ÍTALO SALVATORE DE CASTRO PECCI MADDALENA

SISTEMÁTICA DAS ESPÉCIES DE *Ceracis* MELLIÉ DO GRUPO *furcifer* (COLEOPTERA: CIIDAE)

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: 17 de julho de 2015.

Lucimar Soares de Araújo

Vivian Eliana Sandoval Gómez
(Coorientadora)

Cristiano Lopes Andrade
(Orientador)

Dedico este trabalho aos meus pais Salvatore e Tânia e à memória do professor Maury Pinto de Oliveira, que quando eu era criança, ele um jovem de 88 anos, estimulou em mim o amor pelos besouros...

Mude

Mas comece devagar,
porque a direção é mais importante
que a velocidade.

Sente-se em outra cadeira,
no outro lado da mesa.
Mais tarde, mude de mesa.
Quando sair,
procure andar pelo outro lado da rua.
Depois, mude de caminho,
ande por outras ruas,
calmamente,
observando com atenção
os lugares por onde você passa.
Tome outros ônibus.
Mude por uns tempos o estilo das roupas.
Dê os teus sapatos velhos.
Procure andar descalço alguns dias.
Tire uma tarde inteira
para passear livremente na praia,
ou no parque,
e ouvir o canto dos passarinhos.

Veja o mundo de outras perspectivas.

Abra e feche as gavetas
e portas com a mão esquerda.
Durma no outro lado da cama.
Depois, procure dormir em outras camas.
Assista a outros programas de tv,
compre outros jornais,
leia outros livros,

Viva outros romances!

Não faça do hábito um estilo de vida.
Ame a novidade.
Durma mais tarde.
Durma mais cedo.
Aprenda uma palavra nova por dia
numa outra língua.
Corrija a postura.
Coma um pouco menos,
escolha comidas diferentes,
novos temperos, novas cores,
novas delícias.
Tente o novo todo dia. O novo lado,
o novo método,
o novo sabor,
o novo jeito,
o novo prazer,
o novo amor.
A nova vida.
Tente.
Busque novos amigos.
Tente novos amores.
Faça novas relações.
Almoce em outros locais,
vá a outros restaurantes,
tome outro tipo de bebida
compre pão em outra padaria.
Almoce mais cedo,
jante mais tarde, ou vice-versa.
Escolha outro mercado,
outra marca de sabonete,
outro creme dental.
Tome banho em novos horários.

Use canetas de outras cores.
Vá passear em outros lugares.
Ame muito,
cada vez mais,
de modos diferentes.
Troque de bolsa,
de carteira,
de malas.
Troque de carro.
Compre novos óculos,
escreva outras poesias.
Jogue os velhos relógios,
quebre delicadamente
esses horrorosos despertadores.
Abra conta em outro banco.
Vá a outros cinemas,
outros cabeleireiros,
outros teatros,
visite novos museus.
Mude.
Lembre-se de que a Vida é uma só.
Arrume um outro emprego,
uma nova ocupação,
um trabalho mais light,
mais prazeroso,
mais digno,
mais humano.

Se você não encontrar razões para ser livre,
invente-as.

Seja criativo.

E aproveite para fazer uma viagem despretensiosa,

longa, se possível sem destino.
Experimente coisas novas.
Troque novamente.
Mude, de novo.
Experimente outra vez.
Você certamente conhecerá coisas melhores
e coisas piores,
mas não é isso o que importa.
O mais importante é a mudança,
o movimento,
o dinamismo,
a energia.

Só o que está morto não muda!
(Edson Marques)

Para que eu não esqueça daqui a dez anos: Esta dissertação deu muito trabalho, pois foi toda minha vida, até aqui...

"Fórmula de minha ventura: um sim, um não,
uma linha reta, um objetivo..."
Friedrich Nietzsche em "O crepúsculo dos ídolos"

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SUMÁRIO

RESUMO

MADDALENA, Ítalo Salvatore de Castro Pecci, M.Sc., Universidade Federal de Viçosa, julho de 2015. **Sistemática das espécies de *Ceracis* Mellié do grupo *furcifer* (Coleoptera: Ciidae)**. Orientador: Cristiano Lopes Andrade. Coorientadora: Vivian Eliana Sandoval Gómez.

Poucos organismos são consumidores de *Pycnoporus sanguineus*, uma espécie de fungo tóxica devido a sua alta concentração de cinabarinas e outras substâncias tóxicas. Este fungo concentra elementos que geralmente estão em baixa concentração em ecossistemas terrestres (por exemplo, cádmio). Entre os animais que são capazes de consumir este fungo na região Neotropical, as espécies de *Ceracis* do chamado "grupo *furcifer*" parecem ser as mais freqüentes. No entanto, apesar da sua importância na ciclagem dos componentes de *P. sanguineus*, a taxonomia do grupo furcifer ainda não foi revisada. Sabe-se que o grupo foi proposto a mais de quarenta anos e desde então inclui oito espécies descritas: *Ceracis cornifer* (Mellié), *Ceracis cylindricus* (Brèthes), *Ceracis furcifer* Mellié, *Ceracis hastifer* (Mellié), *Ceracis monocerus* Lawrence, *Cerarcis ruficornis* Pic, *Ceracis simplicicornis* (Pic) e *Ceracis unicornis* Gorham. Porém a descrição e um estudo comparativo da terminalia masculina ainda não foram conduzidos. Além disso, pouco ou nada se sabe a respeito dos padrões de distribuição das espécies do grupo. A presente dissertação tem por objetivo esclarecer a taxonomia do grupo *furcifer*, prover novos dados sobre sua distribuição e discutir os possíveis padrões biogegráficos do grupo, levando também em consideração a sua relação com o fungo *P. sanguineus*. A partir de comparações morfológicas, morfométricas, dissecação e análise de terminálias abdominais de machos e estudo da literatura, o grupo *furcifer* agora é composto por apenas quatro espécies dispostas artificialmente em dois subgrupos: (i) *Ceracis cornifer* e *Ceracis hastifer*; (ii) *Ceracis furcifer* e *Ceracis ruficornis*. Com base em comparações da terminália masculina, nós **(i)** sinonimizamos *Cer. cylindricus*, *Cer. monocerus*, *Cer. unicornis* and *Cer. simplicicornis* com *Cer. cornifer*; **(ii)** designamos lectótipos para *Cer. cornifer*, *Cer. furcifer*, *Cer. hastifer* e *Cer. ruficornis*; **(iii)** confirmamos a sinonimia de *Cer. semipallidus* com *Cer. furcifer* (Lawrence 1967); **(iv)** redescrevemos *Cer. cornifer*, *Cer. hastifer*, *Cer. furcifer* e *Cer. ruficornis*; **(v)** propomos uma chave de identificação para as espécies do grupo *furcifer*.
Tendo como base esse grande número de sinonímias, a inclusão de novas espécies no grupo, com base apenas na morfologia do corno frontoclipeal e coloração do corpo, é

contestada. Discute-se que estes dois aspectos, na verdade, são devido à variação intraespecífica entre os machos, além da ontogenia e outros fatores biológicos que levam também à formação de ecótipos. Apesar desta variação intraespecífica, o grupo *furcifer* apresenta grande homogeneidade morfológica entre as suas espécies. É provável que uma recente separação do grupo tenha ocorrido, o que pode ser uma explicação; este fator temporal associado com uma dieta especializada pode ter levado o grupo *furcifer* a um quadro de estase evolutiva. Esta hipótese pode explicar porque populações disjuntas de *Cer. cornifer* ainda não divergiram. Por outro lado, é possível que as diferenças entre as espécies do grupo *furcifer* sejam polimorfismos; A associação entre polimorfimos dentro de populações espacialmente separadas é um fator que pode levar a especiação. Neste contexto, as variações morfológicas verificadas no grupo *furcifer*, podem ser evidencias de que algumas linhagens agora estejam se divergindo. Este conhecimento demonstra que o grupo *furcifer* pode ser uma ferramenta muito útil em futuros trabalhos de filogeografia.

ABSTRACT

MADDALENA, Ítalo Salvatore de Castro Pecci, M.Sc., Universidade Federal de Viçosa, July, 2015. **Sistematics of *Ceracis* Mellié of the *furcifer* group (Coleoptera: Ciidae)**. Advisor: Cristiano Lopes Andrade. Co-advisor: Vivian Eliana Sandoval Gómez.

Few animals in the Neotropics are consumers of *Pycnoporus sanguineus*, a toxic fungus species due to high concentration of cinnabarins and other toxic substances. Such fungus components (e.g. cadmium and molybdenum) are generally concentrated in low concentration in terrestrial environments. Among the animals that are able to consume this fungus in the Neotropics, species of the *Ceracis* (*furcife*r) group, seem to be the most frequent. However, despite its importance in the cycling of *P. sanguineus* components, the taxonomy of the *furcifer* group has not yet been revised. It is known only the group was proposed more than forty years ago and since then, includes eight species described: *Ceracis cornifer* (Mellié), *Ceracis cylindricus* (Brèthes), *Ceracis furcifer* Mellié, *Ceracis hastifer* (Mellié), *Ceracis monocerus* Lawrence, *Cerarcis ruficornis* Pic, *Ceracis simplicicornis* (Pic) and *Ceracis unicornis* Gorham. However, the description and a comparative study of the male terminalia have not yet been conducted. In addition, little or nothing is known about the distribution patterns of the *furcifer* species group. This work aims to clarify the taxonomy of the *furcifer* group, providing new data on distribution and discuss its possible biogeographic patterns, also taking into account its association with *P. sanguineus*. As a result of morphological and morphometric comparisons, dissection and examination of male abdominal terminalia and study of the literature, we **(i)** synonymize *Cer. cylindricus*, *Cer. monocerus*, *Cer. unicornis* and *Cer. simplicicornis* with *Cer. cornifer*; **(ii)** designate lectotypes for *Cer. cornifer*, *Cer. furcifer*, *Cer. hastifer* and *Cer. ruficornis*; **(iii)** confirmed the synonym of *Cer. semipallidus* with *Cer. furcifer* (Lawrence 1967); **(iv)** provide a redescription of *Cer. cornifer*, *Cer. hastifer*, *Cer. furcifer* and *Cer. ruficornis*; **(v)** Propose an identification key for *furcifer* species-group. Now *furcifer* group consists of only four species artificially arranged into two subgroups: (i) *Ceracis cornifer* and *Ceracis hastifer* (ii) *Ceracis furcifer* and *Ceracis ruficornis*. Based on comparisons of male terminalia, four species (*Cer. cylindricus*, *Cer. monocerus*, *Cer. simplicicornis* and *Cer. unicornis*) were synonymized with *Cer. cornifer*, which is in actually a species widely distributed and with a disjunct distribution. Based on this large number of synonyms,

we definitively contest the inclusion of new species in the group, based mostly in frontoclypeal horn and body coloration. We argued these two aspects, in fact, are due to male intraspecific variations, as well ontogeny and other biological factors, besides the occurrence of ecotypes. Despite this intraspecific variation, the furcifer group shows great morphological homogeneity among their species. We discuss a likely recent separation occurred in this group; this time factor associated with a specialized diet may have led the *furcifer* group to an evolutionary stasis. This hypothesis can explain why disjunct populations of *Cer. cornifer* has not diverged. Besides it is possible that the differences among specimens are polymorphisms; the association between polymorphisms within spatially separate populations is a factor that can lead to speciation. Thus, these morphological variations in the *furcifer* group, may be evidence that some populations currently must to be diverging. The knowledge provide here demonstrates that *furcifer* group is a very useful tool in future studies of phylogeography.

1. INTRODUÇÃO

Ciidae (Coleoptera: Tenebrionoidea) são besouros pequenos (0,5 a 7 mm) que passam a vida no interior ou ao redor de basidiomas corticoides ou poliporoides de macrofungos das ordens Hymenochaetales, Polyporales e Auriculariales. A maioria desses fungos, em especial as espécies com basidiomas poliporoides, são conhecidos vulgarmente como "orelhas-de-pau". Os ciídeos são considerados organismos **micetobiontes**, pois a associação com fungos hospedeiros é obrigatória em todas as fases de desenvolvimento desses besouros. A maioria dos representantes da família pertence à Ciinae, que inclui atualmente 42 gêneros e cerca de 650 espécies descritas, distribuídas por todos os ecossistemas terrestres do planeta, exceto os pólos (Paviour-Smith 1960; Lawrence 1971, 1973; Lawrence & Lopes-Andrade 2010; Graf-Peters *et al.* 2011; Oliveira *et al.* 2013; Lopes-Andrade & Grebennikov 2015).

Nas duas últimas décadas, o conhecimento científico sobre os ciídeos avançou bastante, principalmente no campo da Sistemática (Królik 2002; Kawanabe 2002, 2003, 2005, 2007; Lopes-Andrade 2002; Lopes-Andrade *et al*. 2002; Lopes-Andrade *et al*. 2003a; Lopes-Andrade & Zacaro 2003a,b; Lopes-Andrade & Lawrence 2005; Lopes-Andrade 2007a,b, 2008, 2010a,b, 2011; Lopes-Andrade *et al*. 2009; Lopes-Andrade & Lawrence 2011; Antunes-Carvalho *et al.* 2012; Sandoval-Gómez 2013; Sandoval-Gómez *et al*. 2014; Pecci-Maddalena *et al.* 2014; Lopes-Andrade & Grebennikov 2015) e Ecologia (Guevara *et al*. 2000a,b; Guevara *et al*. 2000c; Komonen 2006; Lopes-Andrade *et al*. 2003b; Gumier-Costa *et al*. 2003; Gumier-Costa 2004; Orledge & Reynolds 2005; Graf-Peters *et al*. 2011; Souza 2013; Araujo *et al*. 2015). Apesar destes avanços, a taxonomia dos dois principais gêneros da família (*Cis* Latreille e *Ceracis* Mellié) ainda é bastante obscura. Alguns grupos de espécies dentro destes dois gêneros foram recentemente revisados (ver Antunes-Carvalho & Lopes-Andrade 2011, 2013; Oliveira *et al*. 2013), porém existem ainda muitos problemas a serem solucionados, principalmente para as espécies da região Neotropical.

1.1. O gênero *Ceracis* Mellié, 1849

Atualmente *Ceracis* inclui 52 espécies descritas, o que o torna o segundo gênero mais rico em espécies dentro de Ciidae, atrás apenas de *Cis* (com cerca de 350 espécies). Mellié (1849) propôs o nome como subgênero de *Ennearthron* Mellié e incluiu cinco espécies. Lacordaire (1857) elevou *Ceracis* a gênero e autores subsequentes adicionaram espécies em ambos os gêneros (*Ennearthron* e *Ceracis*). Somente mais de um século depois, Lawrence (1967) revisou as espécies norte-americanas de *Ceracis*, ampliou os limites morfológicos do gênero e incluiu espécies originalmente descritas em *Cis*, *Ennearthron*, *Octotemnus* Mellié, *Scolytocis* Blair, *Xestocis* Casey e *Xylographus* Mellié. Após esse período, a taxonomia de *Ceracis* avançou pouco, com a publicação de apenas algumas descrições (Lawrence 1971; Miyatake 1982; Lopes-Andrade *et al*. 2002) e, recentemente, dois artigos de revisão de um grupo de espécies (Antunes-Carvalho & Lopes-Andrade 2011, 2013).

As espécies de *Ceracis* apresentam forma do corpo oval e alongada (subcilíndrico), revestimento consistindo de cerdas finas e diminutas (subglabro), antenas com oito a dez antenômeros, margens laterais do pronoto estreitas, ângulos anteriores do pronoto obtusos ou arredondados, prosterno côncavo a achatado ou ligeiramente convexo, processo prosternal laminado, metaventrito medianamente a fortemente convexo, discrimen curto ou ausente, protíbias expandidas na região apical e com uma fileira de espinhos margeando o ângulo apical externo. Machos apresentam marca sexual circular ou oval no primeiro ventrito abdominal (fóvea) e apresentam comumente cornos ou tubérculos conspícuos no ápice do pronoto e na placa frontoclipeal (Lawrence 1967; Antunes-Carvalho *et al.* 2011; Pecci-Maddalena *et al.* 2014).

As relações filogenéticas de *Ceracis* ainda não são claras, mas há indícios de que o gênero seja merofilético (Lopes-Andrade & Grebennikov 2015). Esta situação se agrava considerando o grande número de espécies descritas para o gênero. Em casos como este, o agrupamento das espécies tem se mostrado uma ferramenta útil, pois facilita estudos taxonômicos e permite testar hipóteses taxonômicas e biogeográficas (*e.g.* Lawrence 1967, 1971; Lopes-Andrade *et al.* 2002; Oliveira *et al.* 2013). Neste contexto, quatro grupos baseados exclusivamente em similaridades morfológicas externas, englobando 21 espécies, foram definidos para *Ceracis* (Lawrence 1967; Lopes-Andrade *et al.* 2002) (número de espécies entre parênteses): (i) grupo *furcifer* (8); (ii) *grupo cucullatus* (6); (iii) grupo *furcatus* (4); e (iv) grupo *singularis* (3). As demais 31 espécies do gênero ainda não estão formalmente incluídas em nenhum grupo e devem integrar outros grupos em trabalhos futuros.

Ceracis apresenta distribuição ampla e, apesar de mais diverso nas regiões Neotropical e Neártica, várias espécies ocorrem na Oceania, ilhas do Oceano Pacífico e duas na região Paleártica. Recentemente, duas espécies foram classificadas como invasoras: *Ceracis cucullatus* (Mellié, 1849), nativa do continente sul-americano e introduzida em Galápagos; e *Ceracis tabellifer* (Mellié, 1849), nativa da região Neotropical e introduzida na África e sul e sudeste da Ásia (Antunes-Carvalho & Lopes-Andrade 2013). Ao menos vinte das espécies descritas já foram encontradas no Brasil, mas há várias espécies novas brasileiras em coleções científicas e, possivelmente, os nossos biomas abrigam a maior diversidade do gênero (C. Lopes-Andrade *com. pess.*).

1.2. Hábito alimentar e fungos hospedeiros

Ciídeos têm sido tradicionalmente incluídos em grupos de uso de fungos hospedeiros (Paviour-Smith 1960; Lawrence 1973; Orledge & Reynolds 2005; Graf-Peters *et al*. 2011; Araujo 2014). Estes grupos podem ser definidos por emissões de voláteis características que são compartilhadas pelos seus membros (fungos) e que são geralmente reconhecidas apenas pelas espécies de ciídeos típicas de cada grupo (Orledge & Reynolds 2005). De acordo com Orlegde & Reynolds (2005) atualmente, são reconhecidos seis grupos de fungos hospedeiros para ciídeos. Em quatro deles há registros de *Ceracis*: (i) **Grupo *Trichaptum*** (*e.g Ceracis powelli* Lawrence); (ii) **Grupo *Phellinus*** (*e.g Ceracis pullulus* (Casey), *Ceracis puntulatus* Casey, *Ceracis singularis* (Dury), *Ceracis obrieni* Lawrence); **(iii) Grupo *Trametes*** (*e.g Ceracis dixiensis* (Tanner), *Ceracis monocerus* Lawrence) e **(iv) Grupo *Ganoderma*** (*Ceracis multipunctatus* (Mellié), *Ceracis californicus* (Casey)).

Entretanto a classificação dentro dos grupos supracitados não necessariamente reflete o grau de especialização destes besouros com seus fungos hospedeiros (Araujo 2014). Também é possível classificar os ciídeos quanto aos seus tipos de estratégias alimentares. Uma espécie de ciídeo é considerada **polífaga** quando a porcentagem de ocorrências numa única família de fungos é menor do que 90% do total de registros de ocorrência, **oligófaga** quando essa porcentagem é maior que 90% e **monofága** quando o ciídeo alimenta-se de uma única espécie de fungo hospedeiro (Graf-Peters *et al*. 2011). Neste contexto, algumas espécies de *Ceracis* são reconhecidamente polífagas, por exemplo, as espécies do grupo *cucullatus*, encontradas em fungos da família Ganodermataceae, Meripilaceae, Meruliaceae e Polyporaceae (Antunes-Carvalho & Lopes-Andrade 2013). A espécie *Cer. limai* Lopes-Andrade *et al*., 2002 é considerada oligófaga e associada a algumas espécies dentro de Hymenochaetaceae (Graf-Peters *et al.*2011). A monofagia é pouco conhecida para o gênero (Lawrence 1973; Graf-Peters *et al.*2011). Algumas espécies só foram encontradas em um único fungo hospedeiro, como é o caso de *Ceracis pecki* Lawrence, registrada em *Poria nigra* (Polyporaceae) (Lawrence 1971). Porém, para a uma afirmação precisa sobre níveis mais altos de especialização, é necessário que o maior número possível de fungos hospedeiros seja examinado e a freqüência de espécies de *Ceracis* igualmente verificada.

1.3. O grupo *furcifer*

Originalmente o grupo *furcifer* inclui nove epítetos específicos (Lawrence 1967): *Ceracis cornifer* (Mellié, 1849); *Ceracis cylindricus* (Brèthes, 1922); *Ceracis furcifer* Mellié, 1849; *Ceracis hastifer* (Mellié, 1849); *Ceracis monocerus* Lawrence, 1967; *Cerarcis ruficornis* Pic, 1916; *Ceracis simplicicornis* (Pic, 1916); *Ceracis unicornis* Gorham, 1898 e *Ceracis semipallidus* Pic, 1922. Quando o grupo foi proposto, *Cer. semipallidus* foi sinonimizado com *Cer. furcifer* (Lawrence 1967), o que totaliza, portanto, oito espécies válidas no grupo.

Todas as espécies do grupo *furcifer* possuem corpo alongado, pontoação fina e esparsa no pronoto e nos élitros, pronoto levemente emarginado ou arredondado no ápice e machos armados com um corno frontoclipeal mediano (Lawrence1967). *Cer. cornifer, Cer. cylindricus, Cer. hastifer, Cer. monocerus, Cer. simplicicornis e Cer. unicornis*, possuem nove antenômeros e o corno frontoclipeal dos machos arredondado, truncado ou levemente emarginado no ápice. *Cer. furcifer e Cer. ruficornis,* apresentam oito antenômeros e o ápice do corno frontoclipeal nos machos leve ou profundamente bifurcado. Lawrence (1967) observou pouca diferença entre as espécies com oito antenômeros e entre as espécies com nove, restritas à coloração, pontoação e forma do corno frontoclipeal. O mesmo autor sugeriu a existência de “raças” de duas espécies politípicas, mas preferiu manter a separação de oito espécies com base na distribuição alopátrica conhecida até então.

Recentemente três espécies do grupo *furcifer* (*Cer. cornifer, Cer. furcifer, Cer.simplicicornis*) tiveram uma sequência do gene mitocondrial Citocromo-Oxidase subunidade 1 (COI) analisadas. A análise indicou que essas três espécies são muito próximas, talvez por compartilharem uma história evolutiva recente (Lopes-Andrade & Grebennikov 2015). É possível que o grupo *furcifer* seja de fato um clado. No entanto, baseado exclusivamente nas espécies de *Ceracis* analisadas, e na restrição a apenas um gene mitocondrial, ainda não é possível fazer uma afirmação precisa sobre as relações filogenéticas de *Ceracis,* assim como para as espécies do grupo *furcifer*.

1.3.1. Distribuição

Os dados de ocorrência das espécies do grupo *furcifer* disponíveis nas descrições originais são, em sua maioria, vagos e outros trabalhos com tais informações sobre o grupo são escassos na literatura. Porém, sabe-se que todas as espécies descritas para o grupo ocorrem na região Neotropical (Lawrence 1967; Gumier-Costa *et al.* 2003; Graf-Peters *et al*. 2011). Mellié (1849) descreve a localidade tipo de *Ceracis cornifer* unicamente como "Brasilia" (=Brasil) e os registros desta espécie limitam-se a poucas localidades na região sudeste deste país (ver Gumier-Costa *et al*. 2003; Lopes-Andrade 2004; Souza 2013). *Ceracis simplicicornis* (Pic) foi descrita para Buenos Aires (Argentina) e também registrada em São Francisco de Paula (RS-Brasil) (Graf-Peters *et al*. 2011). *Ceracis cylindricus* (Brèthes), *Ceracis unicornis* (Gorham), *Ceracis hastifer* (Mellié) e *Ceracis ruficornis* Pic, são conhecidas apenas pela localidade tipo, que são respectivamente: General Urquiza (Argentina), Ilha de São Vicente (Caribe), Colômbia (sem detalhes sobre a localidade) e Blumenau (SC-Brasil). A localidade tipo de *Ceracis furcifer* Mellié é Caiena (Guiana Francesa) mas há registros desta espécie no Peru, Suriname e Colômbia (sem detalhes sobre a localidade) e nas localidades de Izabal (Guatemala), Ilha de São Vicente e Guadalupe (Caribe), e Santo Domingo (República Dominicana) (Blackwelder 1945; Lawrence 1967; Lawrence *com. pess.*; Abdullah 1973).

Ceracis monocerus ocorre na Flórida (EUA), mas parece estender sua distribuição para algumas áreas vizinhas a este estado, com registro para o estado de Louisiana (Lawrence 1967). Esta espécie ocorre também em Cuba, que é uma das ilhas das Antilhas mais próxima da Flórida (Lawrence 1967). É interessante notar que a Flórida ora é reconhecida como parte da região Neotropical, ora como parte da região Neártica (Morrone 2006, 2014; Oliveira *et al.* 2013; Escalante *et al.* 2013). Aqui consideraremos a Flórida como parte da região Neotropical e áreas vizinhas como possíveis zonas de transição para a região Neárctica. É possível que tais zonas de transição sejam ecótonos, que de acordo com van der Maarel (1990) e Attrill & Rundle

(2002) são zonas de transição entre dois sistemas ecológicos adjacentes, cada um com tipos diferentes e relativamente homogêneos de comunidades.

1.3.1. Ecologia

Os membros do grupo *furcifer* tem sido frequentemente encontrados em basidiomas de *Pycnoporus sanguineus* (L.) Murrill (Polyporaceae) fungo que pertence ao grupo *Trametes* de fungos hospedeiros (Mellié 1849; Lawrence 1973; Gumier-Costa 2003; Orledge & Reynolds 2005; Graf-Peters *et al*. 2011; Souza 2013; Araujo 2014). Essa espécie de fungo está amplamente distribuída na região Neotropical (Roberts & Evans 2011; Graf-Peters *et al*. 2011) e é muito comum em áreas abertas do Brasil, como no bioma Cerrado (Resende 2013), clareiras de florestas (*obs. pess*.) com registro também em áreas modificadas pelo homem (da Silveira *et al*. 2008). Porém também existem registros do grupo *furcifer* em outros fungos, por exemplo, *Trametes* (Lawrence 1967; Pecci-Maddalena *obs. pess*.), *Coriolus* e *Lenzites* (Lawrence 1973). Por esta razão, talvez, as espécies do grupo *furcifer* sejam oligófagas, especialistas em alguns fungos dentro de Polyporaceae ou adotar diferentes estratégias alimentares, incluindo a monofagia.

A classificação de *Cer. cornifer* como polífaga feita por Souza (2013) é controversa, pois apesar deste ciídeo ter sido registrado em fungos de outras famílias, este registro pode ter sido ocasional (só foi encontrado um espécime em outras três famílias, ao passo que em *P. sanguineus* e *Trametes villosa*, ambos Polyporaceae, foram encontrados oito e três indivíduos respectivamente). É bem provável que *Cer. cornifer* responda mais a voláteis de *P. sanguineus* do que de outros fungos. Existem registros de outros ciídeos associados a *P. sanguineus* (Souza 2013; Araujo 2014), entretanto ao que parece, as espécies do grupo *furcifer* são as únicas, encontradas em grande número neste fungo e como reportado por Gumier-Costa *et al*. (2003), às vezes em populações com mais de cem indivíduos. Outro aspecto interessante é que indivíduos de *Cer. cornifer* podem colonizar *P. sanguineus* antes da fase de esporulação, um indicativo de que esses ciídeos podem ser parasitas deste fungo (Gumier-Costa *et al*. 2003).

P. sanguineus causa prejuízos para produtores de madeira (é um dos causadores da "podridão-branca"), mas também gera benefícios para a indústria farmacêutica por produzir diversos compostos antibióticos (Smania Jr. *et al*. 2003; Oliveira *et al*. 2007; Borderes *et al*. 2011; Modes *et al*. 2012). Seus basidiomas têm uma alta concentração de cinabarinas, substâncias tóxicas com ação antibiótica (Oliveira *et al.* 2007; Graf-Peters *et al.* 2011). Essa alta toxicidade poderia funcionar como uma barreira para o consumo por insetos. Entretanto o uso de *P. sanguineus* por ciídeos sugere que estes organismos podem ser resistentes aos compostos antibióticos deste fungo (Graf-Peters *et al.* 2011). Além de substâncias tóxicas, esses fungos concentram elementos que, normalmente, estão em baixa concentração em ecossistemas terrestres, como o cádmio e o molibdênio. Sendo assim, é possível que o grupo *furcifer* desempenhe um papel importante na ciclagem de tais nutrientes, em especial em áreas abertas, onde esse fungo é mais comum.

Para que futuros estudos sejam realizados é imprescindível a revisão taxonômica das espécies do grupo *furcifer*. Tal revisão deve ser apoiada em características morfológicas externas, o que inclui o exame da terminália abdominal dos machos. Além disso, para determinar os padrões de distribuição geográfica dessas espécies, bem como qual (is) o (s) recurso (os) alimentar (es) utilizado (os) por elas, deve-se examinar o maior número possível de exemplares, provenientes de diferentes localidades.

2. OBJETIVOS

1) Responder à pergunta: Quais as espécies do grupo *furcifer*? A resposta para esta pergunta inclui: (i) Redescrever as espécies; (ii) Resolver problemas de sinonímia; (iii) Fornecer as primeiras descrições dos escleritos da terminália abdominal de machos; (iv) Elucidar os limites morfológicos do grupo e suas diferenças e semelhanças com outros membros de *Ceracis* e outros membros de Ciidae; (v) Propor uma chave de identificação para as espécies do grupo;

2) Baseado na revisão taxonômica, responder às perguntas: Por que existem formas com oito antenômeros e ápice do corno frontoclipeal bifurcado e formas com nove antenômeros e ápice do corno frontoclipeal truncado? A hipótese sugerida por Lawrence (1967) de que o grupo *furcifer* é composto por raças de duas espécies politípicas está correta?

3) Responder às perguntas: Quais organismos na natureza são capazes de se alimentar de *P. sanguineus*? O grupo *furcifer* pode ser considerado "especialista" e neste caso, os únicos especialistas neste fungo?

4) Responder às perguntas: Qual o padrão biogeográfico das espécies do grupo *furcifer*? Qual uma possível explicação para este padrão? Qual a relação entre a distribuição das espécies e seu tipo de estratégia alimentar?

3. RESULTADOS

A presente dissertação é apresentada na forma de um manuscrito a ser submetido para a revista *PlosOne*: ***"Systematics of Ceracis (furcifer) (Coleoptera: Ciidae): A specialist Neotropical group of minute tree-fungus beetles".***

Este manuscrito não constitui e nem 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).

REFERÊNCIAS

Abdullah, M. 1973. The systematic position of Cisidae (Heteromera) including a catalogue of the world and comments on central European families of Cucujoidea (Coleoptera). Zoologische Beiträge (N.F.), 19 (2): 189–246.

Antunes-Carvalho, C. & Lopes-Andrade, C. 2011. Two new Neotropical species of *Ceracis* Mellié (Coleoptera, Ciidae) and redefinition of the cucullatus group. ZooKeys 132: 51-64. doi: 10.3897/zookeys.132.1570.

Antunes-Carvalho, C. & Lopes-Andrade, C. 2013. Two invaders instead of one: the true identity of species under the name *Ceracis cucullatus* (Coleoptera: Ciidae). PlosOne. 8 (8): e72319. doi:10.1371/journal.pone.0072319.

Antunes-Carvalho, C., Lopes-Andrade, C. & Sandoval-Gómez, V. E. 2012. *Grossicis*, a new genus of Neotropical minute tree-fungus beetles (Coleoptera: Ciidae), with a detailed discussion on its systematic position in the family. Comptes Rendus Biologies, 335: 107–119.

Araujo, L. S. 2014. Ecologia De Besouros Micetócolos: Novas Perspectivas para biomas da América do Sul e África. Tese de doutorado, Programa de Pós-Graduação em Entomologia, Universidade Federal de Viçosa.

Araujo, L. S., Komonen, A. & Lopes-Andrade, C. 2015. Influences of landscape structure on diversity of beetles associated with bracket fungi in Brazilian Atlantic Forest. Biological Conservation, 191: 659–666.

Attrill, M. J. & Rundle, S. D. 2002. Ecotone or Ecocline: Ecological Boundaries in Estuaries. Estuarine. Coastal and Shelf Science, 55: 929–936.

Blackwelder, R. B. 1945. Checklist of the Coleopterous Insects of Mexico, Central America the West Indies, and South America. 1544 pp.

Brèthes, J. 1922. "Descripción de varios coleópteros de Buenos Aires." Anales de la Sociedad Científica Argentina 94: 263-305.

Borderes, J., Costa, A., Guedes, A. & Tavares, L. B. B. 2011. Antioxidant Activity of the Extracts from *Pycnoporus sanguineus* Mycelium. Brazilian Archives Of Biology And Technology. 54(6): 1167-1174.

da Silveira., R. M. B., Reck, M. A., Graf, L. V. & Sá, F. N. 2008. Polypores from a Brazilian pine forest in Southern Brazil: pileate species. Hoehnea, 35(4): 619-630.

Escalante, T., Morrone J. J. & Rodríguez-Tapia G. 2013. Biogeographic regions of North American mammals based on endemism. Biological Journal of the Linnean Society, 110: 485–499.

Gorham, H. S. 1898. "On the serricorn Coleoptera of St. Vincent, Grenada and the Grenadines (Malacodermata, Ptinidae, Bostrychidae) with descriptions of new species." Proc. Zool. Soc. London 27: 315-343.

Graf-Peters, L. V., Lopes-Andrade, C., da Silveira, R. M. B., Moura, L. A., Reck, M. A. & Nogueira, F. 2011. Host fungi and feeding habits of Ciidae (Coleoptera) in a subtropical rainforest in southern Brazil, with an overview of host fungi of Neotropical ciids. Florida Entomologist, 94 (3): 553–566.

Gumier-Costa, F. 2004. Influência de alterações antrópicas em besouros ciídeos de floresta amazônica. Dissertação de mestrado, Programa de Pós-Graduação em Entomologia, Universidade Federal de Viçosa.

Gumier-Costa, F., Lopes-Andrade, C. & Zacaro, A. A. 2003. Association of *Ceracis cornifer* (Mellié) (Coleoptera: Ciidae) with the bracket fungi *Pycnoporus sanguineus* (Basidiomycetes: Polyporaceae). Neotropical Entomology. 32(2): 359–360.

Guevara, R., Rayner, A. D. M. & Reynolds, S. E. 2000a. Effects of fungivory by two specialist ciid beetles (*Octotemnus glabriculus* and *Cis boleti*) on the reproductive fitness of their host fungus, *Coriolus versicolor*. New Phytol. 145: 137–144.

Guevara, R., Hutcheson, K. A., Mee, A. C., Rayner, A. D. M. & Reynolds, S. E. 2000b. Resource partitioning of the host fungus *Coriolus versicolor* by two ciid beetles: the role of odour compounds and host ageing. Oikos. 91: 184–194.

Guevara, R., Rayner, A. D. M. & Reynolds, S. E. 2000c. Orientation of specialist and generalist fungivorous ciid beetles to host and non-host odours. Physiological Entomology. 25: 288– 295.

Kawanabe, M. 2002. A Revision of the Genus *Octotemnus* (Coleoptera, Ciidae) from Japan. Japanese Journal of Systematic Entomology. 8: 243-267.

Kawanabe, M. 2003. Notes on the Genus *Euxestocis* (Coleoptera: Ciidae), with Description of a New Species from the Malay Peninsula. Special bulletin of the Japanese Society of Coleopterology. 6: 303–309.

Kawanabe, M. 2005. A New Species of the Genus *Octotemnus* (Coleoptera, Ciidae) from Nantou County, Central Taiwan. Elytra. 33: 47–50.

Kawanabe, M. 2007. *Cis satoi* (Coleoptera, Ciidae, Ciinae), a new ciid species from Thailand. Elytra. 35: 149–152.

Komonen, A. 2006. Local spatial pattern of two specialist beetle species (Ciidae) in the fruiting bodies of *Formitopsis pinicola*. Ecoscience 13:372-377.

Królik, R. 2002. *Cis tauriensis* n. sp. from Turkey (Coleoptera: Ciidae). Genus. 13: 197–202.

Lacordaire, J. T. 1857. Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome IV. Librairie Encyclopédique de Roret, Paris.

Lawrence, J. F. 1967. Delimitation of the genus Ceracis (Coleoptera: Ciidae) with a revision of North American species. Bulletin of the Museum of Comparative Zoology, 136: 91–143.

Lawrence, J. F. 1971. Revision of the North American Ciidae (Coleoptera). Bulletin of the Museum of Comparative Zoology. 142: 419–522.

Lawrence, J. F. 1973. Host preference in ciid beetles (Coleoptera: Ciidae) inhabiting the fruiting bodies of Basidiomycetes in North america. Bulletin of the Museum of Comparative Zoology. 145: 163–212.

Lawrence, J. F. & Lopes-Andrade, C. 2010. Ciidae Leach in Samouelle 1819, pp. 504-514. In R.G. Beutel, & R.A.B. Leshen (eds), Handbook of Zoology. Vol IV Arthopoda: Insecta. Part 39. Coleoptera, Vol. 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, New York.

Lopes–Andrade, C. 2002. Recent Advances in the Study of the Brazilian Ciidae (Coleoptera: Tenebrionoidea). Dugesiana 9, 5–13.

Lopes-Andrade, C., Madureira, M. S., Zacaro, A. A. 2002. Delimitation of the *Ceracis singularis* group (Coleoptera: Tenebrionoidea: Ciidae), with the description of a new Neotropical species. Dugesiana, 9, 59–63.

Lopes-Andrade, C., Gumier-Costa, F., Zacaro, A. A. 2003a. *Cis leoi*, a new species of Ciidae (Coleoptera: Tenebrionoidea) from the Neotropical Region. Zootaxa, 161, 1–7.

Lopes-Andrade, C., Gumier- Costa, F. & Sperber, C. F. 2003b. Why do Male *Xylographus contractus* Mellié (Coleoptera: Ciidae) Present Abdominal Fovea? Evidence of Sexual Pheromone Secretion. Neotropical Entomology 32(2): 217-220.

Lopes-Andrade, C. & Zacaro, A. A. 2003a. The first record of *Ennearthron* Mellié, 1847 (Coleoptera: Tenebrionoidea: Ciidae) in the Southern Hemisphere, with the description of a distinctive new species. Zootaxa, 395, 1–7.

Lopes-Andrade, C. & Zacaro, A. A. 2003b. *Xylographus lucasi*, a new Brazilian species of Ciidae (Coleoptera: Tenebrionoidea). Dugesiana, 10, 1–6.

Lopes-Andrade, C. 2004. Análise Filogenética de Ciidae (Coleoptera: Tenebrionoidea). Dissertação de mestrado, Programa de Pós-Graduação em Entomologia, Universidade Federal de Viçosa.

Lopes-Andrade, C. & Lawrence, J.F. 2005. *Phellinocis*, a new genus of Neotropical Ciidae (Coleoptera: Tenebrionoidea). Zootaxa. 1034: 43–60.

Lopes-Andrade, C. 2007a. Notes on *Falsocis* Pic (Coleoptera: Tenebrionoidea: Ciidae), with the description of an endangered Brazilian species. Zootaxa. 1544: 41–58.

Lopes-Andrade, C. 2007b. *Neoapterocis*, a new genus of apterous Ciidae (Coleoptera: Tenebrionoidea) from Chile and Mexico. Zootaxa. 1481: 35–47.

Lopes-Andrade, C. 2008. The first record of *Cis chinensis* Lawrence from Brazil, with the delimitation of the *Cis multidentatus* species-group (Coleoptera: Ciidae). Zootaxa. 1755: 35–46.

Lopes-Andrade, C. 2010a. Two new species of *Cis* Latreille (Coleoptera: Ciidae) from Chile. Zootaxa. 2441: 53–62.

Lopes-Andrade, C. 2010b. The first record of *Orthocis* Casey (Coleoptera: Ciidae) from the Andean Region, with the description of a distinctive new species. Zoological Science. 27: 830–833.

Lopes-Andrade, C. 2011. The first *Strigocis* Dury (Coleoptera: Ciidae) from the southern Neotropical region and a provisional key to world species. ZooKeys. 81: 27–37.

Lopes-Andrade, C., Matushkina, N., Buder, G. & Klass, K. D. 2009. *Cis pickeri* sp. nov. (Coleoptera: Ciidae) from Southern Africa. Zootaxa, 2117: 56–64.

Lopes-Andrade, C. & Lawrence, J. F. 2011. Synopsis of *Falsocis* Pic (Coleoptera, Ciida), new species, new records and an identification key. ZooKeys. 145: 59–78.

Lopes-Andrade, C. & Grebennikov, V.V. 2015. First record and five new species of Xylographellini (Coleoptera: Ciidae) from China, with online DNA barcode library of the family. ZOOTAXA, 4006 (3): 463–480.

Mellié, J. 1849. Monographie de l'ancien genre Cis des auteurs. Annales de la Société Entomologique de France, 6(2): 205–274, 313–396.

Miyatake, M. 1982. Three new species of the Ciidae from Taiwan (Coleoptera). In M. Satô, Y. Hori, Y. Arita & T. Okadome (eds), Special issue to the memory ofretirement of emeritus professor Michio Chûjô, Nagoya, Japan.

Modes, K. S., Lazarotto, M., Beltrame, R., Vivian, M. A., Santini, E. J. Muniz, M. F. B. 2012. Resistência natural das madeiras de sete espécies florestais ao fungo *Pyconoporus sanguineus* causador da podridão-branca. Cerne, Lavras. 18(3): 6.

Morrone, J. J. 2006. Biogeographic areas and transition zones of latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu. Rev. Entomol, 51:467–94.

Morrone, J. J. 2014. Cladistic biogeography of the Neotropical region: identifying the main events in the diversification of the terrestrial biota. Cladistics, 30 202–214.

Oliveira, L. F. C., Le Hyaric, M., Berg, M. M., de Almeida, M. V. & Edwards, H. G. M. 2007. Raman spectroscopic characterization of cinnabarin produced by the fungus *Pycnoporus sanguineus* (Fr.) Murr. Journal of Raman Spectroscopy, 38 (12): 1628-1632.

Oliveira, E. H., Lopes-Andrade, C. & Lawrence, J. F. 2013. Review of the Neotropical Ciidae (Insecta: Coleoptera) in the *Cis* taurus species-group. ARTHROPOD SYSTEMATICS & PHYLOGENY, 71 (3): 181–210.

Orledge, G. M. & Reynolds, S. E. 2005. Fungivore host-use groups from cluster analysis: patterns of utilisation of fungal fruiting bodies by ciid beetles. Ecological Entomology, 30: 620–641.

Pavior-Smith, K. 1960. The fruiting-bodies of macrofungi as habitats for beetles of the family ciidae (coleoptera). Oikos 11(1): 43–71.

Pecci-Maddalena, Í.S.C., Sandoval-Gómez, V.E. & Lopes-Andrade, C. 2014. *Ceracis zarathustrai* sp. nov. (Coleoptera: Ciidae) from the Atlantic Forest biome. ZOOLOGIA, 31 (5): 482–488.

Pic, M. 1916. Mélanges Exotico-Entomologiques. Bussière.

Pic, M. 1922. Noveautés diverses. Melanges Exotico-Entomologiques, 36: 22.

Roberts, P. & Evans, S. 2011. The Book of Fungi: A Life-Size Guide to Six Hundred Species from around the World.1th ed. United Kingdom: Ivy press. 656 pp.

Ruta, R. 2003. *Rhopalodontus lawrencei* n. sp. – the first *Rhopalodontus* species in the Oriental Region (Coleoptera: Tenebrionoidea: Ciidae). Genus, 14: 363–369.

Sandoval-Gómez, V. E. 2013. Revisão Taxonômica Do Gênero *Xylographus* Mellié, 1847 (Coleoptera: Polyphaga: Ciidae) Da África. Tese de doutorado, Programa de Pós-Graduação em Entomologia, Universidade Federal de Viçosa.

Sandoval-Gómez, V. E., Lopes-Andrade, C., Lawrence, J. F. 2014. Lectotype designations and nomenclatural changes in *Xylographus* Mellié (Coleoptera, Ciidae). ZooKeys, 374: 23–43.

Smania Jr, A., Marques, C. J. S., Smânia, E. F. A., Zanetti, C. R., Carobrez, S. G., Tramonte, R. & Loguercio-Leite, C. 2003. Toxicity and antiviral activity of cinnabarin obtained from *Pycnoporus sanguineus* (Fr.) Murr. Phytother Res 17(9): 1069-1072.

Souza, N. F. R. 2013. A fauna de besouros Ciidae (Insecta: Coleoptera) de Cerrado no Alto Paranaiba, MG. Dissertação de mestrado, Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Viçosa.

van der Maarel, E. 1990. Ecotones and ecoclines are different. Journal of Vegetation Science 1: 135-138.

Systematic of the *Ceracis furcifer* species-group (Coleoptera: Ciidae): A specialist Neotropical group of minute tree-fungus beetles[1]

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Systematic of the *Ceracis furcifer* species-group (Coleoptera: Ciidae): A specialist Neotropical group of minute tree-fungus beetles[1]

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Abstract

Few animals in the Neotropics are consumers of *Pycnoporus sanguineus*, a toxic fungus species due to high concentration of cinnabarins and other toxic substances. Among the animals able to consume this fungus, species of the *Ceracis* (*furcifer)* group, seem to be the most frequent. However, despite its importance, the taxonomy of the furcifer group must also be revised. It is known only the group includes eight species described, but description and a comparative study of the male terminalia have not yet been conducted. In addition, little or nothing is known about the distribution patterns of the *furcifer* group. As a result of morphological and morphometric comparisons, dissection and examination of male abdominal terminalia and study of the literature, the *furcifer* group now encompass four species artificially arranged into two subgroups: (i) *Ceracis* c*ornifer* and *Ceracis hastifer* (ii) *Ceracis furcifer* and *Ceracis ruficornis*. Based on patterns of the external morphology of adults, including male abdominal terminalia, we (i) synonymize *Cer. cylindricus*, *Cer. monocerus*, *Cer. unicornis* and *Cer. simplicicornis* with *Cer. cornifer*; (ii) designate lectotypes for *Cer. cornifer*, *Cer. furcifer*, *Cer. hastifer* and *Cer. ruficornis*; (iii) confirmed the synonym of *Cer. semipallidus* with *Cer. furcifer* (Lawrence 1967); (iv) provide a redescription of *Cer. cornifer*, *Cer. hastifer*, *Cer. furcifer* and *Cer. ruficornis*; (v) Propose an identification key for *furcifer* species-group. We definitively contest the inclusion of new species in the group, based mostly in frontoclypeal horn and body coloration as was done in the past. These two aspects are due to male intraspecific variations, as well ontogeny and other biological and environmental factors. Despite this intraspecific variation, the furcifer group shows great morphological homogeneity. We discuss a likely recent separation occurred and this factor associated with a specialized diet may have led the *furcifer* group to an evolutionary stasis. This hypothesis can explain why disjunct populations of *Ceracis cornifer* has not diverged. Besides it is possible that the differences among specimens are polymorphisms, which within spatially separate populations is a factor that can lead to speciation. Thus morphological variations in the furcifer group, may be evidence that some populations currently must to be diverging. We believe that the knowledge provides here, demonstrate that the *furcifer* group must be a useful tool for future phylogeography studies.

Introduction

Ceracis was described by MELLIÉ (1849) as a subgenus of Ennearthron Mellié, 1847. LACORDAIRE (1857) elevated *Ceracis* to genus and then LAWRENCE (1967) redefined its limits. Currently, *Ceracis* encompasses 52 described species, being the second most speciose genus of Ciidae (ANTUNES-CARVALHO & LOPESANDRADE 2011, 2013; Pecci-Maddalena *et al*. 2014). Four species-groups were defined for the genus (*Cer. cucullatus*, *Cer. furcatus*, *Cer. furcifer*, and *Cer. singularis*), but they encompass only 21 species (LAWRENCE 1967, LOPES-ANDRADE et al. 2002; Pecci-Maddalena *et al*. 2014). Only the *Cer. cucullatus* group was revised. Two of these species have been recognized as invasive: *Cer. cucullatus* (Mellié, 1849), native to the continental South America and introduced in Galapagos, and *Cer. tabellifer* (Mellié, 1849), native to the Neotropical region and introduced in Africa and south and southeast of Asia (Antunes-Carvalho & Lopes-Andrade 2011, 2013). Thus, the systematic of the remaining species of *Ceracis* are until unclear.

The *Ceracis furcifer* species-group (Coleoptera: Ciidae) originally includes nine species names: *Ceracis cornifer* (Mellié, 1849); *Ceracis cylindricus* (Brèthes, 1922); *Ceracis furcifer* Mellié, 1849; *Ceracis hastifer* (Mellié, 1849); *Ceracis monocerus* Lawrence, 1967; *Ceracis ruficornis* Pic, 1916; *Ceracis simplicicornis* (Pic, 1916); *Ceracis unicornis* Gorham, 1898 and *Ceracis semipallidus* Pic, 1922. When the group *furcifer* was proposed, *Cer. semipallidus* was synonymized with *Cer. furcifer* (Lawrence 1967) and then no changes were made to its composition, leaving the group with eight valid species. All species of the *furcifer* group have a similar body form, fine and sparse pronotal and elytral punctation, a rounded or shallowly emarginated pronotal apex and a median frontoclypeal horn in males (Lawrence 1967).

Cer.cornifer, *Cer. cylindricus*, *Cer.hastifer*, *Cer. monocerus*, *Cer. simplicicornis* and *Cer. unicornis*, have nine antennomeres and frontoclypeal horn of males rounded, truncated or shallowly emarginate at apex. *Cer.furcifer* and *Cer.ruficornis*, have eight antennomeres and the frontoclypeal horn of males is deeply incised at apex, forming two lobes (Lawrence 1967). Besides number of antennomeres, there are few differences between *furcifer* species-group, as color, dorsal punctation, shape of male frontoclypeal horn and the allopatric distribution of species based on the known material (Lawrence 1967). For this reason, Lawrence (1967) suggested that *furcifer* species "may well be races of two polytypic species”. He has not discussed further this matter; his work was a revision of the North American *Ceracis* and only briefly discussed taxonomic problems on Neotropical species.

Occurrence data of the *furcifer* species-group available in the original descriptions are very poor and other works with such information about the group are scarce in the literature. However, it is known that all species described for the group occurs in the Neotropical region (Lawrence 1967; Gumier-Costa et al. 2003; Peters et al Graf-2011.). Mellié (1849) describes the type-locality of *Ceracis cornifer* solely as "Brasilia" (= Brazil) and the other records of this species are limited to a few locations in the southeastern of this country (see Gumier-Costa *et al*. 2003; Lopes-Andrade 2004; Souza 2013). *Ceracis simplicicornis* (Pic) was described to Buenos Aires (Argentina) and also recorded in São Francisco de Paula (RS-Brazil) (Graf-Peters et al. 2011). *Ceracis cylindricus* (Brèthes), *Ceracis unicornis* (Gorham), *Ceracis hastifer* (Mellié) and *Ceracis ruficornis* Pic, are known only by the type-locality, which are respectively: General Urquiza (Argentina), St. Vincent (Caribbean), Colombia (type-locality unknown) and Blumenau (SC-Brazil). The type-locality of *Ceracis furcifer* Mellié is Cayenne (French Guiana) but there are records of this species in Peru, Suriname and Colombia (no details on the location) and the localities of: Izabal (Guatemala), St. Vincent and Guadeloupe (Caribbean) and Santo Domingo (Dominican Republic) (Blackwelder 1945; Lawrence 1967; Lawrence pers. obs. .; Abdullah in 1973.).

Ceracis monocerus occurs in Florida (USA), but seems to extend its distribution to nearby areas, as the state of Louisiana (Lawrence 1967). This species also occurs in Cuba, which is one of the Antilles islands closer to Florida (Lawrence 1967). Important to note that Florida is sometimes recognized as part of the Neotropical region, either as part of the Nearctic region (Morrone, 2006, 2014; Oliveira et al 2013;. 2013 Escalante et al.). Here we will consider Florida as part of the Neotropical and surrounding areas as possible transition zones for the Nearctic region. It is possible that such transition zones are ecotones, that are transition zones between two adjacent ecological systems (in our case, the two biogeographic regions), each of them with different types and relatively homogeneous communities (van der Maarel 1990; Attrill & Rundle 2002).

In terms of feeding habitats, members of the *furcifer* group have been recorded mostly in the blood-red bracket fungus *Pycnoporus sanguineus* (L.) Murrill (Polyporaceae) a member of the *Trametes* ciid host-use group (Mellié 1849; Lawrence 1973; Gumier-Costa 2003; Orledge & Reynolds 2005; Graf-Peters *et al*. 2011; Souza

2013; Araujo 2014). This fungus species is widely distributed in the Neotropics (Roberts & Evans 2011; Graf-Peters et al 2011) and is very common in open areas of the Brazil, as in the Cerrado biome (Resende 2013), forest clearings (pers. obs.) with record also in areas modified by humans (Silveira *et al*. 2008). This fungus cause damage to timber producers, being one of the causes of the "white-rot", but it is also beneficial for the pharmaceutical industry, producing antibiotic compounds (Smania Jr. *et al.* 2003; Oliveira *et al.* 2007; Borderes *et al.* 2011; Modes *et al.* 2012). Recently fungus extracts of the *P.sanguineus* have the potential for the production of bioactive substances against larvae of the *Anopheles nuneztovari* Gabaldón (1940), a malaria vector (Bücker *et al*. 2013).

Basidiomes of *P. sanguineus* have a high concentration of cinnabarins, toxic substances with antibiotic action (Oliveira et al 2007; Graf-Peters et al 2011.). Such high toxicity can function as a barrier for consumption by insects. However, the use of *P. sanguineus* by ciids suggests that these organisms may be resistant to antibiotic compounds of this fungus (Graf-Peters *et al*. 2011). Besides toxic substances, these fungi focus elements that usually are in low concentration in terrestrial ecosystems, such as cadmium, one of the most common toxic metals found in industrial effluents (Mashitah *et al*. 2008). However, there are also records of the *furcifer* group in other fungi, as *Trametes*, *Coriolus* and *Lenzites* (Lawrence 1967, 1973; Pecci-Maddalena pers. obs.). For this reason, maybe, the species of the *furcifer* group should be oligophagous, specialists in some fungi within Polyporaceae or adopt different feeding strategies, which can include monophagy.

Here we answer the following questions: **1)** actually, what the species compound the *furcifer* group? This answer included: (i) redescription of the species; (ii) resolution of synonymy problems; (iii) the first descriptions of the abdominal sclerites of the males terminalia; (iv) Elucidation of the morphological limits of the group and their differences and similarities with other *Ceracis* and ciidae members; (v) proposition of an identification key to the species of the *furcifer* group; **2)** Based on the taxonomic revision, answer the questions: Why there are individuals with the frontoclypeal horn of males deeply incised at apex and eight antennomeres and individuals with nine antennomeres and frontoclypeal horn of males rounded at apex? The hypothesis suggested by Lawrence (1967) that the *furcifer* group consists of races of two polytypic species is correct? **3)** What the organisms in the nature are able to feed of *P. sanguineus*? The *furcifer* group, in fact, can be regarded as "specialist," and in this case the only specialist in this fungus? **4)** What is the geographical pattern of distribution of the *furcifer* species-group? What is the possible explanation for this pattern? And finally, what is the relationship between the distribution of the species and their food strategy?

Material and Methods

We examined and dissected the lectotypes (here designated) of *Cer. cornifer*, *Cer. furcifer* and one paralectotype of *Cer. hastifer*. We based the redescription of *Cer. ruficornis* on a plesiotype (*sensu* Evenhuis 2008), because we examined only images of the lectotype, but designated a lectotype with bases in annotations made by John F. Lawrence in 1965, a ciid specialist who directly examined the type series. The type-specimen of *Cer. cylindricus* is considered to be lost (Lawrence 1967). We did not examine the types of *Cer. monocerus* and *Cer. simplicicornis*, but series of the first specimens and closely forms of the second (from localities near the type locality) were examined and a few individuals were dissected. In the case of *Cer. unicornis* we compared available images of type material with individuals of the *furcifer* group we had in hands. Besides type series and historical material (see results, material examined), we examined individuals of 58 localities of the Neotropical region; in most cases, we dissected at least one male individual of each locality for comparing sclerites of male abdominal terminalia.

We use terms for external morphology and male abdominal terminalia of ciids listed by Lopes-Andrade and Lawrence (2005). Range, mean and standard deviation values for measurements (in millimeters) and ratios are provide in the description and the following abbreviations are use: **BW**, basal width of the scutellum; **CL**, length of the antennal club (measured from base of the eighth to apex of the tenth antennomere); **EL**, elytral length (at midline, from base of scutellum to elytral apex); **EW**, greatest elytral width; **FL**, length of the antennal funicle (measured from base of the third to apex of the seventh antennomere); **GD**, greatest depth of the body (from elytra to metaventrite); **GW**, greatest diameter of the eye; **PL**, pronotal length along midline; **PW**, greatest pronotal width; **TL**, total length (=EL+PL; head not included). The ratio **GD/EW** was recorded as an indication of degree of convexity; **TL/EW** indicates degree of body elongation. Besides this terms we included the term **HL**, that is the length of the frontoclypeal horn, measured in lateral view, slightly below of the horn baseline (because this is generally concave) until the apex. We measured a maximum of five males and five females from each locality with focus in distribution extremes. In some cases, wet did not measure specimens from close locations because we considered that representative variations were not present in these cases (see section on variation for selected locations). Differences among specimens are given in the sections on variation, together with standard measurements and ratios.

We examined, compared, measure and photographed specimens under a Zeiss Discovery V20 equipped with a Zeiss AxioCam 506 digital camera. Whole mount preparations of male abdominal terminalia followed the protocol described by Lopes-Andrade (2011) and photography of dissected pieces were made under a Zeiss AxioLab compound microscope equipped with a Zeiss Axiocam MRc digital camera. We created distribution maps using latitude and longitude coordinates estimated by tracking localities in the online database GeoNames (Wick 2010) and plotting them in a map for analysis. The map was made by means the freeware QGIS 2.10.1. We include in the map all localites containing specimens directly examined for us and all records of the *furcifer* species-group cited in literature.

A search in the bases: Web of Knowledge, Scielo, Biodiversity Library and Google (Scholar) was made for the terms *Pycnoporus sanguineus* or *Polyporus sanguineus* (synonymous; but only the first name is valid). Organisms that for sure, feeding of *P. sanguineus* were included in a table and when possible, the occurrence number of these organisms in this host fungus was recorded. Besides, we recorded all host fungi used by species of the *furcifer* group, exanimate directly (when collected for us) and indirectly (literature data).

Specimens examined in this work belong to the following scientific collections:

ANIC Australian National Collection of Insects (Canberra, Australia)

CELC Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleopterada UFV (Viçosa, state of Minas Gerais, Brazil)

MFN Museum für Naturkunde (Berlim, Germany)

MHNG Muséum d'Histoire Naturelle (Géneve, Switzerland)

MNHN Muséum National d'Histoire Naturelle (Paris, France)

MPEG Museu Paraense Emilio Goeldi (Belém, state of Pará, Brazil)

MZSP Museu de Zoologia da Universidade de São Paulo (São Paulo, state of São Paulo, Brazil)

NMNH National Museum of Natural History, Smithsonian Institution (Washington, D. C., USA)

SANC South African National Collection of Insects (Pretoria, South Africa)

Results

Based on patterns of the external morphology of adults, including male abdominal terminalia, we **(i)** synonymize *Cer. cylindricus*, *Cer. monocerus*, *Cer. unicornis* and *Cer. simplicicornis* with *Cer. cornifer*; **(ii)** designate lectotypes for *Cer. cornifer*, *Cer. furcifer*, *Cer. hastifer* and *Cer. ruficornis*; **(iii)** confirmed the synonym of *Cer. semipallidus* with *Cer. furcifer* (Lawrence 1967); **(iv)** provide a redescription of *Cer. cornifer*, *Cer. hastifer*, *Cer. furcifer* and *Cer. ruficornis*; **(v)** Propose an identification key for *furcifer* species-group.Therefore, the *furcifer* species-group now includes the following four species:

Taxonomic synopsis

Ceracis cornifer (Mellié, 1849)

Ceracis cylindricus (Brèthes, 1922), **new synonym**

Ceracis monocerus Lawrence, 1967, **new synonym**

Ceracis simplicicornis (Pic, 1916), **new synonym**

Ceracis unicornis Gorham, 1898, **new synonym**

Ceracis furcifer Mellié,1849

Ceracis semipallidus Pic, 1922

Ceracis hastifer (Mellié, 1849)

Ceracis ruficornis Pic, 1916

The *Cer. furcifer* sp-group. Frontoclypeal ridge in males usually strongly produced forming a median horn, generally laminar in lateral view and bearing several diminute, sparsely setae along it; horn bifurcated or not at apex, its length variable, being almost absent to longer than pronotal length. Antennae with eight or nine antennomeres, never ten. Prosternal process thin but not laminate. Protibia apically expanded and bearing several conspicuous spines, along the outer apical angle; meso and metatibia also with spines, but less prominent. Male abdominal terminalia with sterniteVIII with posterior edge bearing a profund concave emargination at middle; tegmen witha deep longitudinal emargination at apex forming two wide parallel lobes, with rounded or blunt apices; penis cylindrical with rounded apex.

Host fungi. Although there are records in other host fungi, *furcifer* species is associated mostly to *Pyconoporus sanguineus*.

Distribution. Considering data in the literature and here in, from southern Argentina to southern USA, the *furcifer* species-group occur only in the Neotropical region.

Species accounts

The redescriptions of *Cer. cornifer*, *Cer. hastifer*, *Cer. furcifer* and *Cer. ruficornis* are provided below.

Ceracis cornifer (Mellié, 1849)

Figures. 1 A–F; 2 A–G; 3 A–I and 4.

Ennearthron corniferum Mellié, 1849: 371, pl. 4, fig. 18. Type locality: Brazil; Blackwelder 1945: 549 [distribution]; Casey 1898: 90 [taxonomic notes]; Lawrence 1967: 97 [taxomomic status]; Abdullah 1973: 198 [taxonomic status and distribution]

Ceracis cornifer (Mellié, 1849): Lawrence 1967: 99 [taxonomic notes]; Abdullah 1973: 198 [taxonomic status and distribution]; Lopes-Andrade 2002a: 6 [taxonomic notes]; Gumier- Costa *et al.*, 2003: 359 [host fungus and distribution]; Graf-Peters *et al.* 2011: 558 [feeding habit]; Antunes-Carvalho & Lopes-Anadrade 2011: 61 [taxonomic notes]; Pecci-Maddalena *et al.* 2014: 482 [taxonomic notes].

Ceracis unicornis Gorham, 1898: 332, **syn. n.** Type locality: Saint Vincent, West Indies; Blackwelder 1945: 550 [distribution]. Lawrence 1967: 98 [taxomomicstatus]; Antunes-Carvalho & Lopes-Anadrade 2011: 61 [taxonomic notes]; Abdullah 1973: 203 [taxonomic status and distribution].

Ennearthron simplicicorne Pic, 1916: 19 **syn. n.** Type locality: Buenos Aires, Argentina; Blackwelder 1945: 550 [distribution]; Lawrence 1967: 97 [taxomomic status]; Abdullah 1973: 202 [taxonomic status and distribution].

Ceracis simplicicornis (Pic, 1916): Lawrence 1967: 99 [taxonomic notes]; Graf-Peters *et al.*2011: 556 [feeding habitat]; Antunes-Carvalho & Lopes-Anadrade 2011: 61 [taxonomic notes]; Pecci-

Maddalena *et al.* 2014: 482 [taxonomic notes]; Abdullah 1973: 202 [taxonomic status and distribution].

Ennearthron cylindricum Brethes, 1922: 303, **syn. n.** Type locality: General Urquiza, Argentina; Blackwelder 1945: 549 [distribution]; Lawrence 1967: 97 [taxomomic status; location of type unknown]; Abdullah 1973: 199 [taxonomic status and distribution].

Ceracis cylindricus (Brethes, 1922): Lawrence 1967: 99 [taxonomic notes]; Antunes-Carvalho & Lopes-Anadrade 2011: 61 [taxonomic notes]; Pecci-Maddalena 2014: 482 [taxonomic notes]; Abdullah 1973: 199 [taxonomic status and distribution].

Ennearthron unicorne Casey, 1898: 90; *Ceracis monocerus*, new name, Lawrence, 1967: 115, fig. 20., **syn. n.** Type locality: Lake placid, Highlands, Florida, United States; Lawrence 1973: 202 [feeding habitat]; Gumier-Costa *et al.*, 2003: 359 [host fungus and distribution]; Graf-Peters *et al.*2011: 563 [feeding habit]; Antunes-Carvalho & Lopes-Anadrade 2011: 61 [taxonomic notes]; Pecci-Maddalena *et al.*2014: 486 [taxonomic notes]; Abdullah 1973: 200 [taxonomic status and distribution].

Diagnosis. Lateral contour of the frontoclypeal horn usually with a pronounced inflexion near base; horn with apex rounded, extended and subtruncate. Antennal funicle with four antennomeres, the first shorter than the next three together. Pronotum convex, with anterior edge broadly rounded. Hypomera not enlarged toward median portion of the eye. Tegmen with a narrow inner emargination at the anterior edge, less than one half of the total length of tegmen; outer edges with an inflexion at first basal one half; each lobe of anterior portion with one small tip at the inner edge apex and a slight cutting on the outer portion.

Redescription. Male lectotype, **here designated (Fig. 1 A–E)** adult apparently fully pigmented and in good condition. Measurements (in mm): TL 1.21, PL 0.43, PW 0.53, EL 0.78, EW 0.56, GD 0.47.Ratios: PL/PW 0.80, EL/EW 1.38, EL/PL 1.82, GD/EW 0.84, TL/EW 2.14. **Body** glabrous, elongate, subcylindrical; dorsal surface mostly yellowish-brown; ventral surface reddish-brown; basal antennomeres and mouthparts yellowish brown; antennal funicle, tarsi and legs yellowish to reddish-brown; antennal club dark reddish-brown. **Head** barely visible from above; dorsal surface immediately above horn base concave, glabrous, sparsely punctate; frontoclypeal ridge strongly produced forming a long and narrow upward directed median horn (in mm: length 0.29; basal width 0.28) that is laminate in lateral view and bearing several minute, sparsely distributed setae; the horn with a pronounced lateral inflexion near base (Fig. 1 A, black arrows) and a rounded, extended subtruncate apex. **Antennae** (left antennae measured) with FL 0.08 mm, CL 0.15 mm, CL/FL1.9, length of antennomeres 1–9 (in mm) as follows: 0.06, 0.04, 0.03, 0.02, 0.01, 0.01, 0.05, 0.05, 0.05; sensilliferes barely visible. **Eyes** coarsely facetted, with minute slender yellowish setae emerging from the intersection between omatidia; GW 0.12 mm. **Pronotum** with anterior edge uniformly rounded and covering the head; posterior edge sublinear, punctation fine, single, uniform and regularly distributed (Fig. 1 B); distance between puntures from 4 to 5.3 puncture-widths; each puncture bearing a yellowish decumbent minute setae, barely visible even at a magnification of 150x; in between punctures shiny, microreticulate. **Scutellum** small, subtriangular; BW 0.08 mm and SL 0.04 mm. **Elytra** about 1.8x as long as pronotum; sides subparallel at the basal two-thirds, then abruptly converging toward apex; punctation single, similar to pronotal punctation but comparatively finer; vestiture similar to that of pronotum; humeral calli conspicuous. **Hind wings** developed, apparently functional. **Prosternum** in front of coxae shallowly biconcave; prosternal process thin (Fig. 1 A, white arrow), as long as coxae and projected below prosternal disc. **Hypomera** biconcave, with lateral contour emarginate and not enlarged toward median portion of the eye; surface subglabrous and microreticulate. **Protibia, meso and metatibia** as in the diagnosis of the *furcifer*s species-group. **Metaventrite** moderately convex, subglabrous, bearing scattered slender setae; surface microreticulate; discrimen not discernible in this specimen. **Abdominal ventrites** with surface microreticulate; punctuation shallow and vestiture of scattered slender setae, longer than those on dorsal surface; length of ventrites 1–5 (in mm, from base to apex of each ventrite at longitudinal midline): 0.16, 0.06, 0.07, 0.07, 0.07. First abdominal ventrite bearing a circular, marginated, pubescent sex patch at center (Fig. 1 C, arrow) with a transverse diameter of 0.03 mm. **Male abdominal terminalia** (Fig. 1 D, lectotype) with **VIII sternite** with posterior edge bearing a deep concave emargination at middle (Fig. 1 D, VIII sternite, black arrow); posterior corners sclerotized and rounded, bearing bristles; disc membranous; lateral edges diverging from posterior to anterior portion; anterior edge sublinear. **Tegmen** with the inner emargination of anterior edge narrow and shallow, less than one half of the total length (Fig. 1 D, teg, big black arrow); each lobe of the posterior portion bearing one small tip at inner edge apex (Fig. 1 D, teg, big blue arrow) and a small cutting on the outer portion (Fig. 1 D, teg, small blue arrow); lateral edges with an inflexion at first basal one half (Fig. 1 D, teg, small black arrow). **Penis** elongate, subcylindrical, basal edge blunt (Fig. 1 D, pen, black arrows), sides subparallel at basal two thirds and then gradually converging to apex.

Females (Fig. 1 F). Similar to males except in the following features: abdominal sex patch absent; anterior edge of the head shallowly emarginated; frontoclypeal ridge devoid of horn.

Variation. Males, measurements in mm (n= 79, included the lectotype) TL 0.95–1.41 (1.17 ± 0.09); PL 0.34–0.52 (0.42 ± 0.03); PW 0.4–0.6 (0.5 ± 0.04); EL 0.61–0.94 (0.74 ± 0.07); EW 0.44–0.66 (0.53 ± 0.04); GD 0.38–0.55 (0.46–0.04); HL 0.01–0.41 (0.25 ± 0.11). Ratios: PL/PW 0.75–0.93 (0.85 ± 0.04); EL/EW 1.25–1.59 (1.4 ± 0.07); EL/PL 1.47–2.14 (1.74 ± 0.14); GD/EW 0.74–0.94 (0.86 ± 0.03); TL/EW 2.08–2.41 (2.2 ± 0.07). Females, measurements in mm (n = 65) TL 0.95–1.47 (1.19 ± 0.1); PL 0.35–0.55 (0.43 ± 0.04); PW 0.4–0.6 (0.48 ± 0.04); EL 0.6–0.96 (0.76 ± 0.07); EW 0.44–0.66 (0.53 ± 0.04); GD 0.38–0.67 (0.46–0.05); Ratios: PL/PW 0.8–1 (0.89 ± 0.04); EL/EW 1.25–1.54 (1.43 ± 0.07); EL/PL 1.4–2.2 (1.78 ± 0.16); GD/EW 0.78–0.94 (0.87 ± 0.03); TL/EW 2.02–2.38 (2.23 ± 0.06). Specimens of the follow localities were measured (localities inside parentheses): **BRAZIL:** State of Minas Gerais (Carrancas, Guaraciaba, Ipatinga, Jequeri, Juiz de Fora, Pains, Piau, Rio Paranaíba, Sacramento, Ubá, Viçosa); State of Rio de Janeiro (Gruçaí and Seropédica); State of Espírito Santo (Alto Bergamo and Conceição da Barra); State of São Paulo (Ilha da Victoria); State of Mato Grosso do Sul (Campo Grande and Paranhos); State of Santa Catarina (Urubici). **URUGUAY:** Montevideo. **ARGENTINA:** Tucuman. **MEXICO:** Mazatlán. **UNITED STATES:** Florida (Lake Placid Highlands).

Material examined. Lectotype, here designated, male. (MNHN; Fig. 1 A) "*Ennearthron corniferum* ? Cast 72? [circular green label; handwritten]\ 25? [white label; handwritten]\ Brasilia [white label; handwritten] \ LECTOTYPE *Ennearthron corniferum* [red label; handwritten]". **BRAZIL. State of Minas Gerais:** 51 specimens (CELC; including 1 dissected male) "Brazil: MG, Juiz de Fora, Embrapa, 20.ix.2013, Pecci-Maddalena, Í.S.C. leg."\ ex. *Pycnoporus sanguineus*"; 16 specimens (CELC; including 1 dissected male) "Brazil: MG, Jequeri, Grota, 20.i.2011, Sandoval-Gómez, V.E.leg.\ ex. *Pycnoporus sanguineus*"; 15 specimens (CELC; including 1 dissected) "Brazil: MG, Jequeri, Piscamba, vi. 2010, Edigio, E.M. leg.\ ex. *Pycnoporus sanguineus*"; 33 specimens (CELC; including 1 dissected male) "Brazil: MG, Sacramento, Distrito de Manhuaçu, 15.vii.2010, Antunes-Carvalho, C. leg."\ ex.

Pycnoporus sanguineus”; 32 specimens (CELC; including 1 dissected male) “Brazil: MG, Sacramento, Distrito de Manhuaçu, 18.vii.2010\ Antunes-Carvalho, C. leg.”\ ex. *Pycnoporus sanguineus*”; 30 specimens (CELC; including 1 dissected male) “Brazil: MG, Sacramento, Distrito de Manhuaçu, 31.vii.2010\ Antunes-Carvalho, C. leg.”\ ex. *Pycnoporus sanguineus*”; 32 specimens (CELC; including 1 dissected male) “Brazil: MG, Viçosa, UFV-Apiário, 09.vi.2010, Campos, L.A. leg.”\ ex. *Pycnoporus sanguineus*”; 13 specimens (CELC; including 1 dissected male) “Brazil: MG, Viçosa, Campus UFV, 02.i.2008, Campos, L.A. leg.”\ ex. *Pycnoporus sanguineus*”; 1 specimen (CELC) “Brazil: MG, Viçosa, Violeira, 17.xii.2004, Zacaro, A.A. leg.”; 4 specimens (CELC)“Brazil: MG, Viçosa, Atrás do insetário, 14.xi.2003, Zacaro, A.A. & Lopes-Andrade, C. legs. ”; 38 specimens (CELC; including 1 dissected male) “Brazil: MG, Pains, 01.vi.2008, Soares, L.G.S. leg.”\ ex. *Pycnoporus sanguineus*”; 30 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado, ES Ponto 11, CE 11 Tronco caído 24 cm Pote2”, 05.i.2011, Resende, N.F. leg.\ ex. *Pycnoporus sanguineus*”; 30 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado, ES Ponto 11, CE 11 Tronco caído 18 cm Tempo sol, 05.i.2011\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 16 specimens (CELC; including 1 dissected male) “Brazil: MG, Rio Paranaiba, Cerradão C2 (19 cm) Fotos 45-46 6,27g, 26.xii.2011\ Resende, N.F. leg.\” ex. *Pycnoporus sanguineus*”; 1 specimen (CELC) “Brazil: MG, Rio Paranaiba, Cerradão C1 (27 cm) Fotos 47-48-49 107,79g, 26.xii.2011\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 8 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerradão C6 (11 cm) Fotos 291-292 2,32g, 28.xii.2011, Resende, N.F. leg.\” ex. *Pycnoporus sanguineus*”; 7 specimens (CELC; including 1 dissected male) “Brazil: MG, Rio Paranaiba, Cerradão C7 (18 cm) Fotos 52-53 13,54g, 28.xii.2011\ Resende, N.F. leg.\” ex. *Pycnoporus sanguineus*”; 3 specimens (CELC; including 1 dissected male) “Brazil: MG, Rio Paranaiba, Campo limpo P7 (20 cm) Fotos 25-26-27 56,22g, 14.xii.2011\ Resende, N.F. leg.\” ex. *Pycnoporus sanguineus*”; 2 specimens (CELC; including 1 dissected male) “Brazil: MG, Rio Paranaiba, Campo limpo P1 (30 cm) Fotos 5-6 4,82g, 12.xii.2011, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 2 specimens (CELC) “Brazil: MG, Rio Paranaiba, Campo limpo P2 (14 cm), Fotos 8-9 12,18cm, 12.xii.2011, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 2 specimens (CELC) “Brazil: MG, Rio Paranaiba, Campo limpo P1 (15 cm) Fotos 1-2-3-4 5,31g, 12.xii.2011\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 10 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES Ponto 11 CE 11 tronco caído 24 cm tempo sol, 05.i.2011\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 10

specimens (CELC) “Brazil: MG, Rio Paranaiba, Ponto 11 CE 11 tronco caído 18 cm tempo sol, 05.i.2011\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 6 specimens (CELC; including 1 dissected male) “Brazil: MG, Rio Paranaiba, Cerrado ES Ponto 10 CE 10 tronco caído 18 cm tempo sol, 05.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 15 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES 10 CE 11 Fotos 57-58 18 cm 9,039 g”, 05.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 6 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES CE11 Fotos 1701-1702-1703 28cm 1,08 g, 05.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 14 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES CE11 Fotos 59-60 24cm 45,57 g, 05.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 11specimens (CELC; including 1 dissected male) “Brazil: MG, Rio Paranaiba, Cerrado ES CE8 (28cm) Fotos 310-311 50,74g, 03.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 1 specimen (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES CE11 Fotos 217-218-219 16 cm 50,38 g, 05.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 2 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES CE10 Fotos 315-316 18 cm 129,014g, 05.i.2012\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 40 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES árvore vinho/tronco caído 20cm Ponto 12 CE 12, 05.i.2012\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 25 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES Ponto 10 CE 10 Tronco caído 18cm tempo sol, 05.i.2012\ Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 4 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES Ponto 10 Tronco caído 18cm, 05.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 10 specimens (CELC) “Brazil: MG, Rio Paranaiba, Cerrado ES Ponto 10 (CE 10) tronco caído 18 cm, tempo sol, 05.i.2012, Resende, N.F. leg.”\ ex. *Pycnoporus sanguineus*”; 39 specimens (CELC; including 1 dissected male) “Brazil: MG, Ipatinga, 2006, Nolasco, J.P. leg.”\ ex. *Pycnoporus sanguineus*”; 33 specimens (CELC; including 1 dissected male) “Brazil: MG, Ipatinga, 2009, Nolasco, J.P. leg.”\ ex. *Pycnoporus sanguineus*”; 2 specimens (CELC; including 1 dissected male) “Brazil: MG, Ipatinga, RPPN ZACA, 07.xii.2011, Araújo, L.S. leg.\ “código: Trans: 2 Parcela: C Fungo 1”; 18 specimens (CELC; including 1 dissected male) “Brazil: MG, Ubá, 2009, Nolasco, J.P. leg.”\ ex. *Pycnoporus sanguineus*”; 18 specimens (CELC; including 1 dissected male) “Brazil: MG, Ubá, Faz. Córrego do Pari (S21º 08’’W42º 32’, 31m), vii.2000, Gumier-Costa, F. leg.”\ *Ceracis cornifer* (Mellié,1848) det. Cristiano Lopes-Andrade 2003”; 4 specimens (CELC) “Brazil: MG, Ubá, Faz. Córrego do Pari, x.2000, Gumier-Costa, F. leg.”\

Ceracis cornifer (Mellié,1848) det. Cristiano Lopes-Andrade 2003"; 22 specimens (CELC; including 1 dissected male) "Brasil: MG, Piau, 22.vi.2014, Pecci-Maddalena, Í.S.C. leg."\ ex. *Trametes* sp."; 7 specimens (CELC) "Brasil: MG, Piau, 22.vi.2014, Pecci-Maddalena, Í.S.C. leg."\ ex. *Pycnoporus sanguineus*"; 13 specimens (CELC; including 1 dissected male) "Brasil: MG, Carrancas, Complexo da Zilda, cerrado e fragmento de mata 27-29.xii.2012, Oliveira, E.H.leg."; 12 specimens (CELC; including 1 dissected male) "Brasil: MG, Guaraciaba, Chalé do Turvo, 21.v.2012, Lopes-Andrade, C.leg."\ ex. *Pycnoporus sanguineus*"; 20 specimens (CELC) "Brasil: MG, Texeiras, "saindo de Viçosa no restaurante da BR", 12.i.2014, Lopes-Andrade, C.leg."\ ex. *Pycnoporus sanguineus*. **State of Rio de Janeiro:** 71 specimens (CELC; including 1 dissected male) "Brasil: RJ, Seropédica, 2004, Grossi, P.C.leg."\ ex. *Pycnoporus sanguineus*"; 12 specimens (CELC; including 1 dissected male) "Brasil: RJ, Rio das Ostras, Rebio União, 01.iii.2013, Aloquio, S. leg."\ ex. *Pycnoporus sanguineus*"; 12 specimens (CELC; including 1 dissected male) "Brasil: RJ, Grussaí, 01.xi.2003, Souto, L.S. leg."\ ex. *Pycnoporus sanguineus*"; 4 specimens (CELC; including 1 dissected male) "Brasil: RJ, Paraty, Ponta Negra, 5-6.iii.2011, Sandoval, V.E & Idrobo, C.J. leg.". **State of São Paulo:** 3 specimens (ANIC; including 1 dissected male) "Ilha da Victoria, S. Paulo, Brazil, Dec. 1963, Exped. Dep. Zool."\ *Ceracis cornifer* 9 (Mellié) 202\ JFL"; 1 specimen dissected (CELC) "Peruibe, SP, 28.xi a 01.xii.84"\ Exp. MZUSP em fungo\ *Ceracis ruficornis* Pic.Gen 1[handwritten]"; 4 specimens (MZSP; including 1 dissected male) "Raiz da Serra, SP, 28.ix. 1907, Luderwaldt"\ Dep. Zool. São Paulo 1247\ SP"; 3 specimens (CELC) Brasil: SP, São José dos Campos, Parque da cidade, 09.x.2004, leg S.S.P. Almeida & G.S.P. Almeida\ ex. *Pycnoporus sanguineus*. **State of Espírito Santo:** 10 specimens (CELC; including 1 dissected male) "Brasil: ES, Alto Bergamo, João Neiva, 11.v.2008, Furieri, leg."\ ex. *Pycnoporus sanguineus*"; 3 specimens (CELC) "Brasil: ES, Santa Teresa, Reserva Biológica de Santa Lúcia, 03.iii.2003, Barreto, F.C.C & Furieri, K.S. leg."; 10 specimens (CELC) "Brasil: ES, Santa Teresa, Rebio Augusto Ruschi, 17-19.vi.2013, Pereira, M.R. leg."\ ex. *Pycnoporus sanguineus*"; 1 specimen (CELC) "Brasil: ES, Santa Teresa, EBSL, iii.2003, Furieri, K.S. leg."\ ex. *Pycnoporus sanguineus*"; 1 specimen dissected (CELC) "Brasil: ES, Conceição da Barra, Rebio Córrego Grande, 14-19. Xii.2005, Furieri, K.S., Loiola, G.R., Van de Koken, A.F. legs."; 1 specimen dissected (CELC) "Brasil: ES, Conceição da Barra, Floresta Nacional do Rio Preto, 03.xii.2011, Araujo, L.S. leg."\ Trans: 3, Parcela B, Fungo 1"; 2 specimens (CELC) "Brasil: ES, Conceição da Barra, Floresta

Nacional do Rio Preto, 03.xii.2011, Araujo, L.S. leg.”\ Trans: 3, Parcela 0, Fungo 4”; 2 specimens (CELC) Brasil: ES, Conceição da Barra, Floresta Nacional do Rio Preto, 03.xii.2011, Araujo, L.S. leg.”\ Trans: 1, Parcela 0, Fungo 1”; 1 specimen (CELC) “Brasil: ES, Conceição da Barra, “Floresta Nacional do Rio Preto”, 03.xii.2011, Araujo, L.S. leg.”\ Trans: 2, Parcela C, Fungo 1”; 1 specimen (CELC) “Brasil: ES, Conceição da Barra, Floresta Nacional do Rio Preto, 03.xii.2011, Araujo, L.S. leg.”\ Trans: 2, Parcela A, Fungo 5”; 1 specimen dissected (CELC) “Brasil: ES, Aracruz, 04.i.2004, Furieri, K.S. leg.”. **State of Bahia:** 2 specimens (CELC; including 1 dissected male) “Brasil: BA, Porto Seguro, RPPN Pau Brasil, 4-7 Janeiro 2010, Chamorro, J. leg.”\ ex. *Pycnoporus sanguineus*”. **State of Mato Grosso do Sul:** 9 specimens (CELC; including 1 dissected male) “Brasil: MS, Paranhos, Chácara Santo Antônio, Pastagem, vi.2012, Puker, A. leg.”\ ex. *Pycnoporus sanguineus*”; 6 specimens (CELC; including 1 dissected male) “Brasil: MS, Campo Grande, Cerradinho UFMS, 27.v.2015, Chamorro, J. leg.”\ ex. *Pycnoporus sanguineus*”. **State of Santa Catarina:** 24 specimens (CELC; including 1 dissected male) “Brasil, SC, Urubici, Estrada p/Serra do Corvo Branco em placa, 06.iii.2011, Grossi & Perigotto legs.”\ 28º02’53’’S, 49º23’06’’W, 1022 m\ ex. *Pycnoporus sanguineus*”; 30 specimens (CELC) “Brasil, SC, Urubici, Estrada p/Serra do Corvo Branco em placa, 06.iii.2011, Grossi & Perigotto legs.”\ 28º02’53’’S, 49º23’06’’W, 1000 m\ ex. *Pycnoporus sanguineus*”. **State of Rio Grande do Sul:** 3 specimens (CELC; including 1 dissected male) “Brasil: RS, São Francisco de Paula, Flona SFP, 2006, Graf, L.V. leg.”\ ex. *Pycnoporus sanguineus*; 15 specimens (CELC) “Brasil: RS, São Francisco de Paula, Flona SFP, xii. 2006, Graf, L.V. leg.”\ Fungo 1970, sp 29. **ARGENTINA:** 12 specimens (SANC; including 1 dissected male) “Argentina, Misiones Prov. nr. Wanda,25º 58’S, 54º 35’W, 22.x.2007 S. Neser”\ Ex. Orange bracket fungus on old pine logs\ National coll. of insects\ Pretoria, South Africa”; 3 specimens (ANIC; including 1 dissected male) “Arg: Salta Capital, July, 1971, L.A. Stange, Lot 14\ *Pycnoporus cinnabarinus*\ JFL”; 2 specimens (ANIC) “Arg. Tucuman, Rio Urueña, nr, Salta, Border, Dec 1970\ L.A. Stange Lot 4(2)\ *Pycnoporus cinnabarinus*\ JFL”; 2 specimens (ANIC) “Arg. Tucuman, Tafi del Valle, xii.17.1971”\ L.A. Stange Lot 15\ JFL”; 2 specimens (ANIC; including 1 dissected male) “Tucuman, Arg.v.1926, R.C. Shannon”\ ex. *Polyporus sanguineus*\ Ceracis (9) sp 448\ JFL Smithsonian”; 2 specimens (ANIC) Tucuman“Arg. Feb. ’29, R.C. Shannon”\ ex. *Polyporus sanguineus*\ JFL”; 4 specimens (ANIC) “Tucuman, Argentina, L. Castillon, Coll. J.F. Lawrence, Lot. 2007”\ ex. *Polyporus sanguineus*, ex U.S.D.A Herbaria, JFL.

URUGUAY: 7 specimens (ANIC; including 1 dissected male) "Montevideo, Uruguay, F.Felippone, J.F. Lawrence, Lot. 2025"\ ex. *Trametes hispida*, ex U.S.D.A Herbaria\ JFL. **MEXICO:** 6 specimens (ANIC; including 1 dissected male) "Cer furcifer gr. Det. J.F. Lawrence 19"\ Mazatlan Crotch\ JFL. **UNITED STATES:** 3 specimens (ANIC; including 1 dissected male) "4 mi. SE Lake Placid Highlands County Florida, June 30, 1965\ J.F. Lawrence Lot 1532"\ *Polyporus sanguineus*\ JFL.

Remarks. The male specimen from Florida (EUA) was not measured due to its bad condition; nevertheless, it short length, body shape and total length (1.18 mm), and anatomy of male abdominal terminalia make it similar to the large morphs of *Cer. cornifer* from South American localities. In all examined populations of *Cer.cornifer*, male frontoclypeal horn is extremely variable in length. There are small male morphs (with apex of frontoclypeal horn slightly bifurcated or truncated), intermediate morphs and large morphs similar to the lectotype (Fig. 2 A–G, Male morps). We observe that small males with frontoclypeal horn slightly bifurcated at apex are relatively common (Fig. 2 C–E), but bifurcation in large males is rare (one case shown in Fig. 2 G). Some specimens of Ubá (MG-Brazil) and Gruçaí (RJ-Brazil) have lateral contour of the pronotum angulated and anterior edge forming two prominent lobes. The coloration in both sex varies from yellowish-brown or reddish-brown (common in individuals from several localities with different geographic coordinates) to black (especially specimens from southernand southwestern Brazil) (Fig. 3 A–I, ecotypes). Besides these color variations, teneral forms occurs in all populations and have a similar aspect, apparently not pigmented (Fig. 3 E, arrow). Specimens from Campo Grande (MS-Brazil) resemble some *Cer. ruficornis* with horn apex slightly bifurcated and body uniformly shiny black and legs with a somewhat amber color. The male terminalia is apparently uniform, mainly in the shape of penis and sternite VIII. In some cases, the basal contour of tegmen is rounded, and in others the apex of each apical lobe is conspicuously sharp. The cutting on the outer portion of which lobe, in the male specimen from Florida (EUA) is prominent.

Distribution. *Ceracis cornifer* is widely distributed in the southern, southeastern and southwestern Neotropical region, without records in the middle and northern South America, but occurring in southwestern Mexico, in a few Caribbean islands and southern USA (Fig. 4, Map). This species is sympatric with *Cer. furcifer* in Paranhos (southwestern Brazil) and *Cer. ruficornis* in three localities in southeastern Brazil (Paraty, Peruíbe and Ilha da Victória) (Fig. 4, Map). In the case of Paranhos, individuals of *Cer.cornifer* and *Cer.furcifer* were within the same basidiomes of *P. sanguineus*.

***Ceracis furcifer* Mellié, 1849**
Figures. 2 H; 4; 5 A–F and 6 A–C

Ceracis furcifer Mellié, 1849: 379, pl. 4, fig.24. Type locality: Cayenne, French Guyana; Gorham: 1886:359 [taxonomic notes and distribution]; 1898: 332 [taxonomic notes]; Blackwelder 1945: 550 [distribution]; Lawrence 1967: 97 [taxonomic status]; 1973: 202 [feeding habit]; Abdullah 1973 [taxonomic status and distribution]; 199; Mueller 2001: 317 [taxonomic notes and distribution]; Lopes-Andrade 2002a: 6 [taxonomic notes]; Gumier-Costa *et al*., 2003: 359 [host fungus and distribution]; Graf-Peters 2011: 558 [feeding habitat]; Antunes-Carvalho & Lopes-Anadrade 2011: 61 [taxonomic notes]; Pecci-Maddalena 2014: 482 [taxonomic notes].
Ceracis semipallidus Pic, 1922:3. Junior synonym. Type locality: Guadeloupe, Caribbean.

Diagnosis. Apex of the frontoclypeal horn alongated and emarginated at middle, forming two conspicuous rounded lobes; lateral contour of the horn without inflexion near of the base, but in larger morphs conspicuously narrow at middle. Antennal funicle with three antennomeres, being the first equal or superior in length, to three following combined. Tegmen with the internal emargination of the anterior portion short and less than one half of it total length. Lateral edges forming an enlargement before of the apex, with a prominent inflexion at the outer apical portion of the lobes.

Redescription. Male lectotype here designated (Fig. 5 A–C and 5 E). Adult apparently fully pigmented and in good condition. Measurements (in mm): TL 1.2, PL 0.44, PW 0.543, EL 0.76, EW 0.56, GD 0.47. Ratios: PL/PW 0.81, EL/EW 1.36, EL/PL 1.73, GD/EW 0.84, TL/EW 2.14. **Body** glabrous, elongate, subcylindrical; frontoclypeal horn mostly reddish-brown; dorsal surface, to apex of pronotum until the elitral disc, mostly dark reddish-brown; the second half until elytral apex similar in color to frontoclypeal horn; ventral surface mostly dark reddish-brown, except for reddish-brown abdominal ventrites; basal antennomeres, funicle, mouthparts and legs mostly yellowish-brown, antennal club reddish-brown. **Head** barely visible from above; dorsal surface immediately above horn base concave, glabrous, sparsely punctate; frontoclypeal ridge strongly produced forming a long, that is larger in frontal view and laminate in lateral view (in mm: length 0.3, basal width 0.295); horn apex alongated, emarginated at middle, forming two conspicuous rounded lobes (Fig. 5 A, big black arrow); lateral contour of the horn without inflexion near of the base, however, conspicuously narrow at middle (Fig. 5 A, small black arrow); **Antennae** (right antennae measured) with FL 0.08 CL 0.14, CL/FL 1.75, length of antennomeres 1–8 (in mm) as follows: 0.06, 0.04, 0.04, 0.02, 0.02, 0.03, 0.05, 0.06; sensilliferes barely visible. **Eyes** coarsely faceted, with minute slender yellowish setae emerging from the intersection between omatidia, GW 0,11 mm. **Pronotum** subquadrate, with anterior portion produced forward, covering head; anterior edge slightly emarginated at middle, forming two small lobes (Fig. 5 A, white arrow); sides narrow, not visible from above; posterior edge sublinear; punctation fine, single, uniforme and regularly distributed (Fig. 5 B; distance between punctures from 2 to 3 puncture-widths; each puncture bearing a yellowish decumbent minute setae, barely visible even a magnification of 150x; in between punctures, shiny, microreticulate. **Scutellum** small, subtriangular, with few punctures, each one bearing a short, fine, decumbent setae; BW 0.08 mm and SL 0.05 mm. **Elytra** about 1.7x as long as pronotum; sides subparallel at the basal two-thirds, then abruptly converging toward apex; punctation single, more fine than pronotal punctation; humeral calli conspicuous. **Hind wings** developed, apparently functional. **Prosternum** in front of coxae shallowly concave; prosternal process thin (Fig. 5 A, big white arrow), almost as long as coxae and projected bellow prosternal disc. **Hypomera** biconcave, subglabrous and reticulous with lateral contour emarginate; **Protibia, meso and metatibia** absent in Lectotype, but follow the *furcifer* group pattern (with base in material examined). **Metaventrite** moderately convex, subglabrous; surface microreticulate. **Abdominal ventrites** with microreticulate surface; shallow punctures and scattered slender setae, longer than those on dorsal surface; length of ventrites 1–5 (in mm, from base to apex of each ventrite at longitudinal midline): 0.14, 0.06, 0.05, 0.05, 0.08. First abdominal ventrite bearing a circular, marginated, pubescent sex patch at center (Fig. 5 C, white arrow). **Male terminalia** (Fig. 5 D in topotype) with **VIII sternite** with posterior edge bearing a deep concave emargination at middle (Fig. 5 D, VIII sternite, black arrow) posterior corners sclerotized and rounded, bearing bristles; at median portion shallowly membranous; lateral edges diverging from posterior to anterior portion; anterior edge sublinear. **Tegmen** with the inner emargination of anterior portion short, less than one half of it length. Lateral edges forming an enlargement before of the apex (Fig. 5 D, teg, big arrow), with a prominent inflexion at the external apical portion of the lobes (Fig. 5 D, teg, small arrow). **Penis** elongate, subcylindrical with basal edge blunt (Fig. 5 D, pen, small arrows); esclerotized until the first one half and then membranous; sides subparallel at one-half of median portion and then expanding in a membranous portion (Fig. 5 D, pen, big arrow).

Females (Fig. 5 F). Similar to males except in the abdominal sex patch absent; frontoclypeal ridge devoid of horn; Resembles the females of the *Cer. cornifer* species, but former later has nine antennomeres instead eight.

Variation. Males, measurements in mm (n= 32, included the lectotype) TL 1.02–1.35 (1.16 ± 0.09); PL 0.37–0.51 (0.43 ± 0.04); PW 0.44–0.6 (0.52 ± 0.04); EL 0.6–0.88 (0.73 ± 0.07); EW 0.47–0.61 (0.55 ± 0.04); GD 0.4–0.56 (0.47 ± 0.04); HL 0.05–0.38 (0.23 ± 0.07). Ratios: PL/PW 0.76–0.92 (0.83 ± 0.03); EL/EW 1.14–1.52 (1.34 ± 0.1); EL/PL 1.33–1.95 (1.7 ± 0.15); GD/EW 0.78–0.96 (0.86 ± 0.04); TL/EW 1.93–2.33 (2.13 ± 0.1). Females, measurements in mm (n= 19) TL 1.02–1.32 (1.17 ± 0.08); PL 0.37–0.5 (0.43 ± 0.03); PW 0.42–0.55 (0.48 ± 0.03); EL 0.65–0.85 (0.74 ± 0.05); EW 0.44–0.58 (0.52 ± 0.03); GD 0.4–0.52 (0.46 ± 0.03). Ratios: PL/PW 0.83–1 (0.89 ± 0.05); EL/EW 1.28–1.54 (1.42 ± 0.06); EL/PL 1.47–1.88 (1.72 ± 0.1); GD/EW 0.83–0.96 (0.88 ± 0.03); TL/EW 2.14–2.4 (2.25 ± 0.06). Specimens of the following localities were measured: **BRAZIL:** Mato Grosso do Sul (Paranhos); Góias (Mambaí); Pará (Marabá); Tocantins (Araguaína); Amazonas (Manaus). **COLOMBIA:** Casanare (San Luis de Palenque). **COSTA RICA:** Turrialba. **MEXICO:** Veracruz (Coatzacoalcos) and **FRENCH GUYANA:** Cayenne.

Material examined. Lectotype, male here designated (**MNHG) (Fig. 5 A)** [white label] *Furcifer* Kuntze Cayenne Mellié [handwritten]\ [red label] Lectotype *Ceracis furcifer* Mellie [handwritten]. **Historical Material:** 1 specimen [white label] Collomby [handwritten]\ [yellow label] PARALECTOTYPE [printed] *Ceracis furcifer* Mellié [handwritten]"; 1 specimen (MNHG) [white label] *Furcifer* Kuntze Perou Mellié [handwritten]\ [yellow label] PARALECTOTYPE [printed] *Ceracis furcifer* Mellié [handwritten]"; 4 specimens [white label] Collomby [handwritten]\ 1 specimen dissected [white label] *Furcifer* Kuntze mexique Geory Mellié [handwritten]"; 1 specimen [white label] *furcifer* Kuntze Suriname Geory Mellié[handwritten]"; 1 specimen dissected (MFN) [green label] Hist. Coll. (Coleoptera) Nr. 53172 (3.Ex.) Cis furcifer Kunze Zool. Mus. Berlin [printed]"; 1 specimen dissected (MNHN) [green label] MUSEUM PARIS GUYANE FRANÇAISE St-Laurent du Maroni E. Le moult 1911?"; 1 specimen dissected (MNHN) [red label] LECTOTYPE [printed] *Ceracis semipallidus* Pic [handwritten]\ [White label] *Ceracis semipallidus* mp? [handwritten]\ Ciside nº 241.3[handwritten]\ Guadeloup [printed]\ Ex. M. Pic Collection Générale (ex. Anceyiete) Exotique [handwritten]. **BRAZIL. State of Amazonas:** 30 specimens (CELC; including 1 dissected male) "Brasil: AM, Manaus, Campinara, 12.vii.2011, Pereira, M.R.leg."\ ex. *Pycnoporus sanguineus*"; 28 specimens (CELC; including 1 dissected male) "Brasil: AM, Manaus, Tarumã-Mirim Rio Negro, 10.vi.2011, Pereira, M.R. leg."\ ex. *Pycnoporus sanguineus*". **State of Pará:** 30 specimens (CELC; including 1 dissected male) "Brasil: PA, Marabá, Reserva Biológica de Tapirapé, pastagem, 2003, Gumier-Costa, F. leg."; 15 specimens (CELC) "Brasil: PA, Marabá, Reserva Biológica de Tapirapé, Amazônia Legal, 04.xii.2003, Gumier-Costa, F. leg."\ Amostra extra nº 09, Borda; 10 specimens (CELC; including 1 dissected male). **State of Góias:** "Brasil: GO, Mambaí, Fronteira GO/BA, maio 2012, Nilber leg."; 7 specimens (CELC; including 1 dissected male). **State of Mato Grosso do Sul** "Brasil: MS, Paranhos, Chácara Santo Antônio, Pastagem, vi.2012, Puker, A.leg."\ ex. *Pycnoporus sanguineus*"; 1 specimen (CELC) "Brasil: MS, Paranhos, Chácara Santo Antônio, Pastagem, vi.2012, Puker, A. leg.". **State of Tocantins:** 20 specimens (CELC) Brasil: TO, Araguaína, Campos UFT/ EMUZ, vi.2015, Sandoval-Gómez, V.E. leg."\ ex. *Pycnoporus sanguineus*."; **COLOMBIA:** 20 specimens (CELC; including 1 dissected male) "Colômbia, Casanare San Luis de Palenque, 260 m, 30.i.2010, Contreras, J. L leg."\ ex. *Pycnoporus sanguineus*"; 4 specimens (ANIC; including 1 dissected male) "Colômbia: Valle Rio Jamundi entre Cali y Jamundi, 1000 m"\ slipt corn\ JFL. **PANAMÁ:** 4 specimens (FMNH; including 1 dissected male) "Madden Dam, Canal Zone, vii-18-1969, J.F. Lawrence"\ Lot 2901\ ex. *Daedalea elegans*\ JFL"; 5 specimens (FMNH; including 1 dissected male) "R. Panamá: Almirante, 1959, H.S. Dybas, FMNH (HD) # 59-154"\ *Polyporus sanguineus*\ JFL FMNH. **JAMAICA:** 1 specimen dissected (JFL) "Kingston, Jamaica, W.I., A.H. Ritchie, J.F. Lawrence, Lot 1991"\ ex. *Polyporus maximus* ex USDA herbaria\ Ceracis furcifer (8) mellié 203\ JFL. **ANTIGUA:** 2 specimens (JFL; including 1 dissected male) "Gaynor's Gut, Antigua, B.W.I, IX-11.65, A.P. Laska"\ J. F. Lawrence, Lot 1598\ ex. *Polyporus sanguineus*\ JFL. **COSTA RICA:** 3 specimens (JFL; including 1 dissected male) "Turrialba, Costa Rica, ix-5-66"\ JF Lawrence Lot 1851\ Robin Andrews Collector\ ex. *Daedalea elegans*\ JFL"; 4

specimens (JFL; including 1 dissected male) "Smi. S.W. Cañas Guanacaste, Costa Rica, Feb. 3-12.1967"\ J.F. Lawrence Lot.2153\ Robin Andrews Coll.\ ex. *Polyporus sanguineus*\ JFL. **MEXICO:** 1 specimen dissected (ANIC) "Mex: Veracruz, Coatzacoalcos"\ mi.S.vii.10.63\ J.Doyen collector\ JFL.

Remarks. As in male *Cer. cornifer*, the frontoclypeal horn in male *Cer. furcifer* shows great variation, but its apex is almost always bifurcated in small to large morphs. In small morphs, the bifurcation may be very prominent (Fig. 2 H). The occurrence of more than one body color among individuals from the same population is common (Fig. 6 A) and the coloration "half brown half dark-brown" seems to be one of the most common (Fig. 6 A, arrow). However, individuals may be homogeneously black in some populations (Fig. 6 B, arrow), besides intermediate colors that also occur (Fig. 6 C). There are males in which the lobes of tegmen are rounded comparatively larger (*e.g.* specimens from Manaus, Brazil); in other cases these lobes are conspicuously angulated (*e.g.*in a specimen from Antigua, Caribbean Sea).

Distribution. *Ceracis furcifer* occurs on central and northern South America, extending throughout the Antilles until Mexico. It is sympatric with *Cer.cornifer* in Paranhos (Brazil) and with *Cer.hastifer* in San Luis de Palenque (Colombia) (Fig. 4, Map).

***Ceracis hastifer* (Mellié, 1849)**
Figures. 2 I; 4 and 7 A–F

Ennearthron hastiferum Mellié, 1849: 370, pl. 4, fig. 17. Type locality: Colombia; Pic: 1916: 20 [taxonomic notes]; Blackwelder 1945: 549 [distribution]; Lawrence 1967: 97 [taxonomic status]; Abdullah 1973: 199 [taxonomic status and distribution]; Mueller *et al*., 2001: 318 [taxonomic notes].

Ceracis hastifer (Mellié, 1849): Lawrence 1967: 99 [taxonomic notes]; Abdullah 1973: 199 [taxonomic status and distribution]; Mueller *et al*., 2001 : 318 [taxonomic notes]; Antunes-Carvalho & Lopes-Anadrade 2011: 61 [taxonomic notes]; Pecci-Maddalena 2014: 486 [taxonomic notes].

Diagnosis. Base of the frontoclypeal horn without lateral inflexion and expanded until one third of the horn length. Antennal funicle with four antennomeres, being the first inferior in length, to three following combined. Hypomera with lateral contour emarginated and enlarged toward the median portion of the eye. Tegmen with the inner emargination of the anterior portion deep, about two thirds of its length; lateral edges almost linear, without inflexion; outer apical edges apparently without cutting.

Redescription. Male lectotype, here designated (Fig. 7 A–C and 7 E). Adult apparently fully pigmented and in good conditions, but antennae absent. Measurements (in mm): TL 1.39, PL 0.49, PW 0.69, EL 0.9, EW 0.7, GD 0.56. Ratios: PL/PW 0.71, EL/EW 1.3, EL/PL 1.84, GD/EW 0.8, TL/EW 1,94. **Body** glabrous, elongate, slightly extended on discal portion. Dorsal surface mostly dark reddish-brown; ventral surface mostly reddish-brown, except for yellowish-brown hypomera, legs and mouthparts. **Head** barely visible from above; dorsal surface immediately above horn base concave, glabrous, sparsely punctate. Frontoclypeal ridge strongly produced forming a long and narrow upward directed median horn (in mm: length 0.5, basal width 0.32), laminate in lateral view and bearing several diminute, sparsely setae. The horn base is expanded until one third of the horn length (Fig. 7 A, big black arrows) and has no lateral inflexion near of the base; apex rounded, subtruncate. **Antennae** (left antennae measured in a plesiotype) FL 0.09 mm, CL 0.16 mm, CL/FL 1.8, length of antennomeres 1–9 (in mm) as follows: 0.06, 0.04, 0.03, 0.03, 0.02, 0.01, 0.04,0.05,0.07; sensillifers apparently presents but barely visible. **Eyes** coarsely facetted, with minute slender yellowish setae emerging from the intersection between omatidia (barely visible even at a magnification of 150x), GW 0.13 mm. **Pronotum** with anterior portion produced forward, covering head; anterior edge shallowly emarginated, forming two short and acute frontolateral lobes; sides narrow, not visible from above; posterior edge sublinear, punctation single, uniforme and regularly distributed (Fig. 7 B), distance between puntures from 1,25 to 3,75 puncture-widths; each puncture bearing a yellowish decumbent minute setae, barely visible even a magnification of 150x; in between punctures, microreticulate. **Scutellum** small, subtriangular, with few puncture, each one bearing a short, fine, decumbent setae; BW 0,09 mm and SL 0,04 mm. **Elytra** about 1,84x as long as pronotum; sides subparallel at the basal two-thirds, then abruptly converging toward apex; punctation single, more fine than pronotal punctation; humeral calli conspicuous. **Hind wings** developed, apparently functional. **Prosternum** in front of coxae shallowly biconcave; prosternal process thin (Fig. 7 A, white arrow) almost as long as coxae and projected bellow prosternal disc. **Hypomera** biconcave, subglabrous and reticulous with lateral contour emarginate and enlarged toward median portion of the eye (Fig. 7 A, small black arrow). **Protibia, meso and metabia** follow the pattern of *furcifer* species group. **Metaventrite** moderately convex, subglabrous, bearing scattered slender setae, surface microreticulate; discrimen not discernible. **Abdominal ventrites** with microreticulate surface, shallow punctures and scattered slender setae, longer than those on dorsal surface; length of the ventrites 1–5 (in mm, from base to apex of each ventrite at longitudinal midline) 0.19, 0.05, 0.05, 0.06, 0.08. First abdominal ventrite bearing a circular, marginated, pubescent sex patch at center (Fig. 7 C, arrow), with a transverse diameter of 0.06 mm. **Male terminalia** (in paralectotype) (Fig. 7 D). with **VIII sternite** with posterior edge bearing a deep concave emargination at middle (Fig. 7 D, VIII sternite, arrow); posterior corners rounded, scletotized, bearing bristles; discal portion membranous; lateral edges diverging from posterior to anterior portion; anterior edge slightly biconcave. **Tegmen** with the inner emargination of anterior portion deep, about two thirds of it length (Fig. 7 D, teg, arrow); lateral edges almost linear, without inflexion; external apical edges without cutting. **Penis** elongate, subcylindrical, basal and posterior portion membranous; discal portion sclerotized; posterior portion membranous and enlarged (Fig. 7 D, pen, arrows).

Females (Fig. 7 F). Similar to males except in the abdominal sex patch absent and frontoclypeal ridge devoid of horn; Resembles mostly the females of the *Cer.cornifer* species, but apparently larger than it.

Variation. Males, measurements in mm (n= 6, included the lectotype) TL 1.14–1.46 (1.33 ± 0.1); PL 0.43–0.52 (0.47 ± 0.03); PW 0.58–0.69 (0.64 ± 0.03); EL 0.69–0.94 (0.86 ± 0.08); EW 0.6–0.7 (0.65 ± 0.04); GD 0.46–0.56 (0.52 ± 0.04); HL 0.27–0.51 (0.41 ± 0.08). Ratios: PL/PW 0.68–0.78 (0.73 ± 0.03); EL/EW 1.15–1.53 (1.33 ± 0.12); EL/PL 1.53–2.14 (1.84 ± 0.18); GD/EW 0.7–0.85 (0.8 ± 0.05); TL/EW 1.9–2.25 (2.05 ± 1.3). Females, measurements in mm (n= 3) TL 1.27–1.46 (1.35 ± 0.08); PL 0.46–0.57 (0.51 ± 0.04); PW 0.58–0.66 (0.6 ± 0.04); EL 0.77–0.89 (0.85 ± 0.05); EW 0.57–0.69 (0.62 ± 0.05); GD 0.5–0.54 (0.52 ± 0.02). Ratios: PL/PW 0.79–0.86 (0.84 ± 0.03); EL/EW 1.28–1.54 (1.37 ± 0.12); EL/PL 1.54–1.91 (1.67 ± 0.17); GD/EW 0.78–0.89 (0.84 ± 0.04); TL/EW 2.11–2.35 (2.19 ± 0.11). Since that in good conditions we measured all specimens.

Material examined. Lectotype, male here designated (MNHG) (Fig. 7 A)\ [white label] *Hastifer* Kuntze Colombie Mellié [handwritten] \ [yellow label] LECTOTYPE [printed] *Ennearthron hastiferum* Mellié [handwritten]. **COLOMBIA:** 1 specimen male dissected (MNHG) [white label] *Hastifer* Kuntze Colombie Mellié [handwritten]\ [yellow label] PARALECTOTYPE [printed] *Ennearthron hastiferum* Mellié [handwritten]"; 1 specimen male (MNHG) [white label] *Hastifer* Kuntze Colombie Mellié [handwritten]\ [yellow label] PARALECTOTYPE [printed] *Ennearthron hastiferum* Mellié [handwritten]"; 1 specimen female (MNHG) [white label] *Hastifer* Kuntze Colombie Mellié [handwritten]\ [yellow label] PARALECTOTYPE [printed] *Ennearthron hastiferum* Mellié [handwritten]"; 1 specimen dissected (CELC) Colômbia, "Casanare San Luis de Palenque"\ 1247965-1092026, 290.9 m, 20.i.2010, Contreras, J. L leg.\ ex. *Pycnoporus sanguineus*"; 1 specimen dissected (MFN)\ [blue label] Columb Moritz [handwritten]\ [red label] Hist.-Coll. (Coleoptera) Nr. 53171 (4. Ex.) Cis hastifer Kunze Peru – Columb. Zool. Mus. Berlin [printed]. **PERU:** 1 specimen dissected (MNHG) [white label] *Hastifer* Kuntze Perou ?Mellié [handwritten]"; 4 specimens (ANIC; including 1 dissected male) "Peru, "Intercep Miami Florida 14576"\ oct 19, 1960 ex Polyporid. **BRAZIL:** 15 specimens (CELC) "Brasil: PA, Marabá, Reserva Biológica de Tapirapé, Amazônia Legal, 04.xii.2003, Gumier-Costa, F. leg."\ Amostra extra nº 09, Borda; 1 specimen dissected (MPEG) "Brasil: AM, Tapurucuara, Rio-Negro, 1.2.1963, M.P.E. Goeldi, J & B. Bechyné"; 3 specimens (ANIC; including 1 dissected male) "São Roque (Mato Dentro) S. Paulo, Brazil, xi-1963"\ N. Papavero, Coll. **Doubtfully included**.

Remarks. We had few specimens in hands, only 10 males and 5 females which is not enough to observe variation. The frontoclypeal horn of the specimen from Colombia (Casanare San Luis de Palenque) has an inflexion about four fifths of its length and a square shaped apex. In large morphs the frontoclypeal horn is most prominent and the greatest pronotal width is larger than in individuals of *Cer. cornifer* (Figs. 2 I and 7 A). In the paralectotype the anterior edge of the pronotum is slightly emarginated at middle, forming two lobes, as well as in the specimen of the MFN, from Colombia. The laterals of the anterior portion of tegmen have is somewhat thickening and flattened, a condition more evident in the specimen from San Luis de Palenque, (Casanare, Colombia).

Distribution. The only accurate data we have are from "Tapurucuara, Rio Negro" (Manaus, Brazil), Marabá (Pará, Brazil), both of the Amazonian biome; and San Luis de Palenque (Casanare, Colombia), where *Cer. hastifer* is sympatric with *Cer. furcifer*

(Fig. 4, Map). The remaining data are from Colombia and Peru (without details), from the label of the lectotype and historic material examined. We examined three specimens from São Roque (São Paulo, Brazil), being one male and two females, but due to the bad condition of the male terminalia we prefer to consider it as doubtfully included in *Cer. hastifer*.

***Ceracis ruficornis*Pic, 1916**
Figures. 2 J; 4 and 8 A–E

Ceracis ruficorne Pic, 1916: 20. Type locality:Blumenau, Brazil.

Ceracis ruficornis Pic, 1916: Blackwelder 1945: 550 [distribution]; Lawrence 1967: 97 [taxonomic status]; 1973: 202 [feeding habits]; Abdullah 1973: 201 [taxonomic status and distribution] Lopes-Andrade 2002a: 7 [taxonomic notes]; Gumier-Costa *et al*., 2003: 359 [host fungus and distribution]; Antunes-Carvalho & Lopes-Andrade 2011: 61 [taxonomic notes]; Pecci-Maddalena 2014: 482 [taxonomic notes .

Diagnosis. Frontoclypeal horn with apex expanded, slightly emarginated at middle, forming two small rounded lobes. Lateral contour of the horn without inflexion near of the base, instead, shallowly narrow at middle. Antennal funicle with three antennomeres, being the first equal or superior in length, to three following combined. Tegmen with the inner emargination of the anterior portion shallowly enlarged and less than one half of the total length. Lateral edges expanded before of the apex, with a shallow inflexion at outer apical edge of the each lobe.

Redescription. Male plesiotype (Figs. 8 A–C and 8 D). Adult apparently fully pigmented and in good condition. Measurements (in mm): TL 1.22, PL 0.49, PW 0.56, EL 0.73, EW 0.59, GD 0.51. Ratios: PL/PW 0.88, EL/EW 1.24, EL/PL 1.49, GD/EW 0.86, TL/EW 2.07. **Body** glabrous, elongate, subcylindrical, shiny, dorsal surface blackish; ventral surface blackish, except for yellowish-brown legs, mouthparts, funicle and basal antennomeres; procoxae and head (including frontoclypeal horn) mostly reddish-brown; antennal club dark reddish-brown. **Head** barely visible from above; dorsal surface immediately above horn base concave, glabrous, sparsely punctate; frontoclypeal ridge strongly produced forming a long horn (in mm: length 0.29, basal width 0.29) with apex expanded, slightly emarginated at middle, forming two small rounded lobes (Fig. 2 J); contour lateral of the horn without inflexion near of the base, instead, shallowly narrow at middle (Fig. 8 A, black arrows). **Antennae** (right antennae measured) with FL 0.07, CL 0.16, CL/FL 2.29, length of antennomeres 1–8 (in mm) as follows: 0.06, 0.04, 0.04, 0.02, 0.01, 0,04, 0.04.0.08; sensilliferes visible. **Eyes** coarsely facetted, with minute slender yellowish setae emerging from the intersection between ommatidia, GD 0.11 mm. **Pronotum** with anterior portion produced forward, covering head; anterior edge slightly emarginated and forming two very short rounded lobes; sides narrow, not visible from above; posterior edge sublinear; punctation fine, single, uniform and regularly distributed (Fig. 8 B); distance between punctures from 2.5 to 4.7 puncture-widths; each puncture bearing a yellowish decumbent minute setae, barely visible even at a magnification of 150x; in between punctures shiny, microreticulate. **Scutellum** small, subtriangular, with few punctures, each one bearing a short, fine, decumbent setae, barely visible at a magnification of 150x; BW 0.08 mm and SL 0.04 mm. **Elytra** about 1.5x as long as pronotum; sides subparallel at the basal two-thirds an then abruptly converging toward apex; punctation single, similar to pronotal punctation but more fine; vestiture similar to that of pronotum; humeral calli conspicuous. **Hind wings** developed, apparently functional. **Prosternum** in front of coxae shallowly biconcave, microreticulous; prosternal process thin (Fig. 8 A, white arrow), almost as long as coxae and projected below prosternal disc. **Hypomera** biconcave, reticulous, bearing decumbent setae and lateral contour slightly emarginated. **Protibia, meso and metatibia** follow the *furcifer* species pattern. **Metaventrite** moderately convex, subglabrous, bearing scattered slender setae; surface microreticulate; discrimen not visible. **Abdominal ventrites** with microreticulate surface, shallow punctures and scattered slender setae; longer than those on dorsal surface; length of ventrites 1–5 (in mm, from base to apex of each ventrite at longitudinal midline): 0.17, 0.06, 0.07, 0.07, 0.06. First abdominal ventrite bearing a circular, marginated pubescent sex patch at center (Fig. 8 C, arrow), with a transverse diameter of 0.03 mm. **Male terminalia** (Fig. 8 D) with **sternite VIII** with posterior edge bearing a deep concave emargination at middle (Fig. 8 D, sternite VIII, arrow); posterior corners sclerotized and rounded, bearing bristles, median portion membranous; lateral edges diverging from posterior to anterior portion; anterior edge biconcave, forming a strut at middle. **Tegmen** with the inner emargination of the anterior portion shallowly enlarged (Fig. 8 D, teg, red arrow) and less than one half of it length; lateral edges expanded before of it apex (Fig. 8 D, teg, big black arrow), with a shallow inflexion at the external apical portion of the lobes

(Fig. 8 D, teg, small arrow). **Penis** elongate, subcylindrical; basal edge blunt (Fig. 8 D, pen, arrow); sides subparallel, lateral contour emarginated.

Females (Fig. 8 E). Similar to males except in the abdominal sex patch absent and frontoclypeal ridge devoid of horn; Resembles mostly the *furcifer* species, but usually black;

Variation. Males, measurements in mm (n= 9, included the plesiotype) TL 1.11–1.29 (1.21 ± 0.05); PL 0.41–0.51 (0.46 ± 0.03); PW 0.5–0.58 (0.54 ± 0.02); EL 0.7–0.8 (0.76 ± 0.04); EW 0.54–0.61 (0.57 ± 0.02); GD 0.46–0.53 (0.49 ± 0.02); HL 0.09–0.3 (0.21 ± 0.08). Ratios: PL/PW 0.78–0.9 (0.84 ± 0.04); EL/EW 1.24–1.45 (1.31 ± 0.06); EL/PL 1.49–1.95 (1.66 ± 0.14); GD/EW 0.82–0.91 (0.86 ± 0.02); TL/EW 2–2.2 (2.1 ± 0.6). Females, measurements in mm (n= 7) TL 1.17–1.31 (1.23 ± 0.04); PL 0.42–0.5 (0.45 ± 0.02); PW 0.5–0.57 (0.53 ± 0.02); EL 0.72–0.85 (0.78 ± 0.05); EW 0.53–0.62 (0.57 ± 0.02); GD 0.47–0.51 (0.49 ± 0.01). Ratios: PL/PW 0.79–0.94 (0.85 ± 0.05); EL/EW 1.24–1.49 (1.37 ± 0.07); EL/PL 1.44–2.02 (1.76 ± 0.16); GD/EW 0.82–0.92 (0.86 ± 0.03); TL/EW 2.09–2.23 (2.16 ± 0.6). Specimens of the following localities were measured: **Brazil:** Rio de Janeiro (Nova Friburgo and Paraty, "Ponta Negra"); São Paulo (Bertioga, "Praia da Boraceia").

Material examined. Lectotype, male here designated (MNHN) [Blumenau. S.O. Brasilien. (Reitter)]\ [*Ceracis* (antennes 8 art. Probabl.)]\ [Type] yellow\ [Type] red; [*Ceracis ruficorne* Pic]\ Lectotype.\ [Blumenau. S.O. Brasilien. (Reitter)]\ [*Ceracis* (antennes 8 art. Probabl.)]\ [Type] yellow\ [Type] red; [*Ceracis ruficorne* Pic]\ Paralectotype. **BRAZIL:** 23 specimens (CELC; including 1 dissected male) "Brasil: SP, Praia da Boraceia, 13.ix. 2011, Sandoval-Gómez, V.E.leg."\ ex. *Pycnoporus sanguineus*"; 11 specimens (MZSP; including 1 dissected male) "Ilha dos Buzios, São Paulo, Brazil, x.1963"\ Exped. Dep. Zool.\ SP\ *Ceracis ruficornis* Pic Det. J.F. Lawrence"; 2 specimens (MZSP; including 1 dissected male) "Peruibe, SP, 28.xi/01.xii.1984, Exp. MZUSP col."\ *Ceracis ruficornis* Pic Gen 1"; 4 specimens (JFL; including 1 dissected male) "*Ceracis* (8) *ruficornis* Pic 447"\ "Ilha da Victoria, S. Paulo, Brasil, 16-27.iii.1964"\ Exped. Dep. Zool.\ JFL"; 4 specimens (CELC; including 1 dissected male) "Brasil: RJ, Nova Friburgo, xi.2003, Grossi, E.J. leg."\ *Ceracis furcifer* Mellié 1848; det. C. Lopes-Andrade"; 4 specimens (CELC; including 1 dissected male) “Brasil: RJ, Paraty, Ponta Negra, 5-6.iii.2011, Sandoval, V.E & Idrobo, C.J. leg”.

Remarks. We note (by exam of the pictures) that the lectotype is similar to all specimens exanimate for us; differing principally for anterior edge of pronotum, greatly emarginated, instead slightly as in plesiotype. Specimens with the greatest pronotal width (PW) are large, but smaller than the examined *Cer. hastifer*. Individuals are usually black, except for a single specimen from Paraty (Brazil-RJ), which is dark reddish-brown. As in other members of the *furcifer* group, the male frontoclypeal horn also varies in shape and length between morphs and, in like *Cer. cornifer*, a conspicuous bifurcation at the horn apex is common in small individuals; however, a bifurcated male horn also occurs in large morphs, different from what was observed in *Cer. cornifer* (Fig. 2 J). The type locality is Blumenau (SC-Brazil), and in the examined material the closest locality is Peruíbe (SP-Brazil). However, specimens from Bertioga (SP-Brazil) are in better condition, so we used it for the redescription (as a“plesiotype”).

Distribution. We have found *Cer. ruficornis* only at a few localities close to the coastal area of southeastern Brazil, where it was sympatric with *Cer. cornifer* in Paraty (in the state of Rio de Janeiro), Peruíbe and Ilha da Victoria (in the state of São Paulo) (Fig. 4, Map).

Identification key to male individuals of the *Ceracis furcifer* group

1 Antennal funicle with three antennomeres ………. 2

1’Antennal funicle with four antennomeres ………. 3

2 Apex of the frontoclypeal horn elongated and emarginated at middle, forming two conspicuous rounded lobes; lateral contour of the horn without inflexion near base, but usually conspicuously narrow at middle. Tegmen with lateral edges with an enlargement before apex, with a prominent inflexion at the outer apical edge of the each lobe…***Ceracis furcifer***

2’ Frontoclypeal horn with apex expanded but only slightly emarginated at middle, forming two small rounded lobes. Tegmen with lateral edges expanded before apex but with a shallow inflexion at the outer apical edge of the each lobe… ***Ceracis ruficornis***

3 Lateral contour of the frontoclypeal horn usually with a pronounced inflexion near base. Hypomera usually not enlarged toward median portion of the eye. Tegmen with inner emargination of the anterior portion narrow and less than one half of the tegmen length; outer edges usually with a prominent inflexion at first basal one half; each lobe of posterior portion with one small tip at the inner apical edge and a small cutting on the outer edge…***Ceracis cornifer***

3’ Lateral contour of the frontoclypeal horn expanded until one third of the horn length, usually devoid of lateral inflexion. Hypomera with lateral contour enlarged toward the median portion of the eye. Tegmen with inner emargination of anterior portion deep, about two thirds the tegmen’s length; lateral edges almost linear, without or with an inconspicuous inflexion, less prominent than in *Cer.cornifer*; posterior portion of each lobe without tip at inner edge apex and without cutting on the outer edge…***Ceracis hastifer***

Discussion

Species in the *Ceracis furcifer* species-group are very similar externally, even in the morphology of sclerites of male abdominal terminalia. Differences between species are hard to note, mainly for non-specialists. Lawrence (1967) noted the great similarity between *furcifer* species and cited that they would even constitute “races” of two polytypic species, rather than eight species recognized by him. Based in our results, we agree in part with him, butwe see two natural subgroups of *furcifer* species, rather than two polytypic species. In the first subgroup, of species with eight antennomeres (*Cer. furcifer* and *Cer. ruficornis*), males usually have the frontoclypeal horn deeply incised at apex forming two branches; while in the second subgroup, of species with nine antennomeres (*Cer. cornifer* and *Cer. hastifer*), the frontoclypeal horn is usually truncate or shallowly emarginate. There are subtle differences in sclerites of male abdominal terminalia between the two subgroups. In the subgroup with nine antennomeres the tegmen has the outer apical portion of each lobe rounded, sometimes sharp, with a shallow cutting on outeredge. At the other subgroup, of species with eight antennomers, the lateral edges of the tegmen have an enlargement before apex, with an inflexion at the outer apical portion of each lobe.

Intraspecific variation and ecotypes

We found more intraspecific variation in *furcifer* species than previously observed, mainlyin shape of the male frontoclypeal horn, between males of the same or different populations (Fig. 2, Male morphs). Other aspect is the color variation in populations of *Cer. cornifer* and *Cer. furcifer* (Figs. 3 and 6). These variable traits were considered diagnostic for the *furcifer* species recognized before our work (Mellié 1849; Gorham 1898; Casey 1898; Pic 1916; 1922; Brèthes 1922). Despite these differences, the examination of sclerites of male abdominal terminalia, mainly the tegmen, reveals that the *furcifer* group consists only of four species, instead of eight as accepted before. In this context, although the presence of a frontoclypeal horn is diagnostic for the *furcifer* group, the shape of this horn, especially of its apex, is extremely variable between individuals of the *furcifer* species and cannot be used alone to delimit species. The use of body color and shape of male frontoclypeal horn for delimitingciid species has led to the formation of a number of synonyms in the past (for example, see synonymies in Lawrence 1967, 1971). For instance, the specific epithet of *Cer.semipallidus* was a clear allusion to coloration (see Pic, 1922), but it is indeed a variation observed in *Cer. furcifer*, and the synonymization of both, proposed by Lawrence (1967), is completely correct.

The greatest intraspecific variation we observed was between individuals of *Cer. cornifer* and can explain why four species (*Cer.cylindricus*, *Cer. monocerus*, *Cer. simplicicornis* and *Cer. unicornis*) were synonymized with it by us. Pic (1916) described *Enneartrhon simplicicorne* from Buenos-Aires (Argentina) as “nigro-piceus” with a “capite lamina, apice truncate, munito” and has distinguished this species from the closely “*E. hastiferum* Mell” for differences in coloration and horn shape. Similarly *Enneartrhon cylindricum* was described by Brèthes (1922) from the same country, as being “subpiceum” and “Le mâle porte sur le front une corne releveé” with “son extrémité tronqueé”. Now we know that these are just morphs of the same *Cer. cornifer*, that in southern Neotropical areas show black or blackwish coloration. At the other distribution extreme, based in a series from Saint Vincent (Caribbean), Gorham (1898) described *Cer. unicornis* and argued that “The distinguishing character of this little species is the long, simple, lamelliform, and rather narrow horn" that is "similar to that in *C. furcifer*, but longer and not bifurcate or emarginate at its tip". In this case, although Gorham referred to this species as "Nigro-piceus", we examined images from the lectotype and conclude that actually, it seems to be mostly yellowish or reddish-brown, similar to the male *Cer. monocerus* from Florida (EUA) examined by us.

The resemblance of these two morphs (*Cer. unicornis* and *Cer. monocerus*) was already verificated by Lawrence (1967) on the *Cer. monocerus* redescription. In that work, Lawrence also observed that "*C. unicornis* Gorham is a very similar form, and further collecting in the West Indies may well show that it is not distinct from *C. monocerus* even at the subspecific level". Lawrence also remarks that *Cer. cornifer* and *Cer. hastifer* are "also very similar to *C. monocerus*, differing mainly in color and in the shape of the frontoclypeal horn andpronotal apex"; and observe that these two specimens "may not be specicifically distinct". Now based on the examination of sclerites of male abdominal terminalia, we affirm that all these four names (*Cer.cylindricus*, *Cer.monocerus*, *Cer.simplicicornis* and *Cer.unicornis*) are synonyms of *Cer. cornifer*, which shows a disjuntic geographic distribution and a great intraspecific variation.

Although the presence of tubercles and horns on male head or pronotum is common in several species of *Ceracis* (Antunes-Carvalho & Lopes-Andrade 2011, 2013; Pecci-Maddalena *et al.* 2014) and other ciid genera like *Cis, Falsocis* and *Grossicis* (Antunes-Carvalho *et al.* 2012; Oliveira *et al.* 2013; Lopes-Andrade & Lawrence 2011), the role of these secondary sexual characteristics in the behavior of ciid beetles is still unclear. Interestingly we have noted that males of all *furcifer* species are apparently smaller in total length (excluding the horn) than female conspecifics (see Variation). It is possible that horns, tubercles or pronotal projections are useful in combats and used like weapons, as has already been observed in other insects, taking some role in sexual selection (Emlen 2008). So, males possibly relocate part of the energy during growth for the development of these secondary sexual traits, which would ultimately result in increased *fitness*. In this context why these differences occur between adults in single and different populations? And, how often each morph occurs in a given population?

Secondary sexual traits in head and pronotum of male *Ceracis* possibly have an allometric growth (Lawrence 1967), which possibly holds true for *furcifer* species and was already suggested for species in the *Ceracis cucullatus* group (Antunes-Carvalho &

Lopes-Andrade 2013). Besides, female ciids usually oviposit continuously, which leads to generation overlap (Lawrence 1973). In ciid populations maintained in laboratory for a long period, the individuals that develop when resource is depleting are usually smaller and males have smaller or even lack secondary sexual traits (Lopes-Andrade pers. obs.). It is evident that in extreme situations like that (resource depletion) the absence or reduction of secondary sexual traits in male ciids may be the result of polyphenism. But it was already observed that adult males emerged at the same time show variable secondary sexual traits (Lopes-Andrade pers. obs.), which may constitute genetically determined variation (polymorphism).

However, it is usually called polymorphism the variation is discrete, not continuous, and has a genetic base (Ford 1945; Mclean & Stuart-Fox 2014). According to Lawrence (1967) the morph that characterizes a given species is usually the largest male, which constitutes the minority of a population. It ispossible in the case *furcifer* species that large and small morphs are infrequent extremes, with the intermediary morphs being the most common in a given population. In this case, if the variation falling within a single normal distribution (continuous), than likely it is not a case of polymorphism, at other hand, if the horn variations can be clustered into categories and follow a bi-modal or multi-modal curve, than the *furcifer* group would be considered polymorphic. These shall be checked in future morphometrics studies. We even do not know if the variation in shape and size of male horns and tubercles of ciid species is a polymorphism (a phenotype genetically regulated) or a polyphenism (different phenotypes expressed from a single genotype); for instance, as a result of food quality and quantity during development. Or even both, as they are not mutually exclusive.

Differences in body coloration may be a consequence of the relatively long period of time between emergence and attainment of full pigmentation, during which teneral are abundant (Lawrence 1967). As overlay of generations is common in ciids, the consequence is that a mature ciid population may have adults with every degree of pigmentation, from recently emerged and thus light colored adults (tenerals) to fully pigmented adults (Figs. 3 and 6). However, we shall consider environmental and genetics factors may also determine body coloration. In one hand *Cer. cornifer* individuals in a single longitude show different body coloration; at the other hand, individuals from southern are usually black, being conspicuously different from the ones in northern latitudes (Fig. 3). The similar color variations (morphs usually black) occur with individuals of *Cer. furcifer* from some Brazilian localities (*e.g.* Araguaina-

TO, Fig. 6 B; Mambai-GO and Manaus-AM) and mostly of the *Cer. ruficornis* from the Atlantic Forest biome (Figs. 8).

These ecotypes of *Cer.cornifer, Cer. furcifer* and *Cer.ruficornis* may be the result of adaptations leading to changes in developmental time, being slower in colder than in warmer areas. The extended developmental time of ecotypes of colder areas may lead to more food consumed by individuals and, consequently, enhancement of traits like body size and pigmentation. As environmental conditions usually follow latitudinal and altitudinal gradients, the pattern we see is of populations of darker individuals in southern latitudes and higher altitudes. The most conspicuous ecotypes we observed were populations of *Cer. cornifer*, with darker adults in localities with lower winter temperatures, like Paranhos (MS-Brazil) (Fig. 3 C), cold and with higher altitude like Urubici (SC-Brazil) and cold areas in the southern Neotropical region (Fig. 3 F–H) .

Ecotypes may be recognized by other differences, rather than coloration and body size, and may be the result of adaptations not only to colder areas. It is also possible that slight local differences, as in conditions and resource availability and distribution between natural open to clearing areas, lead to specific adaptations and thus to the evolution of ecotypes. Both *Cer.cornifer* and *Cer.furcifer* would be good models to evaluate this, because both has been collected in natural open areas and environments drastically modified by human activities. It is important to note here that these differences in color and male horn shape would be polymorphisms within geographic variations. In this case, the prevalence and nature of geographic variation in polymorphism suggests that polymorphism may be a precursor to and facilitate speciation (Mclean & Stuart-Fox 2014) and can be evidence that speciation process may be occurring in populations of the *furcifer* group.

The *furcifer* group within *Ceracis* and Ciidae

Although species in the *furcifer* group possess most of the diagnostic characteristics currently accepted for the genus *Ceracis*, some remarkable aspects distinguish this group within the genus:

(i) Frontoclypeal ridge strongly produced forming a single median horn (bifurcate or not at apex), laminar in lateral view and bearing several minute, sparse setae along it. The false *furcifer* species, *Cer.zarathustrai* Pecci-Maddalena *et al.*, also has a frontoclypeal horn, butit is subcylindrical and bears a conspicous tuft of yellowish bristles at apex. Species of the *cucullatus* group also have the frontoclypeal ridge produced forward, forming a wide short lamina (Antunes-Carvalho & Lopes-Andrade 2013) and not a horn. In species of other ciid genera, such as *Grossicis*, males have a laminate frontoclypeal projection, wide and conspicuously produced upwards in *Grossicis diadematus* (Mellié) and relatively narrow in *G. laminicornis* Antunes-Carvalho *et al*. .However, in the latter species the horn is curved (as seen in lateral view; Antunes-Carvalho *et al.* 2012) and not so narrow as in *furcifer* species.

(ii) Prosternal process thin, but not laminate. *Ceracis* species can be easily distinguished from *Cis* species and most Ciinae by the possession of spinose protibial apex and a concave prosternal with laminate prosternal process (Lawrence 1967). In all known *Ceracis* species, and even in undescribed Neotropical forms examined by us, the prosternal process is laminate, except for the *furcifer* species, in which it is thin and parallel-sided. As the shape of the prosternal process is somewhat homogenous between species of a ciid genus, hence being traditionally used as generic character, future studies shall evaluate whether the *furcifer* group is a lineage separated from the remaining *Ceracis*. In other words, whether it constitutes a separate genus. Molecular data shows that *Cer. cornifer* and *Cer. furcifer* are a closely related and do not cluster with other *Ceracis* species (Lopes-Andrade & Grebennikov 2015).

(iii) Anatomy of sclerites of male abdominal terminalia. These sclerites are similar between *furcifer* species, except for a few diagnostic differences we cited in their redescriptions, mainly in the shape of tegmen. But there are features in these sclerites that distinguishes the *furcifer* group from the remaining *Ceracis*. In *furcifer* species, the tegmen has a deep longitudinal emargination at apex forming two wide parallel lobes, with rounded or blunt apices; the penis is cylindrical with rounded apex; and the sternite VIII has a conspicuous, deep concave emargination at the middle of the posterior edge. In *Cer.Zarathustrai* and in species of the *cucullatus* group, the sternite VIII has a shallow V-shaped emargination at the posterior edge, the lateral lobes of tegmen are narrow and acute at apex and the penis has a triangular sclerotization at the middle of the apical portion (Antunes-Carvalho *et al.* 2013; Pecci-Maddalena *et al.* 2014).

(iv) The host fungus *Pycnoporus sanguineus* (S1 Fig.). Although we have records of *furcifer* species in other host fungi (see sections onvariation), our study shows that this group are associated almost exclusively with *Pycnoporus sanguineus*, based in records on literature and label data of individuals of *furcifer* species examined by us (Mellié 1849; Lawrence 1967, 1973; Gumier-Costa *et al.*2003; Graf-Peters*et al.*

2011). We also show that such association occurs widely in the Neotropical region (see material examined; and Fig. 4, Map). If they did not perform this environmental service, basidiomes of *P. sanguineus* would persist in nature for years. Nevertheless, besides toxic substances, basidiomes of this fungus have high concentrations of elements that are usually in low concentration in terrestrial ecosystems (*e.g.* cadmium and molybdenum). In this context, the *furcifer* group plays an important role in nutrient cycling, especially in open areas where this fungus is one of the most common.

Another interested ecological aspect from the narrow association of the *furcifer* species with *P. sanguineus* is exactly the specialization or monophagy instead the polyphagy strategies. This ecological tactic contrasts the *furcifer* species with *cucullatus* species and certainly influences on how species of these two *Ceracis* groups colonize new areas. Two species of the *cucullatus* group are remarkably invasive, being native to the Neotropical region and introduced in Galapagos (*Cer. cucullatus*), Africa, South and Southeast Asia (*Cer. tabellifer*). In the same group, *Cer.bicornis* is also polyphagous and it is the most widespread *cucullatus* species in the Neotropical region (Lopes-Andrade obs. pess.). These three *cucullatus* species are remarkdly polyphagous even in a single locality and this biological chacteristic possibly, a sowide diet breadth has probably contributed to their geographic expansion and invasion success (Antunes-Carvalho & Lopes-Andrade 2013). It is to believe that populations in these three species are panmitic, therefore it is plausible to assume that isolation of certain populations had occurred and led to several speciation events in the history of the *cucullatus* group. Indeed, the *cucullatus* group is more diverse than reported in literature and include several undescribed species, most of them being specialists (oligophagous or even monophagous) and with a narrow geographic distribution. At the other hand, *furcifer* species seems to be restricted to the Neotropical region (*sensu* Morrone, 2006, 2014) where it lives associated mostly with a single host fungus and differently from the *cucullatus* group, the *furcifer* group has a relatively low diversity (four recognized species and devoid of new forms in collections).

One of the ecological bases of the evolution of specialization is the environmental constancy (Futuyama & Moreno 1988). The origin of the *Pycnoporus* species is old (Garcia-Sandoval 2011) and it is plausible to assume that the ancestral *Pycnoporus* species need the same environmental conditions to develop as in extant *Pycnoporus* species (open areas with fallen wood directly exposed to sunlight, thus subjected to high temperatures and desiccation). *Pycnoporus sanguineus* is widespread in the southern hemisphere, while the closely related *P. cinnabarinus* is less common but widespread in temperate areas (mainly in the northern hemisphere) and *P. coccineus* is common in Australia and New Zealand; but futher research is needed to assess whether these species are really distinct (Roberts & Evans 2011).

Therefore, considering the distribution of *Pycnoporus* species, specially of *P. sanguineus*, we can assume that this resource are available for ciids for a long time, possibly much before the origin and diversification of *furcifer* species. The great morphological and molecular similarities among *furcifer* species (morphological data presented herein; molecular data by Lopes-Andrade & Grenennikov *in press*), suggest that their divergence might have been recent. The use of a single fungus as resource might have put *furcifer* species in an evolutionary stasis: in all areas occupied by their populations, they use the same resource, which is widely available in most open areas in the Neotropical region. That contrasts with species-group with polyphagous species, in which populations can undergo subsequent specialization, becoming oligophagous or even monophagous, which may act as evolutionary constraint and lead to rapid irradiation of the group, as was possibly the case of species in the *Ceracis cucullatus* group and also in the *Cis taurus* group.

In both *Cer.cucullatus* and *C. taurus* groups, there are a few widespread polyphagous species and several geographically restricted oligophagous species, closely related to the polyphagous species (Graf-Peters *et al.* 2011; Antunes-Carvalho & Lopes-Andrade 2013; Oliveira *et al.* 2013). The evolutionary stasis of *furcifer* species is a plausible hypothesis and may explain why disjunct populations of *Cer. cornifer* has not undergone speciation. But now the question is: What can explain the separation of the recognized *furcifer* group?

Distribution patterns of the *furcifer* group: An historic explanation

According to Garcia-Sandoval *et al.* (2011) the origins of the fungus *Pycnoporus* species dates back to the late Cretaceous, the same period of the origin and expansion of the world rainforests (Morley 2011), that occupied much parts of South America. At this time, Atlantic forest and Amazonian rainforest biomes were attached, beginning to separate in the Pliocene period (DaSilva and Pinto-da-Rocha 2012). The separation of these biomes led to isolation of prior pan mictic populations of species, which resulted in a high level of endemism in these two environments (Carvalho & Almeida 2011). Thus, based on the current environments where *P. sanguineus* occurs, mainly in natural open and clearing areas of the Southern Hemisphere, where there is a great incidence of light and elevated temperature, it's possible that the first *P. sanguineus* has appeared in clearings within the ancient rainforests and border areas. Thus, this food source would be available for a long time, being very possible that has been used for ciid as well as by the ancestor of *furcifer* group. We believe that this ancestral *furcifer* occurred widely in these areas of *P. sanguineus* occurrence, then dispersing throughout the neotropics.

The current distribution patterns of *Cer.furcifer* species reveals that it occupies many areas of the Amazonian biome and also ecotones in middle Brazil (Fig. 4, Map), where it may occur in natural open or in clearing areas. At the other hand, *Cer.cornifer* occurs widely in open areas of the Neotropical region, reaching Caribbean island and southern USA (Fig. 4, Map). We argue that these two current distributions patterns of *Cer. furcifer*and *Cer. cornifer* are not are random, but indicates that this two forms diverged in the past, from a common ancient, resulting in a ancient form similar to *furcifer* and *ruficornis* individuals and another ancient form, similar to *Cer. cornifer and Cer. hastifer* species. The ancient similar to *Cer. furcifer* and *Cer. ruficornis*, must have been isolated in clearing areas within the forest and then gradually diverged in the current *Cer. furcifer* and *Cer. ruficornis* species; After the Amazonian and Atlantic forest separation, *Cer. furcifer* stayed restricted to interior continental areas and *Cer. ruficornis* to some islands and coastal maritime areas, as the current distribution patterns shows (Fig. 4, Map). A similar event can be happened with ancient of the *Cer. cornifer* and *Cer. hastifer*, although in this case, it must have been adapted early, for open areas and coastal maritime areas and this shoul be a motive to explain the presence of *Cer. cornifer* species in Caribbean and Florida (EUA), besides the several open areas that it species also occurs in Brazil (Fig. 4, Map).

The Amazonian and Atlantic forest separation event might explain why species most closely related, seems to be separated from each other, and at other hand, less related individuals, are sympatric in some localities (Fig. 4, Map). *Cer.cornifer* are sympatric with *Cer.ruficornis* in three points of the Brazilian Atlantic Forest Biome (see map) and with *Cer. furcifer* in Paranhos (MS). These localities apparently belong to the same unity of the biogeographic analysis that corresponds to Parana unity (see Morrone 2014b) or in the case of Paranhos, a border area between Parana and Chaco unities. Although currently, these two areas are not connected, these are recognized as sister group of the south eastern Amazônia (Morrone 2014b) and its separation occurs recently in the Pliocene (about 5 Ma). A similar biogegraphic event also must have isolated populations of the *furcifer* group in areas to the north of the Neotropical region, like San Luis de Palenque (Colombia), where *Cer. hastifer* and *Cer. furcifer* are sympatric (Fig. 4, Map). It is plausible that all these sympatry areas recorded here, belong to endemism areas, which are caused by non random historical factors (Sigrist & Carvalho) but for instance, these questios are not clear.

Conclusions

The *Ceracis furcifer* species group now encompasses only four species artificially arranged in two subgroups: *Cer. cornifer* and *Cer.hastifer; Cer.furcifer* and *Cer. ruficornis*. Based on male terminalia comparisons, we synonymize *Cer. cylindricus, Cer. monocerus, Cer.unicornis* and *Cer.simplicicornis* with *Cer. cornifer*, and definitively contest the inclusion of new species in the group, based on frontoclypeal horn and body coloration, as mostly was done in the original descriptions (Gorham, 1898; Casey, 1898; Pic, 1916; Brèthes, 1922). We demonstrate that these two aspects, actually, are due to the conspicuous differences among male morphs and ecotypes, besides of the ontogeny and other biological factors. Other important aspects provide here, is the singularities morphological and ecological, which differs the *furcifer* group from other *Ceracis*. These facts suggest that although the monophyly of *Ceracis* is questionable, in the case of *furcifer* species is very likely that it occurs.

Nevertheless, we show that *furcifer* species are widely distributed along to Neotropical region, as well its host fungus *Pycnoporus sanguineus* and provide evidences of an old association between *furcifer* group and its fungus species, based on current distribution patterns from *furcifer* species. We argue that *furcifer* group diversification, happened recently, likely after Amazonian and Atlantic Forest separation occurred, from the Pliocene period (DaSilva and Pinto-da-Rocha, 2012). This recent separation time would be an explication for the great similarities among the *furcifer* species; this temporal factor associated with a specialized diet, may lead *furcifer* species to an evolutionary stasis, what can explain why disjuntic *Cer. cornifer* populations does not diverged yet. Nevertheles, it’s possible that differences among *furcifer* species are polymorphisms within geographic variations and now, speciation process may be occurring in populations of the *furcifer* group. We believe that the knowledge provides here, demonstrate that the *furcifer* group must be a useful tool for future phylogeography studies.

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References

Antunes-Carvalho C, Lopes-Andrade C (2011) Two new Neotropical species of Ceracis Mellie´ (Coleoptera, Ciidae) and redefinition of the cucullatus group. ZooKeys 132: 51–64. doi: 10.3897/zookeys.132.1570

Antunes-Carvalho C, Lopes-Andrade C (2013) Two Invaders Instead of One: The True Identity of Species under the Name Ceracis cucullatus (Coleoptera: Ciidae). PLOS ONE 8 (8): e72319. doi:10.1371/journal.pone.0072319

Antunes-Carvalho C, Sandoval-Gómez VE, Lopes-Andrade CL (2012) Grossicis, a new genus of Neotropical minute tree-fungus beetles (Coleoptera: Ciidae), with a detailed discussion on its systematic position in the family. CR Biol 335: 107–119. doi: 10.1016/j.crvi.2011.11.006

Borderes J, Costa A, Guedes A, Tavares LBB (2011) Antioxidant Activity of the Extracts from Pycnoporus sanguineus Mycelium. Brazilian Archives Of Biology And Technology 54(6): 1167–1174.

Brèthes J (1922) Descripción de varios coleópteros de Buenos Aires. Anales de la Sociedad Científica Argentina 94: 263–305.

DaSilva MB, Pinto-da-Rocha R (2011) História biogeográfica da Mata Atlântica: opiliões (Arachnida) como modelo para sua inferência. In Biogeografia da America do Sul: Padrões e Processos. Roca, São Paulo

DeCarvalho CJB, Almeida EAB (2011) Biogeografia da America do Sul: Padrões e Processos. Roca, São Paulo.

Emlen DJ (2008) The Evolution of Animal Weapons. Annual Review of Ecology, Evolution, and Systematics Vol. 39: 387-413 DOI: 10.1146/annurev.ecolsys.39.110707.173502

Evenhuis NL (2008) A compendium of zoological type nomenclature: a reference source. Bish Mus Tech Rep 41: 1–23.

Ford EB (1945). Polymorphism. Heredity 20, 73–88.

Futuyma DJ, Moreno G (1988) The Evolution of Ecological Specialization. Annual Review of Ecology and Systematics, Vol. 19, pp. 207–233

Garcia-Sandoval R, Wang Z, BM, Hibbett DS (2011) Molecular phylogenetics of the Gloeophyllales and relative ages of clades of Agaricomycotina producing a brown rot. May-Jun;103(3):510-24. doi: 10.3852/10–209.

Gorham HS (1886). Supplement to Malacodermata. In: Godman, F. D. & Salvin, O. (eds),Biologia Centrali-Americana. Insecta. Coleoptera Vol. 3, Part 2. Porter, London, pp. 313–360.

Gorham HS (1898) On the serricorn Coleoptera of St. Vincent, Grenada and the Grenadines (Malacodermata, Ptinidae, Bostrychidae) with descriptions of new species. Proc. Zool. Soc. London 27: 315–343.

Graf-Peters LV, Lopes-Andrade C, Silveira, RMB, Moura, LA, Reck, MA, Nogueira-de-Sá, F (2011) Host Fungi and Feeding habits of Ciidae (Coleoptera) in a Subtropical Rainforest in Southern Brazil, with an overview of Host-Fungi of Neotropical Ciids. Florida Entomologist 94 (3): 553–566.

Gumier-Costa F, Lopes-Andrade C, Zacaro AA (2003) Association of Ceracis cornifer (Mellié) (Coleoptera: Ciidae) with the Bracket Fungus Pycnoporus sanguineus (Basidiomycetes: Polyporaceae). Neotropical Entomology 32 (2): 359–360.

Lawrence J F (1973) Host preference in ciid beetles (Coleoptera: Ciidae) inhabiting the fruiting bodies of Basidiomycetes in North america. Bulletin of the Museum of Comparative Zoology 145: 163–212.

Lawrence JF (1967) Delimitation of the Genus Ceracis (Coleoptera: Ciidae) with a revision of North America Species. Bulletin of the Museum of Comparative Zoology 136(6): 54.

Lopes-Andrade C (2002a) Recent Advances in the Study of the Brazilian Ciidae (Coleoptera: Tenebrionoidea). Dugesiana 9, 5–13.

Lopes-Andrade C (2011) The first Strigocis Dury (Coleoptera: Ciidae) from the southern Neotropical region and a provisional key to world species. ZooKeys 81:27–37. doi: 10.3897/zookeys.81.940

Lopes-Andrade C, Grebennikov VV (2015) First record and five new species of Xylographellini (Coleoptera: Ciidae) from China, with online DNA barcode library of the Family. Zootaxa, in press.

Lopes-Andrade C, Lawrence JF (2005) Phellinocis, a new genus of Neotropical Ciidae (Coleoptera: Tenebrionoidea). Zootaxa 1034: 43–60.

Lopes-Andrade C, Lawrence JF (2011) Synopsis of Falsocis Pic (Coleoptera, Ciidae), new species, new records and an identification key. Zookeys 145: 59–78 doi: 10.3897/zookeys.145.1895

McLean CA, Stuart-Fox D (2014) Geographic variation in animal colour polymorphisms and its role in speciation. Biol Rev Camb Philos Soc. 89(4): 860-73. doi: 10.1111/brv.12083. Epub 2014 Feb 14

Mellié MJ (1849) Monographie de l'ancien genre Cis des auteurs. Annales de la Société Entomologique 205: 158.

Miiller C, Jaeger B, Kompantsev AV, Uhlig M (2001)Type and species catalogue of the minute tree-fungus beetles of the Museum für Naturkunde in Berlin, with general information on the Coleoptera collection, its curation and “Historical Collection” (Coleoptera, Polyphaga, Ciidae and Pterogeniidae). Zoosystematics and Evolution Volume 77, Issue 2, pages 303–323.

Modes KS, Lazarotto M, Beltrame R, Vivian MA, Santini EJ, Muniz MFB (2012) Resistência natural das madeiras de sete espécies florestais ao fungo Pyconoporus sanguineus causador da podridão-branca. Cerne, Lavras. 18(3): 6.

Morley RJ (2011) Cretaceous and Tertiary climate change and the past distribution of megathermal rainforests. Tropical Rainforest Responses to Climatic Change. doi:10.1007/978-3-642-05383-2

Morrone JJ (2006) Biogeographic Areas and Transition Zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistics analyses of the entomofauna. Annual Review of Entomology 51: 467–494.

Morrone JJ (2014a) Biogeographical regionalisation of the Neotropical region. Zootaxa 3782 (1): 001–110. http://dx.doi.org/10.11646/zootaxa.3782.1.1

Morrone JJ (2014b) Cladistic biogeography of the Neotropical region: identifying the main events in the diversification of the terrestrial biota. Cladistics 30: 202–214

Oliveira EH, Lopes-Andrade C, Lawrence JF (2013) Review of the Neotropical Ciidae (Insecta: Coleoptera) in the Cis taurus species-group. Arthropod Systematics & Phylogeny 71 (3): 181 – 210

Oliveira LFC, Le Hyaric M, Berg MM, Almeida MV, Edwards HGM (2007) Raman spectroscopic characterization of cinnabarin produced by the fungus Pycnoporus sanguineus (Fr.) Murr. Journal of Raman Spectroscopy 38(12): 1628–1632.

Pecci-Maddalena ISC, Sandoval-Gómez VE, Lopes-Andrade C (2014) Ceracis zarathustrai sp. nov. (Coleoptera: Ciidae) from the Atlantic Forest biome. ZOOLOGIA: an international journal for zoology 31 (5): 482–488.

Pic M (1922) Noveautés diverses. Melanges Exotico-Entomologiques 36: 22.

Pic M (1916) Mélanges Exotico-Entomologiques. Bussière.

Roberts P, Evans S (2011) The Book of Fungi: A Life-Size Guide to Six Hundred Species from around the World.1th ed. United Kingdom: Ivy press.

Smânia A Jr, Marques CJ, Smânia EF, Zanetti CR, Carobrez SG, Tramonte R, Loguercio-Leite C (2003) Toxicity and antiviral activity of cinnabarin obtained from Pycnoporus sanguineus (Fr.) Murr. Phytother Res 17(9): 1069–1072.

Wick M (2012) The GeoNames Geographical Database. Available: http://www. geonames.org

Attachment

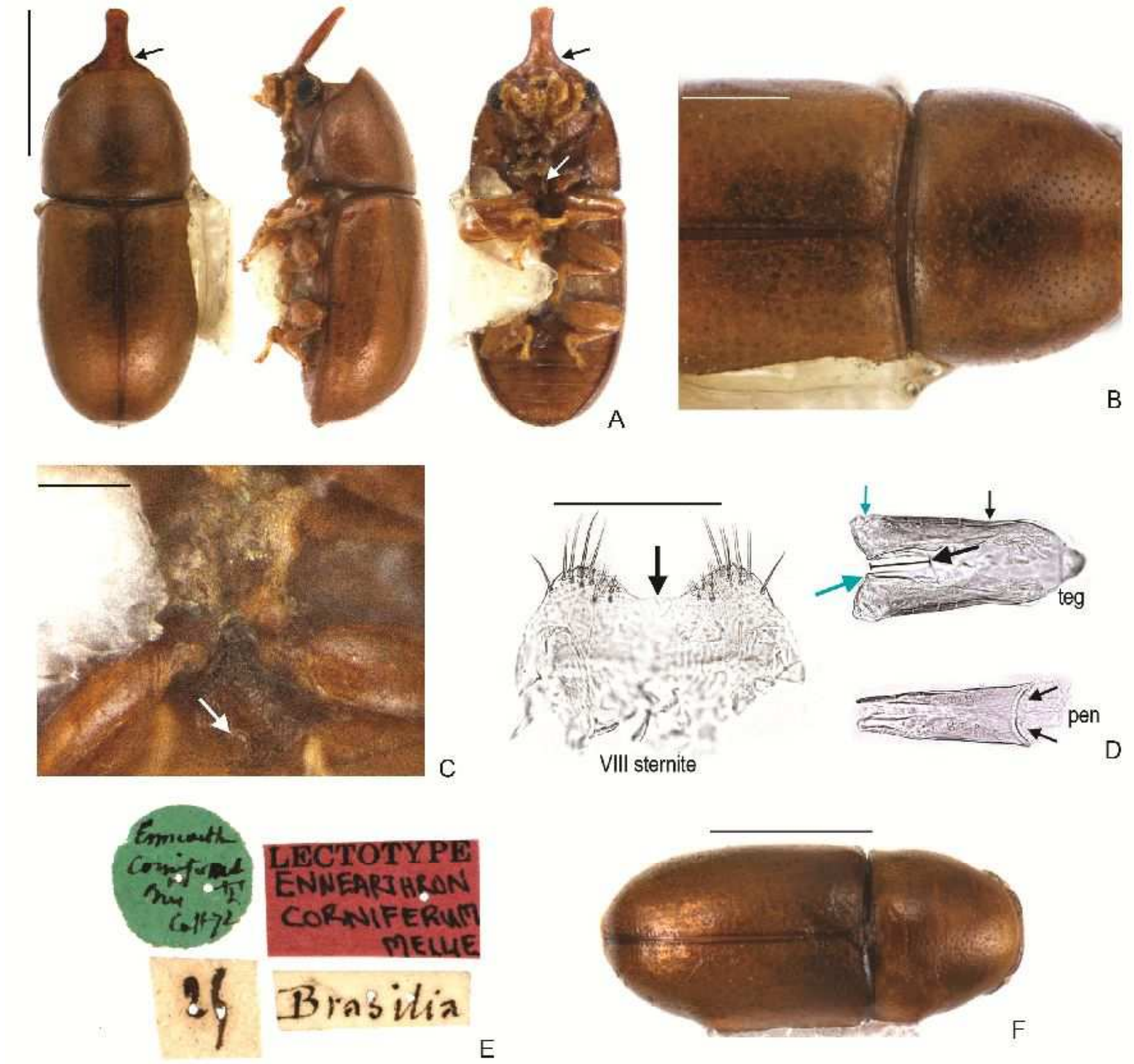


Figure 1. Habitus of *Ceracis cornifer* (Mellié, 1849). A–E Lectotype male (A) dorsal, lateral and ventral view respectively. Lateral inflexion near of the base (black arrows) and the prosternal process thin (white arrow) (B) Pronotum punctuation (C) First abdominal ventrite with a sex patch at center (white arrow) (D) Male terminalia: VIII sternite with a deep concave emargination at middle (black arrow); teg (tegmen) with the inner emargination of the anterior edge narrow and shallow; not deep (big black arrow); Each lobe of the posterior portion bearing one small tip at inner edge apex (big blue arrow); slight cutting on the outer portion (small blue arrow); Lateral edges with an inflexion at first basal one half (small black arrow); pen (penis) basal edge blunt (black arrows) (E) label data (F) female plesiotype from Viçosa, MG, Brazil. Scale bars: A = 0.5 mm, B = 0.2 mm, C–D = 0,1 mm, F = 0.5 mm.

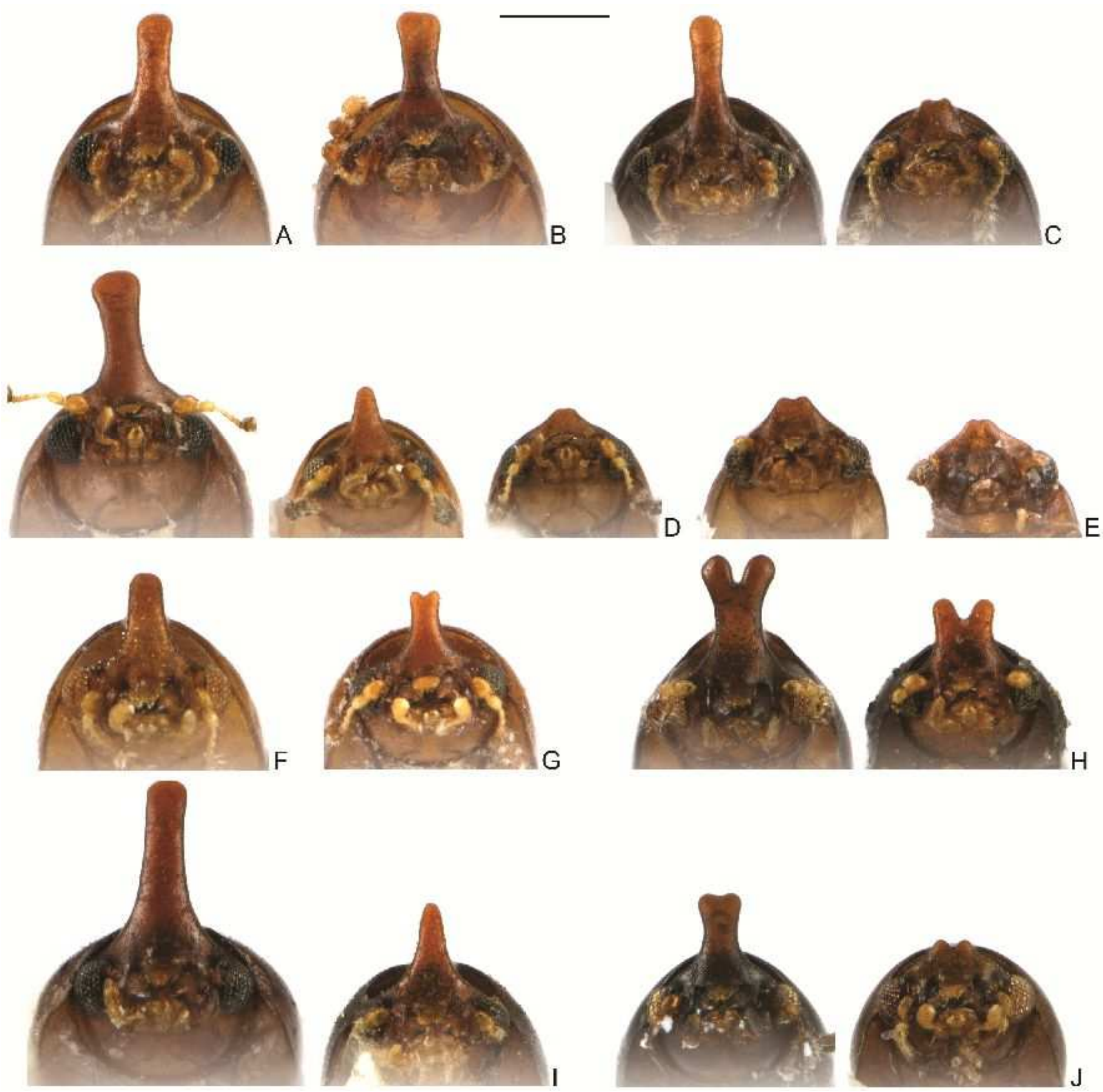


Figure 2. Male morphs of the *furcifer* group from different localities (as see in labels). A–G *Ceracis cornifer*: (A) lectotype (B) Florida, United Sates (C) Urubici, SC, Brazil (D) Juiz de Fora MG, Brazil (E) Jequeri, MG, Brasil (F) São Francisco de Paula, RS, Brazil (G) Tucuman, Argentina. *Ceracis furcifer*: (H) Paranhos, MS, Brazil and Colombia respectively. *Ceracis hastifer*: (I) lectotype and specimen from Colombia, respectively. *Ceracis ruficornis* (J) Peruibe, SP, Brazil and Ilha dos Buzios SP, Brazil, respectively. (Acronyms refers to States, *e.g.* SC = Santa Catarina State, in Brazil). Scale bar: 0.1 mm.

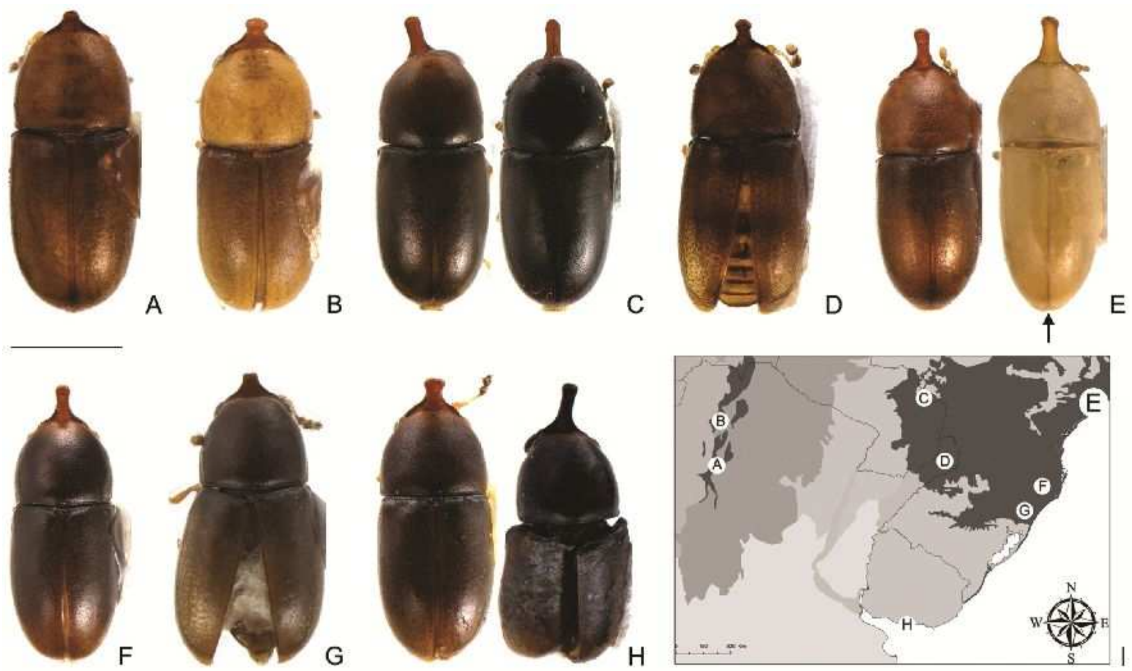


Figure 3. Male ecotypes of *Ceracis cornifer* species from different localities (as see in labels).A–H specimens, (A) Tucuman, Argentina (B) Salta, Argentina (C) Paranhos, MS, Brazil (D) Wanda, Missiones, Argentina (E) specimens from Viçosa, MG and a teneral (arrow) from Jequeri, MG from Brazil, respectively (F) Urubici, SC, Brazil (G) São Francisco de Paula, RS, Brazil (H) Montevideo, Uruguay (I) map showing the localities. Remarks: The letter E, not corresponds to true locality in the map, but refers to a very common ecotype of the *Cer. cornifer* in several north areas since these points. Scale bar = 0.5 mm.

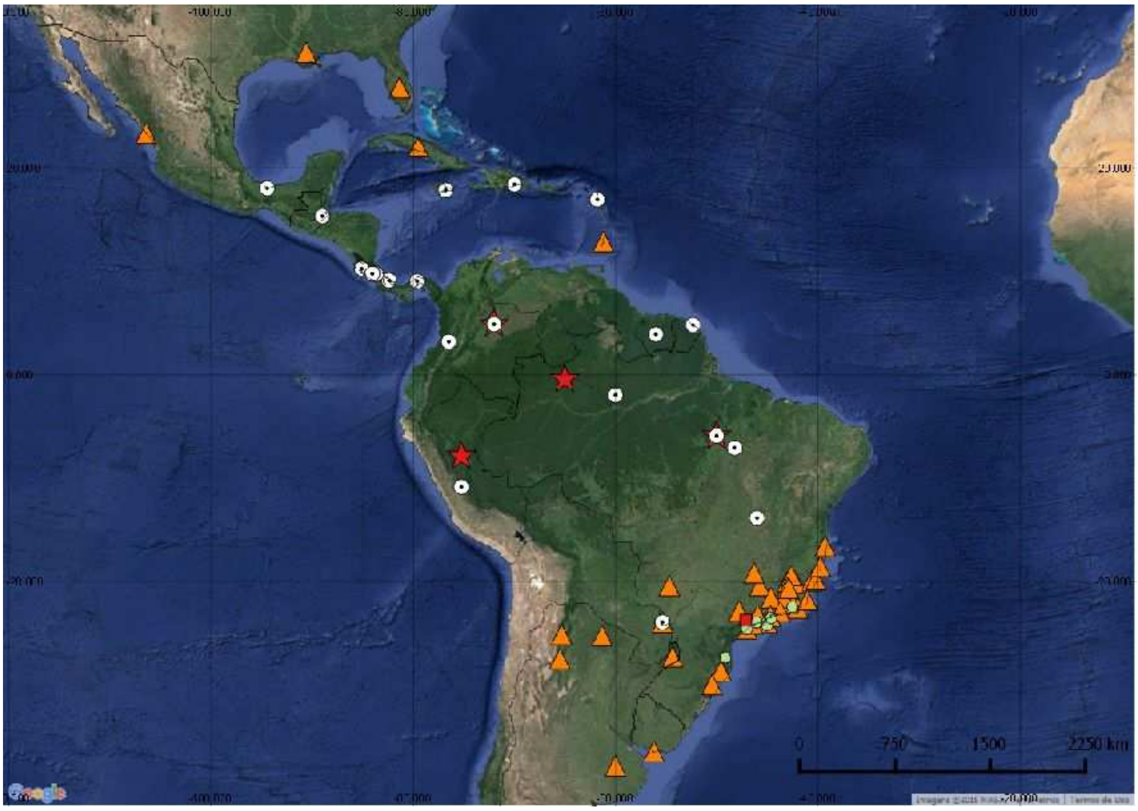


Figure 4. Map showing the distribution of *furcifer* species group: *Ceracis cornifer* (Mellié, 1849) (triangule); *Ceracis furcifer* Mellié, 1849 (white circle with a dot); *Ceracis hastifer* (Mellié, 1849) (red star); *Ceracis ruficornis* Pic, 1916 (green circle). The distribution of *Ceracis cornifer* is disjunct. Overlapped symbols represent spots where two species (in images) are sympatric: *Ceracis cornifer* and *Ceracis furcifer* are sympatric in Paranhos, MS, Brazil; *Ceracis furcifer* and *Ceracis hastifer* are sympatric in San Luis de Palenque, Casanare, Colombia and Marabá, PA, Brazil; *Ceracis ruficornis* are sympatric with *Ceracis cornifer* in three points: Paraty, RJ; Ilha da Vitória, SP and Peruibe, SP, all in Atlantic Forest Biome in southeast of the Brazil. Red square represents a doubtfully included specimen of *Cer. hastifer* of the locality of São Roque, SP, Brazil.

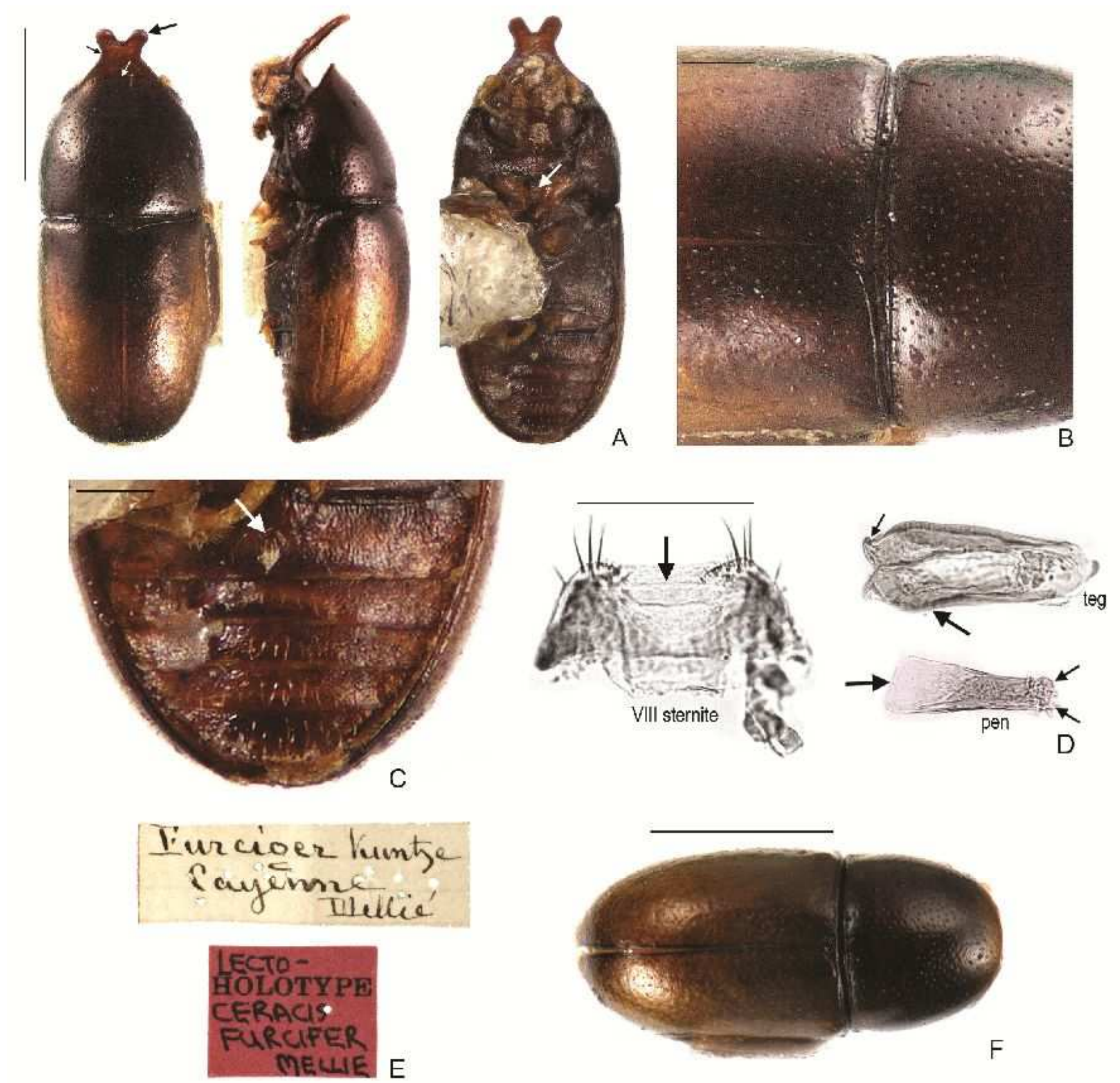


Figure 5. Habitus of *Ceracis furcifer* Mellié, 1849. A–C Lectotype male (A) dorsal, lateral and ventral view, respectively. The two conspicuous rounded lobes in horn apex (big black arrow), lateral contour conspicuously narrow at middle (small black arrow), anterior edge forming two lobes (small white arrow) and the prosternal process thin (big white arrow) (B) Pronotum punctuation (C) First abdominal ventrite with a sex patch at center (white arrow) (D) Male terminalia in topotype: (VIII sternite) with a deep concave emargination at middle (black arrow); Tegmen (teg) with lateral edges forming an enlargement before of the apex (big arrow) and a prominent inflexion at the outer apical portion of the lobes (small arrow). Penis (pen) with basal edge blunt (small black arrows) and a membranous portion (big black arrow) (E) label data of the lectotype (F) female plesiotype from Manaus, AM, Brazil. Scale bars: A = 0.5 mm, B–D = 0.1 mm, F = 0.5 mm.

Fig 6. Color variation in *Ceracis furcifer* species. A–C, (A) specimens from Paranhos, MS (Brazil) showing the occurrence of more than one type of color among individuals from the same population and the coloration half brown half dark-brown (arrow) (B) a teneral and a black individuals (arrow) from Araguaina, TO, Brazil (C) specimen from Mambaí, GO, Brazil showing a intermediate color. Scale bar: 0.5 mm.

Fig 7. Habitus of *Ceracis hastifer* Mellié, 1849. A–C Lectotype male (A) dorsal, lateral and ventral view, respectively. The horn base expanded without inflexion near of the base (big black arrows), prosternal process thin (white arrow) and hypomera enlarged toward median portion of the eye (small black arrow) (B) Pronotum punctuation (C) First abdominal ventrite with a sex patch at center (white arrow) (D) Male terminalia in paralectotype: (VIII sternite) with a deep concave emargination at middle (black arrow); Tegmen (teg) with the innser emargination of the anterior portion deep (arrow). Penis (pen) with posterior portion membranous and enlarged (arrows) (E) label data of the lectotype (F) female plesiotype from Peru. Scale bars: A = 0.5 mm, B–D = 0.1 mm, F = 0.5 mm.

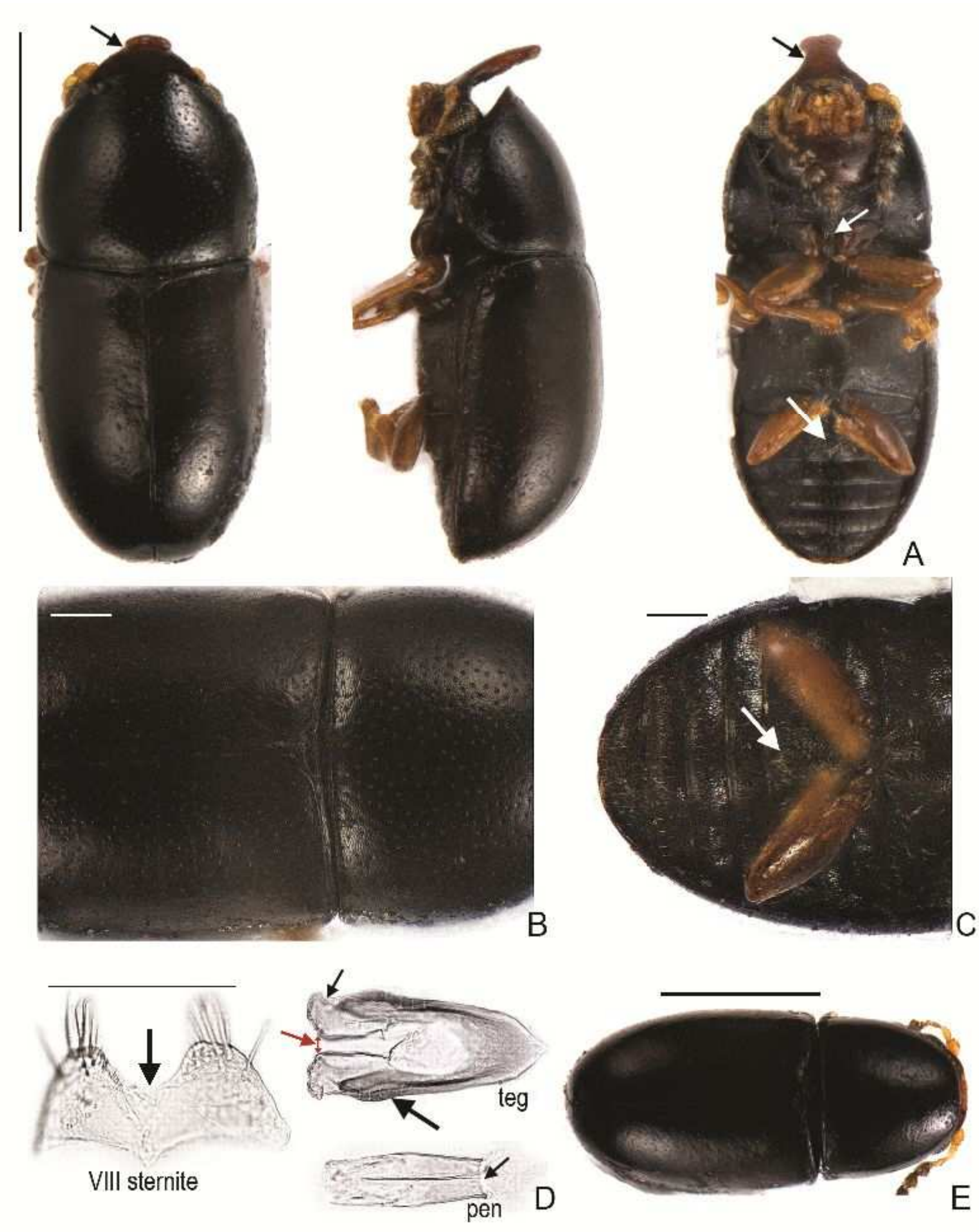
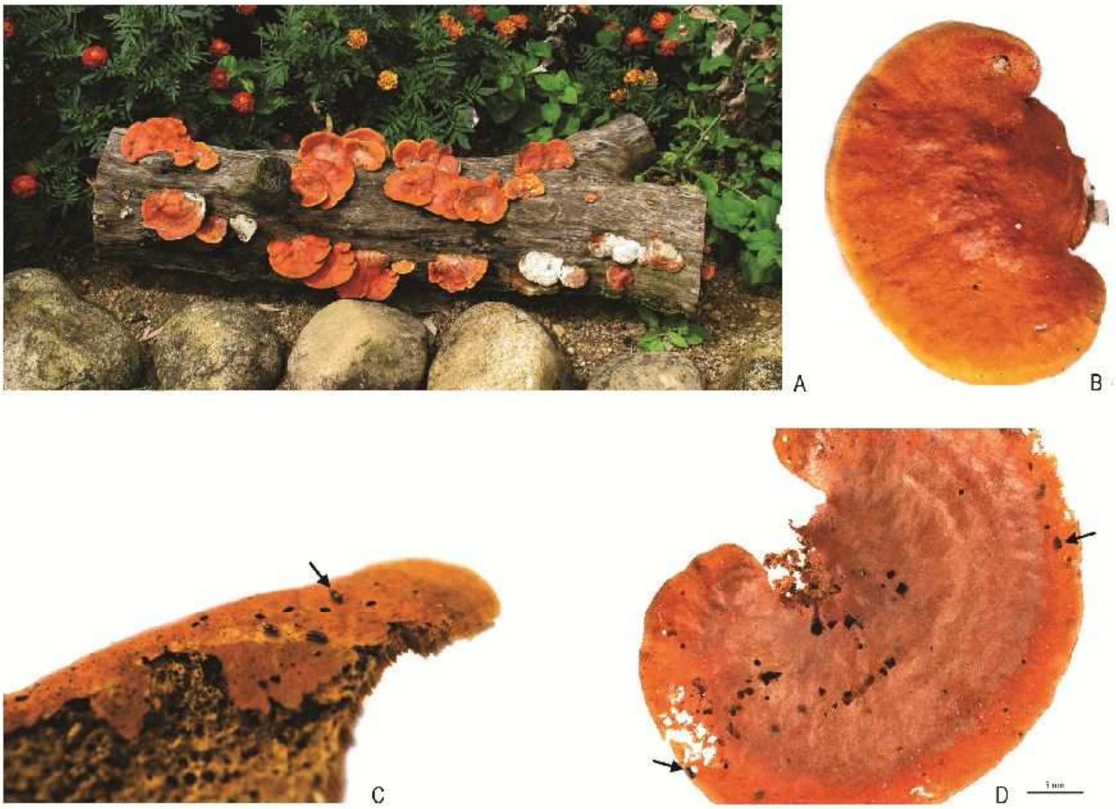


Fig 8. Habitus of *Ceracis ruficornis* Pic, 1916. A–C plesiotype male (A) dorsal, lateral and ventral view, respectively. Contour lateral of the horn shallowly narrow at middle (arrows) and prosternal process thin (white arrow) (B) Pronotum punctuation (C) First abdominal ventrite with a sex patch at center (white arrow) (D) Male terminalia in another plesiotype: (VIII sternite) with a deep concave emargination at middle (arrow); Tegmen (teg) with the inner emargination of the anterior portion shallowly enlarged (red arrow), lateral edges expanded before of it apex (big black arrow), with a shallow inflexion at the external apical portion of the lobes (small black arrow). Penis (pen) with basal edge blunt (arrow) (E) female plesiotype from Praia da Boraceia, SP, Brazil. Scale bars: A = 0.5 mm, B–D = 0.1 mm, F = 0.5 mm.



S1 Figure: The host fungus Pycnoporus sanguineus (A) in a garden in the locality of Juiz de Fora (Brazil) (B) fungus apparently without furcifer species (C) individuals of *Ceracis cornifer* species from Juiz de Fora (Brazil) (arrow) (D) individuals of *Ceracis furcifer* species from Araguaína (Brazil).

4. CONCLUSÃO

• O grupo *furcifer* é formado por 4 espécies (*Cer. cornifer*, *Cer furcifer*, *Cer. hastifer* e *Cer. ruficornis*).

• Dentro do grupo há dois subgrupos de espécies: (i) *Cer. cornifer* e *Cer. hastifer* e (ii) *Cer furcifer* e *Cer. ruficornis*; organizados principalmente quanto ao número de antenomeros, forma do corno frontoclipeal dos machos e aspectos morfológicos da terminália masculina.

• O grupo não é composto por “raças de duas espécies politípicas” e sim por 4 espécies que apresentam grande variação intraespecífica, principalmente quanto à forma do corno frontoclipeal dos machos e coloração do corpo.

• Baseado no presente estudo e em dados da literatura, conclui-se que apenas ciídeos alimentam-se de *P. sanguineus* e o grupo *furcifer* constitui o único grupo de organismos especialistas neste fungo.

• As espécies do grupo *furcifer*, ocorrem apenas na região Neotropical, mas não distribuiem-se igualmente por ela. Espécies próximas (*Cer. cornifer* e *Cer. hastifer*) e (*Cer furcifer* e *Cer. ruficornis*) estão espacialmente separadas e espécies menos próximas são simpátricas em alguns pontos (*Cer cornifer* e *Cer. furcifer* em Paranhos-MS, Brasil; *Cer. furcifer* e *Cer. hastifer* em San Luis de Palenque-Casanare, Colombia e Marabá-PA, Brasil; *Cer. ruficornis* e *Cer cornifer* em Parati-RJ, Ilha da Vitória-SP e Peruibe-SP, Brasil). Este padrão biogeográfico, somado à disjunção espacial de populações de *Cer. cornifer* geram evidências de que a diversificação do grupo *furcifer* ocorreu recentemente, provavelmente depois da separação da Amazônia e da Mata Atlântica, no perído Plioceno.