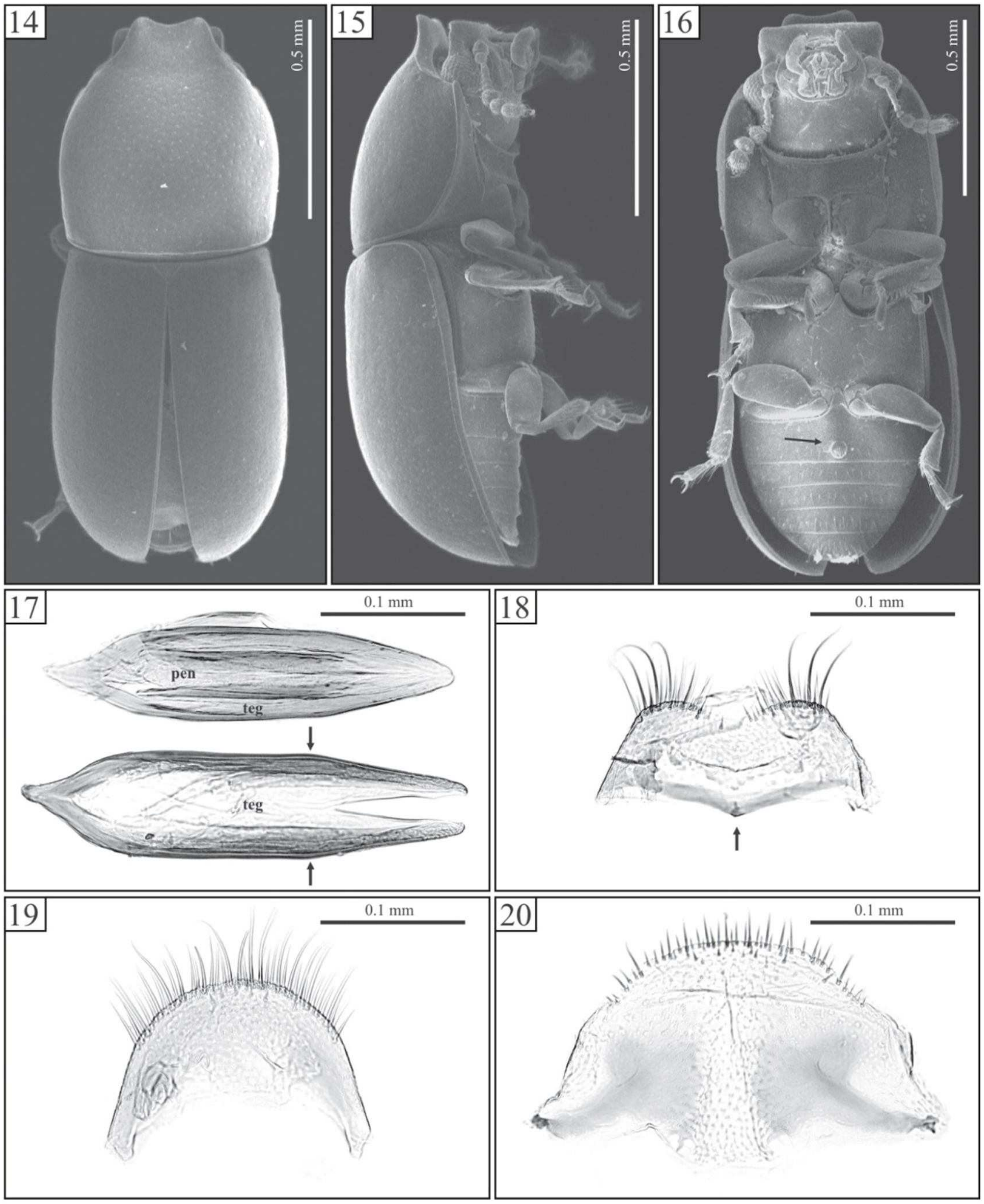
Etymology. The specific epithet is in honor of José Luis Navarrete Heredia, who made available to us the majority of the specimens included in the type series.

Diagnosis. Body with very fine, sparse punctation. Each antenna with nine antennomeres. Pronotum mostly black; elytra and apex of pronotum reddish brown. Pronotal apex projected for- and upward, forming a curve, raised foursquare plate, weakly emarginated at the anterior edge. Elytra with lateral margins subparallel at the basal half, then gradually converging toward the apex. Aedeagus 4× longer than wide (Fig. 17); tegmen with parallel sides at most of their lengths, lateral edges angulate at the beginning of the apical third (Fig. 17, arrows) and then converging in straight line toward the apex.



Figures 11–13. Habitus of *Ceracis navarretei* Antunes-Carvalho & Lopes-Andrade, sp. n., holotype. **11** Dorsal view **12** Lateral view **13** Ventral view.

Description. Male holotype (Figs 11-13), measurements in mm: TL 1.60; PL 0.72; PW 0.64; EL 0.88; EW 0.62; GD 0.56; TL/EW 2.58; PL/PW 1.13; EL/EW 1.42; EL/PL 1.22; GD/EW 0.90. Body subcylindrical, moderately convex; elytra and apex of pronotum reddish brown, remainder of pronotum black; ventral surface reddish brown; legs, mouthparts, basal antennomeres and funicle yellowish brown; antennal club dark brown. Head barely visible from above; dorsal surface flattened, subglabrous, bearing minute, sparsely decumbent fine setae, almost indiscernible; punctation sparse, consisting of shallow coarse punctures; frontoclypeal ridge produced forward, transversely concave, with its anterior margin slightly emarginate at middle, the anterior edge with a row of setae along it. Each eye with a widest diameter of 0.13 mm; some short slender yellowish setae emerging from the intersection between ommatidia. Each antenna with nine antennomeres (FL 0.09, CL 0.15, CL/FL 1.67); length of the antennomeres (in mm) as follows (from base to apex): 0.06, 0.04, 0.04, 0.02, 0.02, 0.02, 0.04, 0.04, 0.06; each antennomere of the club bearing several sparse slender setae, and four conspicuous sensillifers symmetrically positioned at its upper portion. Pronotum with subparallel sides, widest at middle; lateral margins narrow, being a bit thicker at the anterior portion; only the anterior and posterior corners can be seen from above, but the latter is weakly visible; anterior edge projected for- and upward, forming a curve, raised foursquare plate, slightly emarginated at apex (Figs 11, 14); raised plate transversely concave; anterolateral angles slightly produced, moderately obtuse;



Figures 14–20. *Ceracis navarretei* Antunes-Carvalho & Lopes-Andrade, sp. n., SEM of male topotypes (14–16) and slide preparations of male terminalia of topotypes (17–20). **14** Dorsal view **15** Lateral view **16** Ventral view, showing the circular margined sex patch at the first abdominal ventrite (arrow) **17** Above, aedeagus showing penis (pen) and tegmen (teg). Below, a tegmen alone. Arrows indicate the angulation point from which the sides of tegmen converge in straight line toward the apex **18** Eighth sternite, showing the anterior margin weakly produced at middle (arrow) **19** Eighth tergite **20** Fused ninth and tenth tergites.

punctation fine, single, relatively uniform; distance between punctures from 2.5 to 3 puncture-widths; vestiture of yellowish decumbent seta; in between punctures shiny, microreticulate. Scutellum small, triangular, glabrous, with few fine punctures; basal width 0.11mm; length along the longitudinal midline 0.05 mm. Hind wings developed. Elytra with sides subparallel at basal half, then gradually converging to apex; only the most anterior corners visible from above; punctation single, confused, finer and denser than that of pronotum; vestiture consisting of minute, fine, decumbent yellowish setae; in between punctures smooth and shiny. Ventral sclerites microreticulate. Prosternum in front of coxae shallowly concave longitudinally and transversely convex; surface beside coxae weakly concave; prosternal process laminate, almost as long as coxae. Metaventrite moderately convex, bearing sparse slender setae; punctation shallow and sparse, almost indiscernible; discrimen indiscernible. Abdominal ventrites bearing sparse slender decumbent yellowish setae, longer than those on the dorsal surface; punctation shallow and sparse; lengths of abdominal ventrites (from base to apex, at the longitudinal midline) as follows (in mm): 0.19; 0.07; 0.07; 0.07; 0.08; abdominal length 0.50 mm, abdominal width (basal width of the first abdominal ventrite) 0.55 mm; first abdominal ventrite bearing a circular margined sex patch (Fig. 16, arrow), located postered of center, with a transverse diameter of 0.04 mm. Apex of each protibia expanded; outer apical angle rounded and bearing a row of spines.

Male terminalia. (Figs 17–20) Ninth segment (=genital ring) V-shaped. Fused ninth and tenth tergites (Fig. 20) with posterior margin reasonably straight, with small suberect bristles along it; sides diverging, each bearing a small protuberance at middle. Eighth sternite (Fig. 18) with posterior margin weakly emarginate at middle; posterior angles rounded and bearing some bristles; lateral margins diverging; anterior margin biconcave, sclerotized and forming a short median strut (Fig. 18, arrow). Eighth tergite (Fig. 19) with posterior margin rounded, bearing long and medium size bristles along it; lateral margins diverging; anterior margin concave. Aedeagus (Fig. 17) 4× longer than wide; basal piece not observed, possibly membranous. Tegmen slightly longer than and twice as wide as penis; posterior portion subtriangular and then parallel sided at most of its length, either side angulate at the beginning of the apical third (Fig. 17, arrows) and converging in straight line toward apex. Penis elongate, subcylindrical; sides subparallel at the basal three-fourths, with apical one-fourth subtriangular and weakly sclerotized.

Females. Differing from males in the following features: frontoclypeal ridge rounded, not produced. Head with dorsal surface usually convex. Lateral margins of pronotum rounded; anterior margin rounded, not produced; pronotal and elytral punctation slightly finer than in males. Abdominal sex patch absent.

Variation. Males, measurements in mm (n=22, including holotype): TL 1.22–1.74 (1.53 ± 0.13); PL 0.46–0.78 (0.67 ± 0.08); PW 0.50–0.68 (0.61 ± 0.05); EL 0.76–0.96 (0.86 ± 0.05); EW 0.50–0.68 (0.60 ± 0.05); GD 0.40–0.60 (0.53 ± 0.04). Ratios: PL/PW 0.92–1.27 (1.09 ± 0.08); EL/EW 1.38–1.57 (1.44 ± 0.05); EL/PL 1.14–1.65 (1.31 ± 0.12); GD/EW 0.80–0.94 (0.88 ± 0.04); TL/EW 2.43–2.73 (2.56 ± 0.09). Color of pronotum varying from black to reddish brown, usually reddish;

elytra dark reddish to reddish brown. Anterior edge of pronotum weakly developed in the smallest males and strongly projected in the largest ones. In some cases the anterior and posterior corners of the lateral margins of pronotum are not visible from above. Surface of pronotum weakly to distinctly microreticulate. Eighth sternite with anterior margin completely rounded to weakly produced at middle.

Females, measurements in mm (n=18): TL 1.16–1.50 (1.35 ± 0.09); PL 0.44–0.58 (0.51 ± 0.04); PW 0.44–0.60 (0.54 ± 0.04); EL 0.72–0.92 (0.84 ± 0.05); EW 0.46–0.62 (0.55 ± 0.04); GD 0.42 ± 0.54 (0.49 ± 0.04). Ratios: PL/PW 0.88–1.00 (0.95 ± 0.04); EL/EW 1.43–1.59 (1.51 ± 0.05); EL/PL 1.54–1.79 (1.64 ± 0.07); GD/EW 0.81–0.96 (0.89 ± 0.05); TL/EW 2.31–2.57 (2.43 ± 0.08).

Type series. Male holotype (CZUG) "MEXICO: Veracruz Dos Amates 03.vi.1988 S.L. Álavez *leg.*" "*Ceracis navarretei* Antunes-Carvalho & Lopes-Andrade HOLOTYPUS" [printed on red paper]. Paratypes: 19 males, 16 females (11 males and 12 females at CZUG, 8 males and 4 females at LAPC), same data as holotype; 2 females and 2 males (2 females and 1 male at ANIC, 1 male at LAPC) "MEXICO: Veracruz Dos Amates 28/2/1987 polypore 0114 J. Navarrete". All paratypes distinguished labeled "*Ceracis navarretei* Antunes-Carvalho & Lopes-Andrade PARATYPUS" [printed on yellow paper].

Natural history. Dos Amates is surrounded by small villages, being a mosaic of forest remnants and deforested areas apparently far from major urban areas. We have no information on the host-fungus of this new species. We only know that a few specimens were collected in a polypore (see "Type series" above).

Discussion

Organizing morphologically similar species of Ciidae into species-groups has been an useful taxonomic tool, especially in speciose genera as *Ceracis*, *Cis* Latreille and *Scolytocis* Blair (Lopes-Andrade 2008, Lopes-Andrade et al. 2002), as it facilitates the task of recognizing new species or synonyms. Currently, there are four defined species-groups (*cucullatus*, *furcatus*, *furcifer* and *singularis*) for 17 species of *Ceracis*. The *furcatus* group includes *C. furcatus* (Bosc), *C. militaris* Mellié, *C. minutus* Dury and *C. variabilis* (Mellié). These species were discussed together in the work of Lawrence (1967) and called a species-group by Lopes-Andrade (2002), who erroneously included *C. furcifer* Mellié (lapsus calami with *C. minutus*; Lopes-Andrade pers. obs.). *Ceracis furcifer* names another group including *C. cornifer* (Mellié), *C. cylindricus* (Brèthes), *C. furcifer*, *C. hastifer* (Mellié), *C. monocerus* Lawrence, *C. ruficornis* Pic, *C. simplicicornis* (Pic) and *C. unicornis* Gorham (sensu Lawrence 1967). The *singularis* group (sensu Lopes-Andrade et al. 2002) includes *C. furcicollis* (Blair), *C. limai* Lopes-Andrade et al. and *C. singularis* (Dury).

Lawrence (1967) proposed the *cucullatus* group for *C. bicornis* (Mellié) and *C. cucullatus*. He also synonymized *C. bilamellatus* (Pic), *C. lamellatus* (Pic) and *C. tabellifer* (Mellié) with *C. cucullatus* because they were described based on size and development of pronotal characters in the male, features considered variable within the populations examined by the author. *Ceracis cucullatus* and *C. bicornis* can be distinguished by the pronotal apex that is weakly emarginate in *C. cucullatus*, and deeply emarginate in *C. bicornis* forming two distinct horns in males with developed secondary sexual characteristics. Lawrence (1967) suggested that the nearctic *C. thoracornis* (Ziegler) and the palearctic *C. shikokuensis* (Miyatake) and *C. japonus* (Reitter) could be part of the *cucullatus* group, although not formally including them. We have examined named specimens of these three species and concluded that they are not similar enough to either *C. cucullatus* or *C. bicornis* to be included in the group. Here we redefine the *cucullatus* group so to include *C. cassumbensis* sp. n. and *C. navarretei* sp. n., as follows: (i) each antenna with eight or nine antennomeres, (ii) pronotum with fine and sparse punctation, (iii) body moderately long, and (iv) relatively long lamina on the apex of pronotum in males with fully developed secondary sexual characteristics. In the original proposal (see Lawrence 1967), only species with nine antennomeres were included in the *cucullatus* group. However, the number of antennomeres can vary even among morphologically similar species of *Ceracis*, as within the *furcifer* group: *C. furcifer* and *C. ruficornis* have eight antennomeres, while the other species have nine antennomeres (Lawrence 1967).

Among the species in the *cucullatus* group, as proposed here, *C. navarretei* sp. n. is possibly the most similar to *C. cucullatus*, mainly to its African populations. Differences are notable especially on male terminalia: The tegmen of *C. navarretei* sp. n. has the lateral edges parallel at most of their lengths, the apical third converging in straight line toward the apex. In named specimens of *C. cucullatus* examined by us, the sides of tegmen are either subparallel or weakly curved. Moreover, the aedeagus in *C. navarretei* sp. n. is 4× longer than wide, while in *C. cucullatus* it is around 3×. *Ceracis cassumbensis* sp. n. may be distinguished from *C. cucullatus* by its greater depth of the body (most evident when comparing females), antennae with eight antennomeres, elytral punctation denser and abdominal sex patch larger and transversely oval (Fig. 6, arrow). Moreover, either lateral edge of the tegmen in *C. cassumbensis* sp. n. has a peculiar excavation near apex (Fig. 7, arrows). This characteristic is also observed in *C. similis* Horn, although this species is distinguishable from *C. cassumbensis* sp. n. by its reddish body, punctation comparatively coarser and denser and relatively wider pronotal lamina.

The morphological limits of both *C. cucullatus* and *C. bicornis* were not satisfactorily established. The former is one of the most widely distributed ciid species in the tropics and the latter is widespread in the Neotropical region, having been reported in Mexico, Guatemala, Costa Rica, Peru (Lawrence 1967), northeastern, southeastern and southern Brazil (C. Lopes-Andrade pers. obs.). Morphological variation among allopatric populations of these species has been frequently observed and possibly interpreted as polymorphism, which may be overshadowing the recognition of new species. The description of *C. cassumbensis* sp. n. and *C. navarretei* sp. n. is a reflex of this scenario. *Ceracis cucullatus* and *C. bicornis* may be cryptic species complexes and shall be more carefully studied. Other *Ceracis* species, as those in the *furcatus* group, also have strong morphological interpopulational variation and possibly involve undescribed forms.

Acknowledgements

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CAPÍTULO II

Identity and distribution of species previously under the name *Ceracis cucullatus* (Mellié) (Coleoptera: Ciidae), with a discussion on an old case of biological invasion[1]

Caio Antunes-Carvalho & Cristiano Lopes-Andrade

Manuscrito original, apresentado em formato de submissão para publicação.

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[1] **Este manuscrito não deve ser considerado como publicação válida para fins de nomenclatura zoológica, de acordo com as normas do Código Internacional de Nomenclatura Zoológica (Cap. 3, Art. 8.2 e Art. 8.3).**

Identity and distribution of species previously under the name *Ceracis cucullatus* (Mellié) (Coleoptera: Ciidae), with a discussion on an old case of biological invasion[1]

Caio Antunes-Carvalho[a, *] & Cristiano Lopes-Andrade[b]

[a]*Programa de Pós-graduação em Entomologia, Departamento de Entomologia,*
Universidade Federal de Viçosa, 36570-000, Minas Gerais, Brazil
[b]*Departamento de Biologia Animal, Universidade Federal de Viçosa, 36570-000,*
Minas Gerais, Brazil

[*]Corresponding author
Email address: cantunescarvalho@gmail.com

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[1] **This manuscript should not be regarded as a valid publication for purposes of zoological nomenclature, in the sense of the Chapter 3, Article 8.2 and 8.3 of the International Code of Zoological Nomenclature.**

Abstract

The Neotropical obligate fungivore beetle *Ceracis cucullatus* (Mellié) has attracted attention of coleopterists due to the increasing number of records of populations in Africa. Although its disjunct populations have been interpreted as a cohesive taxonomic unit, previous comparisons between African and Neotropical specimens revealed inconsistencies in the external morphology among populations, causing uncertainty about the true unity of the species. Here, we compared the external morphology of specimens named as *C. cucullatus* from several localities of the Neotropical, Afrotropical, Afrotemperate and Oriental region. As results, we invalidate three previous junior synonymies of *C. cucullatus*, proposing *C. lamellatus* (Pic) and *C. tabellifer* (Mellié), both revalidated status, as separate species. We also propose *C. bilamellatus* (Pic) as a new synonym of *C. tabellifer*. In face of these taxonomic changes, we identify *C. tabellifer* as the actual invasive species on African lands, instead *C. cucullatus* as was previously accepted. Then, through historical records gathered from scientific collections and literature, and through examination of recently collected specimens from South Africa, we provide the geographic distribution of *C. tabellifer* and its host fungi species. Based on these data, we discuss possible explanations to the successful invasion of *C. tabellifer* in Africa and elsewhere and its potential threat to native fauna of ciids. This study helps to fill an old gap in the literature on bioinvasions, in which most studies consider predatory species, disease vectors or potential pests of agricultural crops.

1. Introduction

Ceracis cucullatus (Mellié) belongs to Ciidae (Coleoptera: Tenebrionoidea), a family of small obligate fungivorous beetles that live and breed in polypore basidiomes worldwidely. *Ceracis cucullatus* was originally described as *Ennearthron cucullatum* by Mellié in 1849, based on specimens collected in Cayenne (French Guiana) and Cape of Good Hope (South Africa), and posteriorly transferred to *Ceracis* Mellié by Lawrence (1967). It names the *cucullatus* species group, which currently comprises *C. bicornis* (Mellié), *C. cassumbensis* Antunes-Carvalho & Lopes-Andrade, 2011, *C. cucullatus* and *C. navarretei* Atunes-Carvalho & Lopes-Andrade, 2011. It also encompasses the names *C. tabellifer* (Mellié), *C. billamelatus* (Pic) and *C. lamellatus* (Pic), junior synonymies of *C. cucullatus*. These synonymies were proposed by Lawrence (1967) who argued that they were described as new based primarily on differences in size and development degree of male pronotal projections. Such secondary sexual characteristics exhibit a wide variation in size and sometimes even in form, as they have allometric growth. It is common to find males with either conspicuous or weak secondary characteristics coexisting in a single population. This phenotypic plasticity may hamper the delimitation and species identification causing synonymies.

As *C. billamelatus* was described from Madagascar, *C. tabellifer* from South Africa and *C. lamellatus* from Brazil, the synonym of these with *C. cucullatus* led it to be considered a broadly distributed species. The records of populations in areas beyond its native range are old and have accumulated over the years, attracting the attention of ciidologists. Populations have been found in Italy, France and Britain (Abeille de Perrin, 1874; Müller *et al*. 2001, Orledge *et al*. 2010), although they appear not to be free-living in these countries. Various records of populations in islands are also known, such as Galapagos, in the Pacific Ocean, and Reunion, Mauritius, Seychelles and Aldabra, at the western Indian Ocean (Lesne, 1917; Scott, 1926; Lawrence, 1967b). As most species of *Ceracis* inhabits the Neotropical region, and given the absence of other *Ceracis* species in Africa, non-Neotropical populations of *C. cucullatus* have been interpreted as a result of introduction (Scott, 1926; Lawrence, 1967b).

The most reliable way to distinguish ciid species is combining traditional information of the external morphology with that of male abdominal terminalia. High morphological stability and specificity of male terminalia is observed not only in ciids, but in many other animals, especially arthropods (Mayr & Ashlock, 1991) and it is largely explained by its rapid evolutionary divergence among phylogenetically related species (Eberhard, 2010). For this reason, the use of genitalic structures is widespread in animal taxonomy. Despite this, in the taxonomy of subtropical and tropical Ciidae, the use of male terminalia to distinguish species was consolidated mostly over the last decade, during which several new ciid species have had their descriptions largely supported by the morphology of male terminalia (*e.g.* Lopes-Andrade, 2007; Lopes-Andrade, 2008; Lopes-Andrade *et al*., 2009; Lopes-Andrade, 2010; Antunes-Carvalho & Lopes-Andrade, 2011; Lopes-Andrade, 2011). Although the disjunct populations named as *C. cucullatus* have been interpreted as a cohesive taxonomic unit, previous comparisons between African and Neotropical specimens revealed inconsistencies in the external morphology, including male abdominal terminalia, leading us to doubt on the conspecificity of populations under this name. The proposed junior synonymies of *C. cucullatus* were based only on the comparison of types and named specimens of a few populations, and male abdominal terminalia were possibly not dissected and compared.

The present study aims to evaluate the actual status of disjunct populations under the name *C. cucullatus*. Thus, we analysed and compared the general external morphology and male abdominal terminalia of populations from several localities of the Neotropical, Afrotropical, Afrotemperate and Oriental regions. As results, we invalidated *C. bilamellatus, C. lamellatus* and *C. tabellifer* as senior synonyms of *C. cucullatus*, and propose *C. bilamellatus* as a new synonym of *C. tabellifer*. The three species are sustained as valid and here were redescribed. Additionally, based on data of the host fungi and historical records of *C. tabellifer* in the African continent, we conducted a wide discussion on its successful invasion in Africa and other regions.

2. Material and methods

2.1. Comparisons, pictorial documentation and measurements

Comparisons. We examined and compared the external morphology of a representative number of specimens originally named *C. cucullatus* from localities of the Neotropical, Palearctic, Oriental, Afrotropical and Afrotemperate regions, including a number of islands of the western Indian Ocean. We also dissected and carefully compared the morphology of male abdominal terminalia of representative specimens from these regions. Comparisons, examination and measurements of general external morphology were made under a Zeiss Stemi 2000-C stereomicroscope or a Zeiss Axiolab microscope. Terms used here for external morphology, including male terminalia, are explained and discussed by Lopes-Andrade and Lawrence (2005).

Pictorial documentation. Digital photographs of adult specimens were taken with a Canon EOS 1000D attached to a Zeiss Stemi 2000-C stereomicroscope. Final images were the result of joining 20 to 50 photomicrographs at different focal depths using the image stacking software Zerene Stacker (v1.04). The names *C. cucullatus*, *C. lamellatus* and *C. tabellifer* used from now on refer to these species in their new sense, here proposed, unless otherwise specified. Images and redescriptions of *C. cucullatus* and *C. tabellifer* are based on the respective male lectotype, here designated, and those of *C. lamellatus* on a male topotype. The specimen chosen as lectotype of *C. lamellatus*, here designated, was examined but could not be borrowed. The syntypes of the species treated in the present work were all labelled as lectotypes or paralectotypes by John F. Lawrence, but they were not officially designated in the literature. We preferred to maintain Lawrence's labels so to avoid future confusions. Whole mount preparations followed the protocol described by Lopes-Andrade (2011), and photographs were taken under a ZEISS Axiolab A1 compound microscope equipped with a ZEISS Axiocam Erc5S digital camera. Scanning Electron Microscope (SEM) images were taken with a LEO 1430 VP. Specimens examined under SEM were dehydrated in a series of alcohol solutions, dried in a Critical Point Dryer (Balzers CPD 020), mounted on stubs and sputter-coated with gold (Balzers Sputter Module SCA 010). The SEM images of *C. cucullatus* are of specimens from Canarana, Brazil (Figs 26–29) and those of *C. tabellifer* are of specimens from Lubumbashi, Congo (Figs 31–34). Specimens of *C. cucullatus* from Galapagos (Fig. 25) and of *C. tabellifer* from Cape of Good Hope, South Africa (Fig. 30) were examined under variable pressure (SEM-VP) with backscattered electrons detector, without prior dehydration or gold covering.

Measurements. A representative sample of specimens of both species were measured. The values provided for *C. cucullatus* are from populations collected in Brazil, Panama and Galapagos. For *C. tabellifer*, we measured specimens from Brazil, South Africa, Congo and Gambia. Values for *C. lamellatus* are of topotypes. The following abbreviations are used for measurements (in millimeters) and ratios: BW, basal width of the scutellum; CL, length of the antennal club (corresponding to antennomeres eight to ten); EL, elytral length (median length from base of scutellum to elytral apex); EW, greatest elytral width; FL, length of the antennal funicle (corresponding to antennomeres three to seven); GD, greatest depth of the body (from elytra to metaventrite); PL, pronotal length along midline; PW, greatest pronotal width; TL, total length (EL+PL; head not included). The ratio GD/EW was taken as an indication of degree of convexity; TL/EW indicates degree of body elongation. Range, mean and standard deviation are given for each measurement and ratio in the section on “Variation”.

2.2. Dissected material

We dissected males of specimens previously named *C. cucullatus*, or unidentified specimens resembling the species, from the following localities: Canarana, Chapada dos Guimarães and Nova Teutônia (Brazil), Vista Hermosa (Colombia), Cayenne (French Guiana), Fort Sherman (Panama), Santa Rosa (Galapagos Islands), Pretoria (South Africa), Kirungu, Kisantu and Lubumbashi (Congo), Bakau (Gambia), Hanoi (Vietnan) and Befanamy (Madagascar). Therefore, we have representative samples of male abdominal terminalia from populations located at the southern and northernmost distribution of species previously under the name *C. cucullatus* (Figure 1).

2.3. Host fungi and collection data of *Ceracis tabellifer* (Mellié) in South Africa

Field collections of polypore basidiomes were carried out in several localities from South Africa between 2002 and 2010, led by Ottilie Neser as part of her study on *Astichus* Föster (Hymenoptera: Eulophidae), parasitoids of Ciidae (see Neser, 2012). The fungi were collected by the team of Neser opportunistically during walks and travels and taken to the laboratory where ciids were sorted, then mounted on cards or kept in gelatin capsules. All host fungi and associated ciids were identified to the lowest possible taxonomic level (see details in Neser, 2012). The adult ciids found together with *Astichus* were sent for identification to the junior author of the present study. Thus, for each basidiome with *C. tabellifer*, we could record the number of other ciid species and the number of specimens per species habiting the same basidiome or basidiomes of the same host fungus collected together (see Table 1).

2.4. Maps and geographic distribution

Aiming to trace the geographical distribution of *C. cucullatus*, *C. lamellatus* and *C. tabellifer*, we searched for records of these species by direct observation of labels in museum materials and throughout literature. We estimated latitude and longitude coordinates by tracking localities in the online database GeoNames (Wick, 2010) and plotting them in a map using the software ArcGis 9.3 (ESRI, Redlands, CA, USA).

Here, *invasive species* refers to non-native species that establish populations and spread widely beyond the site of initial introduction (as adopted by Kolar & Lodge, 2001; Keller & Taylor, 2008; Walther *et al.* 2009, among many other authors) – this is not necessarily associated to impact.

The acronyms used in this paper are listed below.

ANIC	Australian National Insect Collection; CSIRO Ecosystem Sciences (Canberra, Australia: John F. Lawrence)
CMN	Canadian Museum of Nature (Ottawa, Canada: François Génier)
KMMA	Koninklijk Museum voor Midden Afrika (Tervuren, Belgium: Marc De Meyer)
LAPC	Cristiano Lopes-Andrade Private Collection (Viçosa, Minas Gerais, Brazil)
MFN	Museum für Naturkunde (Berlin, Germany: Manfred Uhlig)
MHNG	Muséum d’Histoire Naturelle (Geneva, Switzerland: Giulio Cuccodoro)
MZLU	Museum of Zoology, Lund University (Lund, Sweden: Roy Danielsson)

MNHN	Muséum national d' Histoire naturelle (Paris, France: Thierry Deuve)
SANC	South African National Collection of Insects (Pretoria, South Africa: Riaan_Stals)
SNSD	Senckenberg Naturhistorische Sammlungen Dresden (Dresden, Alemanha: Klauss Dieter-Klass)

3. Results

3.1. Taxonomy

Based on patterns of the external morphology of adults, including male abdominal terminalia, we (i) revalidate both *C. tabellifer* and *C. lamellatus* as separate species, (ii) invalidate the synonymy of *C. bilamellatus* with *C. cucullatus* and (iii) propose *C. bilamellatus* as a new synonym of *C. tabellifer*, as the populations from continental Africa (*C. tabellifer*) and Madagascar (described as *C. bilamellatus*) do not express consistent morphological differences. Therefore, the *cucullatus* species-group now includes the following six species:

Ceracis bicornis (Mellié, 1849)
Ceracis cassumbensis Antunes-Carvalho & Lopes-Andrade, 2011
Ceracis cucullatus (Mellié, 1849), **new sense**
Ceracis lamellatus (Pic, 1939), **revalidated status**
Ceracis navarretei Antunes-Carvalho & Lopes-Andrade, 2011
Ceracis tabellifer (Mellié, 1849), **new sense and revalidated status**
  Ennearthron bilamellatum Pic, 1916, **new synonym**

The redescriptions of *C. cucullatus*, *C. lamellatus* and *C. tabellifer* are provided below. An identification key for adult males of *Ceracis* of the *cucullatus* species-group is provided in the section 3.2.

3.1.1. *Ceracis cucullatus* (Mellié, 1849), new sense

Figs 2–7, 19, 22, 25–29

Diagnosis. Eighth sternite with anterior margin distinctly produced and angulate at middle, its apex conspicuously beyond the anterolateral angles (Fig. 19). Tegmen with basal portion narrow, differentiated; basal interior margin narrow and rounded. Penis elongate, subcylindrical; basal portion opened, leaving the inferior limits of the lateral margins disconnected; lateral margins narrow, subparallel at the basal three-fourths and abruptly converging at the beginning of the apical one-fourth; apical portion narrowed and weakly sclerotized.

Lectotype, here designated (Figs 2–4). Measurements in mm: TL 1.49, PL 0.64, PW 0.56, EL 0.85, EW 0.58, GD 0.51. Ratios: PL/PW 1.13, EL/EW 1.48, EL/PL 1.33, GD/EW 0.89, TL/EW 2.59. Body elongate, subcylindrical; dorsal and ventral surfaces mostly dark reddish brown; appendices yellowish brown. Head barely visible from above; dorsal surface smooth, with a small salience at middle; frontoclypeal ridge produced forward, transversely concave, its anterior margin weakly emarginated at middle, the anterior edge with a row of setae along it. Eyes coarsely facetted, with minute slender yellowish setae emerging from the intersection between ommatidia. Each antennae with nine antennomeres; length of antennomeres (in mm) as follows (from base to apex): 0.06, 0.04, 0.03, 0.02, 0.02, 0.02, 0.04, 0.05, 0.06 (left antenna measured; FL 0.19 mm, CL 0.15 mm, CL/FL 0.79); each antennomere of the club bearing several sparse slender setae and four conspicuous sensillifers symmetrically positioned at its upper portion. Pronotum with subparallel sides; lateral margins narrow, visible from above only for the posterior corners; anterior edge projected forwards forming a quadrangular plate, slightly emarginated at middle; anterolateral angles obtuse, not produced; disc with relatively fine, single, uniformly distributed punctation; in between punctures from one to two puncture widths; vestiture consisting of yellowish decumbent minute seta. Scutellum small, subtriangular, glabrous; basal width of 0.08 mm; length along the longitudinal midline 0.05 mm. Elytra with lateral margins subparallel at the basal two thirds, then abruptly converging to the apex; only the anterior angles visible from above; punctation single, very fine, confused, denser than pronotal punctation; vestiture consisting of minute decumbent yellowish setae; in between punctures smooth and shiny, shallowly rugose. Hind wings developed. Ventral sclerites with most of their surfaces granulate. Prosternum in front of coxae shallowly concave longitudinally and transversely convex; surface beside coxae weakly concave; prosternal process laminate, almost as long as coxae. Metaventrite moderately convex, subglabrous, with sparse slender setae; punctation not observed; discrimen indiscernible. Each protibia with the apex expanded; outer apical angle rounded and bearing a row of spines. Abdominal ventrites bearing several slender setae, longer than those on dorsal surface; punctation shallow and sparse; lengths of abdominal ventrites (from base to apex, at the longitudinal midline) as follows (in mm): 0.19, 0.07, 0.08, 0.08, 0.07; first abdominal ventrite with a basal width of 0.48 mm and bearing a circular sex patch located postered of center, with a transverse diameter of 0.04 mm.

Male terminalia (Figs 19, 22). Eighth sternite with posterior margin slightly emarginated at middle; posterior corners rounded, bearing bristles; lateral margins diverging from the posterior to their anterior portions; anterior margin distinctly produced and angulate at middle, its apex conspicuously beyond the anterolateral angles (Fig. 19). Tegmen 3 times as long as wide, twice as wide as penis, and 3 times as long as the greatest width of the eighth sternite; basal portion narrowed, differentiated; basal interior margin narrow and rounded; lateral margins subparallel at the two basal thirds of its length, and then angulate at the beginning of the apical third; apex of each lateral margin narrow, with a few sensilla (Fig. 22). Penis elongate, subcylindrical; basal portion opened (=not membranous), leaving the inferior limits of the lateral margins disconnected; lateral margins narrow, subparallel at the basal three-fourths, abruptly converging at the beginning of the apical one-fourth; apical portion narrowed and weakly sclerotized (Fig. 22).

Females (Figs 5–6). Similar to males, but frontoclypeal ridge, lateral and anterior margins of pronotum rounded, not produced. Dorsal surface of head devoid of prominences. Abdominal sex patch absent. Usually smaller than males.

Variation. Males, measurements in mm (n = 43, including the lectotype): TL 0.94–1.53 (1.26 ± 0.14); PL 0.43–0.68 (0.56 ± 0.07); PW 0.40–0.56 (0.48 ± 0.04); EL 0.48–0.85 (0.70 ± 0.07); EW 0.41–0.58 (0.49 ± 0.04); GD 0.38–0.51 (0.44 ± 0.04). Ratios: PL/PW 1.00–1.29 (1.15 ± 0.06); EL/EW 1.12–1.55 (1.44 ± 0.07); EL/PL 1.03–1.47 (1.27 ± 0.09); GD/EW 0.85–0.95 (0.89 ± 0.02); TL/EW 2.21–2.76 (2.58 ± 0.11). Body varying from dark brown or dark reddish brown to black. Frontoclypeal ridge and anterior edge of pronotum varying from strongly projected in large males to weakly or not produced in small ones. In the last case, the frontoclypeal ridge and anterior margins of pronotum are rounded, making the smallest males morphologically similar to females. In males from midwest Brazil, the pronotal projection is usually projected forward, not upward. The body size of specimens from northern of South America and especially from Galapagos islands is greater than those of midwest of Brazil. This difference also occurs with the abdominal male terminalia, which is longer in insular populations. Females, measurements in mm (n = 21): TL 1.00–1.44 (1.18 ± 0.12); PL 0.38–0.64 (0.45 ± 0.06); PW 0.39–0.55 (0.45 ± 0.04); EL 0.63–0.89 (0.72 ± 0.06); EW 0.40–0.59 (0.49 ± 0.04); GD 0.36–0.51 (0.43 ± 0.04). Ratios: PL/PW 0.91–1.28 (1.01 ± 0.07); EL/EW 1.38–1.56 (1.49 ± 0.04); EL/PL 1.25–1.80 (1.60 ± 0.11); GD/EW 0.86–0.92 (0.89 ± 0.02); TL/EW 2.23–2.67 (2.42 ± 0.09).

Host fungi. The following records of host fungi were taken from labels, mainly from specimens collected in Panama, and updated consulting *Index fungorum* (http://www.indexfungorum.org): *Rigidoporus* sp., *Polyporus conchoids*, *Trametes corrugata* (Pers.) Bres., *Trametes cirrifer Picnoporus sanguinus* (L.) Murrill, *Hexagonia hydnoides* (Sw.) M. Fidalgo, *Trichaptum sector* (Ehrenb.) Kreisel, *Ganoderma applanatum* (Pers.) Pat.

Distribution (Fig. 35). From southern Mexico to midwest Brazil. Also in the Galapagos islands (possibly introduced).

Material examined. Lectotype, here designated (MNHN)\ Coll. Olivier [handwritten]\ [red label] LECTOTYPE [printed] Ennearthron cucullatum Mellie [handwritten]\ (see Fig. 5); 2 paralectotypes, here designated (MNHN)\ [blue circular label] Enneartho cucullatum [handwritten] [words difficult to interpret]\ [yellow label] PARALECTOTYPE [printed] Ennearthron cucullatum Mellie [handwritten]\. **French Guiana**: 7 specimens (MNHN)\ Cayenne [handwritten]\ [blue label] MUSEUM PARIS, Collection Léon Fairmaire, 1906\ Ennearthron cucullatum [handwritten]. **Guadeloupe**: 1 specimen (MNHN)\ [blue label] MUSEUM PARIS, GUADELOUPE, Env. De Trois-Riviéres, LEO DUFAU 1904 [printed]\ Ceracis cucullatus (Mellie) [handwritten] 1969 J.F. Lawrence\. **Cuba**: 1 specimen (MNHN)\ Cuba, Ennearthron cucullatum [handwritten]. **Panama**: 2

specimens (ANIC)\ Barro Colorado Is. CANAL ZONE July [printed] 6 [handwritten] 1969 [printed]\ J.F. Lawrence Lot. [printed] 2791 [handwritten]\ Rigidoporus sp.\; 3 specimens (ANIC)\ Barro Colorado Is. CANAL ZONE Feb. 14, 1968\ J.F. Lawrence Lot. [printed] 2412 [handwritten]\ Polyporus conchoids\; 2 specimens (ANIC)\ Fort Sherman Canal Zone Panama, IV-2-67\ J.F. Lawrence Lot. [printed] 2079 [handwritten]\ Trametes corrugata\; 1 specimen (ANIC)\ Barro Colorado Is. CANAL ZONE Feb. 23, 1968\ J.F. Lawrence Lot. [printed] 2474 [handwritten]\ Trametes cirrifer\; 1 specimen (ANIC)\ Barro Colorado Is. CANAL ZONE Feb. 23, 1968\ J.F. Lawrence Lot. [printed] 2263 [handwritten]\ Trametes cirrifer\; 1 specimen (ANIC)\ Barro Colorado Is. CANAL ZONE Aug. [printed] 6 [handwritten] 1969 [printed]\ J.F. Lawrence Lot. [printed] 2996 [handwritten]\ Trametes corrugata [printed]\; 1 specimen (ANIC)\ Madden Dam CANAL ZONE VII-18-1969\ J.F. Lawrence Lot. [printed] 2903 [handwritten]\ Polyporus sanguineus\; 1 specimen (ANIC)\ Madden Dam CANAL ZONE VII-18-1969\ J.F. Lawrence Lot. [printed] 2905 [handwritten]\ Polyporus hydnoides\; 4 specimens (ANIC)\ Madden Dam CANAL ZONE VII-18-1969\ J.F. Lawrence Lot. [printed] 2908 [handwritten]\ Hexagona sp.\; 1 specimen (ANIC)\ Barro Colorado Is. CANAL ZONE July [printed] 25 [handwritten] 1969 [printed]\ J.F. Lawrence Lot. [printed] 2961 [handwritten]\ ex Polyporus sector\; 1 specimen (ANIC)\ Barro Colorado Is. CANAL ZONE July [printed] 10 [handwritten] 1969 [printed]\ J.F. Lawrence Lot. [printed] 2833 [handwritten]\ Ganoderma sp.\; 2 specimens (ANIC)\ Fort Sherman Canal Zone Panama, IV-2-67\ J.F. Lawrence Lot. [printed] 2085 [handwritten]\ Rigidoporus sp.\; 2 specimens (ANIC)\ Barro Colorado Is. CANAL ZONE July [printed] 3 [handwritten] 1969 [printed]\ J.F. Lawrence Lot. [printed] 2750 [handwritten]\ Ganoderma sp.\; 2 specimens (ANIC)\ Fort Sherman Canal Zone Panama, IV-2-67\ J.F. Lawrence Lot. [printed] 2079 [handwritten]\ Trametes corrugata\; 3 specimens (ANIC)\ CANAL ZONE: 5mi. SW Fort Sherman Mas. 2, 1975 Lawrence, Erwin\ J.F. Lawrence [printed] Lot 3841 [handwritten]\. **Ecuador** : 2 specimens (ANIC)\ ECUAD: Pichincha Rio Palenque, 47 km.s Sto.Domingo May 18-29, 1975\ J.F. Lawrence Lot No. [printed] 4055 [handwritten]\ A. Forsyth S.&J. Peck collectors\ Rigidoporus\ ; 1 specimen (ANIC)\ ECUAD: Pichincha Rio Palenque, 47 km.s Sto.Domingo July 20-30, 1975[handwritten]\ J.F. Lawrence Lot No. [printed] 4062 [handwritten]\ A. Forsyth S.&J. Peck collectors\ Rigidoporus\. **Galapagos Islands**: 1 specimen (CMN)\ ECU: Galap; St. Cruz 2KmN Bellavista 360m, guavathicket 14.V-13.VII.85, S&J Peck Agricultural area, FIT\ [yellow label] CMN 108\; 2 specimens (ANIC)\ ECU: Galap; St. Cruz 2KmN Bellavista 360m, guavathicket 14.V-13.VII.85, S&J Peck Agricultural area, FIT\; 1 specimen (CMN)\ ECU: Galapagos Isabela, Sto. Tomas 4-15.III.89, 330m humidforest, FIT Peck&Sinclair, 89-100\ [yellow label] CMN 112\; 1 specimen (CMN)\ ECU: Galapagos SantaCruz, Sta. Rosa., Scalesia [underlined] zone bracketfungi 5.II.89, S. Peck, 89-100\ [yellow label] CMN 111\; 1 specimen (CMN)\ ECU: Galapagos SantaCruz, Sta. Rosa. ,Scalesia [underlined] zone bracketfungi 5.II.89, S. Peck, 89-100\ [yellow label] CMN 109\; 1 specimen (CMN)\ ECU: Galapagos SantaCruz, 5KmN Pto. Ayora, trans.z. III.89, bracketfungi S. Peck 89-192\ [yellow label] CMN 110\; 2 specimens (ANIC)\ Santa Cruz Is., Galapagos II-1964\ J.F. Lawrence Lot. [printed] 1293 [handwritten]\ R.L.Usinger Coll. [handwritten]\ ex Ganoderma applanatum\. **Colombia**: 1 specimen (LAPC)\ Colombia: Meta, Vista Hermosa, Vda. La Reforma PNN La Macarena iv.2010 [printed] .2-3 [handwritten] leg J.L. Contreras \ 2°37’52’’N 75°44’10.3’’W 269 m\. **Brazil**: 50 specimens (LAPC)\ BRASIL: MT Canarana; “Faz. Santa Marta” 22.xii.2008 C.M. Mews *leg*.\.

3.1.2. *Ceracis lamellatus* (Pic, 1939), revalidated status

Figs 8–12, 20, 23.

Diagnosis. Eighth sternite with posterior corners rectangular; anterior margin sinuous, slightly produced at middle but apex at the same height of the anterolateral angles. Tegmen with basal portion narrow, differentiated; lateral margins converging gradually to apex. Penis elongate; basal portion opened; lateral margins narrow, subparallel at the basal one-third, converging gradually along the second-third of its length, and abruptly converging at beginning of the apical third, following parallel and very close at final extension of the apex.

Male topotype (Figs 8–10). Measurements in mm: TL 1.80, PL 0.78, PW 0.70, EL 1.03, EW 0.68, GD 0.66. Ratios: PL/PW 1.11, EL/EW 1.52, EL/PL 1.32, GD/EW 0.98, TL/EW 2.67. Body elongate, convex; elytra, apex of pronotum, proventrite, mesoventrite and abdomen reddish brown, remainder of pronotum and metaventrite dark reddish brown; appendices yellowish brown. Head barely visible from above; dorsal surface smooth, with a slight salience at middle; frontoclypeal ridge produced forward, transversely concave, its anterior margin weakly emarginated at middle, the anterior edge with a row of setae along it. Eyes coarsely facetted; some minute slender yellowish setae emerging from the intersection between ommatidia. Each antenna with nine antennomeres; length of antennomeres (in mm) as follows (from base to apex): 0.07, 0.04, 0.03, 0.02, 0.02, 0.02, 0.04, 0.05, 0.07 (right antenna measured; FL 0.20 mm, CL 0.16 mm, CL/FL 0.80); each antennomere of the club bearing several sparse slender setae and four conspicuous sensillifers symmetrically positioned at its upper portion. Pronotum with subparallel sides; lateral margins narrow, visible from above only for the anterior corners; anterior edge projected forwards forming a quadrangular plate, slightly emarginated at middle (see the section on "variation"); anterolateral angles obtuse, not produced; disc with relatively fine, single, uniformly distributed punctation; in between punctures from 1.50 to three puncture widths; vestiture consisting of yellowish decumbent minute seta. Scutellum small, triangular, glabrous; basal width of 0.10 mm; length along the longitudinal midline 0.06 mm. Elytra with lateral margins subparallel at the basal half, then gradually converging to the apex; only the anterior angles visible from above; punctation single, very fine, confused, denser than pronotal punctation; vestiture consisting of minute decumbent yellowish setae; in between punctures smooth and shiny, shallowly rugose. Hind wings developed. Ventral sclerites with most of their surfaces granulate. Prosternum in front of coxae shallowly concave longitudinally and transversely convex; surface beside coxae weakly concave; prosternal process laminate, almost as long as coxae. Metaventrite moderately convex, subglabrous, with sparse slender setae; punctation indiscernible; discrimen not visible. Each protibia with the apex expanded; outer apical angle rounded and bearing a row of spines. Abdominal ventrites bearing several slender setae, longer than those on dorsal surface; punctation indiscernible; length of the abdominal ventrites (from base to apex, at the longitudinal midline) as follows (in mm): 0.22, 0.07, 0.07, 0.07, 0.09; first abdominal ventrite with a basal width of 0.59 mm and bearing a circular sex patch located postered of center, with a transverse diameter of 0.06 mm.

Male terminalia (Figs 20, 23). Eighth sternite with posterior margin barely emarginated at middle; posterior corners rectangular, bearing bristles; lateral margins diverging from the posterior to their anterior portions; anterior margin sinuous, slightly produced at middle but apex at the same height of the anterolateral angles (Fig. 20). Tegmen 3 times as long as wide, about 1.6 times as wide as penis, and about 1.3 times as long as the greatest width of the eighth sternite; basal portion narrowed, differentiated; lateral margins converging gradually to apex; apex of each lateral margin narrow, sensilla indiscernible (Fig. 23). Penis elongate; basal portion opened (=not membranous); lateral margins narrow, subparallel at the basal one-third, converging gradually along the second-third of its length, and abruptly converging at beginning of the apical third; apical portion narrowed and moderately sclerotized (Fig. 23).

Females (Figs 11–12). Similar to males, but frontoclypeal ridge, lateral and anterior margins of pronotum rounded, not produced. Dorsal surface of head devoid of prominences. Abdominal sex patch absent. Usually smaller and with coloration darker than males.

Variation. Males, measurements in mm (n = 2): TL 1.65–1.80 (1.73 ± 0.11); PL 0.70–0.78 (0.74 ± 0.05); PW 0.65–0.70 (0.68 ± 0.04); EL 0.95–1.03 (0.95 ± 1.03); EW 0.64–0.68 (0.66 ± 0.03); GD 0.59–0.66 (0.63 ± 0.05). Ratios: PL/PW 1.08–1.11(1.09 ± 0.02); EL/EW 1.49–1.52 (1.50 ± 0.02); EL/PL 1.32–1.36 (1.34 ± 0.02); GD/EW 0.92–0.98 (0.95 ± 0.04); TL/EW 2.59–2.67 (2.63 ± 0.06). Body varying from dark reddish brown to reddish brown; pronotum and elytra sometimes with the same coloration, but the first being often darkest. Frontoclypeal ridge and anterior edge of pronotum extremely projected in the largest males and weakly produced in smallest ones. Female, measurements in mm (n = 1): TL 1.38; PL 0.48; PW 0.53; EL 0.90; EW 0.60; GD 0.55. Ratios: PL/PW 0.90; EL/EW 1.50; EL/PL 1.89; GD/EW 0. 92; TL/EW 2.29.

Host fungi. Unknown

Distribution (Fig. 35). Known only from Nova Teutônia, southern Brazil.

Material examined. 3 specimens (ANIC)\ Nova Teutonia Sta. Catalina BRAZIL [printed] XI [handwritten] -1964 FritzPlaumann [printed]\; 6 paralectotypes, here designated (MNHN)\ BRASILIEN Nova Teutonia FritzPlaumann [handwritten]\ [yellow label] PARALECTOTYPE [printed] Ennearthron lamellatum Pic [handwritten]\.

3.1.3. *Ceracis tabellifer* (Mellié, 1849), new sense and revalidated status

Ennearthron bilamellatum Pic 1916: 20, **new junior synonym**

Figs 13–18, 21, 24, 30–34

Diagnosis. Eighth sternite with anterior barely projected at middle, almost straight. Tegmen with basal portion subtriangular; basal interior margin thick and V-shaped; lateral margins subparallel at the basal two-thirds of their lengths, angulate at the beginning of the apical third and then slightly curved to apex; apex of each lateral margin converging inwards, bearing several sensilla. Penis with basal portion closed, membranous; lateral margins narrow, subparallel at the basal three-fourths, with the apical portion forming well sclerotized arcs.

Lectotype, here designated (Figs 13–15). Measurements in mm: TL 1.40, PL 0.55, PW 0.55, EL 0.85, EW 0.55, GD 0.50. Ratios: PL/PW 1.00, EL/EW 1.55, EL/PL 1.55, GD/EW 0.91, TL/EW 2.55. Body elongate, reasonably robust, subcylindrical; pronotum and ventral surfaces mostly dark reddish brown; elytra reddish brown; appendices yellowish brown. Head barely visible from above; dorsal surface smooth, with a small salience at middle; frontoclypeal ridge produced forward, transversely concave, its anterior margin weakly emarginated at middle, the anterior edge with a row of setae along it. Eyes coarsely facetted; minute slender yellowish setae emerging from the intersection between ommatidia. Each antenna with nine antennomeres; length of antennomeres (in mm) as follows (from base to apex): 0.06, 0.04, 0.03, 0.02, 0.02, 0.01, 0.04, 0.04, 0.05 (left antenna measured; FL 0.18 mm, CL 0.13 mm, CL/FL 0.72); each antennomere of the club bearing several sparse slender setae and four conspicuous sensillifers symmetrically positioned at its upper portion. Pronotum with subparallel sides; lateral margins narrow, visible from above only for the anterior corners; anterior edge projected forwards forming a plate, slightly emarginated at middle (see the section on "variation"); anterolateral angles obtuse, not produced; disc with relatively fine, single, uniformly distributed punctation; in between punctures from 1.25 to 2.00 puncture widths; vestiture consisting of yellowish decumbent minute seta. Scutellum small, subtriangular, punctate, glabrous; basal width of 0.08 mm; length along the longitudinal midline 0.04 mm. Elytra with lateral margins subparallel at the basal second third, then abruptly converging to the apex; only the anterior angles visible from above; punctation single, very fine, confused, denser than pronotal punctation; vestiture consisting of minute decumbent yellowish setae; in between punctures smooth and shiny, shallowly rugose. Hind wings developed. Ventral sclerites with most of their surfaces granulate. Prosternum in front of coxae shallowly concave longitudinally and transversely convex; surface beside coxae weakly concave; prosternal process laminate, almost as long as coxae. Metaventrite moderately convex, subglabrous, with sparse slender setae; punctation very shallow and sparse, almost imperceptible; discrimen indiscernible. Each protibia with the apex expanded; outer apical angle rounded and bearing a row of spines. Abdominal ventrites bearing several slender setae, longer than those on dorsal surface; punctation shallow and sparse; length of the abdominal ventrites (from base to apex, at the longitudinal midline) as follows (in mm): 0.17, 0.06, 0.07, 0.08, 0.08; first abdominal ventrite with a basal width of 0.48 mm and bearing a circular sex patch located postered of center, with a transverse diameter of 0.04 mm.

Male terminalia (Figs 21, 24). Eighth sternite with posterior margin slightly emarginated at middle; posterior angles rounded, bearing bristles; lateral margins diverging; anterior margin weakly projected at middle, almost straight (Fig. 21). Tegmen almost 3 times as long as wide, twice as wide as penis, and 1.2 times as long as the greatest width of the eighth sternite; basal portion subtriangular; basal interior margin thick and V-shaped; lateral margins subparallel at their basal two-thirds, angulate at the beginning of the apical third and then slightly curved to apex; apex of each lateral margin converging inwards, bearing several sensilla (Fig. 24). Penis elongate, subcylindrical; basal portion closed, membranous; lateral margins narrow, subparallel at the basal three-fourths, with the apical portion forming well sclerotized arcs (Fig. 24).

Females (Figs 18–19). Similar to males, but frontoclypeal ridge, lateral and anterior margins of pronotum rounded, not produced. Dorsal surface of head devoid of prominences. Abdominal sex patch absent. Usually smaller than males.

Variation. Males, measurements in mm (n = 56, including the): TL 1.06–1.78 (1.42 ± 0.13); PL 0.39–0.73 (0.58 ± 0.07); PW 0.40–0.66 (0.55 ± 0.05); EL 0.64–1.08 (0.84 ± 0.08); EW 0.45–0.69 (0.56 ± 0.04); GD 0.36–0.61 (0.50 ± 0.04). Ratios: PL/PW 0.78–1.16 (1.06 ± 0.06); EL/EW 1.11–1.62 (1.48 ± 0.07); EL/PL 1.09–2.00 (1.44 ± 0.13); GD/EW 0.81–0.96 (0.88 ± 0.02); TL/EW 2.13–2.74 (2.52 ± 0.10).

Body varying from dark brown to dark reddish brown, sometimes almost black. Frontoclypeal ridge and anterior edge of pronotum strongly projected in the largest males and weakly or not produced in smallest ones. In the last case, the frontoclypeal ridge and anterior margins of pronotum are rounded, making the smallest males morphologically similar to females. In general, the specimens that live outside neotropical lands have the body size and male terminalia larger than the neotropical form. However, despite also having a longer male terminalia, some specimens that inhabit the tropical African savannah have a similar body size to the neotropical specimens. We also identified a curious morphological variation in specimens from Vietnam: the lack of prosternal process. In addition, this specimens have eight antennomeres, instead nine (see section 4.2). Females, measurements in mm (n = 24): TL 1.13–1.61 (1.32 ± 0.12); PL 0.41–0.59 (0.49 ± 0.04); PW 0.41–0.61 (0.50 ± 0.05); EL 0.70–1.03 (0.83 ± 0.08); EW 0.48–0.65 (0.55 ± 0.04); GD 0.43–0.61 (0.49 ± 0.04). Ratios: PL/PW 0.95–1.05 (0.99 ± 0.03); EL/EW 1.44–1.61 (1.52 ± 0.05); EL/PL 1.58–1.86 (1.69 ± 0.07); GD/EW 0.86–0.94 (0.89 ± 0.02); TL/EW 2.33–2.59 (2.42 ± 0.07).

Host fungi. See Table 1.

Distribution (Fig. 35). Widespread in subsaharan Africa and in several islands of the western Indian Ocean (Comoros, Mayotte, Madagascar, Reunion, Mauritius and Seychelles). Records also from Europe (France, possibly not free-living, and Italy), Asia (Sri Lanka, India and Vietnan) and Brazil (Chapada dos Guimarães).

Material examined. Lectotype, here designated (MNHN)\ [blue circular label] *Ennearthro tabellifer* Cap? 41 Caf? Cast. 72? [handwritten] (see Fig. 16)\ [blue label] Kunze 28 [handwritten]\ [blue label] Cis tabellifer Kunz pr. b. sp. [handwritten]\ (see Fig.16). **South Africa:** 9 specimens (6 SANC, 3 LAPC)\ SOUTH AFRICA: NW Mhlabatini Kloof, Magaliesberg 25°49'S 27°19'E 12.v.2002 O.C. Neser\ Adults ex bracket fungus\ NATIONAL COLL OF INSECTS Pretoria, South Africa\ BF#17/18 [handwritten]\; 8 specimens (6 SANC, 2 LAPC)\ SOUTH AFRICA: GAU Lynnwood Glen, Pretoria 25°46'S 28°16'E 3.xi.2002 S& O.C. Neser\ Adults emerged from bracket fungus *Ganoderma applanatum* BF#10/11\ NATIONAL COLL OF INSECTS (SANC) Pretoria, South Africa\; 2 specimen (1 SANC, 1 LAPC)\ SOUTH AFRICA: GAUTENG Rietondale Experimental Farm, Pretoria 25°43'S 28°14'E 1330m 14.ii.2003 S. Neser\ Ex bracket fungus *Phellinus* sp. on *Gleditsia triacanthos* CAESALPINIACEAE BF# 6\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 10 specimens (7 SANC, 3 LAPC)\ SOUTH AFRICA: NW Dome Kloof, Magaliesberg 25°45'S 27°33'E 27.vii.2003 S. Neser\ Adults ex bracket fungus on fallen log of probably *Faurea saligna* (PROTEACEAE) \ Ex bracket fungi *Stereum hirsutum* & *Stereum* sp. BF#1\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 28 specimens (19 SANC, 9 LAPC)\ SOUTH AFRICA: NW Castle Gorge, Magaliesberg 25°49'S 27°35'E 3.viii.2002 S. Neser\ Ex bracket fungus *Polyporus dictyopus* on dead tree trunk BF#2\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 5 specimen (4 SANC, 1 LAPC)\ SOUTH AFRICA: KZN Mpisini Nature Res. 30°12'S 30°48'E 9.vii.2008 S. & O. C. Neser\ Ex bracket fungus *Funalia* sp. BF#110\ NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 26 specimens (18 SANC, 8 LAPC)\ SOUTH AFRICA: NW Marethwane Magaliesberg 25°47'S 27°29'E 24.viii.2002 S. Neser\ Adults ex bracket fungus\ NATIONAL COLL OF INSECTS Pretoria, South Africa\ BF# 9/16 [handwritten]\; 26 specimens (21 SANC, 5 LAPC)\ SOUTH AFRICA: GAU Pretoria, Rietondale Experimental Station 25°44'S 28°13'E 12.viii.2004 S. Neser\ Ex bracket fungus *Ganoderma applanatum* BF# 25\ NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 10 specimens (7 SANC, 3 LAPC)\ SOUTH AFRICA: NW Mhlabatini Kloof, Magaliesberg 25°49'S 27°19'E 16.vi.2002 S. Neser\ Ex bracket fungus *Ganoderma* sp. on dead Croton gratissimus EUPHORBIACEAE BF#19\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 8 specimens (6 SANC, 2 LAPC)\ SOUTH AFRICA: NW Castle Gorge, Magaliesberg 25°49'S 27°35'E 21.iv.2002 O.C. Neser\ Adults emerged from bracket fungus *Phaeolus schweintzii* BF#13\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 6 specimens (4 SANC, 2 LAPC)\ SOUTH AFRICA: KZN

Umlalazi Nature Res Mtunzini, 28°57’S 31°46’E 13. vii.2008 R.P. Urban\ Ex bracket fungus *Coriolus hirsutus* BF#87\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 8 specimens (6 SANC, 2 LAPC)\ SOUTH AFRICA: MPU Alkmaar, W. Nelspruit 25°27’S 30°50’E 10.ii.2008 OC Neser\ Ex bracket fungus *Trametes versicolor* BF#45\ NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 20 specimens (14 SANC, 6 LAPC)\ SOUTH AFRICA: GAU Pretoria, Rietondale Experimental Station 25°44’S 28°13’E ix.2003 S. Neser\ Ex bracket fungus *Ganoderma lunidum* BF# 27\ NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 2 specimen (1 SANC, 1 LAPC)\ SOUTH AFRICA: MPU Mooihoek Farm, nr. Wakkerstroom 27°13’S 30°32’E 15.vii.2008 O&S. Neser\ Ex bracket fungus *Coriolus versicolor* BF# 135\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 11 specimens (8 SANC, 3 LAPC)\ SOUTH AFRICA: MPU Alkmaar, W. Nelspruit 25°27’S 30°50’E 10.ii.2008 OC Neser\ Ex bracket fungus *Trametes* sp. BF#47\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 20 specimens (14 SANC, 6 LAPC)\ SOUTH AFRICA: LIMP Blouberg Mt. NW Polokwane 23°04’S 29°00’E 27.iv.2007 O.C. Neser\ Adults ex bracket fungus on fallen log\ Ex bracket fungus *Trametes* sp. on fallen tree trunk BF#34\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 45 specimens (30 SANC, 15 LAPC)\ SOUTH AFRICA: MPU Mooihoek Farm nr Wakkerstroom 27°13’S 30°32’E 15.vii.2008 O&S Neser\ Ex bracket fungus *Trametes* sp. BF#113\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 12 specimens (8 SANC, 4 LAPC)\ SOUTH AFRICA: MPU Alkmaar, W. Nelspruit 25°27’S 30°50’E 10.ii.2008 O.C. & S. Neser\ Ex bracket fungus on *Dombeya rotundifolia* BF# 68\ Ex bracket fungus *Trametes* sp. BF#68\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 16 specimens (11 SANC, 5 LAPC)\ SOUTH AFRICA: LIMP Otter’s Den, 16km frm Hoedspruit 24°24’S 30°49’E 18.vii.2008 D. van Heerden\ Ex bracket fungus *Coriolus versicolor* BF# 136\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 10 specimens (7 SANC, 3 LAPC)\ SOUTH AFRICA: KZN Mpisini Nature Res Umkomaas, 30°12’S 30°48’E 9.vii.2008 S. & O.C. Neser\ Ex bracket fungus *Coriolus hirsutus* BF# 134\ NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 9 specimens (LAPC)\ SOUTH AFRICA: MPU Mooihoek Farm, nr. Wakkerstroom 27°13’S 30°32’E 15.vii.2008 O&S Neser\ Ex bracket fungus *Coriolus versicolor* BF#143\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 4 specimen (3 SANC, 1 LAPC)\ SOUTH AFRICA: GAU Wilgepoort, NE of Bronkhorstspruit 25°37’S 29°00’E 23.iii.2010 S. Neser\ Ex bracket fungus # 225 on fallen tree trunk\ Ex bracket fungus *Lenzites elegans* on *Acacia karroo* BF#225\ NATIONAL COLL. OF INSECTS Pretoria, South Africa\; 14 specimens (11 SANC, 3 LAPC)\ SOUTH AFRICA: MPU Die Hel Nature Res. nr. Loskop Dam 25°31’S 29°48’E 10.viii.2008 S. & O.C. Neser\ Ex bracket fungus *Trametes* sp. BF#147\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 20 specimens (15 SANC, 5 LAPC)\ SOUTH AFRICA: MPU Mooihoek Farm, nr. Wakkerstroom 27°13’S 30°32’E 15.vii.2008 O&S Neser\ Ex bracket fungus *Stereum ostrea* BF#144\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 4 specimen (3 SANC, 1 LAPC)\ SOUTH AFRICA: MPU Nelspruit 25°29’S 30°59’E 14.viii.2009 D van Heerden\ Ex bracket fungus #178 on *Acacia sieberiana* var *woodii*\ Ex bracket fungus *Trametes* sp. BF# 178\; \NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 3 specimen (2 SANC, 1 LAPC)\ SOUTH AFRICA: MPU Mooihoek Farm, nr. Wakkerstroom 27°13’S 30°32’E 15.vii.2008 O&S Neser\ Ex unidentified bracket fungus BF# 168\ NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 15 specimens (9 SANC, 6 LAPC)\ SOUTH AFRICA: KZN Twin Streams Nursery Forest, nr Mtunzini 28°57’S 31°54’E 13.vii.2008 RP Urban\ Ex bracket fungus *Coriolus versicolor* BF#167\ NATIONAL COLL OF INSECTS Pretoria, S. Afr.\; 3 specimen (2 SANC, 1 LAPC)\ SOUTH AFRICA LIM Wesfalia Estate nr Politsi 23°44’S 30°07’E 13.x.2009 D van Heerden\ Ex bracket fungus # 223 on avocado tree\ Ex bracket fungus *Lenzites elegans* BF# 223 \NATIONAL COLL OF INSECTS Pretoria, South Africa\; 4 specimen (3 SANC, 1 LAPC)\ SOUTH AFRICA LIM Wesfalia Estate nr Politsi 23°44’S 30°07’E 13.x.2009 D van Heerden\ Ex bracket fungus # 220 on avocado tree\ Ex bracket fungus *Lenzites elegans* BF# 220 \NATIONAL COLL OF INSECTS Pretoria, South Africa\; 4 specimen (3 SANC, 1 LAPC)\ SOUTH AFRICA LIM Wesfalia Estate nr Politsi 23°44’S 30°07’E 13.x.2009 D van Heerden\ Ex bracket fungus # 218 on avocado tree\ Ex bracket fungus *Coriolus versicolor* BF# 218\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 4 specimen (3 SANC, 1 LAPC)\ SOUTH AFRICA WCAPE Prince Alfred’s Pass N of Knysna 33°58’S 23°09’E 5.xi.2009 S& OC Neser\ Ex bracket fungus # 214 on fallen tree trunk\ Ex bracket fungus *Lenzites elegans* BF# 214\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 3 specimen (2 SANC, 1 LAPC)\ SOUTH AFRICA WCAPE Montagu Pass N of George 33°54’S 22°24’E 4.xi.2009 S& OC Neser\ Ex bracket fungus # 211 on *Brachylaena* neriifolia\ Ex bracket fungus *Coriolus hirsutus* BF# 211\; 5 specimen (4 SANC, 1 LAPC)\ SOUTH AFRICA WCAPE Montagu Pass N of George 33°54’S 22°24’E 4.xi.2009 S& OC Neser\ Ex bracket fungus *Coriolopsis polyzona* BF# 202\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 2 specimen (1 SANC, 1 LAPC)\ SOUTH AFRICA WCAPE Montagu Pass N of George 33°54’S 22°24’E 4.xi.2009 S& OC

Neser\ Ex bracket fungus *Coriolus versicolor* On fallen tree trunk BF# 197\ NATIONAL COLL OF INSECTS Pretoria, South Africa\; 1 specimen (MZLU)\ RSA: Cape Prov. Nature's Valley, at Groot Rivier 33°58'S. 23°33' E. 15-17.X.1994 loc.21 leg. R. Danielsson\ Ciidae gen. sp. Det. Mandelshtam, 2002\ [blue label] LUND 286 [printed]\; 1 specimen (MZLU)\ S. Afr. Cape Prov Tzitzikama Forest. Stormsrivierpiek 13.I.51 No 137\ Swedish South Africa Expedition 1950-1951 Brinck-Rudebeck\ [blue label] LUND 284 [printed]\; 6 specimens (SNSD)\ [blue label] Cell. Maerkel [printed] ? [handwritten, information not understood]\ Staatl. Museum für Tierkunde Dresden\; 1 specimen (SNSD)\ [blue label] Cell. Maerkel [printed] ? [handwritten, information not understood]\ Staatl. Museum für Tierkunde Dresden\ *Cis tabellifer* Cap. [handwritten]\; 1 specimen (SNSD)\ Peers Cave, Fish hoek, C.T. Cape P., South Africa 26.12.95, leg. R. Predel\; 2 specimens (MNHN)\ *tabelliferum*, Kunse Mell -, Cap bon spei. [handwritten]\ Ex Coll REITTER\ ; 1 specimen (MFN)\ *tabellifer* kunze, cap. [handwritten]\ Coll. L.W. Schaufuss\ *tabelliferum* Mellié, Cap bom spei [handwritten]\ ; 1 specimen (MHNG)\ *Tabellifer* Kuntze, Cap. B.E. Kuntze Mellié [handwritten]\. **Republic of Mozambique:** 7 specimens (MNHN)\ [blues label] MUSEUM PARIS, ZAMBÉZE, INHACORO, PRÉS CHEMBA, P. LESNE 1929\. **United Republic of Tanzania:** 34 specimens (27 KMMA, 7 LAPC)\ [blue label] dans Polypore sur Cupressus\ COLL. MUS. CONGO Tanganyika Terr.: Kilimanjaro, N. de Marangu, verst. S.E., 1700m. 16-VII-1957\ Mission Zoolog. I.R.S.A.C. en Afrique orientale (P. Basilewsky et N. Leleup)\. **Republic of Rwanda:** 156 specimens (126 KMMA, 30 LAPC)\ MUSÉE DU CONGO Urundi: Masaka [printed] (1500m) VI-193[printed]3[handwritten] A. Becquet [printed]\; 2 specimens (KMMA)\ MUSÉE DU CONGO Urundi: Masaka [printed] (1500m) VI-193[printed]3[handwritten] A. Becquet [printed]\ No scolytidae [handwritten] Det. K.E.Schedi [printed]; 5 specimens (KMMA)\ [blue label] s/ Champignon N° 678 [handwritten]\ MUSÉE DU CONGO Urundi: Masaka [printed] (1500m) VI-193[printed]3[handwritten] A. Becquet [printed]\; 3 specimens (1 KMMA, 2 LAPC)\ [green label] s/ Champignon N° 678 [handwritten]\ MUSÉE DU CONGO Urundi: Masaka [printed] (1500m) VI-193[printed]3[handwritten] A. Becquet [printed]\. **Democratic Republic of Congo:** 140 specimens (93 KMMA, 47 LAPC)\ MUSÉE DU CONGO Elisabethville [printed] -1932 [handwritten] De Loose [printed]\; 1542 specimens (1253 KMMA, 289 LAPC)\ MUSÉE DU CONGO Elisabethville [printed] -1932 [printed or handwritten] De Loose [printed] Ch. 10 [or Ch. 19, Ch. 33, Ch. 34, Ch. 39, Ch. 40, Ch. 41, Ch. 42, Ch. 44, Ch. 45, Ch. 46, Ch. 47, Ch. 49; handwritten]\; 2 specimens (KMMA)\ MUSÉE DU CONGO Eala [printed] -V-1936 [handwritten] J. Ghesquière [printed] 2639 [handwritten]\; 2 specimens (KMMA)\ MUSÉE DU CONGO Eala [printed] -XI-1936 [handwritten] J. Ghesquière [printed]\; 1 specimen (KMMA)\ MUSÉE DU CONGO Eala [printed] -XI-1936 [handwritten] J. Ghesquière [printed]\ [green label] ex Rigidoporus [handwritten]\; 33 specimens (29 KMMA, 4 LAPC)\ MUSÉE DU CONGO [printed] Kisantu 1925 (R.P.Vanderyst) sur polypore [handwritten]\; 10 specimens (6 KMMA, 4 LAPC)\ [green label] Récolté sur [printed] Polypore [handwritten] \MUS. ROY. AFR. CENTR. [printed] Bas. Congo: Kisantu 1925 (R.P.H. Vanderÿst) [handwritten]\; 1 specimen (KMMA)\ Yangambi. 1951 C. DONIS z. [printed] 306 [handwritten]\ COLL. R. MAYNÉ COM. ÉT. BOIS CONGO R. [printed] 2326 [handwritten]\ COLL. MUS. TERVUREN don R. Mayné\; 1 specimen (KMMA)\ MUSÉE DU CONGO [printed] Monga (Uele) III-1931 (Lebrum) ch. 2316 [handwritten]\; 2 specimen (KMMA)\ MUSÉE DU CONGO [printed] Monga (Uele. Itimbiri) III-1931 (Lebrum) [handwritten]\ [label with a piece of fungus, without information]\; 1 specimen (KMMA)\ MUSEÉ DU CONGO Volcap Nyamlagira (Kivu) [printed] IX-1936 [handwritten] J. Ghesquière [printed] 52 53 [handwritten]\; 5 specimens (KMMA)\ MUSÉE DU CONGO [printed] angodia (Uele. Itimbiri) V-1931 (Lebrum) H.2973 [handwritten]\; 1 specimen (KMMA)\ MUSÉE DU CONGO [printed] angodia (Uele. Itimbiri) V-1931 (Lebrum) H.2997 [handwritten]\; 6 specimens (5 KMMA, 1 LAPC)\ MUSÉE DU CONGO [printed] Flandria -IV-1935 [handwritten] J. Ghesquière [printed] 547 [handwritten]\ [green label] Eclos de champignons rouges [handwritten]; 3 specimens (KMMA)\ MUSÉE DU CONGO [printed] Flandria -IV-1935 [handwritten] J. Ghesquière [printed] 547 [handwritten]\; 27 specimens (22 KMMA, 5 LAPC)\ Congo Belge, P.N.G Miss. H. De Saeger PFSK. 22/8, 10-VI-52 H. De Saeger 3609\; 1 specimen (KMMA)\ Congo Belge: P.N.A. 30-VII-1-VIII-1955 P. Vanschuytbroeck 13.727-28\ Mont Hoyo grotte Matetu; 1.160m\; 1 specimen (KMMA)\ [blue label] Dans terreau au Berlese\ COLL. MUS. CONGO Kivu: T. Lubero, Biambwe riv. Lubeu, 1000m [printed] (for) [handwritten] R.P.M.J. Célis V-1955 [printed]\; 4 specimens (KMMA)\ [blue label] Récolté dans polypore [handwritten]\ COLL. MUS. CONGO Katanga: Kakontwé Sar. bois. VIII-1948 N. Leleup\. 81 specimens (65 KMMA, 16 LAPC)\ [blue label] Dans polypore\ COLL. MUS. CONGO Baudouinville VIII-1953 H. Bomans\; 9 specimens (7 KMMA, 2 LAPC)\ COLL. MUS. CONGO Tanganika: Kamsabala 1200m. VIII-1953 H. Bomans\. **Republic of Kenya:** 1 specimen (MZLU)\ Kenya. M. ? [only half of the writing is visible; the label is torn] 2050 [handwritten] m T. Palm [printed]\ Ciidae gen. sp. det. Mandelshtam, 2002\ [blue label] LUND 263 [printed]\; 1 specimen (MZLU)\ 2050 [handwritten] m T.Palm Kenya, 1660m [printed]\ [blue label] LUND 269 [printed]\. **Togolese Republic Listen:** 4 specimens (MHNG)\ TOGO PALIME, Forêt de Klouto, 20-24-IV-74 S. Vit\ *Ceracis* sp. [handwritten] J.F. Lawrence [printed]\. **Republic of The Gambia:** 6 specimens (MZLU)\ Gambia: Bakau 6-26.XI.1984 leg. T. Palm\ *Ceracis cucullatus* Mellié [handwritten] C.Lopes-Andrade det. 2007 [printed]\ [blue label] LUND 406 [printed]; 7 specimens (MZLU)\ Gambia: Bakau 6-26.XI.1984 leg. T. Palm\ *Ceracis cucullatus* Mellié [handwritten] C.Lopes-Andrade det. 2007 [printed]\ [blue label] LUND 243 [printed]. **Madagascar:** 1 specimen (MNHN)\ Madagascar, Amanarivo, (Sikora)\ [yellow label] Type [handwritten]\ [red card] TYPE\ [red card] LECTOTYPE [printed] *Ennearthrom bilamellatum* Pic [handwritten]\ *Ennearthrom bilamellatum* Pic [handwritten]\ *Ceracis cucullatus* [handwritten] O. ROSE det. [printed] 2010 [handwritten]\; 1 specimen (KMMA)\ Ambodivoangy [printed] VI-1959 [handwritten] (Lavage de terre) [printed] 39. [handwritten]\ MUS. ROY. AFR. CENTR. Madagascar Est: Baie d' Antongil J. Vadon\. 5 specimens (MNHN)\ MADAGASCAR, Befanamy, Prov. Tullan, 20.VI.1921, H. Poisson, petit polypore n.17\; 1 specimen (MNHN) \ Madagascar, Diego-Suarez, Ch. Alluaud 1893\ *Ceracis* sp. (cucullatus gp.) [handwritten] Det. J.F. Lawrence [printed]\; 1 specimen (MNHN) \ Madagascar\; 1 specimen (MFN)\ Type\ Madagaskar\ *Cis laminicollis* Fairm [handwritten]\ coll. L.W. SchaufuB\; 7 specimens (MFN)\ Madagaskar\ coll. L.W. SchaufuB\. **Mayotte:** 1 specimen (MNHN)\ Mayotte [handwritten]\ [blue label] MUSEUM PARIS, Collection Léon Fairmaire, 1906\. **Reunion :** 3 specimens (MNHN)\ Bourbon, Cucullatus [handwritten]\ ex Coll. Mellié [handwritten]\; 1 specimen (MNHN)\ Ex : Musaeo Miniszech [printed]\ *Cucullatus* Dej. I. Bourbon [handwritten]\. **Democratic Socialist Republic of Sri Lanka:** 2 specimens (MHNG)\ CEYLAN Central [printed], Hanguranketa 27.I.70 750m [handwritten], MUSSARD BESUCHET LÖBL\ *Ceracis cucullatus* (Mell) [handwritten] det. J.F. Lawrence [printed]\. **Republic of India:** 1 specimen (MHNG)\ Coll. Melly [handwritten] \ *Cucullatum* Dej Bonibay Mellié [handwritten]\. **Vietnan:** 3 specimens (MNHN)\ MUSEUM PARIS, TONKIN, RÉG DE HOA BINH, A DE COOMAN 1927\; 32 specimens (MNHN) \3171. [handwritten]\ Hanoi [handwritten]\ [blue label] MUSEUM PARIS, Coll. A. CROUVELLE 1915 [printed]\. **Brazil:** 11 specimens (LAPC)\ BRASIL: MT Chapada dos Guimarães i.2004 leg. C. Ribas & R. Campos\.

3.2. Key to adult males of *Ceracis* of the *cucullatus* species-group with secondary sexual characteristics fully developed.

1 Lateral margins of pronotum rounded. First abdominal ventrite with a broad transversely oval sex patch. Tegmen with apex bearing a small excavation on each side. Known only from "Ilha da Cassumba" (Cassumba island) in Caravelas, northeastern Brazil... ***C. cassumbensis* Antunes-Carvalho & Lopes-Andrade**

1' Lateral margins of pronotum subparallel. First abdominal ventrite bearing a circular margined sex patch. Tegmen with apex devoid of excavations… **2**

2 (1') Apex of pronotum projected forward, with its anterior margin deeply emarginate forming two diverging horns, which may be circular in cross-section and narrower at apex. From Mexico to southern Brazil... ***C. bicornis* (Mellié)**

2' Apex of pronotum projected forward, forming a raised foursquare plate, slightly emarginated at apex... **3**

3 (2') Aedeagus about 4 times as long as wide. Anterior third of tegmen with sides converging in straight line toward apex. Known only from southern Mexico and norther Brazil... ***C. navarretei* Antunes-Carvalho & Lopes-Andrade**

3' Aedeagus about 3 times as long as wide. Sides of tegmen moderately curved at the anterior third... **4**

4 (3') Tegmen with basal portion subtriangular; basal interior margin thick and V-shaped; apex of each lateral margin pointing inwards, bearing several sensilla distributed. Penis with basal portion closed, membranous; lateral margins forming a well sclerotized arc at the apical portion. Western Europe, Africa, southern Asia and

islands of the western Indian Ocean. Also known from Chapada dos Guimarães in Midwest Brazil… ***C. tabellifer*** **(Mellié)**

4’ Tegmen with basal portion narrowed, differentiated; basal interior margin rounded. Penis with basal portion opened, leaving the inferior limits of the lateral margins disconnected; apical portion narrowed and weakly sclerotized, not forming an arc…**5**

5 (4’) Eighth sternite with anterior margin biconcave, producing a remarkable subtriangular protuberance that extends beyond the inferior limits of the lateral margins. Tegmen twice as wide as penis and 3x as long as the greatest width of the eighth sternite. Penis with lateral margins subparallel at the basal three-fourths and abruptly converging at beginning of the apical one-fourth. Galapagos Islands and from Mexico to southern Brazil… ***C. cucullatus*** **(Mellié)**

5’ Eighth sternite with anterior margin irregular, not produced. Tegmen about 1.6x as wide as penis and about 1.3x as long as the greatest width of the eighth sternite. Penis with lateral margins subparallel at the basal one-third, converging gradually along the second-third of its length, and abruptly converging at beginning of the apical third. Known only from Nova Teutônia, southern Brazil… ***C. lamellatus*** **(Pic)**

3.3. Host fungi and collection data of *Ceracis tabellifer* (Mellié) in South Africa

A total of 2208 adult specimens of 19 Ciidae species were recorded in basidiomes of 30 species of host fungi, of which 60% were *C. tabellifer*. The remainder specimens are of 17 species of *Cis* Latreille, and of *Xylographus seychellensis* Scott. Basidiomes of 26 species of host fungi had at least one adult *C. tabellifer*. Therefore, *Ceracis tabellifer* is a true polyphagous species. Only basidiomes of *Pycnoporus sanguineus*, *Trametes cingulata*, *Trametes meyenii*, cf. *Coriolus*. sp. and a unidentified fungus species were devoid of adults *C. tabellifer*. Of the species that had basidiomes inhabited by *C. tabellifer*, in 17 there were at least one more ciid species (not necessarily in the same basidiome). In 13 species of host fungi the number of adult specimens of *C. tabellifer* exceeded 50% of the total of ciids recorded. These data are provided in Table 1.

4. Discussion

4.1. Taxonomy

The amazing morphological similarity between *C. cucullatus*, *C. lamellatus*, *C. navarretei* and *C. tabellifer* challenges the skills of any taxonomist. They are not only very similar, but there is a high intraspecific morphological variability, notable by the secondary sexual characteristics expressed in males, as the pronotal projections. The confused taxonomic history involving *C. cucullatus* and species previously synonymized with it appears to be a reflex of such scenario. And it reinforces the potential and relevance role of the comparative morphology of male abdominal terminalia for solving taxonomic problems between morphologically similar Ciidae species.

Here we analyse, for the first time, the morphology of male abdominal terminalia of *C. cucullatus*, *C. lamellatus* and *C. tabellifer*. The latter has a comparatively smaller tegmen with basal portion subtriangular and basal interior margin thick and V-shaped. Additionally, *C. tabellifer* has penis with basal portion membranous and apical portion forming a well sclerotized arc (Fig. 24). In *C. cucullatus* and *C. lamellatus*, the basal portion of the tegmen is narrowed, and the basal interior margin is rounded and not ticked (Figs 22, 23). Both species are similar in the membranous basal portion of penis, but the apical portion is different. The penis in *C. cucullatus* is narrowed along the apical one-fourth of its length, and in *C. lamellatus* it is narrowed at the apical third (Figs 22, 23). Moreover, in *C. lamellatus* the eighth sternite has the posterior corners rectangular, while it is rounded in *C. cucullatus*.

4.2. Has *Ceracis tabellifer* a Neotropical or an Afrotropical origin?

Ceracis tabellifer was described in 1849 from Cape of Good Hope, at the southern tip of the African continent (Mellié, 1849). Populations may be collected throughout subsaharan Africa and we report here dozens of historical records outside the Neotropics and a single record from South America (Fig. 35). At first, and considering that the Neotropical specimens is not quite typical in form compared to African populations (see *variation* in 3.1.3), one might suggest that *C. tabellifer* is an autochthonous Afrotropical species. However, considering the absence of any other *Ceracis* on Africa and the great diversity of the genus in the New World, including all the species morphologically similar to *C. tabellifer*, we support the alternative explanation to the remarkable presence of *C. tabellifer* in subsaharan Africa and other regions: a successful invasion from the neotropics.

Among the six species that currently comprises the *cucullatus* group, three are known to be polyphagous and have a wide geographic distribution: *C. bicornis*, *C. cucullatus* and *C. tabellifer*. The latter two are successful invaders and individuals of their invasive populations have the largest body size and male abdominal terminalia (see *variation* in the section 3.1.1 and 3.1.3), and are more frequently found than their conspecific native populations. By responses to selective pressures in new habitats or due to stochastic events (Lee, 2002; Keller & Taylor, 2008; Westley, 2011), phenotypic variation between native and invasive populations is quite common in the literature on biological invasion (*e.g.* Huey *et al*. 2000; Bossdorf *et al*. 2005; Ahern *et al*. 2009). Species introduced into new habitats by human activities often face foundation events, which entails in genetically based shifts in phenotypic traits, among other effects (Dlugosch & Parker, 2008; Keller & Taylor, 2008). For instance, it is possible that the reduction of number of antennomeres and drastic reduction (or even loss) of prosternal process in the population from Vietnam were a consequence of foundation effect and genetic drift. These specimens were collected almost a century ago and they are possibly a subsample of the non-indigenous fauna of *C. tabellifer* that occupies the African mainland. Therefore, the curious lack of prosternal process seems to be an adverse effect of inbreeding. To our knowledge, this is the first record of a ciid without that structure.

Considering (i) that the greatest morphological variability of species in the *cucullatus* group is found in the neotropics, (ii) the easternmost record of *C. tabellifer* (Vietnan) is a morphologically impoverished population, so we assume it might be a subsample of the African populations and (iii) the absence of other *Ceracis* in Africa, we sustain here that *C. tabellifer* is a Neotropical species introduced elsewhere, and not the inverse. Note that we cannot prove it, but our arguments are strong enough to sustain it as the most robust explanation at the moment.

4.3. Spread and current distribution of *C. tabellifer* outside the Neotropical region

During the nineteenth and twentieth century, the collection of *C. tabellifer* varied substantially over time and space (Fig. 35). For this reason, they do not depict the chronological advance of populations on the space, but merely a variation in collection effort. Nevertheless, the historical records we provide here may be informative and reveal how old is the colonization of some areas by *C. tabellifer*.

The first *C. tabellifer* recorded in African lands date back to the beginning of the nineteenth century, although it is possible that its arrival occurred in the previous century or even before. Until the first half of the twentieth century, populations had been recorded at various localities from Democratic Republic of Congo and neighbouring countries. Currently *C. tabellifer* is widely distributed in subsaharan Africa and possibly one of the most frequently collected ciid species in the continent (Fig. 35). Several islands at the western Indian Ocean are also inhabited by *C. tabellifer* (Scott, 1926; Lawrence, 1967b Lopes-Andrade, 2008) and its presence in Sri Lanka and India suggests a possible route of introduction through these islands. Considering it has reached Vietnam in the first half of the twentieth century, if not before, it would not be a surprise to find the species at the remaining Oriental region, or even at the Australotropical, Neoguinean and Neozelandic regions. In contrast to the success of this species in tropical zones, there are few records of *C. tabellifer* in temperate zones (see section 4.5). Each record in Britain and France were noted as introductions, but populations are possibly not free-living in both countries (Abeille de Perrin, 1874; Orledge & Booth, 2006), and that is possibly the case for the records in Italy either.

4.4. Causes for success and potential threat

Examine the invasiveness of a species and predict whether it would succeed in new habitats is still a rather complex task (see Williamson & Fitter 1996; Rosecchi *et al*. 2001; Heger & Trepl, 2003; Hayes & Barry, 2008). However, comparisons between autochthonous and invasive species in a given ecosystem may be a way to identify features determining invasion success (Kolar & Lodge 2001). Despite information on life history and reproductive behaviour of tropical ciids are scarce, we hypothesized below some characteristics that may underly, at least partially, the successful establishment and spread of *C. tabellifer* during the invasion process, and that continue allowing its dissemination.

Most ciids are mycetobionts, with some species exploiting several host fungi, while others are restricted to a few or even one host fungus (Guevara *et al*. 2000). We show that *C. tabellifer* is a remarkably polyphagous species in South Africa

(Table 1). The available data suggest that this ciid is able to exploit more host species than native ciids, and even more than other species of Ciidae as a whole (see Lawrence, 1973; Majka, 2007 for host fungi of Nearctic ciids; Graf-Peters *et al*. 2011 for Neotropical ciids; Orlegde & Reynolds, 2005 for ciids from Britain, Germany, North America and Japan). It is noteworthy that polyphagy is common among widely distributed species of Ciidae, as in *C. bicornis* (Graf-Peters *et al*. 2011), which also belong to the *cucullatus* species group, and other ciids such as *C. thoracicornis* (Ziegler) (Lawrence, 1973), *Cis bilamellatus* Wood (Orledge *et al*. 2010) and *Cis creberrimus* Mellié (Lawrence, 1973), the latter two introduced in Britain (Orledge *et al.* 2010) and Galapagos Islands (Lawrence, 1971), respectively. The diet breadth has been seen as a characteristic involved in the invasion success of animals (*e.g*. Blackburn *et al.* 2009), including beetles (*e.g.* Yan *et al.* 2005; Majerus *et al.* 2006; Orledge *et al*. 2010). Polyphagy has probably contributed to the invasion success of *C. tabellifer*.

Ceracis tabellifer is a multivoltine species (as well as *C. cucullatus*) and may be easily collected throughout the year in South Africa, where it is usually the numerically dominant ciid species within its broad host range (Table 1). Populations have been encountered from areas near the coast to heights of up to 1700 meters, and from urban areas and cultivated lands to endemic forest and savannah (Scott, 1926; Neser 2012). The polyphagous feeding habit and the wide range of habitats which *C. tabellifer* is able to self-sustaining suggest a strong adaptive potential. Allied to it, the notable presence of populations in islands separated by long stretches of ocean indicate the high ability to transpose long distances, either by active migration or through human intervention. However, it is still unclear which are the actual adverse effects derived from the outstanding presence of *C. tabellifer* in invaded habitats, or even if it offers any threat to autochthonous species.

4.5. Global warming: prospects for distribution expansion of *C. tabellifer*

Despite its eurytopic nature, most populations of *C. tabellifer* are concentrated on tropical zone or in marginally tropical areas as the southernmost Africa. We have no knowledge of free-living populations in Europe, and each single record from Italy and mainly from France and Britain can be treated as “outliers”, the latter two being very old records. The supposed record from Britain was, indeed, in a fungus from

Zambia (Orledge & Booth, 2006). Low temperatures may be an impediment to successful establishment of populations in the Palaearctic region. In addition to *C. tabellifer*, the morphologically related *C. cucullatus* and *C. bicorni*s are also restricted to tropical lands. This scenario is subjected to changes. Several studies have discussed how the effects of climate change, including global warming, may affect invasive species (*e.g.* Dukes & Mooney, 1999; Chen, 2008; Hellmann *et al.* 2008; Walther *et al*. 2009; Thomas 2010; Huang *et al*. 2011; Smith *et al*. 2012). Among potential consequences addressed by these authors, the increase in successful establishment rate of invasive species and the range expansion into new habitats previously unsuitable may be important here. In face of changes in Earth's temperature, the synergism between a polyphagous feeding habit and ability to overcome long distances can facilitate successful establishments and the spread of *C. tabellifer* northward into the Palaearctic and even the Nearctic region in a not so distant future.

4.6. Other introduced or invasive ciids

Other invasive ciid species have been recorded in several regions. The Autralasian fungivore *Cis bilamellatus* was accidently introduced in England during the nineteenth century and is currently distributed across England, Wales and southern Scotland, with further records from Ireland, Channel Island and France (Orledge *et al.* 2010). The invasion success of this beetle in northern Europe is associated to its capacity to exploit a range of under-used fungal resources, survive under both wet and dry conditions, and the low levels of parasitoid attack. So far, there is no proof that *Cis bilamellatus* is responsible for any ecological impact in Britain (Orledge *et al.* 2010). *Cis creberrimus*, widespread in the neotropics, is considered an introduced species in Galapagos Islands. Together with *C. cucullatus*, they are the unique ciid species that occupy these islands (Lawrence, 1971). Interestingly, in the population of *C. cucullatus* we reared in laboratory, we have observed contamination by *Cis creberrimus* in a few basidiomes. These species coexisted in the same basidiome for a long time, where they appear to have partitioned the resource temporally. We noted that *C. cucullatus* had greater activity in the morning and afternoon, while *Cis creberrimus* was more active in the late afternoon. Moreover, *Cis creberrimus* is able to exploit the fungus in more advanced stages of decomposition. Temporal partitioning of a host fungus by ciids are not uncommon (*e.g.* Guevara *et al*. 2000) and would not be a surprise to report this behaviour in the wild. *Cis fuscipes* Mellié, an abundant and widely distributed ciid in North America, has been interpreted as an invasive species into Cuba, Hawaii, Madeira, Australia and New Zealand, with several parthenogenetic populations (Lawrence 1967a; Lawrence & Lopes-Andrade 2010). In North America, the parthenogenetic populations are numerically dominant and concentrated mainly in the Midwest, while bisexual populations are more abundant in the Northwest and also occur along the east coast and in some areas of the Gulf Coast states (Lawrence 1967b). *Hadreule elongatula* (Gyllenhal) is recorded throughout the Old World and northern Africa, and the presence of this minute beetle in North America has been cited as an invasion from Europe (Lawrence, 1971; Majka, 2007), although it is still uncertain. A very interesting case of a ciid that has recently turned to be invasive is that of *Cis chinensis* Lawrence. It was described based on specimens found in commercial dried fungi exported to USA (Lawrence 1991; Madenjian *et al*. 1993), but it is apparently not free-living there. At the same year, the species was recorded to Europe based on specimens found free-living in Italy in 1978, and breeding in Tofu at restaurant in Germany in 1990, but formerly identified as *Cis multidentatus* (Pic) (Lohse & Reibnitz 1991). *Cis chinensis* was found free-living in Brazil and it was suggested that it might be conspecific with ciids named *Cis multidentatus* from Europe (Lopes-Andrade 2008). The examination of the type of *Cis multidentatus* confirmed that hypothesis (Rose 2009) and nowadays it is accepted that *Cis chinensis* is free-living in Europe (Germany, Italy, France and Malta), China and Thailand (possibly authocthonous in eastern Asia), southeastern Brazil and La Reunión, in the western Indian Ocean (Lopes-Andrade 2008; Rose 2009). Other species are possibly also invasive, as *Ennearthron victori* Lopes-Andrade & Zacaro, the unique true *Ennearthron* found in the South Hemisphere. Most species of the genus are from Asia, and it is interestingly to note that in at least one Brazilian locality (Ipatinga, in the state of Minas Gerais) *E. victori* is found together with *Cis chinensis* (Lopes-Andrade, 2008). Morphological variation between allopatric populations appear to be common for many of these ciid species and it is possible that at least *Cis fuscipes* and *Cis creberrimus* constitute species complex rather than single species (Lawrence, 1967a, 1971).

5. Conclusion

We refute an ancient scenario in which the broadly distributed populations under the name *C. cucullatus* were interpreted as a cohesive biological unity, and demonstrate that this ciid in fact hid for a long time two additional similar species, which we have validated: *C. lamellatus* and *C. tabellifer*, the latter being the true invasive *Ceracis* in Africa. Due to the morphological similarity, *C. cucullatus* and *C. tabellifer* were historically confused in the literature since they were described (*e.g*. Lesne, 1917; Scott, 1926), and even the descriptor was "deceived" by the similarity of these small beetles (see *Introduction*). We show that the comparative analysis of male abdominal terminalia is the most effective way to distinguish these species.

Since the first record of *C. tabellifer* in Africa, and based on the number of records in the continent and on information drawn from the recent field collections in South Africa, it becomes evident that this ciid overcame the sequential transitions of the invasion process successfully (see Kolar & Lodge, 2001), at least in African lands and islands of the western Indian Ocean. However, although its biological characteristics seem to confer a great competitive ability and suggest a potential threat to native fauna, it is yet unclear whether the remarkably presence of *C. tabellifer* in Africa implies in any ecological impact. Due to its potential to colonize new habitats and ability to transpose long distances, it is probable that *C. tabellifer* will spread across tropical lands, but be limited by the low temperatures of the temperate zones. But in a warmer scenario, it is plausible to speculate that *C. tabellifer* will also be able to populate the Palearctic region.

Future researches should evaluate the relatedness of invasive and native populations of *C. tabellifer* through molecular approaches. *Ceracis tabellifer* offer an exciting opportunity to study the effects of a non-pest micetobiont organism to native community. Our study helps to fill an obvious gap in the literature on biological invasions, as most studies dealing with biological invasions consider mainly predatory species, vectors of diseases or herbivores potential pests of agricultural crops.

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Table 1. Occurrence of adult ciids in polypore basidiomes collected in South Africa, between 2002 and 2010.[a]

Host fungi	Native ciids			*Ceracis tabellifer*		N
	No. of species	No. and percentage of specimens (%)		No. and percentage of specimens (%)		
Fomitopsidaceae						
Fomitopsis lilacino-gilva	0	-	-	1	100	1
Phaeolus schweinitzii	1	1	11.11	8	88.89	9
Ganodermataceae						
Ganoderma applanatum	3	41	33.33	82	66.67	123
Ganoderma lucidum	0	-	-	20	100	20
Ganoderma sp.	1	18	46.15	21	53.85	39
Hymenochaetaceae						
Phellinus sp.	0	-	-	2	100	2
Polyporaceae						
Coriolopsis polyzona	1	1	1.39	71	98.61	72
Coriolus hirsutus	6	180	64.98	97	35.02	277
Coriolus versicolor	4	166	35.85	297	64.15	463
Funalia sp.	2	32	76.19	10	23.81	42
Lenzites elegans	1	17	7.14	221	92.86	238
Pycnoporus sanguineus	1	19	100	0	0	19
Polyporus dictyopus	0	-	-	132	100	132
Trametes cingulata	4	89	100	0	0	89
Trametes versicolor	1	1	11.11	8	88.89	9
Trametes sp.1	1	1	4.76	20	95.24	21
Trametes sp.2	1	1	8.33	11	91.67	12
Trametes sp.3	0	-	-	12	100	12
Trametes sp.4	2	5	4.55	105	95.45	110
Trametes sp.5	2	9	7.96	104	92.04	113
Trametes sp.6	2	19	37.25	32	62.75	51

Stereaceae						
Stereum hirsutum & *Stereum* sp.[b]	0	-	-	10	100	10
Stereum ostrea	4	240	92.31	20	7.69	260
Thelephoraceae						
Thelephora sp.	4	32	96.97	1	3.03	33
Not Identified	1	1	100	0	0	1
Not identified	1	1	25	3	75	4
Phaeolus schweinitzii & *Coriolus versicolor*[b]	0	-	-	29	100	29
Trametes meyenii & cf. *Coriolus* sp.[b]	1	17	100	0	0	17
TOTAL		891	40.35	1317	59.65	2208

a One sample was lost

b It was not possible to know the exact number of ciids from each host fungus

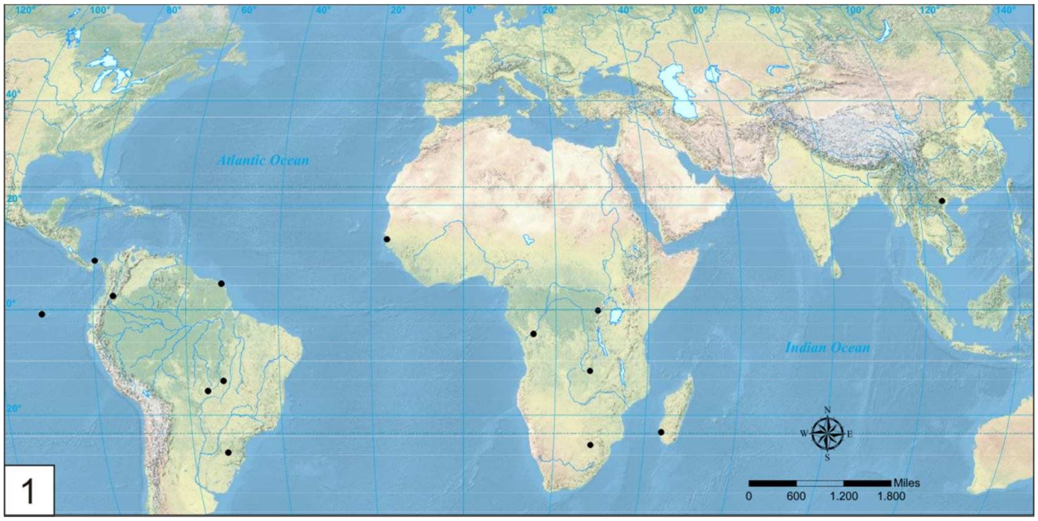
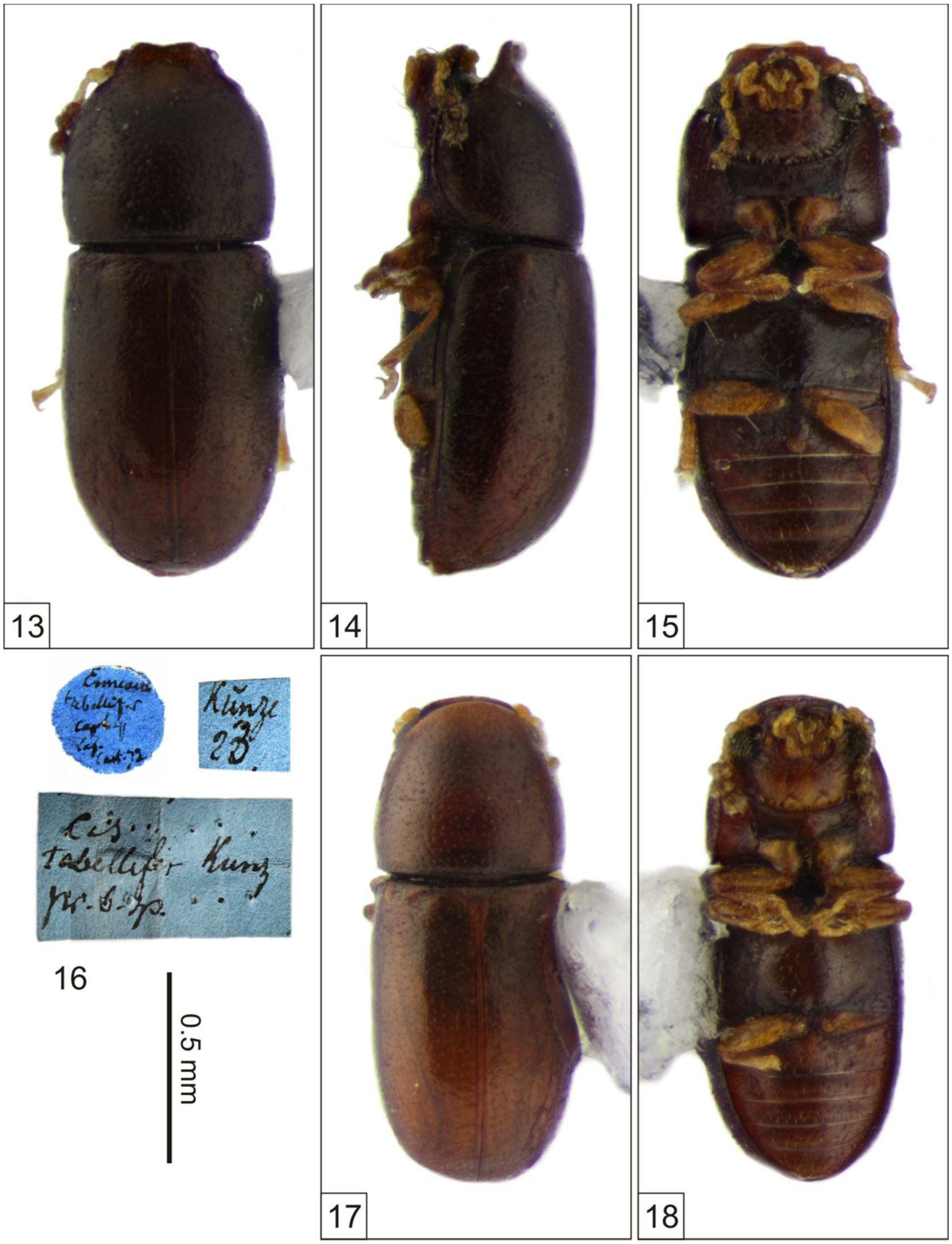


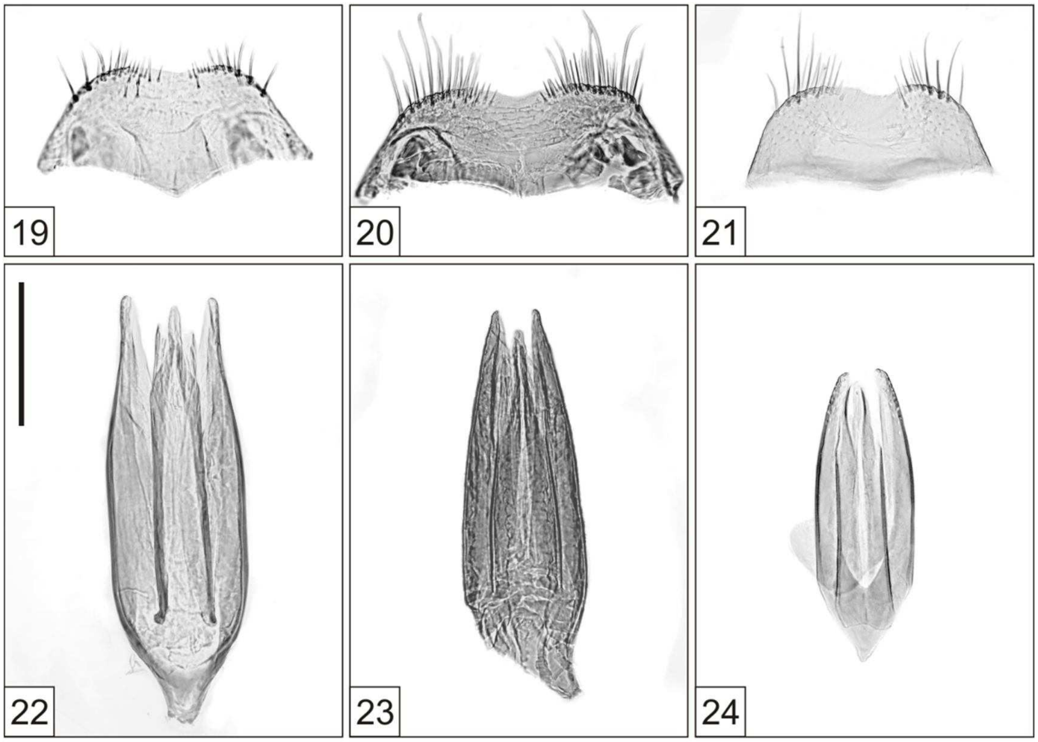
Figure 1. Geographic location of the dissected male specimens.

Figures 2–7. Habitus of *Ceracis cucullatus* (Mellié). Lecotype male (2–5). **2** Dorsal view. **3** Lateral view. **4** Ventral view. **5** Label data. Paralectotype female (6–7).**6** Dorsal view. **7** Ventral view. All figures are in the same scale, except the labels.

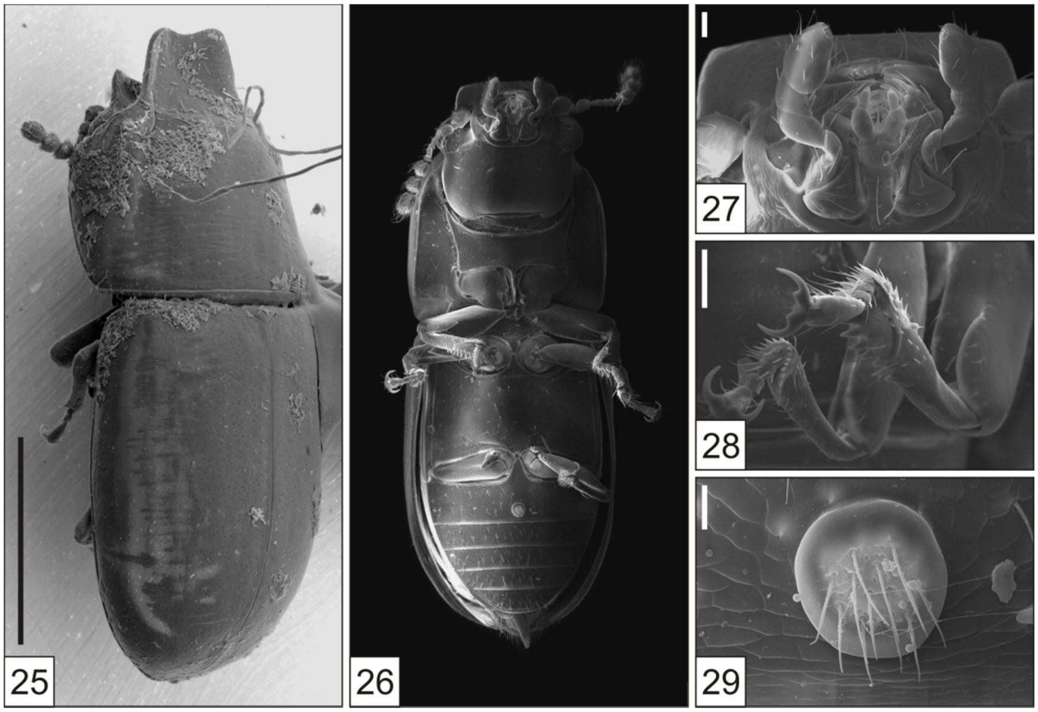
Figures 8–12. Habitus of *Ceracis lamellatus* (Pic). Topotype male (8–10). **8** Dorsal view. **9** Lateral view. **10** Ventral view. Topotype female (11–12). **11** Dorsal view. **12** Ventral view. All figures are in the same scale, except the labels.



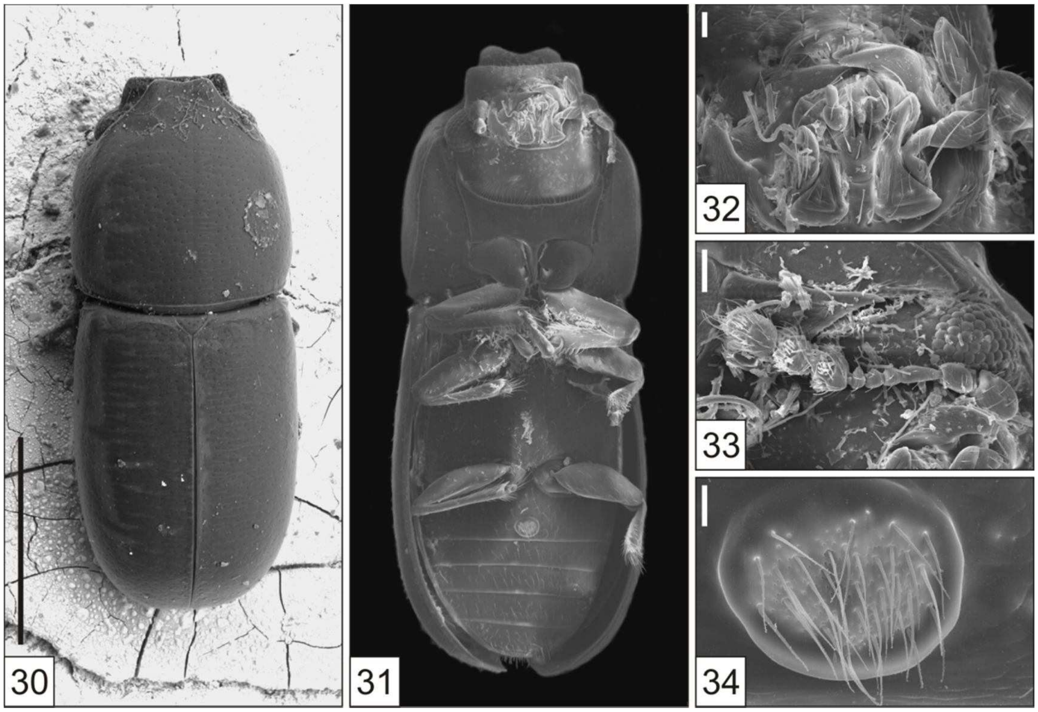
Figures 13–18. Habitus of *Ceracis tabellifer* (Mellié). Lectotype male (13–15). **13** Dorsal view. **14** Lateral view. **15** Ventral view. **16** Label data. Paralectotype female (17–18). **17** Dorsal view. **18** Ventral view. All figures are in the same scale, except the labels.



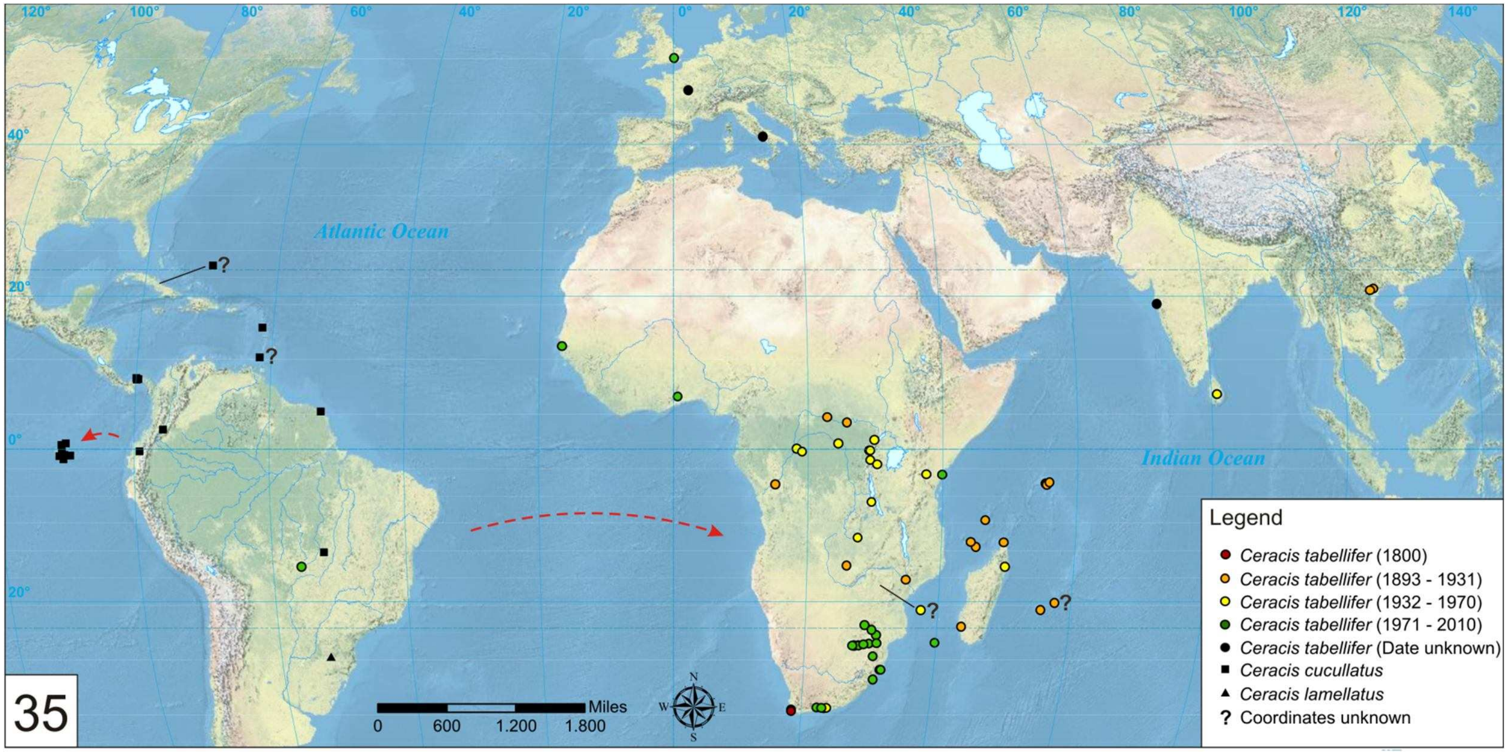
Figures 19–24. Whole mount preparations of eighth sternite (19–21) and aedeagus (22–24) showing penis and tegmen of *Ceracis cucullatus* (Mellié) (**19**, **22**), *C. lamellatus* (Pic) (**20**, **23**) and *C. tabellifer* (Mellié) (**21**, **24**). All figures are in the same scale. Scale bar = 0.1 mm.



Figures 25–29. SEM of male specimens of *Ceracis cucullatus* (Mellié). **25** Dorsolateral view. **26** Ventral view. **27** Ventral view of the mouthparts. **28** Anterior and median legs. **29** Abdominal sex patch. Scale bars: 0.5 mm (25–26); 0.05 mm (27); 0.02 mm (26, 28).



Figures 30–34. SEM of male specimens of *Ceracis tabellifer* (Mellié). **30** Dorsal view. **31** Ventral view. **32** Ventral view of the mouthparts. **33** Ventrolateral view of the head showing an antenna. **34** Abdominal sex patch. Scale bars: 0.5 mm (30–31); 0.05 mm (27); 0.02 mm (26, 28).



Figures 35. Geographic distribution of *Ceracis cucullatus* (Mellié), *C. lamellatus* (Pic) and *C. tabellifer* (Mellié). The records of *C. tabellifer* are divided into four time periods, represented by different colors – records undated are represented by black circles (see map legend). Between 1800 and 1893, no record was found. Records of *C. cucullatus* from Cuba and Grenada, and of *C. tabellifer* from Zimbabwe and Mauritius Island are indicated by "?", because it was not possible to know the exact location of collection. Arrows indicate the probable direction of introductions of *C. cucullatus* and *C. tabellifer* in Galapagos Islands and Africa, respectively.