CONTRIBUIÇÃO À SISTEMÁTICA DE SYNDESINAE MACLEAY, 1819 (COLEOPTERA: LUCANIDAE)

por

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RESUMO

Lucanidae ou “cervos voadores” são um grupo chamativo de escaravelhos amplamente conhecidos por taxônomos tradicionais e colecionadores amadores. Embora seja uma família que sempre chamou a atenção de diversos cientistas ao longo da história, existem muitas lacunas na classificação em nível supragenérico. Este é o caso de Syndesinae MacLeay, 1819, uma das subfamílias menos diversificadas em Lucanidae, da qual não há evidências atualmente que suportem a sua monofilia, já que as análises filogenéticas apresentadas nunca contemplaram os quatro gêneros que a compõem. Além da falta de informação em termos filogenéticos, o estudo do grupo também sofre com inconsistências sobre a classificação de *Syndesus* e *Psilodon* e com a falta de definição das suas tribos. No presente trabalho a monofilia da subfamília foi testada através da reconstrução filogenética com base em dados morfológicos, que revelou a polifilia da mesma. Com base nesses resultados, os limites genéricos entre *Syndesus* MacLeay, 1819 e *Psilodon* Perty, 1830, foram definidos. Considerados por diversos pesquisadores como um único táxon, neste trabalho são fornecidas evidências que suportam a separação dos gêneros, restringindo *Syndesus* à região Australiana e *Psilodon* à América do Sul. Com base em esta precisão se revisou pela primeira vez *Psilodon*, descrevendo seis espécies novas e um novo gênero de Syndesinae para Venezuela e Trindade e Tobago.

PALAVRAS-CHAVE: Morfometria geométrica, Panbiogeografia, Nova espécie, Novo gênero, Filogenia.

CONTRIBUTION ON THE SYSTEMATICS OF SYNDESINAE MACLEAY, 1819 (COLEOPTERA: LUCANIDAE)

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ABSTRACT

Lucanidae or Stag beetles, are a remarkable group of scarabs widely known for traditional taxonomists and amateur collectors. Although it is a family that has caught the attention of several scientists throughout history, there are significant gaps in classification at the suprageneric level. This is the case of Syndesinae MacLeay, 1819, one of the less diversified subfamilies in Lucanidae, of which there is no evidence to support its monophyly, since phylogenetic analyses previously performed never analysed the four genera that compose it. In addition to the lack of information in phylogenetic terms, the definition of tribes and inconsistencies in the classification of *Syndesus* and *Psilodon* remain to this day. In the present work, the monophyly of the subfamily was tested by constructing a morphological phylogeny that revealed its polyphyly. Additionally, the generic limits between *Syndesus* MacLeay, 1819 and *Psilodon* Perty, 1830, which are still considered by several researchers as a single taxon, are defined. Showing evidence that supports the separation of both genera, restricting *Syndesus* to the Australian region and *Psilodon* to South America. Based on these results, *Psilodon* is revised for the first time, with the description of six new species and a new genus of Syndesinae for Venezuela and Trinidad and Tobago.

KEY WORDS: Geometric morphometrics, Panbiogeography, New species, New genus, Phylogeny.

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Tese apresentada ao Programa de Pós-Graduação em Entomologia, da Universidade Federal Rural de Pernambuco, como parte dos requisitos para obtenção do grau de Doutor em Entomologia.

RECIFE - PE

Fevereiro - 2023

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Dados Internacionais de Catalogação na Publicação
Universidade Federal Rural de Pernambuco
Sistema Integrado de Bibliotecas
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C118c Cáceres, Juan Sebastián Dueñas Cáceres

CONTRIBUIÇÃO À SISTEMÁTICA DE SYNDESINAE MACLEAY, 1819 (COLEOPTERA: LUCANIDAE) / Juan Sebastián Dueñas Cáceres Cáceres. - 2023.

228 f.

Orientador: Paschoal C. Grossi.
Coorientador: Hugo A. Benitez.
Inclui referências e apêndice(s).

Tese (Doutorado) - Universidade Federal Rural de Pernambuco, Programa de Pós-Graduação em Entomologia Agrícola, Recife, 2025.

1. Morfometría Geométrica. 2. Panbiogeografía. 3. Nova espécie. 4. Novo gênero. 5. Filogenia. I. Grossi, Paschoal C., orient. II. Benitez, Hugo A., coorient. III. Título

CDD 632.7

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CAPÍTULO 1

INTRODUÇÃO

Os cervos voadores (Coleoptera: Lucanidae) são uma família pequena de Scarabaeoidea representada por aproximadamente 1500 espécies em 115 gêneros (Bouchard *et al*. 2017). Os besouros da família Lucanidae representam uma das primeiras linhagens de Scarabaeoidea a ter se diversificado (Scholtz 1990). Morfologicamente caracterizam-se principalmente pela forma das antenas com escapos fortemente alongados e a presença de três a sete lamelas e pelo forte dimorfismo sexual principalmente representado pelas mandíbulas conspícuas dos machos. A família é cosmopolita e os espécimes encontram-se associados à madeira em decomposição onde os adultos colocam seus ovos para as larvas se desenvolverem no interior de troncos descompostos (Ratcliffe 2002).

Apesar de que a família tenha recebido ampla atenção por parte de colecionadores amadores e taxônomos tradicionais, as relações filogenéticas para a grande maioria dos táxons conhecidos não tem se determinado dificultando a resolução de inconsistências nomenclaturais no nível de tribo e a definição dos limites taxonômicos de alguns gêneros (Holloway 2007; Kim & Farrell 2015).

De acordo com Holloway (1960; 1968; 1969; 1972; 2007), Lucanidae é composto de quatro subfamílias. A grande maioria das espécies descritas pertencem a Lucaninae Latreille, 1804, com cerca de 1200 espécies (contemplando mais ou menos 90% da diversidade). As subfamílias restantes são, Aesalinae MacLeay, 1819 que compreende ao redor de 55 espécies, classificadas em sete gêneros (Holloway 2007); Lampriminae MacLeay, 1819 é a menor com cinco gêneros e 11 espécies restritas à Austrália, Nova Guiné, Nova Zelândia e o sul da América do Sul (Holloway 2007; Paulsen 2010). Syndesinae MacLeay, 1819 com mais ou menos 30 espécies descritas em quatro gêneros, *Sinodendron* Hellwig, 1792 e *Ceruchus* MacLeay, 1819, ambos restritos à região holoártica (Howden & Lawrence 1974); *Syndesus* MacLeay, 1819, considerado neste trabalho como um gênero exclusivo da Austrália, Nova Caledônia e Nova Zelândia e *Psilodon* Perty, 1830 da América do Sul, tratado por vários autores como um sinônimo de *Syndesus* (Benesh 1960; Maes 1992; Krajcik 2001; Krajcik 2003; Holloway 2007; Onore, Bartolozzi & Zilioli 2011).

Lucanidae nos estudos filogenéticos.

Embora sejam escassos os estudos evolutivos sobre a família, a monofilía de Lucanidae e as suas relações com outros grupos basais de escaravelhos, tem sido discutidas e suportadas por diferentes hipóteses filogenéticas, como é o caso de Iablokoff-Khnzorian (1977), que sugere a forte relação filogenética de Lucanidae, Passalidae e Pleocomidae; Howden (1982), recuperou Lucanidae como grupo irmão de Passalidae; Lawrence & Newton (1982) descreveram a forte relação filogenética entre Lucanidae, Passalidae, Trogidae e Pleocomidae; Scholtz (1990) resumiu o emprego de diferentes caracteres na filogenética de Scarabaeoidea fortalecendo as hipóteses de relacionamentos previamente propostas.

d´Hotman & Scholtz (1990), estudando estruturas das genitálias masculinas para inferir as relações entre as diferentes famílias de Scarabaeoidea, estabeleceram no caso de Lucanidae, recuperou Aesalinae como grupo irmão das demais subfamílias, considerando Sinodendrinae como uma subfamília válida e próxima de Lampriminae, e *Ceruchus* (sem a definição de uma subfamília), conformando um clado com Lucaninae. Neste trabalho não foram incluídos *Syndesus* e *Psilodon.*

A classificação utilizada em d´Hotman & Scholtz (1990) foi previamente proposta em Sharp & Muir (1912), definindo quatro subfamílias para Lucanidae: Aesalinae, Lampriminae, Sinodendrinae e Lucaninae. Holloway (1960; 1968; 1972) manteve a classificação em quatro subfamílias, considerando Diphyllostomatidae como um táxon separado, e como subfamílias válidas Aesalinae, Lampriminae, Lucaninae, agrupando os gêneros *Sinodendron*, *Ceruchus* e *Syndesus* na subfamília Syndesinae.

Com estas bases taxonômicas Browne & Scholtz (1995) utilizando caracteres das asas posteriores recuperaram um clado constituído por Diphyllostomatidae e Lucanidae, ambos como grupo irmão de Passalidae. Este trabalho inclui a última filogenia baseada em caracteres morfológicos, até a publicação de Lawrence *et al*. (2011) que oferece uma filogenia para Coleoptera que suportam os resultados previamente encontrados por Browne & Scholtz (2006).

Após os trabalhos realizados na década de 1990, o desenvolvimento de novas ferramentas para análises com base em dados moleculares permitiram novas abordagens para a reconstrução de filogenias sobre Scarabaeoidea. O primeiro exemplo encontra-se em Smith *et al*. 2006, que publicaram uma filogenia preliminar, que corroborou mais uma vez a hipótese da monofilia de Lucanidae, considerando as quatro subfamílias propostas em Holloway (1968) e *Diphyllostoma* como membros do mesmo táxon.

Filogenias posteriores de escaravelhos foram publicadas por Ahrens *et al*. (2014); Gunter *et al*. (2016); Zhang *et al*. (2018), e recentemente Cai *et al*. (2022), sustentando hipóteses de relacionamentos previamente propostas, assim como a monofilía da família. Apesar disto, a falta de estudos filogenéticos específicos para a família tem dificultado o esclarecimento das relações internas e a sua posição em relação a outras famílias de Scarabaeoidea, limitando a elaboração de propostas para a classificação de Lucanidae nos níveis de subfamília e tribo, produzindo o abandono temporário do uso de tribos até mais revisões taxonômicas e filogenias para os táxons menos estudados em Lucanidae sejam desenvolvidas (Holloway 2007).

Embora menos comuns, alguns estudos filogenéticos específicos para Lucanidae foram desenvolvidos por Ratcliffe (1984), que construiu uma filogenia de Penichrolucaninae Arrow, 1950 (hoje classificada em Lucaninae), recuperando a monofilia do táxon contendo os gêneros *Penichrolucanus* Deyrolle, 1863 e *Brasilucanus* Vulcano & Pereira, 1961. Hosoya & Araya (2005) reconstruíram a filogenia dos Lucanidae japoneses onde não foi suportada a monofilia das subfamílias. Em Paulsen (2013) encontra-se a descrição de um novo gênero para Aesalinae da região Neotropical, e ao mesmo tempo apresenta-se a primeira filogenia molecular específica para esta subfamília, recuperando-a como grupo natural, sustentando ao mesmo tempo a monofilia para Lucaninae e a conformação de um clado composto por Lampriminae e Syndesinae com poucos terminais.

Por último Kim & Farrell (2015) apresentaram pela primeira vez uma filogenia para Lucanidae abrangendo um grande número de terminais em comparação com trabalhos prévios, sendo assim um dos maiores aportes recentes à sistemática da família. Embora o foco do estudo tenha sido Lucaninae, a reconstrução filogenética recuperou Lampriminae como um grupo monofilético, sendo Aesalinae e Syndesinae polifiléticos

Considerando Syndesinae, o único trabalho que trata da classificação e composição da subfamília é o de Holloway (1968), onde a autora propôs a classificação atual com base em estudos da morfologia do aparelho bucal e da genitália. Desde então, durante 50 anos, não foram mais publicados trabalhos que possam comprovar ou não o relacionamento dos gêneros de Syndesinae, muito menos se os mesmos estão corretamente incluídos na subfamília. É a partir do presente trabalho que se pretende responder a estas perguntas, sendo o foco Syndesinae MacLeay, 1819.

O caso de *Syndesus* MacLeay, 1819 e *Psilodon* Perty, 1830.

Os cervos voadores da subfamília Syndesinae MacLeay, 1819 (Coleoptera: Lucanidae) representam uma das famílias menos diversificadas de Lucanidae (Holloway 2007). Historicamente Syndesinae tem sido constituído por três ou quatro gêneros dependendo dos autores, com cerca de 30 espécies descritas até hoje, sem um consenso definido para a classificação tribal dos mesmos. As espécies de *Sinodendron* Hellwig, 1792 e *Ceruchus* MacLeay, 1819 estão restritos à região Holoártica (Howden & Lawrence 1974); *Syndesus* MacLeay, 1819 se distribui na Austrália, Nova Caledônia e Nova Zelândia; por último *Psilodon* Perty, 1830, encontra-se distribuído ao longo da América do Sul, sendo esses dois gêneros muito próximos morfológicamente, o qual fez com que alguns autores os considerem sinônimos.

Enquanto *Sinodendron* e *Ceruchus* tem tido uma classificação estável ao nível genérico, *Syndesus* e *Psilodon* tem sido sujeito de diversas mudanças que dificultam o estabelecimento de uma classificação supragenérica confiável. *Syndesus* foi descrito como o gênero-tipo de Syndesidae, hoje considerada subfamília de Lucanidae. De acordo à descrição feita por MacLeay (1819) da espécie *Syndesus cornutus* (Fabricius, 1801) (espécie-tipo), os machos apresentam um corpo alongado e cilíndrico, com forma convexa; cabeça pequena e transversa; labro difícil de distinguir; mandíbulas quase retas; antenas glabras com sete lamelas; tibias serradas. As fêmeas descritas como muito próximas dos machos exceto pelo formato das mandíbulas. É importante destacar que MacLeay descreveu *S. cornutus* baseado em *Sinodendron cornutum* Fabricius, 1801, ambos aparentemente provenientes da Tasmânia, mas não é claro se os dois autores tiveram acesso ao mesmo material uma vez que *S. cornutum* foi originalmente descrito com seis lamelas na antena, característica que foi empregada depois para distinguir entre as espécies da América do Sul alocadas em *Hexaphyllum* Gray, 1832, e as Australianas.

Por outra parte *Psilodon* Perty, 1830 foi descrito para o Brasil baseado em uma fêmea coletada por K.F.P. von Martius e J.B. von Spix durante sua expedição no Brasil entre os anos 1817 e 1820 (Papavero 1971). *Psilodon schuberti* Perty, 1830 foi a primeira espécie descrita, definida como próxima de *Sinodendron* e incluindo as seguintes características: corpo escuro com tons marrons nas antenas; cabeça rugosa e mais ou menos escavada no fronte; pronoto ponteado com um sulco bem definido; placa escutelar lisa; élitros carenados; mandíbulas com cerdas eretas; e tíbias serradas e expandidas no ápice. O epiteto genérico proposto por Perty foi provavelmente baseado na ausência de cerdas ao longo da projeção dentiforme laminar das fêmeas de *Psilodon* (e *Syndesus*). Outra interpretação pode estar relacionada com a presença da projeção denteforme do laminar, sendo fino e presente longitudinalmente ao longo da porção dorsal. Se apresenta de uma forma diferente das mandíbulas fortemente dentadas presentes em Lucanidae. Perty não mencionou na sua diagnose o número de lamelas na clava antenal.

Dois anos depois Gray (1832) descreveu um novo gênero para o Brasil, sendo a espécie tipo *Hexaphyllum brasiliensis*, neste caso, baseado num macho coletado no estado de Rio de Janeiro e, apesar da sua similitude com a fêmea descrita por Perty não foi estabelecida nenhuma conexão entre os dois espécimes. Van Roon (1910) é o primeiro autor que estabelece esta relação sendo assim o macho e a fêmea de *H. schuberti* (como foi registrado no catálogo). O epiteto proposto por Gray se baseou na presença de seis lamelas na clava antenal. Depois deste trabalho, autores posteriores continuaram usando *Hexaphyllum* como o nome válido, principalmente baseados nesta característica, distinguindo assim das espécies de *Syndesus* que até então tinham sido descritas com sete lamelas (Hope 1840; Buquet 1840; van Roon 1910; Luederwaldt 1935; Didier 1929).

Didier & Séguy (1953) no seu catalogo e outros autores como Holloway (1968; 1997) Howden & Lawrence (1974), e Ratcliffe (2002) continuaram reconhecendo a validez de *Psilodon*, citado nestes trabalhos como os representantes sul americanos de Syndesini MacLeay, 1819. Em Benesh (1960), *Psilodon* e *Hexaphyllum* são considerados pela primeira vez como sinônimos de *Syndesus*, provavelmente concordando com as observações de Burmeister (1847) e Arrow (1938) que discutiram que dada a alta proximidade morfológica entre *Syndesus* e *Hexaphyllum* (=*Psilodon*), considerá-los como táxons diferentes representaria uma separação não natural, discutindo também, que o número de lamelas antenais, seis para *Hexaphyllum* e sete *Syndesus* não era suficiente para estabelecer uma divisão entre os espécimes da América do Sul e os Autralasiáticos, já que as espécies de Nova Caledônia de *Syndesus* apresentam seis lamelas.

Depois de Benesh (1960), duas linhas de pensamento em relação a estes dois gêneros foram desenvlvidas, a primeira reconhece *Syndesus* como um gênero distribuído na Austrália, Nova Caledônia, Nova Zelândia e América do Sul (Maes 1992; Krajcik 2001; Krajcik 2003; Holloway 2007; Onore, Bartolozzi & Zilioli 2011), a outra mantêm o proposto em Holloway (1968; 1997), Howden & Lawrence (1974), e Ratcliffe (2002), que reconhecem *Psilodon* como o gênero restrito a América do Sul, como é o caso de diversos autores que continuaram descrevendo novas espécies neste táxon, sendo o caso de Martínez & Reyes-Castillo (1985), Boucher (1993), Pardo-Locarno & Ríos-Málaver, 2011, e mais recentemente, Grossi & Aguiar (2014).

Sem dúvida *Syndesus* e *Psilodon* estão fortemente relacionados, inclusive são difíceis de serem diferenciadas por não-especialistas, mas considerar eles como um único táxon, ignoraria a distribuição disjunta desde o Cretáceo Médio (há ca. 90 milhões de anos) e outras diferenças morfológicas pouco estudadas na literatura, isto devido à falta de revisões taxonômicas e estudos genéticos e a dificuldade para ter acesso a material de coleções. Para estabelecer os limites entre os dois gêneros e fornecer suporte ao uso de Syndesini como a tribo Autralasiática e Neotropical de Syndesinae, são necessárias abordagens integrativas que ofereçam respostas para preencher as lacunas perpetuadas nos estudos de Lucanidae, abordagem que é proposta neste trabalho a partir do uso da morfometria geométrica, como ferramenta para suportar os estudos taxonômicos.

***Psilodon* Perty, 1830, Syndesinae Neotropical.**

Como foi discutido previamente a falta de revisões taxonômicas dificulta a definição da classificação supragenérica, e inclusive tem limitado a definição correta de gêneros menos estudados, como é o caso de *Syndesus* e *Psilodon*. Assim, um dos principais objetivos deste trabalho é revisar o gênero *Psilodon* Perty, 1830, considerado aqui como o único táxon de Syndesinae da região Neotropical.

Psilodon foi originalmente descrito por Perty (1830) com a espécie tipo *Psilodon schuberti*, a partir de uma fêmea coletada na “província Piahuiensi” no nordeste brasileiro. Gray (1832) descreveu um novo gênero, *Hexaphyllum*, usando um macho coletado no Rio de Janeiro no sudeste brasileiro, com a espécie tipo *Hexaphyllum brasiliensis*, sendo ambas espécies muito próximas, porém Gray na sua descrição original, não discutiu nada sobre esta relação.

Hope (1840) descreveu brevemente uma nova espécie classificada no género proposto por Gray, *Hexaphyllum westwoodii* de “Nueva Granada” (Atualmente Colômbia); pouco depois no mesmo ano, Buquet (1840) fez duas contribuições para a taxonomia dos Syndesinae sul americanos, a primeira foi a descrição de uma nova espécie, *Hexaphyllum aequinoctiale*, posteriormente considerado por Burmeister (1847) como sinônimo de *H. westwoodii* Hope, porém esta espécie é incluída em *Syndesus*. A segunda contribuição foi definir *Hexaphyllum brasiliensis* como a única espécie válida para o Brasil, discutindo que Perty (1830), na sua descrição revisou unicamente um espécime feminino, deixando como opção válida o gênero proposto por Gray, o qual foi baseado num macho. Aparentemente Hope interpretou que a fêmea descrita por Perty e o macho referenciado no trabalho de Gray pertenciam a mesma espécie, observação suportada posteriormente por vários autores.

Embora no catálogo de van Roon (1910) manteve o uso de *Hexaphyllum* como o gênero válido, *H. brasiliense* é listado como sinônimo e, *Hexaphyllum schuberti* (Perty) define-se como a espécie do Brasil, oficialmente relacionando a fêmea de *P. schuberti* com o macho descrito em 1832 por Gray. Luederwaldt (1935) na sua monografia sobre os Lucanidae brasileiros usou esta classificação.

Posteriormente Didier (1929) descreveu *Hexaphyllum seguyi*, a terceira espécie do gênero, sendo esta a primeira espécie do Equador. Ele discutiu a aparente proximidade com *H. aequinoctiale*, baseando-se principalmente nas caraterísticas das mandíbulas, claramente diferentes da espécie brasileira. Didier & Seguyi (1953) incluíram estas três espécies, porém, consideraram como válido o uso de *Psilodon*.

Benesh (1960) sinonimizou *Psilodon* e *Hexaphyllum* com *Syndesus*, concordando como foi discutido previamente com Burmesiter (1847 e Arrow (1938), no entanto autores posteriores continuaram descrevendo novas espécies considerando ainda válido *Psilodon* para a região Neotropical.

Após uns 50 anos, Martínez & Reyes-Castillo (1985) descreveram *Psilodon xerophilicum* para o estado de Bahia no nordeste brasileiro, baseando-se em duas fêmeas. Boucher (1993) adicionou uma nova espécie dos Andes bolivianos, *Psilodon gilberti*, sendo esta a primeira e única espécie do gênero que apresenta sete lamelas na clava antenal, da mesma forma que foi descrito para as espécies australianas de *Syndesus*.

Os catálogos posteriores a Benesh (1960), incluíram *Psilodon* e *Hexaphyllum* como sinônimos de *Syndesus*, estendendo a distribuição das espécies sul-americanas para Venezuela e Argentina. Krajcik (2001; 2003) mantem a mesma sinonímia e Holloway (2007) autora que previamente reconheceu a separação entre o gênero australasitático e o neotropical (Holloway 1968; 1997), resolve adotar a classificação proposta nestes catálogos.

Nos últimos anos foram descritas três novas espécies, a primeira *Psilodon paschoali* Pardo-Locarno & Ríos-Málaver, 2011 da Colômbia; *Syndesus luki* Onore, Bartolozzi & Zilioli, 2011 do Equador, sendo esta última a única descrição original que reconhece *Syndesus* como um gênero Australasiático e Sul-americano. Por último *Psilodon buhrnheimi* Grossi & Aguiar, 2014, descrevem a primeira espécie do gênero distribuída na Amazônia.

Psilodon nunca foi objeto de uma revisão taxonômica e dadas as inconsistências nos limites entre as espécies Australianas, junto com as da América do Sul é clara a necessidade de estudar a fundo as espécies sul-americanas, desde uma abordagem comparativa que aporte para o esclarecimento das diferencias entre os dois gêneros e melhor definição das espécies de *Psilodon*. Desta forma este trabalho pretende pela primeira vez propor um estudo que possa oferecer as bases para a classificação supragenérica a partir da revisão taxonômica de *Psilodon* junto com a descrição de novas espécies depositadas na Coleção Entomológica da Universidade Federal Rural de Pernambuco (CERPE) em Recife.

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CAPÍTULO 2

DEFINING GENERIC LIMITS IN SYNDESINI MACLEAY, 1819 (COLEOPTERA: LUCANIDAE: SYNDESINAE) THROUGH TAXONOMY AND GEOMETRIC MORPHOMETRICS [1]

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[1] [Cáceres, J.S.D., P.C. Grossi & H.A. Benítez. Defining generic limits in Syndesini MacLeay, 1819 (Coleoptera: Lucanidae: Syndesinae) through Taxonomy and Geometric Morphometrics. Zoologischer Anzeiger

Defining generic limits in Syndesini MacLeay, 1819 (Coleoptera: Lucanidae: Syndesinae) through Taxonomy and Geometric Morphometrics

Abstract. A comparative taxonomic study was performed between the Syndesini genera *Syndesus* MacLeay, 1819 and *Psilodon* Perty, 1830. Both taxa are redescribed, with the addition of more precise diagnostic traits, including the description of male and female genitalia. We provide comparative remarks to support the separation of both genera, with additional information obtained through the application of geometric morphometric analysis to the following morphological structures: right mandible of males (RMM); lateral view of left mandible of males (LMM); lateral view of males pronotal tubercle (PT); dorsal face of male and female pronotum (DFP); dorsal face of male and female elytra (DFE). The shapes of all analysed traits showed to be different through the performance of Principal Component Analyses producing two well-define clusters, except for the elytral shape which showed a high superposition, however all Procrustes and Mahalanobis distances showed significant differences, supporting the existence of two Syndesini genera instead of one. It was also possible to register a significant influence regarding the biogeographic distribution of the specimens, obtaining statistical differences when comparing the shape data from the Australasian and Neotropical biogeographic dominions, suggesting a strong relation between *Syndesus* and *Psilodon* divergence and the Gondwanan vicariant events. Finally, a checklist was provided including all the described species for both genera.

Key words: Stag beetles; Checklist; Biogeographic dominion; *Psilodon*; *Syndesus*.

Introduction

Stag beetles from Syndesinae MacLeay, 1819 (Coleoptera: Lucanidae) represent one of the less diversified subfamilies in Lucanidae (Holloway 2007). Historically Syndesinae has been composed of three or four genera depending on the author, with around 30 described species. The first two genera are *Sinodendron* Hellwig, 1792 and *Ceruchus* MacLeay, 1819 which are restricted to the Holarctic region (Howden & Lawrence 1974), the third, *Syndesus* MacLeay, 1819 is distributed in Australia, New Caledonia and New Zealand, with some authors extending its distribution to South America, and the last one, *Psilodon* Perty, 1830, distributed along South America and considered by several authors as a synonym of *Syndesus* due to the high resemblance shared by both taxa.

While *Sinodendron* and *Ceruchus* have had a stable classification at the generic level, *Syndesus* and *Psilodon* lacks a consensus. *Syndesus* was described as the type genus of Syndesidae, now recognized at the subfamily level. According to MacLeay´s (1819) description of *Syndesus cornutus* (Fabricius, 1801) (type species), male specimens present an elongate and cylindrical body, with convex shape; small and transverse head; labrum hardly distinct; mandibles almost straight; antennae glabrous with seven lamellae; tibiae serrate. Females are close to males except for the mandibular shape. MacLeay described *S. cornutus* based on *Sinodendron cornutum* Fabricius, 1801, both apparently from Tasmania but it is not clear if both authors had access to the same material as *S. cornutum* was described with antennal club six-lamellate and *S. cornutus* with seven lamellae.

Psilodon Perty, 1830 was described for Brazil based on a female collected by K.F.P. von Martius and J.B. von Spix during their expedition in Brazil (1817-1820) (Papavero 1971).

Psilodon schuberti Perty, 1830 was the first described species, defined as being close to *Sinodendron* with the following characteristics: body dark with brownish tones at antennae; head rugose and somewhat excavate at frons; pronotum punctate with well-defined discal groove; scutellar shield smooth; elytra carinate; mandibles with erect setae; tibiae serrate and enlarged apically. The epithet proposed by Perty was probably based on the lack of well-define teeth of the specimen. Perty never mention the number of antennal lamellae.

Two years later Gray (1832) described a new genus from Brazil with the type species *Hexaphyllum brasiliensis*, in this case, based on a male collected in the state of Rio de Janeiro, and despite the high resemblance between Perty´s and Gray´s specimens, there were only considered as belonging to the same species by van Roon (1910). The epithet proposed by Gray was based on the presence of six lamellae at the antennal club. After this work, posterior authors continue to use *Hexaphyllum* as the valid genus, based on the number of lamellae (Hope 1840; Buquet 1840; van Roon 1910; Luederwaldt 1935; Didier 1929).

Didier & Seguy (1953) in their catalogue, and other authors such as Holloway (1968; 1997), Howden & Lawrence (1974), and Ratcliffe (2002) continued recognizing *Psilodon* as a valid genus, being the only South American representative of Syndesini MacLeay, 1819. In Benesh (1960), *Psilodon* and *Hexaphyllum* are considered for the first time synonyms of *Syndesus*, as he probably agreed with the observations made by Burmeister (1847) and Arrow (1938) who stated that, given the high morphological resemblance between *Syndesus* and *Hexaphyllum* (=*Psilodon*), considering them as different taxa would represent an unnatural separation, they also argued that the number of antennal lamellae, six for *Hexaphyllum* and seven for *Syndesus* was not enough to establish a division between the South American specimens and the Australasian ones.

After Benesh´s work in 1960, different authors such as Maes 1992; Krajcik 2001; Krajcik 2003; Holloway 2007; Onore, Bartolozzi & Zilioli 2011, continued recognizing *Syndesus* as the only valid taxon, however, new species for *Psilodon* continued to be described (Martínez & Reyes-Castillo 1985; Boucher 1993; Pardo-Locarno & Ríos-Málaver 2011; Grossi & Aguiar 2014) and some authors, as Holloway (1968; 1997), Howden & Lawrence (1974), and Ratcliffe (2002) maintained the use of both genera as independent taxa.

There is no doubt that both genera are strongly related, they are even difficult to separate by non-specialists, but considering them as a unique taxon would be obscuring the disjunct distribution and morphological differences among both taxa (Woodruff 2009). In addition the lack of genetic studies, taxonomic revisions for both genera, the difficulty to accessing type material for most species, and the low representation of these specimens in most world entomological collections hinder the possibility of establishing the generic limits between *Psilodon* and *Syndesus*.

The lack of a taxonomic consensus for these genera represents a limitation for the definition of the Syndesini tribe and the development of evolutionary studies at a suprageneric level. In order to reduce these inconsistencies, a taxonomic study was conducted with *Syndesus* and *Psilodon* specimens which were deposited in different entomological collections, redescribing both genera, defining new diagnostic traits, and offering a novel additional morphological support using geometric morphometric analysis. An updated checklist is also provided.

Materials and Methods

Specimens and Taxonomic Material.

A total of 81 specimens from all species of *Psilodon* and *Syndesus* were examined. Specimen of *Syndesus macleayi* Boileau, 1905 and *Syndesus punctatus* Boileau, 1905 were studied using high quality photographs of Holotypes deposited in the Muséum national d'Histoire naturelle of Paris, which were gently offered by Mr Christophe Rivier. Dry collection material is deposited in the following collections.

AMBC Ayr Bello collection, included at the CEIOC (Coleção Entomológica do Instituto Oswaldo Cruz). Brazil, Rio de Janeiro, Rio de Janeiro.

CEMT Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso. Brazil, Mato Grosso, Cuiabá.

CERPE Coleção Entomológica da Universidade Federal Rural de Pernambuco. Brazil, Pernambuco, Recife.

CZPB Coleção Zoológica Paulo Buhrnheim, UFAM, Brazil, Amazonas, Manaus Brazil.

EPGC Everardo and Paschoal Grossi Collection. Brazil, Rio de Janeiro, Nova Friburgo.

HEC Hope Entomological Collections, Oxford University Museum of Natural History. UK, Oxford.

MNHN Muséum national d'Histoire naturelle. France, Paris.

MNRJ Museu Nacional Rio de Janeiro. Brazil, Rio de Janeiro.

MZUEFS Museu de Zoologia Universidade Estadual de Feira de Santana. Brazil, Bahia, Feira de Santana.

NZAC New Zealand Arthropod Collection. New Zealand, Auckland.

UMSP University of Minnesota – Saint Paul Insect Collection. United States, Minnesota, St. Paul.

ZIN Zoological Institute of Russian Academy of Sciences. Russia, St. Petersburg.

Morphological characters

Descriptions for both genera are based on the following conventions. Specimens were studied using a dissecting microscope Zeiss Stemi 508 at 0.63 to 0.50x under fibber optic illumination. ***Size*** was determined using a 0-150 mm digital calliper. ***Length*** was measured from the apex of the mandible to the apex of elytra. ***Width*** was measured at the widest point of the body, mainly across the pronotum and the elytral humeri. ***Colour*** as determined under LED spot illumination. The characteristics of the body surface such as the presence of punctures or setae were based on the described macroscopic types by Holloway (1997; 2007) and. ***Vestiture*** appearance is based on description made under light magnification. ***Puncture size*** is defined according to Paulsen (2005) under 40 x magnification who proposed four categories, coarse, present as pits (above 0.10 mm), large (0.06-0.10 mm), moderate (0.03-0.05 mm) and fine (less than 0.03 mm). ***Puncture density*** *is* also based on Paulsen (2005), and defined as contiguous, dense (punctures separated by less than 2 puncture diameters), moderate (punctures separated by 2-4 puncture diameters), sparse (separated by 4 puncture diameters), or shagreened. ***Discrimen***, is defined as a discrete longitudinal groove present along metaventrite concavity, nevertheless, this trait is not present as a complete suture in most specimens, instead is possible to see a superficial groove or a glabrous longitudinal region. All male and female ***Genitalic*** structures are named according to Holloway (1960, 1961, 1998 and 2007), Lawrence *et al.* (2011), and Cristovão & Vaz-de-Mello (2020) consisting on the 9th and 10th abdominal segment. Descriptions of male genitalia were made considering the ventral, dorsal and lateral views including characteristics based on the basal piece, parameres, median lobe and everted sac. For the females there was included information related to a portion of the sclerotized structures on the 9th and 10th abdominal segments, and reproductive structures *per se*, only considering the ventral view. Dissections of male and female genitalia were conducted as proposed by Grossi & Aguiar 2014.

Geometric Morphometric analysis

As a complement for the taxonomic descriptions, geometric morphometrics tools were performed using 81 specimens of *Psilodon* Perty, which were photographed, and represents all the described species according to the *sensu* proposed in Grossi & Aguiar (2014) (n=51), and several undetermined specimens from Brazil, Venezuela and Trinidad and Tobago (n=30). In the case of *Syndesus* MacLeay, a total of 25 images were used.

All photographs were taken using a digital camera coupled to a DIGILAB DI-150B stereoscopic microscope. Each image was posteriorly edited when needed, using GIMP v.2.10.30.

In order to capture the male and female shape of specimens from both genera, a series of landmarks were defined, standardized and digitalized using the curves tool with equidistant points of TPSdig2 v.2.30 (Rohlf 2017). The analysed traits were the **right mandible of males (RMM)** with 20 landmarks (Figure 1a. M1-M20); lateral view of **left mandible of males (LMM)** with 17 landmarks (Figure 1b. M1-M17); lateral view of **pronotal tubercle (PT)** with 13 landmarks (Figure 1b. P1-P13); dorsal face **of male and female pronotum (DFP)** using 14 landmarks (Figure 1a. P1-P14); dorsal face of **male and female elytra (DFE)**, with 24 landmarks (Figure 2a. E1-E24).

Each analysis was performed separately. In several cases, it was not possible to use the total number of images obtained, as the original position or photographs of some specimens coming from historical collections hindered the standardization and definition of all landmarks, furthermore, given the origin and importance of some specimens, we tried to avoid excessive manipulation. Thus the number of images used for dorsal surface of pronotum and elytra were higher than the used for mandibles and lateral view images**.**

Before conducting the morphometric analysis, all traits were digitized twice in order to test every landmark against definition error through the performance of a Procrustes ANOVA, comparing the values of the mean squares of the error component of variation and individuals.

Using the software MorphoJ v.1.07a (Klingenberg 2011), a Procrustes Superposition analysis was performed to all analysed specimens, in order to remove the influence of size, position and orientation to shape variables (Rohlf & Slice 1990). With these variables a covariance matrix of the individual shape was performed in order to proceed with all corresponding multivariate analysis.

To graphically visualize the shape space, a Principal Component Analysis (PCA) was performed for all the digitalized traits covariance matrices independently (Pearson 1901). Additionally, a Canonical Variate Analysis (CVA) was performed as a discriminant analysis using the classifiers *Genus* and *Biogeographic dominion*. A permutation test (10 000 runs) between groups was used to calculate the statistical relationship between groups using Mahalanobis and Procrustes distances showing the respective *p* values.

Results

Taxonomic results

Checklist of Syndesini MacLeay, 1819 genera

Syndesus MacLeay, 1819

Figure 3 a-f

Syndesus cornutus (Fabricius, 1801) (*Sinodendron*) – **Australia and New Zealand**

=*Lucanus parvus* Donovan, 1805

Syndesus cancellatus (Montrouzier, 1860) (*Rhyssonotus*) – **New Caledonia**

Syndesus macleayi Boileau, 1905 - **Australia**

Syndesus punctatus Boileau, 1905 - **New Caledonia**

***Psilodon* Perty, 1830**

=*Hexaphyllum* Gray, 1832

=*Syndesus* MacLeay, 1819 (partim)

Figure 4 a-l.

Psilodon schuberti Perty, 1830 - **Brazil**

=*Hexaphyllum brasiliensis* Gray, 1832

Psilodon westwoodii (Hope, 1840) - **Colombia**

=*Hexaphyllum aequinoctiale* Buquet, 1840

Psilodon seguyi (Didier 1929) (*Hexaphyllum*)- **Ecuador**

Psilodon xerophilicum Martinez & Reyes-Castillo, 1985 - **Brazil**

Psilodon gilberti Boucher, 1993 - **Bolivia**

Psilodon paschoali Pardo-Locarno & Ríos-Málaver, 2011 - **Colombia**

Psilodon luki (Onore, Bartolozzi & Zilioli 2011) (*Syndesus*) - **Ecuador**

Psilodon buhrnheimi Grossi & Aguiar 2014 – **Brazil**

Syndesus MacLeay, 1819

Examined material: *S. cornutus*: Australia, VIC Mitcham / Melbourne, 27.ii.1994, at light, Leg.G.J. Krake 1♂ (CERPE); same data except: 14.i.1995 1♂ 1♀ (CERPE); Australia, Acacia Plateau, 2.i.1994 – N.NSW, De Keyzer Leg. 1♂ 1♀ (CERPE); “Automontage Image FNZ/61 2007 / *Syndesus cornutus* (Fabricius, 1801), Holloway / Infesting Oak door, Post Kings College, Chapel, Otahuhu, NZ, 29.i.1968. 1♂ (NZAC); NZ Arthropod Collection, Private Beg 92170, Auckland, New Zealand, NZAC04193716 / Illustrated, D.W. Helmore, 5.ii.90 / In cop, 30.iv.1982 / New Zealand AK, Papatoetoe, iv.1982, F.J. Muller, in old Eucalyptus logs. 1♂ (NZAC); NZ Arthropod Collection, Private Beg 92170 , Auckland, New Zealand, NZAC04195439 / New Zealand AK, Whenuapai, 5.iii.1989, M. Manning / Attracted to light inside house at night. 1♂

(NZAC); NZ Arthropod Collection, Private Beg 92170 , Auckland, New Zealand, NZAC04195823 / caught in light trap, m research sta. / New Zealand AK, Pakekche, 27.ii.1992, TJB Herman. 1♂ (NZAC); *Syndesus cornutus*, (Fabricius, 1801) ♂, det. S.E. Thorpe 2003 / NZ Arthropod Collection, Private Beg 92170 , Auckland, New Zealand, NZAC04191849 / New Zealand AK, Glen Innes, Tahuna Torea Res, on wing in evening, 4.iii.2003, Se Thorpe. 1♂ (NZAC); NZ Arthropod Collection, Private Beg 92170, Auckland, New Zealand, NZAC04193548 / New Zealand AK, Glen Innes, Tahuna Torea Res, ex rotten tree slump, 4.iii.2003, SE Thorpe / *Syndesus cornutus*, (Fabricius, 1801) ♀, det. S.E. Thorpe 2003. 1♀ (NZAC); NZ Arthropod Collection, Private Beg 92170, Auckland, New Zealand, NZAC04196298 / New Zealand WO between Eureka and Newsteak iii.1970, Mr. Appelton. / In building lavatory. 1♂ (NZAC) / NZ Arthropod Collection, Private Beg 92170, Auckland, New Zealand, NZAC04193118 / Adult em 27.ii.1991, Reared: B.A. Holloway / New Zealand AK, Birkenhead Larva: 22.x.1990, D. Longworth. / Larva in old post, Chelsea, Sugar refinery. 1♂ (NZAC); same data except: Adult em. 24.ii.1991. Larva: 23.x.1990. 1♂ (NZAC); NZ Arthropod Collection, Private Beg 92170, Auckland, New Zealand, NZAC04192479 / *Syndesus cornutus* (Fabricius, 1801) Holloway 2007 / Ex. Rotting, Floor Boards, Permrose, Auckland, 26.iii.1969, Termite Insp. 1♀ (NZAC); same data: 2♂ (NZAC). Holotype male of *Syndesus punctatus* (Examined by photographs by Antoine Montilleri – 2013 and Christophe Rivier - 2022) labelled: a) old white handwritten label, cancellatus, ?????; b) Ex coll Armitage; c) Type, H.B.; d) Muséum Paris , 1937, coll. R. Didier (ex. coll. H. Boileau).; e) TYPE; f) Holotype, *Syndesus punctatus* Boileau, 1905; g) Holotype; h) MNHN, EC3911. Holotype male of *Syndesus macleayi* (Examined by photographs by Christophe Rivier - 2022) label: a) Victoria; b) Type H.B.; c) TYPE; d) Muséum Paris; e) Holotype; f) HOLOTYPE, *Syndesus macleayi* Boileau, 1905; g) MNHN, Paris, EC14288; *Syndesus cancellatus* labelled: MNHN, no further data 1♂ (MNHN); a) Ex: Musaeo GAMBEY 1892; b) Muséum Paris, 1952, Coll. R. Oberthur. 1♀(MNHN).

Diagnosis: specimens with strong sexual dimorphism at mandibles, labrum, antennae and pronotum. Males and females with sub-cylindrical (Australian species) to somewhat robust body (New Caledonian species). Head anteriorly emarginate, with strongly punctate surface. Supra-antennal projection with conspicuous carinae. Antennae with six to seven lamellae. Male mandible with one external strong tooth located medially, internal face with a laminar tooth, in New Caledonian species extended form base to apex, for Australian species ending before apex, producing in some specimens a reduce tooth-like projection; females mandibles curved upwards, with almost acuminate apex, also with a somewhat laminar tooth extended form base to apex along dorsal face, stronger at base. Gula conspicuous, convex, visible on lateral view. Labrum with concave and almost smooth surface, sometimes with a strong excavation, apex truncate or bilobed. Shape of pronotum convex; antero-lateral angles rounded to somewhat oblique; discal groove strong and complete, sometimes more superficial in females; pronotal tubercle conspicuous, in males, extended anteriorly covering median portion of head, sometimes extended beyond labrum, reduced in females and strongly transverse. Elytral striate, with strong punctation, also with interstrial costae, varying in number depending on the species. Ventrally with a narrow and inconspicuous prosternal process; meso and metaventrite convex; discrimen present as a shallow groove, mainly visible posteriorly. Abdominal ventrites with fine and contiguous punctuation, also with a transverse carina extended through posterior margin of every ventrite. Male aedeagi symmetric, narrowed anteriorly; median lobe enlarged basally; dorsal cross bar "V" to somewhat "U" shaped, sometimes forming a subtriangular median structure. Female genitalia with elongate styli and gonocoxites abruptly narrowed anteriorly.

Description Male: ***Size*****:** *Total length*: 6.85-16.01mm. *Total width*: 2.79-6.52. ***Colour*****:** Most specimens with light brown tones to dark-red, sometimes somewhat black. ***Head*****:** Transverse, anteriorly strongly emarginate, partially concealed by ponotum; surface strongly punctate, some species with a partially smooth area at anterior portion of head; punctures dense and coarse with inconspicuous to somewhat conspicuous strongly curved setae; anterior edge with smooth to shagreened surface; labrum projected between mandibles, smooth, rounded to truncate at apex. Mentum subtrapezoidal, with two lobes at anterior edge, producing an emargination, also with large to somewhat coarse punctures. Gula conspicuous, sub-trapezoidal, from strongly transverse to elongate, with an almost entirely carinate surface, carina smooth, anterior portion with contiguous large to coarse punctures and appressed to strongly curved setae. Gena with dense to moderate coarse punctuation and long appressed setae. Mandibles symmetric with one external tooth, and one internally, internal tooth laminar, complete or almost from base to apex; internal and external face with dense, large to coarse punctuation, internal and external face with suberect to curved setae, some species with a continuous line of conspicuous setae from base to apex of internal portion; apex acute to truncate. Supra-antennal projection present, strongly carinate in some species, when carinae reduced apex of projections truncate. Antennae with six to seven lamellae. ***Pronotum*****:** Shape convex, sometimes with lateral constrictions, anterior margin projected anteriorly, with a narrow and conspicuous tubercle, distinctly extended anteriorly, reaching anterior margin of head; anterior angles reaching posterior margins of eyes; discal groove present, from complete and strong to superficial or absent; surface with moderate to coarse punctuation, dense to contiguous; lateral pronotal carina present, separating disc from hypomeron, almost complete and continuous with posterior and anterior margins, only interrupted at median portion of anterior margin, with scalloped surface and minute simple setae. ***Elytra*****:** Elytral humeri not striate, with tooth-like projections; surface with several striae, each with coarse punctures and minute barbed setae; also with interstrial costae ending at an apical interstrial joint. Epipleuron complete to apex, distinctly visible in lateral view, with a concave surface, and contiguous to dense punctuation, moderate to somewhat coarse. ***Legs*****:** Tibiae serrate. Protibiae with strong teeth from base to apex and suberect to decumbent setae. Meso and metatibiae with similar appearance, serrate, with several teeth increasing in size distally, more acute than protibial ones, with suberect setae; apex enlarged with variable number of tooth-like projections. ***Venter*****:** Prosternal anterior and posterior margins carinate, especially at median portion, also with a continuos line of appressed setae; surface with dense to contiguous punctation, punctures from large to coarse with strongly curved to appressed setae; prosternal process convex, narrowed distally, basally somewhat enlarged, continuous with prosternal surface, producing a convex region. Mesoventrite convex with coarse punctures, dense to contiguous, also with strongly curved to appressed setae. Metaventrite convex, somewhat flattened along disc, with large to coarse punctures, varying in distribution, sometimes mainly distributed anteriorly, stronger along sides with strongly curved, long to short setae; posterior edge with a fine median projection producing a declivity, projected between metacoxae. ***Genitalia*****:** Genital capsule symmetric. Aedeagus symmetric. Phallobase subtriangular, wide to somewhat elongate, with a fine constriction separating anterior and posterior phallobase. Median lobe enlarged and covered by parameres at base; Parameres subparallel, rounded apically; with a V to U-shaped dorsal cross bar.

Description Female *Size*: *Total length*. 8.58-10.77 mm. *Total width.* 3.46-4.16 mm. ***Colour:*** as males, sometimes with darker tones. ***Head***: Shape as males, apparently bigger than males, dorsally more exposed due to reduction in pronotal projection; mandibles symmetric, narrow, only presenting a laminar, longitudinal tooth-like structure along dorsal surface, basally somewhat expanded, dorsal face concave; surface punctate, punctures large to somewhat coarse, mainly densely distributed, with some moderate to sparse areas, also with erect to curved setae, distributed along internal and external surface. ***Pronotum*****:** close to males in appearance with less projected anterior angles; pronotal tubercle strongly reduced and transverse, present as a somewhat conspicuous lobe; discal groove shallow; surface strongly punctate, punctures coarse and dense, almost uniformly distributed. ***Elytra*****:** as males. ***Legs*****:** as present in males with a reduction in meso and metatibiae teeth. ***Venter:*** very close to males except for presenting more conspicuous setae; prosternal process sometimes reduced, almost interrupted by procoxae. Abdominal ventrites similar to males getting narrower distally. ***Genitalia:*** Styli elongate and somewhat wide, rounded apically. External edge of gonocoxites concave distally, becoming convex proximally, anterior portion abruptly narrowed producing a slender projection. Lateral paraprocts forming a C-Shaped plate.

Psilodon Perty, 1830

=*Hexaphyllum* Gray, 1832

Examined material: Holotype female (reviewed by photographs) ***P. schuberti*** 1♀ (HEC) **(Figure 3b)**; Holotype *H. brasiliense* 1♂ (HEC) **(Figure 3b)**; *P. schuberti* Brasil, RJ, Nova Friburgo A: 1100m S. Caturama 8.i.1999 E. & P. Grossi leg. 1 ♂ (CERPE); Brasil – Rio de Janeiro Mun. Resende – Serrinha de Alambari – xii. 2008 U. Caramaschi & H. de Niemeyer col. 1 ♂; Florestinha do Cabo Frio 08/12/1999 (CERPE); Brasil, RJ. Macaé de Cima Alt. 1500m 28.xii.2000 Isabel Miller leg. 1 ♂ (EPGC); Brasil, RJ, Nova Friburgo A: 1100m S. Caturama 3.i.1999 E. & P. Grossi leg.1 ♂ (CERPE); same data except 5.i.1999 1 ♂ (CERPE); same data except 1100m, 15.ii.2009, Interceptação, E. Grossi Leg. 1♀ (CERPE); Brasil, RJ, Nova Friburgo 10.i.2001 E. & P. Grossi leg. 1♀ (CERPE); Brasil, RJ, V. de Mauá, i.97, 1100m, E. & P. Grossi Leg 1♀ (CERPE); Brasil, Nova Friburgo, SESC, Luz, 800m, 19.xii.2008, L.P.C. Grossi Leg. 1♀ (CERPE). - Lectotype male ***P. westwoodii*** Colombie, Ibague, Fr. Claver / "Handwriting" Hexaphyllum Brasiliense Grey / Ex. coll. Boileau 1♂ (MNHN). – ***P. seguyi*** Ecuador, Loja iii.2002, P. Arnaud leg. 1♂, 1♀ (CERPE). - ***P. xerophilicum*** Paratype / Encruzilhada, Bahia, Brasil, xii.1980 A. Martinez & M. Alvarenga leg. / "Handwriting" Psilodon xerophilicum sp.n Martinez & Reyes C. 1♀ (CERPE); Encruzilhada, 980 m, Bahia Brasil, xi.1978, M. Alvarenga leg. 1♂ (EPGC); Encruzilhada, Estr. Torres, 15.xii.2012 1♀ (CERPE); Brasil, MG, Águas Vermelhas, xii.1997, Alt. 850m A. Bello & F.Z. V. Mello leg. 1♀ (CERPE); Brasil, BA. Ituberá, 11/13.vi.2002, F. Bravo& I. Castro 2♂ (MZUEFS); Brasil, Bahia, Serra da Jibóia, 12°50´S/39°28´W, 820m 27-28.v.2000, Frerdy leg. 1♂ (MZUEFS). – ***P. gilberti*** Bolivia Nor. Yungas. Caravani-Coroico. Xi.2009. 1.800 m. B. Cavelius leg. 1♂ (CERPE). – ***P. paschoali*** Venezuela, Altos de Pipe, 12.viii.2011, 1650m, C. Ríos-Málaver leg. 1♂ (CERPE); Venezuela, Miranda, Oripoto, v.2004, 1400 m D. Garcia col. – ***P. luki*** Paratypes Ecuador Pichincha Province, Tandayapa (2100 m.a.s.l), ii.2010. legit G. Onore 1♂1♀ (CERPE). – ***P. buhrnheimi*** Holotype labelled: Brasil, Amazonas, Coari/Rio Urucu, próx. IMT-1,/ 4°49′33.00″S S\ 65°01′49″W,/ 24–25-ix-1995, 89 m, P.F./ Buhrnheim and N.O.Aguiar/ BLB [black light bulb] – Pennsylvania 1♂ (CZPB); Paratype labelled: Brasil, AM, Guajará,/Ramal do Gama km 12,/ 07°27′16″/72°38′56″,/06–19.xi.2006, tronco,/ F°. [Filho] F. F. Xavier leg. 1♂ (EPGC); Brasil, Rondônia. Porto Velho. MUIE 9° 33´41.85´´S, 65°01´28´´W. 02.x.2004, Luminosa M.A.P.A. Silveia leg. 1♂(CERPE); Peru, Satipo, Junín, Río desconocido 1.2003, 1600 m. R.R. Koike col. 1♂(CERPE); Obidos, Pará, Brasil, x.1938 1♂(MNRJ). – **Not determined species:** Brasil, CE, Fortaleza**?**, Nativas. No more data available 1♂ (CERPE); Brasil, GO, São João d´Aliança, 11.xi.1986, 14.7114°S, 47.5161°W, 1000m, R.R. Koike col. 1♂ (EPGC).Brasil, ES, Linhares, P.N. Soretama A: 650m 31.xii.1982 1♂ (EPGC); Brasil, Espirito Santo Linhares, Caliman Agricola S/A, Sede, 23.x.2003, Luz. P.C. Grossi Leg. 1♀ (CERPE); 11/12/99. Linhares Esp. Santo, Brasil 1♂ (CERPE); RFCVRD, Linhares. Brasil, Date. 24/11/89 JSS Col. 1♂(CERPE) / same data except Date: 23.11.88 1♂(CERPE); Brasil, ES. Linhares P.N. Soretama A: 650m F.Z.V. Mello Leg. 1♂(CERPE); Brasil, ES, Linhares, RFCVD, 24.xi.1989, A: 700m JSS Leg. 1♂(CERPE); Local. Viçosa, MG. Data 27/11/82. Col. Martins 1♂(CERPE); Manhu-Mirim. Minas/Col. J. Guerin. S. Paulo Brasil. 1♂ (CEAH); Brasil, RJ, Macaé de Cima 02.i.2002, Altitude: 1600 m, Isabel Miller leg. 1♂ (EPGC); Brasil, Rio de Janeiro, Nova Friburgo, Macaé de Cima i.2002, 1400 m, I. Miller leg. 1♂ (EPGC); Brasil, RJ. Petrópolis, Morim, Morro da Bandeira, 1600 m, Torres da Petrobras 02-10.ii.2010 1♂ (CERPE); Brasil, RJ, Nova Friburgo, A: 1600 m, Cascatinha 1.ii.1999 E & P Grossi leg. 1♂ (CERPE); Botucatu, São Paulo – Brasil, 23.i.1976, Mantovani col. 1♂ (CERPE); Itapema, SC-Brasil, i.1993, Col. J. Carlos. 1♂ (CERPE); Hansa St. Cath. xii.1939 / Psilodon schuberti (Perty) ♀ P. Pereira det. 1♀ (MNRJ); Hansa, St Cat. xii.1939 / Hexaphylum schuberti / Psilodon schuberti (Perty) ♂ P. Pereira det. 1♂ (MNRJ); Olho d´Agua, Ponta Grossa, Parana, v.1943 / Hexaphylum schuberti (Perty) ♂ P. Pereira det. 1♂ (MNRJ); Brasil, SC, Porto Belo, 28.ii.1961 1♂ (MZUEFS); Itapema SC-Brasil, i.1994, Col. J. Carlos 1♂ (AMBC); Pto. Bertoni, Paraguay, Col. Bertoni / Psilodon schuberti Pty, AW.B.d., Hexaphyllum Gray. / MNHP A.W. Bertoni N – 93 Garcete rev. 1♂ (MNHNP);Brasil, Alagoas, Murici, v.1984 D.F. de Moraes Jr. 1♂ (MNRJ). Venezuela, Monagas State 10°10.332´N, 63°33.315´W, 1110 m, Guachero Cave N.P. 20-21.vii.2010 Holzenthal, Thomson, Cressa, UV lights; VZ10-07-21-02B 1♂ (UMSP); “Handwriting”: ?, 50. Trinidad / k. ɓuɗɗepa /?Hexaphyllum 1♂(ZIN).

Diagnosis: Specimens with strong sexual dimorphism in mandibles and pronotum. Males and females with brown to black colour, and dark-red tones in most species. Head anteriorly emarginate, dorsally with a v-shaped excavation along frons, extended anteriorly; vertex convex, concealed under pronotal projection. Labral sufrcae convex with rounded apex, projected between mandibles. Supra-antennal projection variable. Antennae with six to seven lamellae (one species). Eyes conspicuous, strongly developed. Mandibles with an external median tooth (Alpha), sometimes located close to apex forming a concave region (in Andean species), a basal lobe (Beta) and an internal tooth (Gamma). Pronotum projected anteriorly, with a pronotal process covering median surface of head, reduced in females; surface with a longitudinal groove, usually complete, sometimes interrupting females process, punctuation variable, from moderate to coarse, sometimes with shallow excavations and lateral constrictions. Elytra with well-define striae and interstrial costae; humeri not-striate, with tooth-like projections projected laterally, absent in some Andean species. Anterior tibiae distally enlarged with several strong teeth and tooth-like projections; meso and metatibiae with two to several acute teeth and tooth-like projections, setose, with enlarged apex. Mentum subtrapezoidal. Gula conspicuous and convex, visible on lateral view. Male aedeagi symmetric, phallobase subtriangular, with a strong to somewhat fine anterior constriction, with subparallel to slightly convex sides; median lobe distinctly enlarged basally except for Andean species. Female genitalia with elongate and setose styli, with undivided gonocoxites. Gonoxites abruptly narrowed proximally.

Description Male. ***Size:*** *Total length*. 10.29-14.81mm. *Total width*. 4.34-6.61 mm. ***Colour*:** Body entirely black to somewhat brown, often with dark-red tones. ***Head*:** Shape transverse, emarginate; labral surface smooth, elongate, convex to somewhat flattened in some species, rounded at apex with a tuft of conspicuous setae; anterior margin with shagreened surface, somewhat carinate, glabrous; frons slightly excavate; vertex concealed, covered by anterior portion of pronotum. Mentum trapezoidal with a somewhat lobed anterior edge, with few large to coarse punctures, also with yellowish curved setae. Gula conspicuous, strongly convex, sub-trapezoidal to oblong, easily visible in lateral view, surface strongly and almost entirely carinate, carina smooth, sometimes with sparse fine punctuation. Gena with coarse to large punctures, dense, with yellowish, strongly curved to appressed setae. Mandibles symmetric, with a median to subapical tooth (Alpha), a basal internal tooth (Gamma) and a basal lobe (Beta); strongly curved inwards and directed upwards apically; base of mandibles enlarged in most species, producing a dorsal surface, reduced in Ecuadorian species. Antennae with six or seven lamellae. ***Pronotum*:** shape convex, anterior margin projected anteriorly, with a convex, and frequently conspicuous tubercle; posterior margin sinuate; anterior angles reaching posterior portion of eyes; discal groove present, shallow to deep; surface with moderate, large or coarse punctures, dense to contiguous, sometimes with two to four distinct excavations; lateral pronotal carina distinct, separating disc from hypomeron, complete and continuous with posterior and anterior margins, except at anterior projection, with a somewhat scalloped surface, and minute simple setae. ***Elytra*:** Elytral humeri not striate, with or without a tooth-like projection, mostly present in Brazilian species; surface strongly punctate with well-defined striae; striae with coarse punctures and minute setae; interstriae forming longitudinal costae with moderate to large and dense to contiguous punctuation; epipleuron complete to apex, concave to somewhat flat, with dense to contiguous punctuation, large or coarse basally, becoming moderate at apex; elytral apex with a interstrial, convex joint. ***Legs:*** all tibiae serrate, with stronger and higher number of teeth at protibiae; meso and metatibiae with few strong teeth, normally varying from three to four well-defined teeth, always with several tooth-like projections, sometimes with two serrate lines along external portion of tibiae; apex enlarged with tooth-like projections. ***Venter*****:** Prosternum carinate along anterior and posterior margins; with a convex, somewhat conspicuous process; surface with coarse to large punctures densely distributed. Mesoventrite convex, with contiguous to dense coarse punctuation and conspicuous appressed setae. Metaventrite distinctly convex, medially somewhat smooth, frequently with conspicuous appressed setae; lateral portions with coarse to large punctuation, dense to sparsely distributed; discrimen not present as a narrow groove, instead present as a complete or incomplete superficial one, with a declivity at posterior end. Abdominal ventrites with fine, dense to contiguous punctuation, sometimes with moderate to large punctuation across posterior margins; porterior margin of I-IV ventrites with a transverse carina; last ventrite with conspicuous setae at apex. ***Genitalia*****:** Genital capsule symmetric; dorsally divided into three regions, discal plate sub-trapezoidal, distally almost truncate; dorso-lateral plates sub-triangular, but extending anteriorly as a single strut with sharp apex; ventral plate transverse to oblong, becoming narrower anteriorly, forming a single strut at proximal portion; distal edge rounded to almost truncate, surface with simple appressed setae, densely distributed, projected to median axis. Aedeagus symmetric, with subparallel sides; shape from strongly elongate (approx. 4.0X longer than wider) and narrow to moderately elongate (approx. 2.5X longer than wider). Anterior and posterior phallobase divided by a strong constriction forming two well-defined regions. Anterior phallobase rounded apically, varying from sub-trapezoidal to subtriangular shape. Posterior phallobase with almost subparallel sides, also with slightly convex to somewhat concave sides. Parameres with straight sides in most species, on lateral view from strongly to slightly concave, apically rounded. Median lobe enlarged at base, gradually narrowed apically; when Aedeagus strongly elongate penis slender.

Description Female: ***Size*****:** *Total length.* 11.51–15.27mm. *Total width.* 4.49–6.54mm. ***Colour:*** as males. ***Head:*** shape as males, size bigger than males head, more visible on dorsal view, anteriorly emarginate; vertex somewhat excavate; mandibles symmetric, narrow, distinctly different from males, almost straight, concave at dorsal portion, without teeth, instead with a longitudinal external carina from base to apex maxillary and labial palps shorter when compared with males; surface punctate, mainly basally, punctures large to somewhat coarse, denser at base, getting sparse distally, with simple, erect to slightly curved yellowish setae. ***Pronotum*****:** as males but presenting less distinct anterior angles; anterior edge less projected anteriorly; also with a considerable reduction in pronotal tubercle, with sub-trapezoidal shape on dorsal view; discal groove deep, often complete to apex, sometimes reaching pronotal process dividing it in two portions. ***Elytra*****:** as males. ***Legs:*** as males except for presenting subequal and smaller apical spurs at meso e metatibiae. ***Venter:*** very close to males except for presenting more conspicuous setae; prosternal process sometimes reduced, almost interrupted by procoxae. Abdominal ventrites similar to males getting narrower distally. ***Genitalia:*** Styli elongate and setose, with undivided and somewhat convex gonocoxites, showing almost the same width except proximally where each gonocoxite is abruptly narrowed, producing a slender projection. Lateral paraprocts enlarged proximally, rounded with globous to somewhat "C" shaped.

Comparative remarks on *Syndesus* and *Psilodon*: Given the strong resemblance between both genera it is difficult to determine the limits between them. It is also hard to identify good diagnostic traits at species and generic level due the intraspecific variation of some characteristics, such as the presence of species with six or seven lamellae in both genera, fine variations in mandibular teeth, elytral humeri, interstrial costae, metaventrital disc and some genitalic characteristics in both males and females. First of all it is important to summarize the main shared traits by *Syndesus* and *Psilodon*, which can define Syndesini MacLeay, 1819: Strong sexual dimorphism. Head emarginate, dorsal surface partially concealed by pronotum, medially excavated forming a "V" shaped region. Clypeus indistinct, instead with an intermandibular projection between mandibles. Labrum dorso-ventrally projected between mandibles, with rounded to truncate apex. Gula conspicuous, strongly convex and almost entirely glabrous. Eyes conspicuous, almost entirely extended through sides. Male mandibles strongly to somewhat curved inwards; dorsally curved in females. Pronotal antero-lateral angles rounded to oblique, anteriorly with a variable in shape tubercle, reduced in females; lateral pronotal carina present and complete, with scalloped surface. Elytra with well-defined striae and variable number of interstrial costae; epipleuron somewhat concave, abruptly narrowed basally, complete to apex. Legs serrate, with stronger teeth at protibiae. Meso and metatibie acute teeth and tooth-like projections. Prosternal process narrow. Meso and metaventrite finely to strongly convex abdominal ventrites with fine and contiguous to densely distributed punctuation, also with a transverse carina along posterior margin of every ventrite.

Based on the previous characters is possible to describe the principal differences between *Syndesus* and *Psilodon*. The sexual dimorphism is present in the same structures but *Syndesus* shows differences between male and female lamellae, being finely reduced in females. Male mandibles are probably the main difference between both genera, in Australasian species, mandibles only present one strong external tooth and an a laminar one across internal face, extended from base to apex, in New Caledonian this tooth is antero-posteriorly constricted producing a tooth-like projection. In *Psilodon* species male mandibles show a basal enlargement, forming a narrow dorsal surface, this trait allows the presence of a basal internal tooth, defined by

Didier (**1929**) as the γ (Gamma) tooth, a basal, external β (Beta) lobe, and a median to subapical external α (Alpha) tooth, being this one the strongest.

Geometric Morphometrics analyses

The values of the mean squares from Procrustes ANOVA showed to be lower for the error component of variation than the individual component in every analysed trait (*IndividualError>TotalError*) (Table 1), discarding definition errors for the proposed Landmarks.

Table 1. Comparison between mean square values of error components from Procrustes ANOVA of all analysed traits. Individual error are higher in all cases.

	RMM	**LMM**	**PT**	**DFP**	**DFE**
Individual Error	0.0020859548	0.0020637583	0.0015946985	0.0006454029	0.000094667
Total Error	0.0002147154	0.0000113199	0.0000318851	0.0000711143	0.0000260213

Right Male Mandible comparison

Most of the total shape variation for **RMM** (Figure 5a. and b.) was explained by de PC 1 (40.388%), which clearly separate two well-define clusters for each Syndesini genus. The PC2 explained 18.839%, showing an apparent influence separating the species examined. According to the results mandible curvature do not seems to have a strong influence over shape variation, on the other hand, mandible apex (LM: 10-13), alpha (LM: 6-9) and gamma (LM: 15-19) teeth shape and presence or absence of beta lobe (LM: 2-5) have a strong influence on PC scores. *S. cancellatus* represents the highest score across PC1 (0.254), such value responds to a strongly truncate apex, the absence of beta lobe, reducing basal expansion of mandible, the strong alpha tooth located medially and the unique configuration of gamma tooth, which is present as a laminar tooth extended from base to apex. Changes in mandibular shape of *Syndesus* species also seem to respond to the upwards projection of internal face involving LM: 14-20. The lowest score of PC1 (-0.233) was define by the Ecuadorian species *P. luki*, this values are presumably related with the presence of an acute apex, producing narrower mandibles when compared with New Caledonian species, it also responds to the preapical position and almost perpendicular orientation of alpha tooth, a reduction in the basal expansion due to the fusion of gamma tooth and beta lobe, a typical trait of the Ecuadorian *Psilodon*. In general terms the mandibular shape variation of *Psilodon* species responds to a narrower surface represented by a reduction of the distances between the continuous line of LM: 1-9 and the internal line of LM: 14-20, this configuration produces a uniformly concave internal face of mandibles, making it less exposed from dorsal view.

Shape variation through PC2 presents a less abrupt variation, but morphological changes respond to similar patterns, as is the case of mandibular apex, being rounded to somewhat truncate at the lowest value (-0.312), represented by *P. westwodii*, which also presents the more conspicuous configuration of gamma tooth represented by antero-lateral projection of LM: 14-19. The distribution of the internal landmarks produces a clear basal dorsal surface, followed by the strong internal projection of gamma tooth and a uniform concave region apical, perpendicular in relation to gamma tooth. The highest score of PC2 (0.140), defined by one specimen of *S. cornutus,* is not represented by a strong variation of landmark distribution, and as is the case of the other specimens from the Australasian region, the basal configuration of external (1-9) and internal (14-20) landmarks allows a high exposition of internal face from dorsal view.

Using as the main classifier *biogeographic dominion* (Figure 4b.), was observe a somewhat a well-define cluster for Parana dominion, with close PC scores showed by the only record from the Chacoan dominion, and superposition with two specimens from the South Brazilian one (2 males of *P. burnheimi*). The other record from the South Brazilian dominion was represented by the Bolivian Yungas specimen, *P. gilberti* registered a score closer to the Pacific dominion values.

The remaining specimens distributed along the Pacific dominion showed highly variable scores mainly influenced by PC2, with the lowest scores represented by *P. westwoodii* from Colombia and an undetermined species from Venezuela. It is interesting that the two records of *P. paschoali*, a species with distribution data from Colombia and Venezuela registered PC scores (record 1: PC1: -0.061; PC2: -0.034 / record 2: PC1: -0.047; PC2: 0.046) with high superposition with the Parana dominion.

The pairwise distances of the Discriminant Analysis for RMM showed to be significant for Mahalanobis distances (P: 17.57, *p* <0.0001) and Procrustes distances (P: 0.2452, *p* <0.001) using *genera* as classification criterion. The comparison of Mahalanobis distances through the *biogeographic dominions* CVA (see Table 2) showed significant differences within the Australasian dominions, however, Procrustes distances only registered significant differences between New Zealand (*S. cornutus*) and New Caledonian (*S. cancellatus* and *S. punctatus*) species. Neotropical dominions showed a similar pattern, presenting significant differences between Mahalanobis distances of most dominions except between Pacific and Chacoan, and Parana and Chacoan. In regard to Procrustes distances there were only registered significant differences between Parana and Pacific dominions. When comparing the Neotropical Australasian dominions there were recorded significant differences between most comparisons of Mahalanobis and Procrustes distances (Table 2), except among Chacoan and Australasian ones.

Table 2. p-values from permutation tests (10000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **RMM**. Significant differences: p **<0.01**.

	Australia	Chacoan	New Caledonia	New Zealand	Pacific	Parana

Chacoan	0.0336/ *0.2022*					
New Caledonia	**0.0073**/ *0.0200*	0.0483/ *0.1993*				
New Zealand	**<0.0001**/ *0.0580*	0.0177/ *0.0827*	**0.0002**/ ***<0.0001***			
Pacific	**<0.0001**/ *0.0161*	0.0239/ *0.6684*	**0.0077**/ ***0.0080***	**<0.0001**/ ***0.0001***		
Parana	**<0.0001/** ***<0.0001***	0.0402/ *0.0351*	**<0.0001/** ***<0.0001***	**<0.0001/** ***<0.0001***	**<0.0001**/ ***0.0077***	
South Brazilian	**0.0088**/ *0.0591*	**<0.0001**/ *0.5040*	0.0153/ ***0.0061*****	**0.0009*****/ ***0.0008*****	**0.0023**/ *0.07175*	**<0.0001**/ *0.1093*

Left Male Mandible (on lateral view) comparison

The 44.627% variation of **LMM** was explained by PC1, and PC2 explained the 17.282% (Figure 6a. And b.). While PC1 appeared to facilitate the separation among species, PC2 showed to influence the separation between *Syndesus* and *Psilodon*. The lowest score along PC1 (-0.32), represented by the Dominican fossil *Syndesus ambericus* Woodruff, 2009, responds to a strong variation at mandibular apex where alpha tooth (LM: 9-13) presents a preapical position and an almost perpendicular orientation, it also seemed to be related to a reduction between landmarks 7 and 8 which produced a narrower mandibular apex in relation to the other examined specimens.

The highest score recorded for PC1 (0.27) represented by an undetermined species of Brazilian Atlantic Forest is related with the median location of alpha tooth (LM: 9-13), presenting a higher distance from LM: 8 when comparing with *S. ambericus*; there is also a strong shape variation regarding apical landmarks (6-9) that are projected anteriorly and presents a distinct configuration that produces a wider mandibular apex. Median scores respond to changes on alpha tooth represented by fine migrations (closer or not to apex) and orientation, from almost perpendicular to anterodorsally projected. Variation along PC2 is related with changes on the distances between the ventral (LM: 1-7) and the dorsal (LM: 8-17) line of landmarks, producing narrower mandibular shapes at low scores and wider ones at higher scores. There is also a strong influence represented by beta lobe (LM: 14-17) variation, entirely absent in *Syndesus*, producing a flat region and a dorsal projection of landmarks 15 and 16 in *Psilodon*, which produce a convex region.

PCA failed to produce a clear separation between the Neotropical and Australasian dominions, showing a fine separation through PC2 between New Zealand and New Caledonian specimens Neotropical taxa. Australian specimens registered a high superposition with Parana dominion. PC1 showed a clear separation between LMM shape of *S. ambericus*, from the Antillean province and the remaining specimens.

The pairwise distances of the Discriminant Analysis for LMM was significant for Mahalanobis (P: 14.6380, *p* <0.0001) and Procrustes distances (P: 0.1265, *p* 0.0009) under the criterion *genus*. Using the *biogeographic dominions* as the main classification criterion for CVA (Table 3.), Mahalanobis and Procrustes distances were significant between most comparisons involving Australasian and Neotropical dominions, being the South Brazilian one, the only which not registered significant differences between New Zealand, New Caledonian and Australian specimens.

Table 3. p-values from permutation tests (10000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **LMM**. Significant differences: p **<0.01**.

	Australia	Antillean	Chacoan	New Caledonia	New Zealand	Pacific	Parana

Antillean	**<0.0001**/ *0.1794*						
Chacoan	**0.0858**/ *0.1363*	**<0.0001**/ *1.000*					
New Caledonia	**<0.0001**/ *0.0182*	0.1809/ *0.1981*	0.1828/ *0.0318*				
New Zealand	**0.0036**/ ***0.0098***	**<0.0001** / *0.0164*	0.0104 / *0.1340*	**0.0016**/ ***0.0006***			
Pacific	**0.0018/** *0.0114*	0.1696/ *0.3109*	0.1267/ *0.1114*	**0.0011**/ ***0.0084***	**0.0006**/ **<0.0001**		
Parana	**0.0001**/ *0.0217*	0.0474/ *0.0763*	**0.0013**/ *0.0882*	**0.0002**/ ***0.0062***	**<0.0001**/ ***0.0021***	**<0.0001**/ *0.0762*	
South Brazilian	0.1901/ *0.4044*	**<0.0001/** *1.0000*	**<0.0001**/ *1.0000*	0.0351/ *0.3945*	0.0367/ *0.0905*	0.1567/ *0.9972*	0.0268/ *0.9344*

Pronotal Tubercle comparison

The PCA for **PT** shape (Figure 7a and b) successfully represented the shape variation between *Syndesus* and *Psilodon.* PC 1 represented the 62.647% and PC 2 the 22.990% of the total variance. It was possible to obtained two well-defined clusters, one represented by *Syndesus* species and Australasian dominions, and another for the Neotropical genus *Psilodon*. The superposition of both clusters along the PC1, was mainly given by the *S. ambericus* fossil score (0.14) from the Antillean dominion, whose shape is closer to *Psilodon* species, showing less projected landmarks (LM: 4-11) anteriorly, and a typical dorsal projection represented by LM: 11-13, only presented in the studied specimens from North-East Venezuela and Trinidad and Tobago. The pairwise distances of the discriminant analysis of **PT** showed significant differences for both Mahalanobis (P: 3.978, p <0.0001) and Procrustes distances (P: 0.1463, p <0.0001), which are the result of strong differences between *Syndesus* and *Psilodon* PT projection, which is clearly stronger in all *Syndesus* specimens, represented by LM: 2-12.

In regard to the *biogeographic dominions* comparison, there were recorded significant differences between most Australasian and Neotropical Mahalanobis distances. It is interesting to point out that *Syndesus* fossil from Dominican Republic shows differences from the Australasian members of the genus, differences that are also present between Parana and Pacific Neotropical dominions.

There were only identified significant differences between the Mahalanobis distances (Table 4.) of Antillean-Australia, Chocoan and Parana; Antillean-New Caledonia and South Brazilian; New Caledonia-Parana; New Zealand Parana. In the case of Procrustes distances for the same criterion it was only possible to observe significant differences between New Caledonia and Parana dominions. There were not significant differences of Procrustes distances within Neotropical dominions.

Table 4. p-values from permutation tests (10000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **PT**. Significant differences: p **<0.01**.

	Australia	Antillean	Chacoan	New Caledonia	New Zealand	Pacific	Parana
Antillean	**<0.0001**/ *0.0984*						
Chacoan	**<0.0001**/ *0.0842*	1.000/ *1.000*					
New Caledonia	**0.0004**/ *0.0533*	**<0.0001/** *0.1810*	0.1484/ *0.1993*				
New Zealand	**0.0022**/ *0.7213*	0.1079/ *0.1062*	0.0853/ *0.0328*	**0.0025**/ ***0.0018***			
Pacific	**0.0063**/ *0.1281*	**0.0018**/ *0.8319*	0.1606/ *0.8281*	**0.0010**/ ***0.0071***	**0.0023**/ ***0.0040***		

Parana	**<0.0001**/ *0.0107*	0.0349/ *0.1718*	**0.0026**/ *0.4604*	**<0.0001**/ **<0.0001**	**<0.0001**/ ***0.0008***	**0.0008**/ *0.5051*	
South Brazilian	0.0784/ *0.2633*	**<0.0001/** *1.000*	1.0000/ *1.0000*	0.0168/ *0.2015*	0.1190/ *0.0701*	0.0861/ *1.0000*	**0.0046**/ *0.9745*

Dorsal Face of Pronotum comparison

PCA for **DFP** (Figure 8a and b.), two somewhat well-defined clusters for each genus. PC 1 explained the 37.467% and PC 2 the 16.725% of the total shape variation. Despite the high superposition it was possible to perceive the strong influence of LM: 1-5 and 11-14 along the anterior margin of the pronotum. As it was observed for **PT**, the shape variation was influenced by changes in the projection degree. **DFP** showed a similar pattern, with the lowest scores along PC1 (-0.15 and 0.13) representing a strong anterior projection of LM: 1-3 and 13,14, which form a convex region including the pronotal tubercle, present in *P. xerophilicum* and the *Psilodon* specimen from Trinidad and Tobago. The shape variation in this cases is also influenced by a regression of LM: 4 and 12, reducing the projection of antero-lateral angles of the pronotum. With higher scores (e.g. 0.10) of PC 1, the general shape of the pronotum becomes subquadrate with a clearly reduction in anterior projection of the anterior margin, represented by *S. cornutus* specimens. Variation along PC 2 showed similar patterns to PC1, with low scores influenced by a strong projection of pronotal tubercle characteristic of *Syndesus* species, becoming less projected at higher scores, which show the typical shape of most *Psilodon* species.

The pairwise distances of the discriminant analysis performed for **DFP**, showed sigjnificant differences between Mahalanobis (P: 4.7692, *p* <0.0001) and Procrustes (P: 0.0851, *p* <0.0001) distances of *Syndesus* and *Psilodon*. When using as classifier the *biogeographoc dominions* (Table 5) there were obtained significant differences between most Mahalanobis and Procrustes distances from Australasian and Neotropical dominions, suggesting a strong influence of the biogeographic component. It was also possible to identify significant differences in pronotal shape variation between most *Psilodon* specimens distributed across different biogeographic dominions.

Table 5. p-values from permutation tests (10000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **DFP**. Significant differences: p **<0.01**.

	Australia	Chacoan	New Caledonia	New Zealand	Pacific	Parana
Chacoan	**0.0037**/*0.0363*					
New Caledonia	**0.0004**/*0.2945*	**0.0073**/*0.1466*				
New Zealand	**<0.0001**/ *0.1471*	0.0148/*0.0511*	**0.0006**/ *0.2721*			
Pacific	**<0.0001**/ **<0.0001**	0.0386/*0.3875*	**0.0007**/ *0.0973*	**<0.0001**/ ***0.0002***		
Parana	**<0.0001**/ **<0.0001**	0.8052/ *0.9751*	**<0.0001** / *0.0028*	**<0.0001**/ **<0.0001**	**<0.0001**/ ***0.0062***	
South Brazilian	**<0.0001**/ ***0.0029***	0.4233/ *0.4801*	**0.0001**/ *0.0607*	**0.0002**/ ***0.0012***	**<0.0001**/ *0.0551*	**0.0028**/ *0.0880*

Dorsal Face of Elytra comparison

PCA for **DFE** (Figure 9a and b.) failed to separate both *genera* and *biogeograohic dominions*, resulting in a high data superposition. The PC 1 represented 41.4% of the total variation and PC2 the 22.2%. The pairwise comparison under the criterion *genus,* showed to be significant for Mahalanobis distances (P: 3.871; *p*<0.001), but not for the Procrustes ones (P: 0.0218; *p* 0.0127). Shape differences responds tu a reduction in distance between LM 1-2, and 20-21 which results in a more cylindrical elytral shape at low PC scores (*Syndesus* species), and a more robust one for higher scores (*Psilodon* species). For *biogeographic dominions*, Mahalanobis distances showed significant differences between Australasian and Neotropical dominions, there were also recorded differences within regions, suggesting a specific elytral shape for almost every analysed biogeographic dominion.

Table 6. p-values from permutation tests (10000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **DFE**. Significant differences: p **<0.01**.

	Australia	Chacoan	New Caledonia	New Zealand	Pacific	Parana
Chacoan	**0.0014**/*0.4018*					
New Caledonia	**<0.0001**/*0.018*	0.0334/*0.0264*				
New Zealand	**<0.0001**/ *0.0467*	**0.0056**/*0.6334*	**0.0006**/ ***0.0071***			
Pacific	**<0.0001**/ ***0.0074***	0.0132/*0.8181*	**0.0006**/ *0.2476*	**<0.0001**/ *0.166*		
Parana	**<0.0001**/ **<0.0001**	**0.0003**/ *0.5260*	**<0.0001**/ *0.0639*	**<0.0001**/ *0.0631*	**<0.0001**/ *0.1740*	
South Brazilian	**<0.0001**/ **0.0159**	0.0339/ *0.5042*	**0.0017**/ *0.2986*	**0.0004**/ *0.3302*	**0.0001**/*0.7083*	**<0.0001**/ *0.9665*

Discussion

With this study it was possible to identify a significant variation for mandibular, pronotal and elytral shape between the two genera currently positioned in Syndesini. Using geometric morphometrics and strict taxonomic comparisons, this research offers now a strong support to define the limits between the Australasian and Neotropical members of this Syndesinae tribe.

The diagnostic traits identified through the taxonomic evaluation, mainly represented by strong shape variations at male mandibles and male and female pronotum and pronotal tubercle were consistent with the geometric morphometrics analysis results. Changes among these structures are difficult to describe, as it is hard to define good reference points which reflect its relative position, size and shape. This is specially true for the teeth position along male mandibles, and also the shape and degree of projection of pronotal tubercle, and pronotal antero-lateral angles. In these cases, geometric morphometric techniques showed to be highly effective in assisting the taxonomic descriptions, which with the other studied traits, offer a well-supported and less subjective description.

Previous works involving geometric morphometric methods within Lucanidae, studied the shape variation of similar body structures used in this work, showing to be effective for the evaluation of allometric patterns and sexual dimorphism of different Lucaninae genera such as *Prosopocoilus* (Tatsuta *et al*. 2004), *Chiasognathus* (Vergara *et al*. 2014), *Colophon* (Eldred *et al*. 2016), *Lucanus* (Romiti *et al*. 2016), and *Odontolabis* (Matsumoto & Knell 2017). With our study, now is possible to conclude, that geometric morphometric are also useful to resolve taxonomic inconsistencies.

The examples cited above, as most Lucanidae studies, are centred in Lucaninae, being this, the first time in which it is offered a geometric morphometric dataset for Syndesini, as the only available data regarding Syndesinae was provided by Zhang *et al*. (2019), and only included Ceruchini Jacquelin du Val & Fairmaire, 1859 and Sinodendrini Mulsant, 1842 in their evolutionary study. The absence of *Syndesus* and *Psilodon* in this study, reflects not only its under-representation in most entomological collections, but also the limitations concerning evolutionary interpretations within the subfamily, as the Ceruchini and Sinodendrini morphologies are considerably different from Syndesini, suggesting a clear separation between the Holarctic and Austral Syndesinae, which has not been studied so far.

Additional to the morphological comparisons using each genera as classifiers, the same comparisons were conducted from a biogeographic approach using biogeographic dominions as the comparative factor. Due the lack of larger series of specimens for each dominion, biogeographic interpretations are to some extent limited at this level, however, if we consider the results from a regional perspective, the statistical differences between the shape data (Mahalanobis and Procrustes distances) from the Neotropical and Australasian regions, it is possible to support the existence of two Syndesini genera instead of one.

When Burmeister (1847) and Arrow (1938) stated that considering *Syndesus* and *Psilodon* as different taxa would represent an unnatural separation, they were only considering the strong morphological resemblance between both genera, ignoring the vicariance events, that interrupted the connection between Australia and South America at the Cretaceous, around 65 MYA (Grimaldi & Engel 2005).

Woodruff (2009), supported this observations when he described *S. ambericus* fossil*,* stating that considering *Syndesus* and *Psilodon* as synonyms, would totally ignore the biogeographical influence in taxa divergence processes. In spite of this, Woodruff decided to place the fossil species in *Syndesus*, which presents a closer morphological resemblance with *Psilodon* species.

Now, considering this separation between Syndesini genera, it is possible to hypothesize about the biogeographic history of the tribe, suggesting a Gondwanan origin inferred from the results obtained by Paulsen (2013) and Kim & Farrell (2015) for other Stag Beetles genera such as *Casignetus* MacLeay, 1819; *Chiasognathus* Stephens, 1831; *Streptocerus* Dejean, 1833; *Sphaenognathus* Buquet, 1838; *Hilophyllus* Paulsen & Mondaca, 2006, among others which, together with their related Australasian taxa, conforms tribes as Lamprimini MacLeay, 1819;

Chiasognathini Burmeister, 1847; Ceratognathini Sharp, 1899 and Casignetini Reid, 1999. Similar patterns has been registered for other beetle taxa, as is the case of *Araucaria*-associated bark beetles (Sequeira & Farrell 2001), water scavenger beetles (for West Gondwana vicariance) (Toussaint *et al*. 2017), and ground beetles (Sota *et al*. 2022).

With our results we establish the basis for defining the limits between both Syndesini genera, with *Syndesus,* including four species restricted to the Australasian region and *Psilodon* with eight species from the Neotropical region. Given the limitations related to the lack of available material, especially for *Syndesus* species, to offer more robust results, further efforts must be focused on collecting new material, not only for dried conservation but also for the obtention of DNA samples, which would help to clarify the evolutionary relationships within Lucanidae. While conducting our study we observed several undetermined species of *Psilodon*, which remarks the need for a taxonomic revision. We also identify some important morphological divergences presented between the Australian and New Caledonian species of *Syndesus* that should be studied deeper.

Acknowledgments

We would like to thank Richard Leschen and Svetlana Malysheva from the New Zealand Arthropod Collection, who shared with us a series of excellent photographies of several *Syndesus cornutus* specimens. We also thank Antoine Mantilleri and Christophe River from the MNHN who also provided us photographies of the New Caledonian *Syndesus* species. In last we thank to the "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior" – CAPES for the Doctoral Scholarship of the Academic Excellence Programme PROEX, which made possible the conduction of this work.

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Appendix I – List of Figures

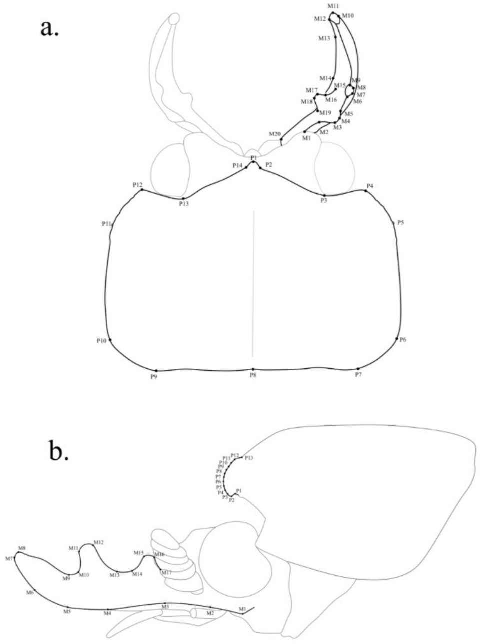

Figure 1. Proposed landmarks for a) RMM (M1-M20) and DFP (P1-P14). b) LMM (M1-M17) and PT (P1-P13).

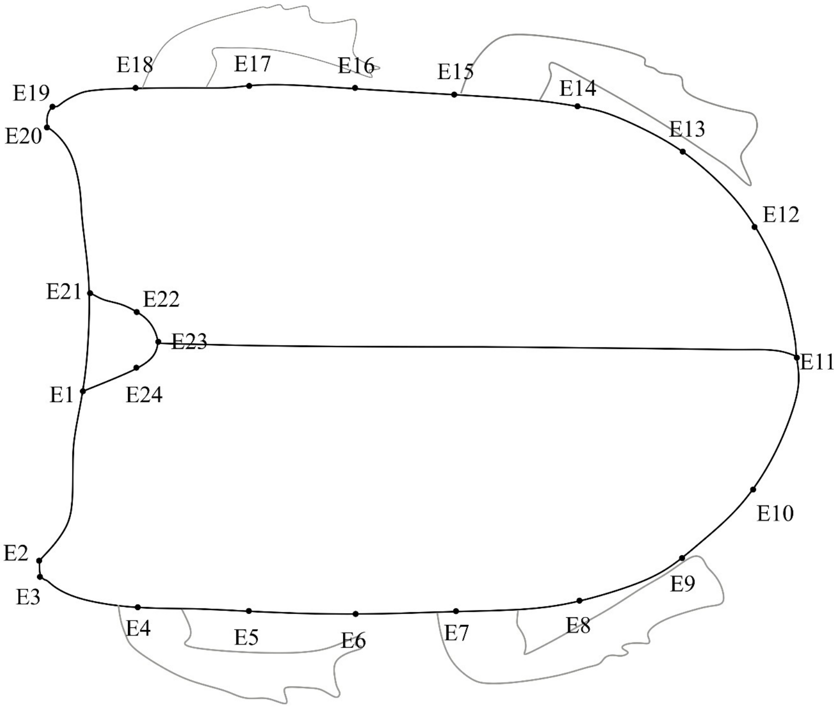

Figure 2. Proposed landmarks for DFE (E1-E24).

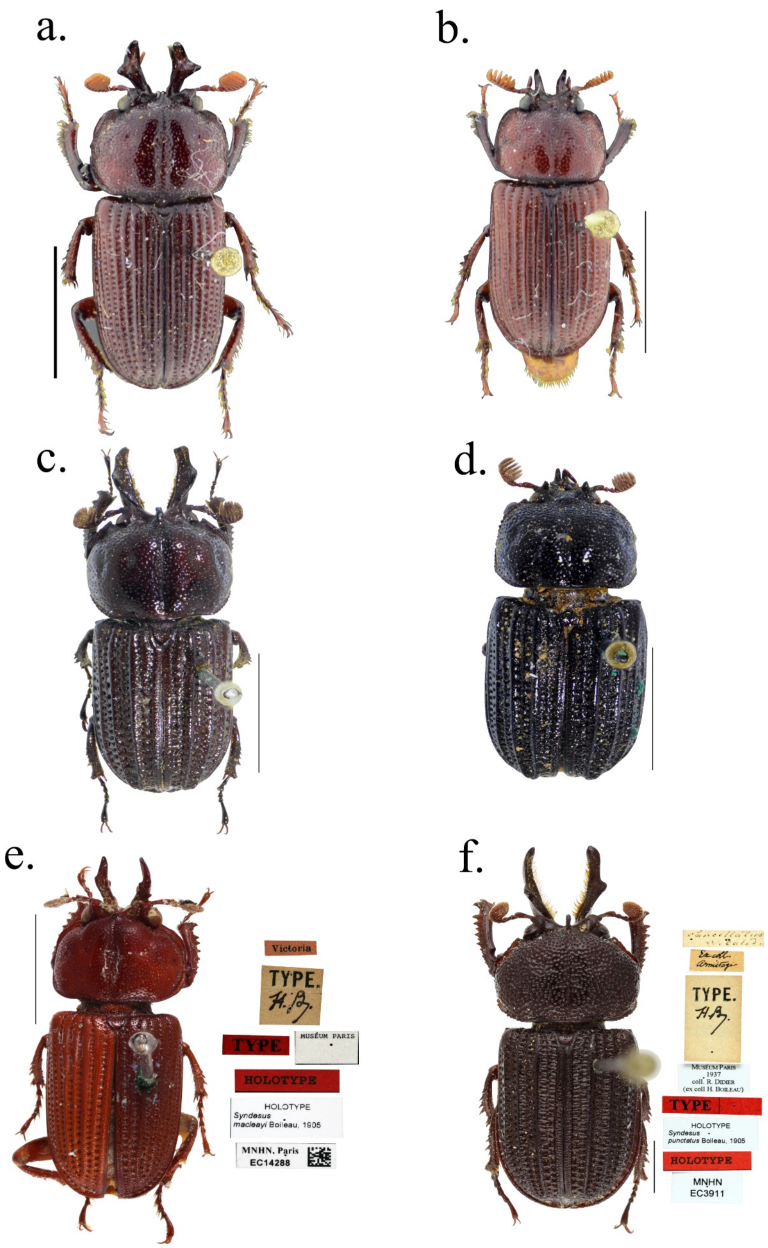

Figure 3. Dorsal habitus of Syndesus MacLeay, 1819 species. **a)** *S. cornutus* Male. **b)** *S. cornutus* Female. **c)** *S. cancellatus* Male. **d)** *S. cancellatus* Female. **e)** Holotype male. MNHN *S. macleayi* (Photo by C. Rivier 2022). **f)** Holotype male. MNHN *S. punctatus* (Photo by A. Mantilleri 2013). Scale bars 5mm except f) 2mm.

Figure 4. Dorsal habitus of *Psilodon* Perty, 1830 species. **a)** *P. schuberti* Male. **b)** *P. schuberti* Female. **c)** *P. xerophilicum* Male. **d)** *P. xerophilicum* Female. **e)** *P. buhrnheimi* Male. **f)** *P. gilberti* Male. **g)** *P. wetwoodii* Male. **h)** *P. paschoali* Male. i**)** *P. seguyi* Male. **f)** *P. seguyi* Female. **g)** *P. luki* Male. **h)** *P. luki* Female. Scale bars 5mm.

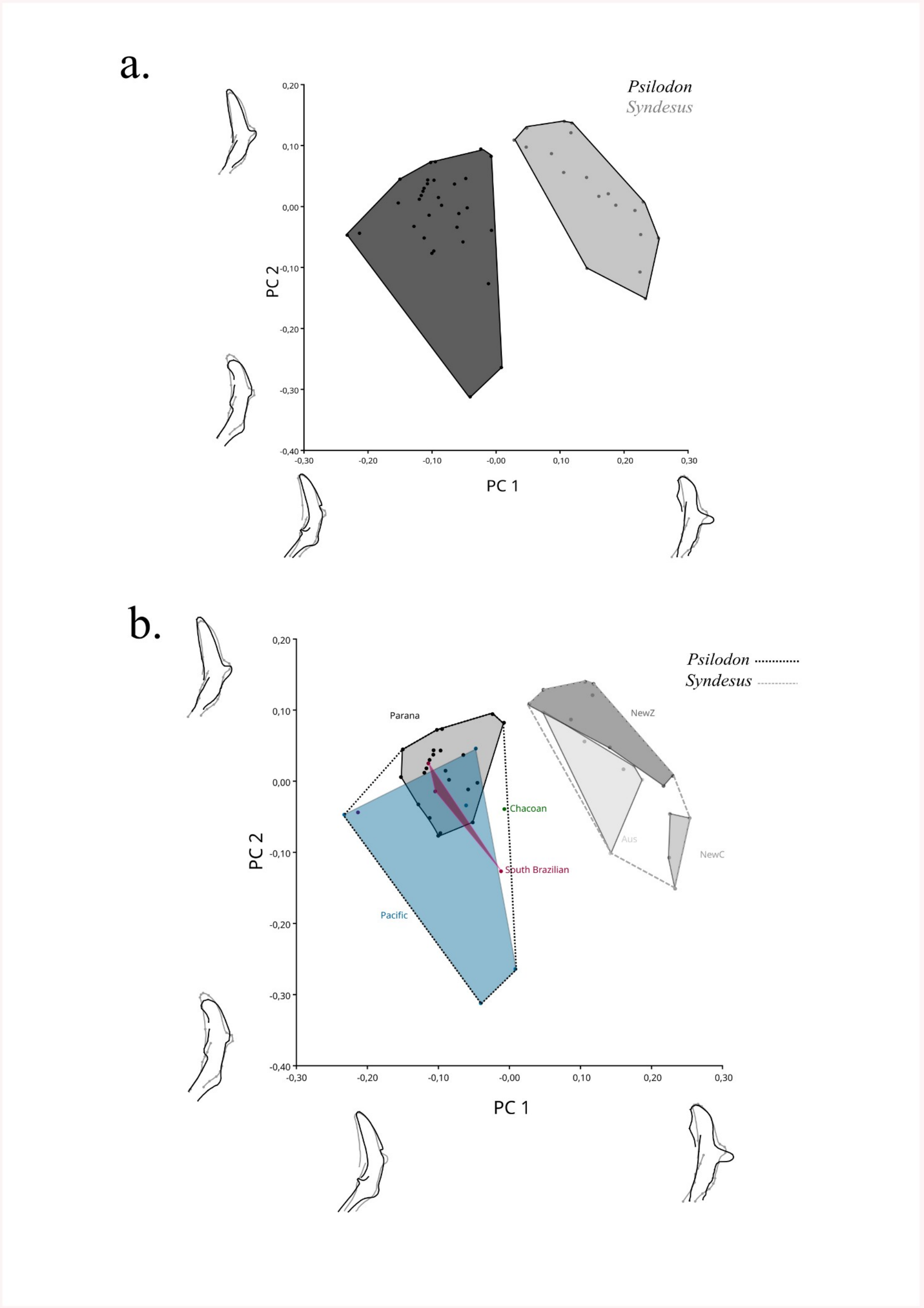

Figure 5. Principal component analysis (PCA) of the shapes of the right mandible of males (RMM), calssified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

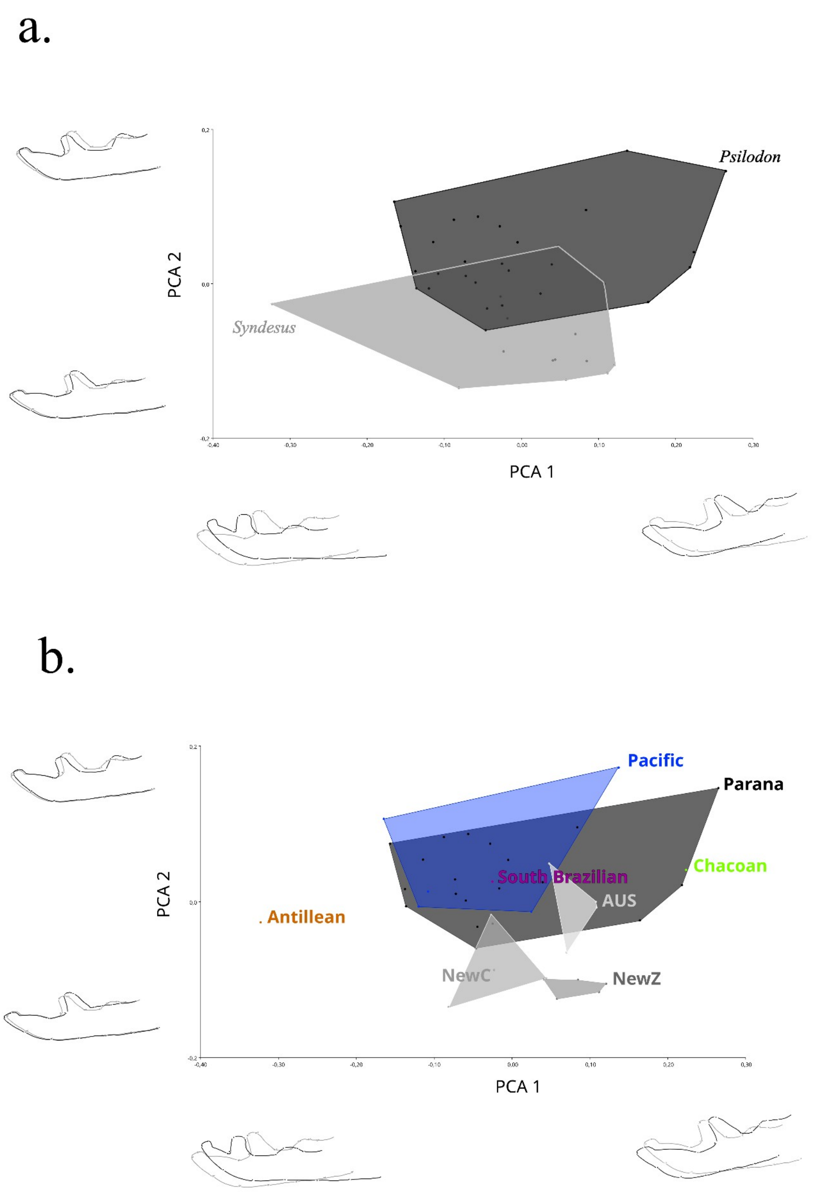

Figure 6. Principal component anlysis (PCA) of the shapes of the lateral view of the left mandible of males (LMM) classified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

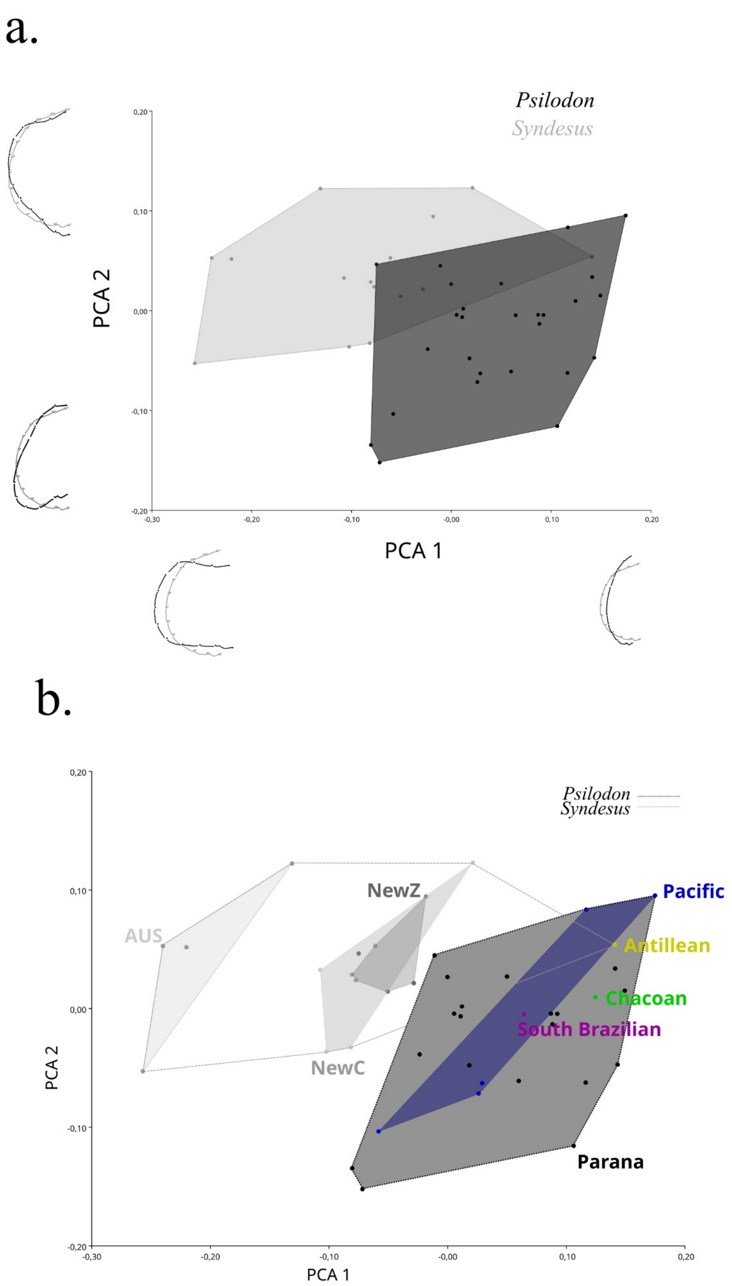

Figure 7. Principal component anlysis (PCA) of the shapes of the lateral view of the pronotal tubercle of males (PT) classified by **a)** *Genus*, and b) the biogeographic dominions of Neotropical and Australasian regions.

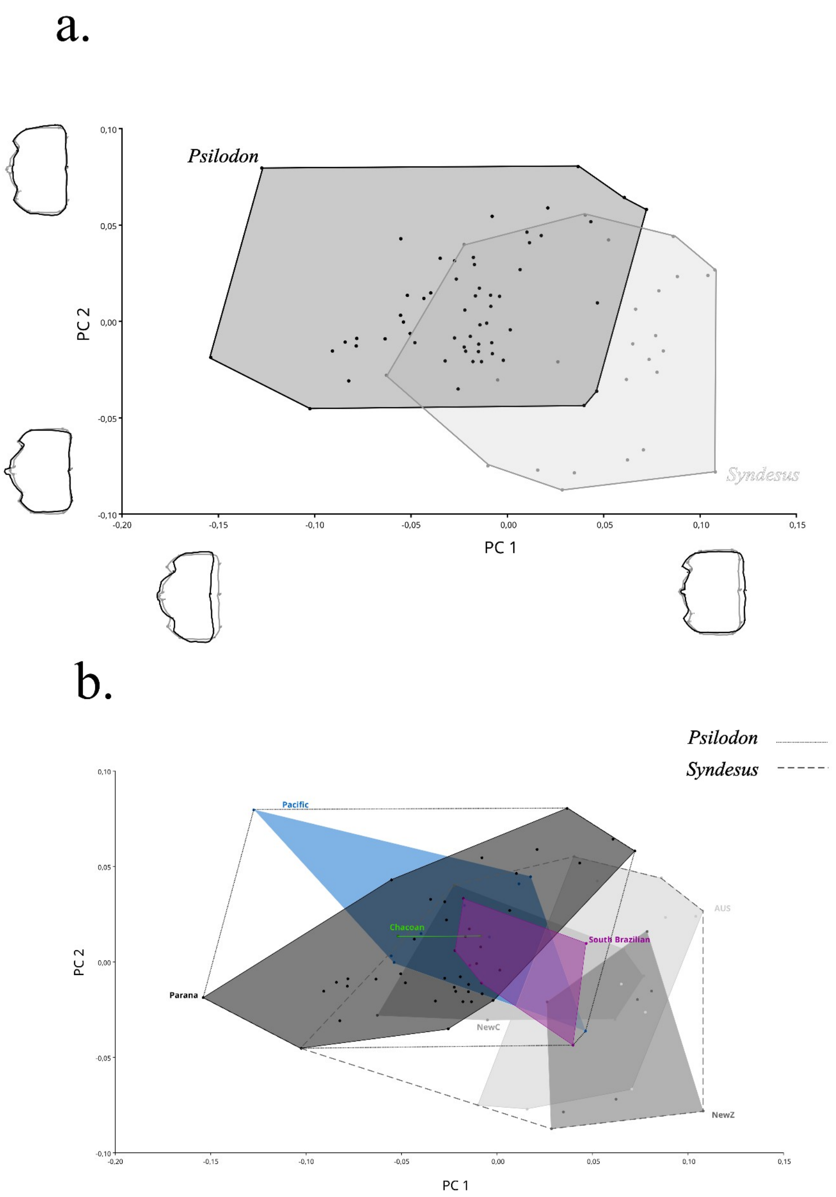

Figure 8. Principal component anlysis (PCA) of the shapes of the dorsal face of pronotum (DFP) classified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

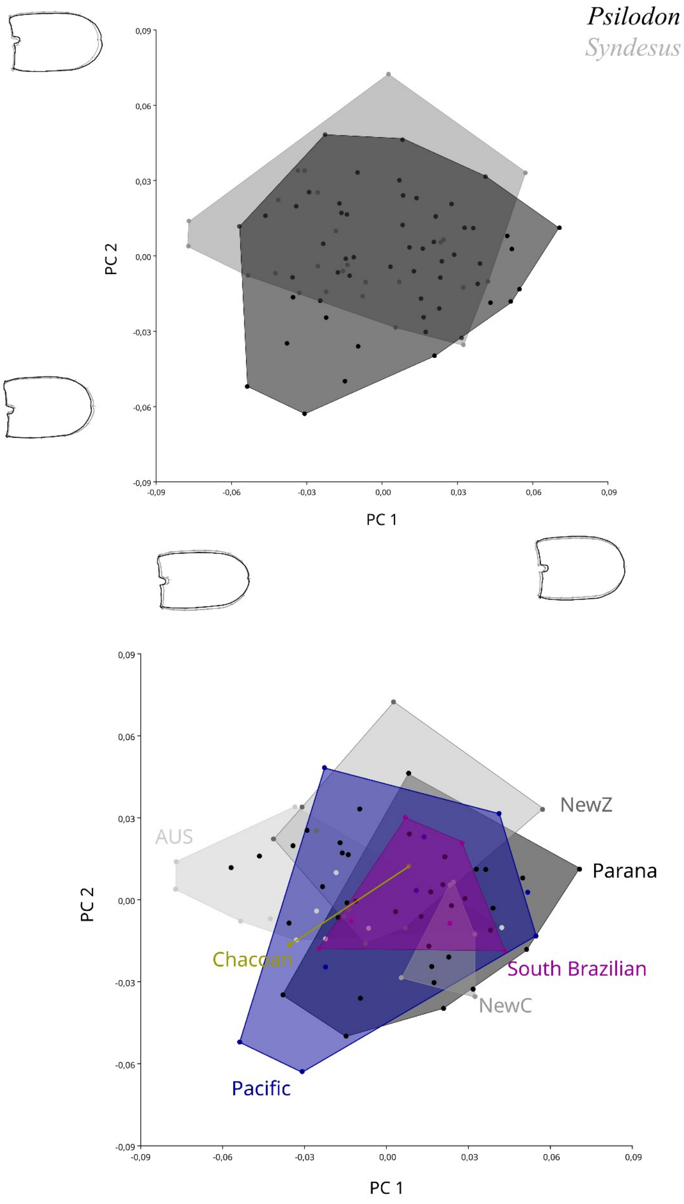

Figure 9. Principal component anlysis (PCA) of the shapes of the dorsal face elytra (DFE) classified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

CAPÍTULO 3

TAXONOMIC REVISION OF *PISLODON* PERTY, 1830 (COLEOPTERA: LUCANIDAE: SYNDESINAE) WITH NOTES ON BIOGEOGRAPHY AND THE DESCRIPTION OF A NEW SOUTH AMERICAN GENUS[1]

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[1] **Cáceres, J.S.D. & P.C. Grossi.** Taxonomic revision of *Psilodon* Perty, 1830 (Coleoptera: Lucanidae: Syndesinae) with notes on biogeography and the description of a new Syndesini genus. European Journal of Entomology.

Taxonomic revision of *Psilodon* Perty, 1830 (Coleoptera: Lucanidae: Syndesinae) with notes on biogeography and the description of a new Syndesini genus.

Abstract

Psilodon Perty, 1830 is revised for the first time. We provide an identification key for males and females and include new diagnostic traits for all species by adding morphological information regarding genitalic structures. Six new species *Psilodon* n. sp. 1, *Psildon* n. sp. 6, *Psilodon* n. sp. 2, *Psilodon* n. sp. 3, *Psilodon* n. sp. 4*,* *Psilodon* n. sp. 5, and are described from North-East, Central-West, South-East and South Brazil. With our results, *Psilodon* is now composed of 14 species, all restricted to South America. A male specimen from Venezuela and Trinidad and Tobago, previously thought to belong to *Psilodon*, led to the description of N. gen. 1 with only one species N. gen. 1 n. sp. 7. In order to infer the biogeographic history of the South American Syndesini and possible insect-plant associations we conducted a panbiogeoraphic analysis including both Neotropical Syndesini genera and all the genera in the plant order Fagales with records from South America. The results showed a high convergence between the individual track of *Psilodon* and the generalized tracks of the Fagales genera, suggesting that besides the South American biogeographic dynamics from the Tropical Andes, the Atlantic rainforest and the recurrent connections between eastern Brazil and the Amazonian region, the possible ecological association with this plant order, could have modeled the current distribution of *Psilodon*. It was not possible to identify similar patterns for N. gen. 1, but given the existence of a highly resemblant amber fossil from Dominican Republic, further studies focused on the Antilles could bring new biogeographic insights for this new genus.

Key words: Stag beetles; Syndesini; Panbiogeography; New species; New genus

Introduction

Stag beetles in the subfamily Syndesinae MacLeay, 1819 (Coleoptera: Lucanidae) represent one of the less diversified subfamilies in Lucanidae (Holloway 2007), only composed by three or four genera, depending on the author, and around 30 species. *Sinodendron* Hellwig, 1792 and *Ceruchus* MacLeay, 1819, both restricted to the Holarctic region (Howden & Lawrence 1974); *Syndesus* MacLeay, 1819 from Australia, New Caledonia and New Zealand; and *Psilodon* Perty, 1830, from South America, treated by several authors as a synonym of *Syndesus* (Benesh 1960; Maes 1992; Krajcik 2001; Krajcik 2003; Holloway 2007; Onore, Bartolozzi & Zilioli 2011; Grossi & Aguiar 2014).

Psilodon was originally described by Perty (1830) with the type species *Psilodon schuberti*, based on a female from "provincia Piahuiensi" in Northeast Brazil. Gray (1832) described a new genus, *Hexaphyllum*, using a male specimen from the state of Rio de Janeiro (Southeast Brazil) defining it *Hexaphyllum brasiliensis* Gray, 1832 as the type species. In spite of the high resemblance between the male of *H. brasiliensis* and the female of *P. schuberti*, Gray did not suggest any connections between both taxa, probably ignoring that Perty´s specimen existed.

Hope (1840) briefly described a new species for this genus, *Hexaphyllum westwoodii* Hope, 1840 from "New Granada" (Colombia). Later, but in the same year, Buquet (1840) made two contributions to the taxonomy of South American Syndesinae, the first one was the description of a new species, *Hexaphyllum aequinoctiale* Buquet, 1840, posteriorly considered a synonym of *H. westwoodii* Hope, by Burmeister (1847), but transferring it to *Syndesus*; the second contribution was to define *Hexaphyllum brasiliensis* as the valid species from Brazil, arguing that Perty (1830) did not have access to specimens of both sexes making his description incomplete, considering as the valid genus the one described by Gray (1832).

Van Roon (1910) kept *Hexaphyllum* as a valid genus in his catalogue, *H. brasiliense* is corrected and listed as a synonym of *Hexaphyllum schuberti* (Perty). Luederwaldt (1935) in his study of Brazilian Lucanidae also kept van Roon's classification.

Posteriorly Didier (1929) described *Hexaphyllum seguyi* Didier, 1929, the third species of the genus and the first one from Ecuador. He discussed the apparent resemblance with *H. aequinoctiale* (both from the Tropical Andes), mainly based on the mandibular aspect of males that differed from the Brazilian species. Didier & Séguy (1953) included these three species, considering *Psilodon* Perty as a valid genus.

Benesh (1960) catalogued *Psilodon* and *Hexaphyllum* as synonyms of *Syndesus*. Previous authors such as Burmeister (1847) and Arrow (1938), discussed that considering *Hexaphyllum* and *Syndesus* different taxa, would represent an unnatural separation as both genera present a strong resemblance. This is probably the reason why Benesh and some other authors maintained this synonymy, but *Psilodon* continued to be used by other authors. Besides the later description of new species it is possible to find the use of *Psilodon* in Holloway (1968; 1997), Howden & Lawrence (1974), and Ratcliffe (2002).

Almost 50 years later, a new species was described, *Psilodon xerophilicum* Martínez & Reyes-Castillo, 1985 from the state of Bahia in Northeast Brazil, based on two female specimens. A few years later, Boucher (1993) added a new species from the Bolivian Andes, *Psilodon gilberti* Boucher, 1993. This is the only species of *Psilodon* with seven antennal lamellae, a trait that has been historically attributed to *Syndesus*, even though species in New Caledonia present six lamellae.

The catalogues published after Benesh (1960), included *Psilodon* and *Hexaphyllum* as synonyms of *Syndesus*, extending the distribution of the South American species to Venezuela and

Argentina, probably based upon the comments on *Psilodon schuberti* made by Martínez & Reyes-Castillo (1985), suggesting that this species was also present in northeastern Argentina. Krajcik (2001; 2003) maintains the same synonymy and Holloway (2007), who previously recognized *Psilodon* and *Syndesus* as separated taxa, only recognized three genera within Syndesinae: *Sinodendron*, *Syndesus*, and *Ceruchus* MacLeay, 1819.

In recent years there have been three new species described: *Psilodon paschoali* Pardo-Locarno & Ríos-Málaver, 2011 from Colombia; *Syndesus luki* Onore, Bartolozzi & Zilioli, 2011 from Ecuador, being the only original description that recognizes *Syndesus* as an Australasian and South American genus. Finally, *Psilodon buhrnheimi* Grossi & Aguiar, 2014, which is the first and the only species of *Psilodon* known from the Amazon region.

Psilodon has never been the object of a taxonomic revision, and the isolated descriptions of new species, as well as the divergent generic classifications, make it difficult to define the inter-specific limits in Syndesini. There is also a significant gap in regard the knowledge about the life history of the tribe in South America, and in the absence of ecological data, we propose the use of panbiogeographic analyses, not only to infer the biogeographic history of this taxon, but also to identify possible insect-plant associations for future studies. We provide the first taxonomic revision of *Psilodon* Perty, 1830, with the description of six new species from Brazil and an updated distribution map for all the known species. We also describe a new South American Syndesini genus.

The generalised tracks obtained for the Fagales plants showed to be highly congruent with the *Psilodon* track, suggesting that besides the allopatric events across the Andes, the physical barriers of the Brazilian Atlantic rainforest, and the recurrent connections between Eastern Brazil and the Amazonian region, the insect-plant association between *Psilodon* species and Fagales plants has strongly influenced the historical distribution of the genus. It was not possible to recover similar patterns for N. gen. 1, but given its high resemblance with the *Syndesus* fossil from the Dominican Republic, it is expected that the answers regarding the biographic history of this taxon would be found along the Antilles.

Materials and methods

Specimens and Taxonomic Material.

A total of **67** specimens from all species of the genus were studied from the following collections.

CEMT	Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, MT, Brazil.
CERPE	Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, PE, Brazil.
CZPB	Coleção Zoológica Paulo Buhrnheim, UFAM, Manaus, AM, Brazil.
EPGC	Everardo and Paschoal Grossi Collection, Nova Friburgo, Rio de Janeiro.
HEC	Hope Entomological Collections, Oxford University Museum of Natural History, Oxford, UK.
MCN	Museu de Ciências Naturais, Fundação Zoobotanica do Rio Grande do Sul, Porto Alegre, RS, Brazil.
UNSM	University of Nebraska State Museum, Lincoln, NE, USA.
MNHN	Muséum national d'Histoire naturelle. Paris, France.
MNRJ	Museu Nacional Rio de Janeiro, Rio de Janeiro, RJ, Brazil.

MZUEFS	Museu de Zoologia Universidade Estadual de Feira de Santana. Feira de Santana, BA, Brazil.
UMSP	University of Minnesota – Saint Paul Insect Collection. Minneapolis, MN, USA.
ZIN	Zoological Institute of Russian Academy of Sciences. Moscow, Russia.

Morphological characters. Specimens were viewed under a dissecting microscope Zeiss Stemi 508 at 0.63 to 0.50x under fiber optic illumination. The species descriptions are based on the following conventions. ***Size*** was determined using a 0–150 mm digital calliper. ***Length*** was measured from the apex of the mandible to the apex of elytra. ***Width*** was measured at the widest point of the body, mainly across the pronotum and the elytral humeri. ***Colour*** as determined under LED spot illumination. The characteristics of the body surface such as the presence of punctures or setae were based on the described macroscopic types by Holloway (1997; 2007). ***Vestiture*** appearance is based on description made under high magnification. ***Puncture size*** was determined at 40 x magnification and according to Paulsen (2005) who proposed four categories, coarse, present as pits (above 0.10 mm), large (0.06–0.10 mm), moderate (0.03–0.05 mm) and fine (less than 0.03 mm). ***Puncture density*** is also based on Paulsen (2005), and defined as contiguous, dense (punctures separated by less than two puncture diameters), moderate (punctures separated by 2–4 puncture diameters), sparse (separated by four puncture diameters), or shagreened. ***Discrimen***, is defined as a discrete longitudinal groove present along the metaventral concavity, nevertheless, this trait is not present as a complete groove in most specimens of *Psilodon*; instead, it is possible to see a variable shallow groove. All male and female ***Genitalic*** structures are named according to Holloway (1960, 1961, 1998 and 2007), Lawrence *et al.* (2011), and Cristovão & Vaz-de-Mello (2020) consisting of the 9th and 10th abdominal segment. Descriptions of male genitalia were made considering the ventral, dorsal and lateral views, including characteristics of the basal piece, parameres, median lobe and everted sac. For the females we included information related to a portion of the sclerotized structures on the 9th and 10th abdominal segments, and reproductive structures *per se*, only considering the ventral view. Dissections of male and female genitalia were conducted as proposed by Grossi & Aguiar 2014.

Specimens Pictures were obtained with a Leica® DFC 500 digital camera attached to a stereomicroscope Leica® MZ 16. Images were captured by using the IM 50 (Image Manager) software, and then manipulated using Combine ZP v.1.0 (Hadley 2010). Posterior edition was made using GIMP v.2.10.30 (Kimball & Mattis 1995-2018).

Distribution map was built using different shapefiles as layers. The base layer is conformed by the *South America* shapefile from the Environmental Systems Research Institute (ESRI), available at http://tapiquen-sig.jimdo.com. The second layer is composed by the shapefile of the *Biogeographic regionalization of the Neotropical region* produced by Morrone *et al*. (2022), which is available at http://neotropicalmap. atlasbiogeografico.com. The last layer contains a *Digital Elevation Model* (DEM) for South America, published by the Center for Earth Resources Observations and Science, available at http://databasin.org/datasets/d8b7e23f724d46c99db1421623fd1b4f. We also add a layer including the geological structures from eastern Brazil obtained at the Brazilian Geological Service (https://geosgb.cprm.gov.br/geosgb/). The remaining layer are the result of the addition of *distributional data* from collection data from all specimens and verified data from the iNaturalist platform. We also generated *individual and generalized tracks* for *Psilodon* and South American Fagales that was produced according to the following information.

Track analyses were performed in order to identify geographic patterns of distribution for *Psilodon* Perty, 1830 and N. gen. 1 Cáceres & Grossi, based on distributional patterns of plant species thought to be strongly related with different lucanid taxa, as is the case of different genera of the order Fagales (beeches). The data used for the Fagales Track Analysis were obtained from the Global Biodiversity Information Facility (GBIF) including data from 77 datasets (GBIF.org. 29 July 2022. Download https://doi.org/10.15468/dl.zzkkut) under the search conditions: Occurrence / Preserved specimens / Material sample from Argentina, Bolivia, Brazil, Colombia, Ecuador, Paraguay, Peru and Venezuela, countries with *Psilodon* and N. gen. 1 occurrences. After obtaining the data we only kept the records with available coordinates. Additionally, we performed Track analysis for all described species in this work, except for *Psilodon seguyi* (Didier, 1929); *Psilodon gilberti* Boucher, 1993; *Psilodon kanynde* Cáceres & Grossi, 2022 **new species**, and *Psilodon amati* Cáceres & Grossi**,** which only have one recorded locality. All analyses were obtained using the MartiTracks algorithm (Echeverría-Londoño & Miranda-Esquivel 2011), which is executed using a command-line (bash-like) interface. It calculates the minimum spanning tree, representing an individual track for every analysed species. Afterwards it looks for the spatial congruence among segments of the minimum spanning trees for producing a generalised distribution pattern, that corresponds to the generalised tracks. Individual and generalised tracks for South American Syndesini were compared with the distribution patterns obtained for South American Fagales genera (*Alfaroa* Standl. (Juglandaceae); *Carya* Nutt. (Juglandaceae); *Castanea* Mill. (Fagaceae); *Casuarina* L. (Casuarinaceae); *Juglans* L. (Juglandaceae); *Morella* Lour. (Myricaceae); *Nothofagus* Blume (Nothofagaceae); *Quercus* L. (Fagaceae); *Trigonobalanus* Forman (Fagaceae) aiming to evaluate the relation between plant and Syndesini distribution in South America.

Results:

Taxonomy:

Psilodon Perty, 1830

Hexaphyllum Gray, 1832 (synonymy)

Syndesus MacLeay, 1819 (partim)

Type-species: *Psilodon schuberti* Perty, 1830 (by monotypy)

Diagnosis

Genus extremely close to the Australasian genus *Syndesus* MacLeay, 1819. With strong sexual dimorphism in mandibles, antennal lamellae, and pronotal tubercule. Males and females with brown to black colour, with dark-red tones in most species, sometimes with dark and light specimens from the same species. Head anteriorly emarginate (see Fig. 1f.), dorsally with a v-shaped excavation along frons, extended anteriorly; vertex convex, concealed under pronotal projection. Labrum convex, with rounded apex, projected between mandibles. Mentum sub-trapezoidal. Gula conspicuous and convex, visible in lateral view. Antennae non-geniculate (see Fig. 3f.), with six or seven lamellae. Eyes conspicuous, almost as long as sides of head. Mandibles of males with one median tooth (denominated Alpha), sometimes located close to apex forming a concave region (in Andean species), a basal lobe (denominated Beta) and an internal tooth (denominated Gamma) (see Fig. 1b.); females with narrow mandibles, slightly enlarged dorsally; with no teeth, instead withby a longitudinal tooth-like surface from base to apex dorsally. Pronotum projected anteriorly, with a pronotal tubercle covering head medially (see Fig. 5b. and c.), reduced in females; dorsal surface with a longitudinal medial groove, usually complete, sometimes interrupting females' tubercle, punctation variable, from moderate to coarse, sometimes with shallow excavations and lateral constrictions. Elytra with well-defined striae and interstrial costae; humeri not-striate, with tooth-like lateral projections, absent in some Andean species. Anterior tibiae distally enlarged with several strong teeth and tooth-like projections among teeth; meso and metatibiae with two to several acute teeth and tooth-like projections, setose, with enlarged apex. Male aedeagi (Fig. 5e-g.) symmetric, phallobase sub-triangular, with a strong to somewhat fine anterior constriction, with subparallel to slightly convex sides; median lobe enlarged at base except in Andean species. Female genitalia (Fig. 5d.) with elongate and setose styli, with undivided gonocoxites, extended beyond lateral paraprocts.

Description male ***Size*****:** *Total length*. 10.29-14.81 mm *Total width*. 4.34-6.61 mm. ***Colour*****:** Body varying from entirely black to somewhat brown, also with reddish tones. ***Head*****:** Shape transverse, anteriorly emarginate; labral surface smooth, shape elongate, convex to somewhat flattened in some species, rounded at apex, with a tuft of conspicuous setae. Mentum trapezoidal with a somewhat lobed anterior margin, with few large to coarse punctures, also with yellowish curved setae. Gula conspicuous, strongly convex, sub-trapezoidal to oblong, easily visible in lateral view, surface smooth, sometimes with sparse fine punctation. Gena with coarse to large punctures, dense, with yellowish, strongly curved to appressed setae. Anterior margin of head with shagreened surface, somewhat carinate, glabrous; frons slightly excavate; vertex concealed, covered by anterior portion of pronotum. Eyes strongly developed, extended from anterior to posterior margins of head; interocular distance 1.7- times longer than head sides. Mandibles symmetric, with a median to subapical tooth (Alpha), a basal internal tooth (Gamma) and a basal lobe (Beta); strongly curved inwards and apically directed upwards directed apically; base of mandibles expanded in most species, producing a reduced dorsal surface (Fig. 1a-c.) reduced in Ecuadorian species (Fig. 7b; 11b.). ***Pronotum*****:** shape convex, anterior margin projected anteriorly, with a convex, and frequently conspicuous tubercle; posterior margin sinuate; anterior angles reaching posterior portion of eyes; discal groove present, shallow to strong; surface with moderate, large or coarse punctures, dense to contiguous, sometimes with two to four distinct excavations; lateral pronotal carina distinct, separating disc from hypomeron, complete and continuous with posterior and anterior margins, except at anterior projection, with a somewhat scalloped surface, and minute simple setae. ***Elytra*****:** Elytral humeri not striate, with or without a tooth-like projection; surface strongly punctate with well-defined striae; striae with coarse punctures and minute barbed setae rising from anterior portion of pits; interstriae forming longitudinal costae, with moderate to large, and dense to contiguous punctation; epipleuron complete to apex, concave to somewhat flat, with dense to contiguous punctation, large or coarse basally, becoming moderate at apex; elytral declivity convex at interstrial joint. ***Legs:*** Tibiae serrate, with stronger and higher number of teeth at protibiae; meso and metatibiae with few strong teeth, normally varying from three to four well-defined teeth, always with several tooth-like projections, sometimes with two serrate lines along external surface of tibiae; apex enlarged with tooth-like projections. ***Venter*****:** Prosternum carinate along anterior and posterior margins; with a convex, somewhat conspicuous process; surface with coarse to large punctures, densely distributed. Mesoventrite convex, with contiguous to dense coarse punctation and conspicuous appressed setae. Metaventrite distinctly convex, medially somewhat smooth, frequently with conspicuous appressed setae; lateral portions with coarse to large punctation, dense to sparsely distributed; discrimen not present as a groove, instead present as a complete or incomplete shallow groove, with a declivity at posterior end. Abdominal ventrites with fine, dense to contiguous punctation, sometimes with moderate to large punctation across posterior margins;

posterior margin of ventrites I—-IV ventrites with a transverse carina; last ventrite with conspicuous setae at apex. ***Genitalia*:** Genital capsule symmetric; dorsally divided into three regions, discal plate sub-trapezoidal, distally almost truncate; dorso-lateral plates sub-triangular, extending anteriorly as a single strut with sharp apex; ventral plate transverse to oblong, becoming narrower anteriorly, forming a single strut at proximal portion; distal margin rounded to almost truncate, surface with simple, appressed setae, densely distributed, projdirected to median axis. Aedeagus symmetric, with subparallel sides; shape from strongly elongate (approx. 4.0 times longer than wider) and narrow to moderately elongate (approx. 2.5 times longer than wider). Anterior and posterior phallobase divided by a strong constriction, forming two well-defined regions. Anterior phallobase rounded apically, varying from a sub-trapezoidal to sub-triangular shape. Posterior phallobase almost subparallel-sided, with slightly convex to somewhat concave sides. Parameres with straight sides in most species;, oin lateral view from strongly to slightly concave, apically rounded. Median lobe enlarged at base, gradually narrowing apically, slender in strongly elongate aedeagi.

Females: ***Size*:** *Total length*. 11.51–15.27 mm. *Total width.* 4.49–6.54 mm. General morphological aspect as males, except in the following. ***Head:*** Dorsally more exposed, showing frons and a portion of vertex, anteriorly emarginate; vertex somewhat excavate; mandibles symmetric, narrow, almost straight, concave at dorsal portion, toothless, instead with a longitudinal external carina from base to apex; dorsal surface punctate, mainly basally, punctures large to somewhat coarse, denser at base, getting sparse distally, with simple, erect to slightly curved yellowish setae. ***Pronotum*:** Anterior angles less distinct than in males; anterior margin less projected forward, with pronotal tubercle reduced, sub-trapezoidal shaped in dorsal view; discal groove deeper than in males, often complete to apex, sometimes reaching pronotal tubercle, dividing it in two portions. ***Legs:*** Spurs at meso- e and metatibiae subequal, and smaller. ***Venter:*** Surface with more conspicuous setae; prosternal process sometimes reduced, almost interrupted by procoxae. ***Abdomen:*** Abdominal ventrites narrower distally. ***Genitalia:*** Styli elongate and setose, with undivided gonocoxites, extended beyond lateral paraprocts,. showing almost the same width, except proximally where each gonocoxite is abruptly narrowed, producing a slender projection. Lateral paraprocts enlarged proximally, usually strongly curved showing an almost "C" shape, with apex rounded to somewhat truncate apically.

Distribution: South America, Argentina, Brazil, Bolivia, Peru, Ecuador, Colombia and Venezuela.

Remarks: *Psilodon* Perty, 1830 is probably the Llucanidae genus with the more extensive distributional range known for Neotropical Sstag beetles, with records of occurrences in most South American countries. Its strong resemblance with the Australasian genus *Syndesus* MacLeay, 1819 suggests a Gondwanan origin of *Psilodon*. Some authorsThere haves been discussed by some authors that *Syndesus* and *Psilodon* must be considered synonyms instead of independent taxa but, besides the early separation between the Australasian and Neotropical regions, it is possible to recognize several diagnostic traits that allow the characterization of *Psilodon*. *Psilodon* species can be distinguished from Syndesus by the followingThese traits: are the more robust instead of the cylindrical habitus of male and female bodies; less conspicuous punctation along most body surfaces; presence of Alpha, Gamma, and Beta teeth (Didier 1929) in male mandibles; more rounded antero-lateral angles of pronotum; a considerable reduction in pronotal tubercle, making it less projected anteriorly; less strong tibiale teeth; metaventrital shape strongly convex, among others.

Lucanidae: Syndesinae: Syndesini: *Psilodon*

Key to *Psilodon* species

Specimens with conspicuous mandibles curved inwards, with three teeth,; with conspicuous pronotal tubercle **(*Males*)... 1**

Specimens with reduced mandibles dorsally concave, with a longitudinal laminar tooth; pronotal tubercle distinctly reduced, not covering frontal surface **(*Females*)... 14**

1. Apex of mandibles concave, with a conspicuous and dense tuft of yellowish setae (*Andean species*) **Figure 1a.. 2**

1´. Apex of mandibles without distinct tuft of setae (*Brazilian species*)**....................................... 6**

2. Base of mandibles with Gamma tooth and Beta lobe free, distinctly separated **Figure 1b**; elytral humeri with a tooth-like projection**... 3**

2´. Base of mandibles narrow, Gamma tooth and Beta lobe merged; lacking tooth-like projections at elytral humeri (*Ecuadorian species*) **Figure 1c...5**

3. Antennal club with seven lamella**... *Psilodon gilberti*** (Figure 9.)

3´. Antennal club with six lamellae (*Colombian species*)**.. 4**

4. Body colour black with reddish tones; body mostly covered with coarse punctation; pronotal surface with contiguous punctures, also with a shallow discal groove and a somewhat reduced pronotal tubercle; antero-lateral angles of pronotum and median portion not strongly projected anteriorly, producing an almost quadrate shape; elytral humeri with somewhat reduced tooth-like projections**...** ***Psilodon westwoodii*** (Figure 6.)

4´. Specimens with blackish tones; punctures of different sizes and distribution, not contiguous along pronotum; pronotal tubercle distinct; antero-lateral angles not strongly projected anteriorly, medially distinctly projected covering frons. Elytral humeri with tooth-like, acuminate projections, highly resemblant to Brazilian species morphology, distributed at Colombian "Cordillera Oriental" and "Altos Mirandinos" in Northern Venezuela**...** ***Psilodon paschoali*** (Figure 10).

5. Body colour dark-brown; pronotum with strong and complete discal groove, also with four excavations at disc; scutellar shield with large to somewhat coarse and dense punctation, almost uniformly distributed, not narrowed posteriorly; elytra with one interstrtial costa for each striae**...** ***Psilodon seguyi*** (Figure 7 b, c, e-g.)

5´. Body colour black; pronotum with a strong discal groove, complete; surface with four strong excavations; discal surface with large to coarse punctation, becoming stronger and contiguous at sides; scutellar shield narrowed posteriorly, with few large punctures, mainly distributed anteriorly; elytra with one interstrial costa for every two striae**...** ***Psilodon luki*** (Figure 11b, c, e-g.)

6. Apex of mandibles acute, almost acuminate in some species**...7**

6´. Apex of mandibles rounded, with a dorsal, fine preapical tooth-like projection **(Figure 1d.)**, visible in lateral view; Metaventrital convexity somewhat smooth and glabrous, laterally with conspicuous, strongly curved to appressed setae. State of Rio de Janeiro**....... *Psilodon schuberti*** (Figure 4c; 5 b, c, e-g.)

7. Males with mandibles abruptly curved distally, distinctly enlarged basally; body with reddish tones; pronotal groove somewhat strong with coarse and dense punctation; aedeagus robust. States of São Paulo and Santa Catarina**....................... *Psilodon* n. sp. 5 New species** (Figure 17 b, c, e-g)

7´. Males with curved mandibles but never abruptly curved distally, remaining traits with different configuration**... 8**

8. Body colour dark-purple with some dark-red tones, sometimes apparently black; mandibles narrow, Alpha tooth somewhat slender, antero-dorsally projected; pronotal disc with two to four shallow excavations, pronotal sides somewhat constricted; discal groove strong and complete. State of Rio de Janeiro**.. *Psilodon n. sp. 4* New species** (Figure 12)

8´. With different combination of traits from step 8**... 9**

9. Procoxal carina reduced, only visible proximally or complete from antero-proximal portion to postero-distal end of coxae**.. 10**

9’. Procoxal carina medially interrupted, continuing as an almost straight line distally **(Figure 1e.)**; supra-antennal projections antero-laterally oriented, rounded apically with a weakly carinate surface; in lateral view mandibles with rounded apex, Beta lobe sub-trapezoidal, extended through base. State of Ceará**..** ***Psilodon n. sp. 1*** **New species.** (Figure 13)

10. Antero-lateral angles of pronotum projected anteriorly, reaching posterior portion of eyes, medially with a well-defined projection, extended beyond apex of anterior angles, sometimes reaching anterior margin of head**...** **11**

10´. Shape of pronotum subquadrate, median projection not extended or only finely extended beyond apex of anterior angles. Supra-antennal projection with distinctly truncate apex, projected laterally **(Figure 1f.)**. In lateral view, mandibular apex acuminate; Beta lobe obsolete; Epipleuron strongly sinuate, visible in lateral view. States of Pará, Amazonas, and Rôndonia……. ***Psilodon buhrnheimi*** (Figure 12)

11. Pronotal groove somewhat shallow, present as a wide longitudinal depression, complete or incomplete**...** **12**

11´. Pronotal groove narrow and shallow, never reaching anterior or posterior margins of pronotum **(Figure 2a.)**. Metaventrite with shallow, wide groove along posterior portion of metaventrital convexity **(Figure 2b.)**. State of Bahia**...** ***Psilodon xerophilicum*** (Figure 8 b, c, e-g.)

12. In lateral view, mandibular appearance robust, almost as wide as eyes diameter**....................** **13**

12´. In lateral view, mandibles distinctly slender; pronotal tubercle convex; anterior and posterior angles of pronotum almost straight, forming oblique angles. Aedeagus with a strongly transverse and slender dorsal cross-bar. State of Goiás................... ***Psilodon*** **n. sp. 2 New species.** (Figure 14).

13. Dorsal face of head distinctly exposed; pronotal groove shallow, medially deeper with coarse and contiguous punctation. Procoxal carina forming a convex curve proximally, gradually projected to posterior portion of coxae distally **(Figure 2c.)**. Aedeagus and median lobe distinctly slender. State of Alagoas... ***Psilodon*** **n. sp. 6** (Figure 18)

13´. Pronotal groove with dense punctation, never contiguous, shallow but complete from posterior margin to proximal portion of pronotal tubercle. Procoxal carina straight, forming an oblique angle (**Figure 2d.**). Scutellar shield with coarse punctation, only distributed proximally. States of Espirito Santo and Minas Gerais (in part)....... ***Psilodon*** **n. sp. 3 New species** (Figure 15 b, c, e-g.)

14. Females with well-defined excavations (four) at pronotal surface **(Figure 2e.)** (*Ecuadorian species*).. **15**

14´. Females without pronotal concave spots (*Brazilian species*).. **16**

15. Body with brownish to dark-red tones. Supra-antennal carina projected antero-dorsally **(Figure 2f.)**. Pronotal surface with dense and coarse punctation. Metaventrital convexity with a longitudinal shallow groove, wider posteriorly, forming a sub-triangular spot **(Figure 3a.)**.. ***Psilodon seguyi*** (Figure 7a, d.)

15´. Body entirely black. Supra-antennal carina projected upwards **(Figure 3b.)**. Pronotal surface with contiguous and coarse punctation, also with a strong and conspicuous longitudinal groove. Metaventrital convexity with a shallow groove, almost reaching anterior margin, uniformly wide, medially stronger **(Figure 3c.)**.. ***Psilodon luki*** (Figure 11 d, e.)

16. Supra-antennal carina projected upwards; pronotum strongly convex.................................... **17**

16´. Supra-antennal carina projected dorso-medially, also finely projected posteriorly; pronotum slightly flattened; pronotal tubercle partially interrupted by discal groove **(Figure 3d.)**... ***Psilodon xerophilicum*** (Figure 8 a, d.)

17. Metaventrital convexity with shallow groove, sometimes obsolete.. **18**

17´. Metaventrital convexity with shallow groove, getting wider posteriorly, medially with a fine, but well-defined groove, resembling a discrimen (**Figure 3e.**). State of Espirito Santo.. ***Psilodon* n. sp. 3** (Figure 15 a, d.)

18. Surface of vertex and frons with two distinct smooth spots **(Figure 3f.)**, forming a v-shaped region projected towards antero-lateral angles. State of Rio de Janeiro**……..** ***Psilodon schuberti*** (Figure 4 a, b; 5 a, d.)

18´. Head surface entirely punctate, punctures coarse and dense, sometimes with two fine smooth spots, not reaching frontal surface **(Figure 3g.)**. Head surface and mandibles highly setose**..** ***Psilodon*** **n. sp. 5** (Figure 17 a,d.)

Psilodon schuberti **Perty, 1830**

Hexaphyllum brasiliense Gray, 1832 (synonymy proposed by van Roon (1910))

Figures 4 and 5

Examined material: Holotype of *Hexaphyllum brasiliense* Gray (examined by photographs) labels: a) old, white, handwritten label, “Rio”; b) old, white, handwritten label, “brasiliense/ Gray Type” (HEC). Holotype of *Psilodon schuberti* labels: a) Type, Grey, Griffith, [not possible to read], 1832.p 536 T.46 14, Coll. Hope Oxon; b) BLC; c) old, red, handwritten label, Hexaphyllum Brasiliense ♂, Gray in Griff.,/ Psilodon schuberti Perty.- ♀; d) old, white, handwritten label, Psilodon schuberti, Perty dep.; e) Type Col: 335 ½, Hexaphyllum brasiliense Gray, (HEC).

Additional material: BRAZIL: Rio de Janeiro, Nova Friburgo A: 1100m S. Caturama 8.i.1999 E. & P. Grossi leg. 1 ♂ (CERPE); Mun. Resende – Serrinha de Alambari – xii. 2008 U. Caramaschi & H. de Niemeyer col. 1 ♂; Florestinha do Cabo Frio 08/12/1999 (CERPE); Macaé de Cima Alt. 1500m 28.xii.2000 Isabel Miller leg. 1 ♂ (EPGC); Nova Friburgo A: 1100m S. Caturama 3.i.1999 E. & P. Grossi leg.1 ♂ (CERPE); same data except 5.i.1999 1 ♂ (CERPE); same data except 1100m, 15.ii.2009, Interceptação, E. Grossi Leg. 1♀ (CERPE); Nova Friburgo 10.i.2001 E. & P. Grossi leg. 1♀ (CERPE); V. de Mauá, i.97, 1100m, E. & P. Grossi Leg 1♀ (CERPE); SESC, Luz, 800m, 19.xii.2008, L.P.C. Grossi Leg. 1♀ (CERPE); Nova Friburgo, 2015, P. Grossi Leg. 1♀ (CERPE).

Diagnosis: males and females dark-brown with reddish tones, sometimes violet red, with darker tones, head transverse, anteriorly emarginate and concealed by anterior region of pronotum. Antennae with six lamellae. Mandibles with rounded apex, wider at preapical portion; Alpha tooth somewhat elongate and erect, with truncate apex, sometimes sub-trapezoidal, not easily distinguished in dorsal view; Gamma tooth opposite to Beta lobe, both extended laterally. Pronotum projected anteriorly, with somewhat conspicuous tubercle. Elytra strongly punctate, humeri with tooth-like projection. Anterior phallobase narrower than posterior one, rounded at sides, and distally truncate; temones convergent and tubular; median lobe basally enlarged, getting narrower distally, with fine punctation. Females as males except for a more exposed head and straight mandibles, with no teeth, instead with laminar carina along dorsal portion. Pronotal tubercle reduced, sometimes medially interrupted by discal groove. Also with more conspicuous punctation. Genitalia somewhat trapezoidal, elongate posteriorly; coxites continuous, proximally abruptly narrowed.

Description Male ***Size*****:** *Total length*. 14–19 mm *Total width*. 6–6.1 mm. ***Colour*****:** dorsally dark brown, with somewhat reddish tones; ventrally brown, with reddish tones. ***Head*****:** Shape transverse, strongly emarginate anteriorly; surface punctate, punctures large, dense, with somewhat conspicuous, erect to slightly curved yellowish setae; antennae with six lamellae, supra-antennal projection carinate, with rounded, setose apex. Mandibles symmetric, curved inwards, apex rounded and directed upwards; external face punctate, punctures moderate, with yellowish curved to decumbent setae; inner surface almost smooth except at apex, punctures moderate to somewhat dense with slightly curved to decumbent yellowish setae distributed along the dorsal portion through apex; Gamma tooth medially projected; Beta lobe projected through external face, wider than Gamma tooth, with a sub-trapezoidal shape; Alpha tooth suberect with rounded to somewhat truncate apex. ***Pronotum:*** Pronotal tubercle conspicuous, covering median portion of head, reaching anterior margin of head in some specimens; surface punctate, punctures large to moderate and dense, with minute setae; discal groove shallow, somewhat broad; anterior and posterior angles rounded. ***Elytra*****:** scutellar shield exposed, surface mainly smooth, with some moderate punctures, margins slightly carinate, anterior margin with somewhat continuous transverse carina; elytral humeri not striate, with fine to somewhat moderate punctation, and a rounded to somewhat acuminate tooth-like projection; interstriae carinate, forming longitudinal costae with moderate to large punctures, moderately to sparsely distributed; epipleuron concave, with complete, scalloped, and posteriorly narrowed carina; epipleuron with large to somewhat coarse punctures, proximally with yellowish and appressed to strongly curved setae, getting shorter and suberect distally, carina with fine, decumbent setae. ***Legs:*** dorsal face of protibiae carinate; external face irregularly serrate, with variable number of strong teeth and tooth-like projections, decreasing in size basally, always with two apical strong teeth and one apical spur; external and internal face setose, externally with conspicuous yellowish curved setae increasing in size distally. Mesotibiae with distinct yellowish suberect setae along whole surface; dorsally with two lines of teeth, anterior line with strong teeth, increasing in size distally, also with tooth-like projections between teeth; posterior line with several inconspicuous tooth-like projections; apex expanded with variable number of apical teeth and two subequal apical spurs, being the posterior one slightly slender and acuminate. Metatibiae with yellowish, suberect to decumbent setae; externally with line of variable number of somewhat strong teeth, increasing in size distally, also with row of tooth-like projections along the posterior portion, apex enlarged, resembling a broad strong tooth. ***Venter*****:** Prosternum anteriorly carinate, with a continuous line of yellowish appressed setae, punctate, punctures coarse and dense, with yellowish appressed setae; prosternal process narrow, slightly convex, inconspicuous; procoxae with a transverse and finely setose carina. Mesoventrite with moderate and dense punctation, and yellowish appressed setae, becoming longer posteriorly. Metaventrite convex with large to somewhat coarse punctures, mainly dense but sparse in some portions; discrimen absent, instead with longitudinal, almost smooth region, enlarged posteriorly. Abdominal ventrites carinate along posterior margins, showing a continuous line of yellowish, strongly curved to decumbent setae, along posterior margins; surface highly finely and densely punctate. ***Genitalia:*** Aedeagus symmetrical, subparallel, narrower proximally, anterior margin truncate to slightly rounded; phallobase sub-triangular, narrower at base; parameres with almost straight sides, rounded at base, apex somewhat truncate and poorly sclerotized; median lobe enlarged basally, with a three lobed apex, laterally with some fine punctation. Dorsal cross bar with two strong emarginations along posterior margin, anterior margin concave.

Females: ***Size*****:** *Total length*. 11–22.2 mm. *Total width.* 5–7mm ***Colour:*** *as males.* ***Head:*** larger than males head, more visible in dorsal view, emarginate; frons excavated; mandibles symmetric, almost straight, dorsally concave; finely carinate at base; reduced when compared with males, as long as the first half of males' mandibles, narrower, with no teeth, and rounded apex; maxillary and labial palpi shorter than in males; surface punctate, mainly basally, punctures large to somewhat coarse, denser at base and getting sparse distally, with simple, erect to slightly curved yellowish setae. ***Pronotum*****:** as males but presenting less distinct anterior angles; anterior margin less carinate and finely projected anteriorly; discal groove more distinct, deeper distally. ***Legs:*** as males except for presenting subequal and smaller apical spurs at meso- and metatibiae. ***Genitalia:*** Styli elongate, internally with an oblique angle at apex, also with strongly punctate surface and conspicuous setae with undivided gonocoxites, extended beyond lateral paraprocts. Gonocoxites showing almost same width except proximally where each one is abruptly narrowed, producing slender projection. Lateral paraprocts C-shaped, enlarged proximally.

Distribution: Brazil, State of Rio de Janeiro – Atlantic Province, Parana Province (partially) (Morrone 2022).

Remarks: *Psilodon schuberti* is the type species of this genus. The original description made by Perty (1830) was based on a female specimen with locality “Provincia Piauhiense” now known as the State of Piauí, located in North-East Brazil, nevertheless all recent records for *P. schuberti* are from the Rio de Janeiro state (South-East Brazil), suggesting that the female Holotype of this species is actually from South-East Brazil. The Holotype male of *Hexaphyllum brasiliense* described by Gray (1832) from Rio de Janeiro matches the description of *P. schuberti* males in this work, which supports the synonymy of both genera. According to the identification labels of the female originally described for the State of Piauí deposited at the University of Oxford, it was associated with Gray´s male, and even though we cannot entirely deny the presence of this species in Piauí, according to *personal communications* made by Professor Fernando Vaz-de-Melo (Universidade Federal do Mato Grosso), it is probable that the material collected by Karl F. von Martius and Johann B. von Spix between 1817 and 1820, later studied by M. Perty, got mixed during the transportation to Europe, and some information regarding localities could be mistaken. Given the strong similarities shown by females of all *Psilodon* species and the lack of enough information from the first described female, we prefer to consider *P. schuberti* as a species restricted to the State of Rio de Janeiro.

Psilodon westwoodii (Hope, 1840) (*Hexaphyllum*)

=*Hexaphyllum aequinoctiale* Buquet, 1840

Figure 6.

Examined material. Lectotype, defined here labeled: Colombie, Ibague, Fr. Claver / "Handwriting" Hexaphyllum Brasiliense Grey / Ex. coll. Boileau 1♂ (MNHN).

Diagnosis: Male colour black with some dark-red reflections mainly distributed ventrally. Head and pronotal surface strongly punctate, punctures dense to contiguous. Frons and vertex excavate. Mandibles with concave apex, in lateral view somewhat truncate, also with conspicuous tuft of setae internally; Gamma tooth strong, located medially and almost directed upwards; Beta lobe also strong, sub-trapezoidal and projected laterally. Pronotal tubercle somewhat reduced, surface with strong contiguous punctation. Odd-numbered interstriae not reaching elytral apex; humeri with somewhat rounded projections, extremely reduced. Ventrally strongly punctate; metaventrital discrimen present as a longitudinal shallow groove.

Description Lectotype Male: ***Size***: *Total length*. 1.9 mm. *Total width.* 6 mm. ***Colour***: dorsally mainly black with some dark-red and brownish tones. Venter dark-red. ***Head:*** Shape transverse, strongly emarginate anteriorly; surface punctate, punctures large to coarse, dense, with simple, curved yellowish setae. Antennae with six lamellae; supra-antennal projection carinate, with acuminate and directed upwards apex, setose. Mandibles with truncate apex, forming a concave region with Alpha tooth; external face with moderate to large punctures, also with slightly curved to decumbent simple setae; dorsal surface finely excavated, with contiguous large to moderate punctures, and erect yellowish setae; inner face with a conspicuous tuft of erect to slightly curved setae at apex; Gamma tooth sub-conical, located medially, directed outwards; Beta lobe located at base, directed outwards, sub-triangular to somewhat trapezoidal; Alpha median tooth located close to apex, producing a continuous concave region with mandibular apex. ***Pronotum*:** Pronotal tubercle reduced, not covering median region of head; surface with contiguous punctation, large to coarse, with minute setae; discal groove shallow; anterior and posterior angles rounded. ***Elytra*:** scutellar shield exposed, with dense, moderate to large punctures, not carinate; elytral humeri not striated, with dense moderate to coarse punctures, and a somewhat truncate tooth-like projection; striae with coarse punctation; interstrial costae with moderate to large punctures, densely to sparsely distributed; epipleuron concave, with a scalloped carina, complete to apex, narrow at apex, with large to somewhat coarse punctures, mainly contiguous and somewhat shallow, with yellowish decumbent setae. ***Legs*:** dorsal face of protibiae with a longitudinal carina; external face serrate, with several strong teeth, increasing in size distally, and with few tooth-like projections between strong ones, also with two apical strong teeth and one apical spur; external and internal face setose, with yellowish curved to decumbent setae. Mesotibiae with yellowish conspicuous suberect to decumbent setae increasing in size distally; external face serrate with several tooth-like projections, most of them covering base of setae, also with one to three preapical strong teeth, increasing in size distally, apex expanded with variable number of strong tooth-like projections, and two subequal apical spurs. Metatibiae with yellowish decumbent setae; surface covered by several tooth-like projections; apex expanded as Mesotibiae, also with two apical spur, being the anterior one shorter. ***Venter*:** Prosternum carinate along anterior margin, with a continuous row of yellowish appressed setae, punctate, punctures coarse and dense with minute setae; prosternal process wide and carinate becoming narrower posteriorly, more conspicuous when compared with other *Psilodon* species. Mesoventrite punctate, except for a smooth spot located medially, punctures large, dense with short yellowish appressed setae, anterior portion convex, getting somewhat concave posteriorly. Metaventrite convex, with moderate punctures, going from dense at margins to moderate and sparse medially; discrimen present as a shallow groove dividing metaventrite into two portions, posterior portion with a sub-triangular projection. Abdominal ventrites slightly carinate along posterior margins, surface shagreened, with decumbent setae, always longer at posterior portions. ***Genitalia*****:** Aedeagus symmetrical, subparallel, anterior margin somewhat rounded. Phallobase sub-triangular**,** lateral margins slightly concave. Parameres with almost straight sides, convergent distally, posterior margin rounded, with some dark setae visible dorsally. Median lobe, enlarged at base, with strongly curved apex, somewhat sclerotized along margins and apically. Dorsal cross bar "U" shaped, strongly convex with three apparent projections at posterior margin.

Distribution: Colombia, Cordillera Central – Magdalena Province (Morrone 2022).

Remarks: Even though *Psilodon westwoodii* shares several traits with other Andean member of the genus, this species shows several unique characteristics, as the strong and contiguous punctation along head and pronotum, also the strong development of all mandibular teeth, especially of Beta lobe, which is normally reduced in most *Psilodon* species; other mandibular traits which are also present in Ecuadorian species, is the almost the truncate to slightly concave apex produced by the distinct distal position of the Alpha tooth, and the apical tuft of conspicuous setae. In the original description of *P. westwoodii*, Hope (1840) did not mention a specific locality in "New Granada". In his description, Buquet (1840) defines Santafé de Bogotá as the type location but the lectotype studied here from the MNHN, was collected at the city of Ibagué (Tolima), which is located at the Central "cordillera" with an altitude of 1.300 m, in contrast to Bogotá which is located at the Eastern "cordillera" at 2.600 m. More recent records are from two municipalities of the department of Huila located at the southern portion of Magdalena River valley, the first one, a female from Gigante (Pardo-Locarno & Ríos-Málaver 2011), which we were not able to study, collected at 1.650 m, and a male from Pitalito (-manuelfernando- from iNaturalist) at 1.318 m. Given the differences between the localities recorded for the type series and recent collections it is difficult to consider Bogotá as part of the distribution range of *P. westwoodii*, nevertheless we do not totally deny the possibility of the presence of the species in ecosystems located at a lower altitudinal range close to this city, even with the presence of Magdalena Valley that represents a strong geographical barrier that could have isolated this species from Eastern "cordillera".

Psilodon seguyi **(Didier, 1929) (*Hexaphyllum*)**

Figure 7.

Examined material: Ecuador, Loja iii.2002, P. Arnaud leg. 1♂, 1♀ (CERPE)

Diagnosis: Males and females with dark-red to brownish tones. Head concealed, distinctly covered by pronotum; mandible apex directed upwards, concave due to Alpha tooth position which is close to apex. Internal face with a tooth of conspicuous setae, Gamma tooth subconical, directed upwards and merged with an extremely reduced Beta lobe. Pronotal surface with moderate to somewhat large, dense punctation, also with a strong groove, reaching pronotal tubercle base, disc with four excavations. Elytral humeri without tooth-like projections. Prosternal process narrow, somewhat carinate at anterior portion, setose. Metaventrite with few setae. Abdominal ventrites with a shagreened surface, posterior margins slightly and entirely carinate, ventrites II and III somewhat convex posteriorly. Females close to males, general habitus of body less wide than males; head and pronotal punctation stronger, dense to contiguous in some regions; head more exposed; supra-antennal projection with almost truncate apex, carinate, carina conspicuous and antero-dorsally projected; mandibles subparallel with highly conspicuous setae; pronotum with a less strong pronotal tubercle; discal groove strongly excavated; pronotal excavations less distinct than males.

Description Male. ***Size*****:** *Total length*. 15 mm *Total width.* 6 mm. ***Colour*****:** dorsally black with dark-red to brownish tones mainly distributed along antennae and legs. Venter black with dark-red tones. ***Head:*** surface with coarse to large punctures, densely distributed with yellowish curved setae. Antennae with six lamellae; supra-antennal projection with a strong sub-triangular carina, and somewhat acuminate apex. External face of mandibles with large to moderate punctures, and decumbent yellowish setae mainly at base; basally slightly expanded, producing a distinctly narrow dorsal surface; inner surface with conspicuous erect setae forming a tuft at apex; Gamma tooth located at base, sub-conical, almost straight and upwards directed, with rounded apex, opposite to Beta lobe; Beta lobe extremely reduced, merged with Gamma tooth; Alpha median tooth located apically, merged with apex producing a concave region. ***Pronotum*****:** Shape convex, somewhat anterio-posteriorly constricted; pronotal tubercle distinct, reaching anterior margin of head; discal groove complete, dividing pronotum in two differentiate regions; surface with moderate to large punctures, densely distributed, also with four distinct excavated spots; anterior and posterior angles rounded. ***Elytra*****:** scutellar shield exposed, with dense and large punctation; elytral humeri not striate, with no tooth-like projection; interstrial costae, with dense to contiguous, moderate to large punctures; epipleuron somewhat concave, carinate, complete to apex and gradually narrowed, with contiguous large to coarse punctures and suberect to decumbent yellowish setae, mainly distally distributed. ***Legs*****:** protibiae basally carinate**,** external face serrate, with several teeth, increasing in size distally, also with few tooth-like projections, mainly at base; external and internal face setose, inner face with yellowish appressed to suberect setae, externally with curved ones. Mesotibiae with yellowish suberect setae, external face with several tooth-like projections associated with setae of variable size, medially with a line of somewhat strong, merged projections, resembling bifurcate teeth; apex expanded with several projections and two subequal apical spurs, also with conspicuous setae. Metatibiae setose, setae increasing in size distally, decumbent to erect, conspicuous at apex; external face with tooth-like projections and pits containing setae; apex expanded with several serrate projections and two apical spurs being the anterior one shorter ***Venter*:** Prosternum carinate along anterior margin, with a continuous line of yellowish appressed setae, surface with coarse punctures, dense to contiguous with yellowish strongly curved setae; prosternal process narrow and convex, somewhat conspicuous, with large and dense punctation, covered by strongly curved setae increasing in size anteriorly. Mesoventrite convex, with large to coarse punctures, dense, with short strongly curved setae, posterior portion with longer and appressed yellowish setae. Metaventrite convex, medially with a wide sub-trapezoidal projection, producing a strong declivity; surface with moderate to somewhat large punctures, densely to moderately distributed; discrimen incomplete, hardly visible, present medially as a shallow excavation. Abdominal ventrites slightly carinate along the mid portion of posterior margins, ventrite I to IV with yellowish reflections along carina; surface with fine to moderate punctures, dense to contiguous; yellowish erect setae distributed along posterior margins of all abdominal ventrites, ventrite V with more conspicuous setae apically. ***Genitalia:*** Aedeagus symmetric, shape somewhat rhombic, rounded proximally; in lateral view mostly straight, somewhat concave proximally. Phallobase elongate with concave sides, also with a strong constriction between anterior and posterior regions. Parameres narrow, with rounded apex, laterally with a fine excavation, ventral portion concave. Median lobe slender, enlarged basally, in lateral view strongly convex. Dorsal cross bar

“V” shaped, medially expanded, producing a sub-triangular shape, also enlarged at lateral portions.

Females: ***Size*****:** *Total length*. *Total width.* ***Head:***surface with dense and coarse punctures; frons and vertex excavated, visible from above; supra-antennal projection strongly carinate, carina projected anteriorly; mandibles symmetric with rounded apex, almost straight, concave in lateral view, also with conspicuous setae, with no teeth, instead with a continuous tooth-like carina across dorsal portion, stronger at base resembling males Beta lobe. ***Pronotum*****:** anterior margin less projected, pronotal tubercle reduced. ***Genitalia:*** Styli convergent, with elongate shape, internal face forming an oblique angle at apex, also with conspicuous setae. Gonocoxites strongly elongate, converging apically, externally with a fine distal concavity, basally abruptly narrowed. Lateral paraprocts strongly curved with a “C” shape.

Distribution: Southern Ecuador – Paramo Province (South American Transition zone) (Morrone 2022).

Remarks: *Psilodon seguyi* was the first species described for Ecuador, and the second described for Tropical Andes. In spite of the geographical proximity with *P. westwoodii*, both species are distinctly different sharing few characteristics, the main one is the concave and highly setose apex of mandibles. One distinctive trait of *P. seguyi* is the strong reduction of Beta lobe which is merged with Gamma tooth thus, reducing the dorsal face present at base of mandibles. Even though the records of this species belong to the Páramo province, the elevation of the type locality is around 2000 m, suggesting that *P. seguyi* is distributed along Andean Forests (Pre-montane forests), instead of the truth Paramos that are located above 3000 m, and present higher levels of endemism.

Psilodon xerophilicum* Martinez & Reyes-Castillo, 1985

Figure 8.

Examined material: Paratype labelled: / Encruzilhada, Bahia, Brasil, xii.1980 A. Martinez & M. Alvarenga leg. / “Handwriting” Psilodon xerophilicum sp.n Martinez & Reyes C. 1♀ (CERPE).

Additional material: BRAZIL: BAHIA: Encruzilhada, 980 m, xi.1978, M. Alvarenga leg. 1♂ (EPGC); Encruzilhada, Estr. Torres, 15.xii.2012 1♀ (CERPE); Ituberá, 11/13.vi.2002, F. Bravo& I. Castro 2♂ (MZUEFS); Serra da Jibóia, 12°50´S/39°28´W, 820m 27-28.v.2000, Frerdy leg. 1♂ (MZUEFS). **MINAS GERAIS**: Águas Vermelhas, xii.1997, Alt. 850m A. Bello & F.Z. V. Mello leg. 1♀ (CERPE).

Diagnosis: Specimens apparently black but usually with brown to dark-red tones. Mandibles slightly curved inwards, mainly distally; apex narrowed and somewhat directed upwards; Alpha tooth directed upwards with truncate apex, Beta lobe sub-trapezoidal and Gamma tooth apex located medially. Supra-antennal projection with truncate to somewhat rounded apex, poorly carinate. Pronotal groove complete; dorsal face of pronotal tubercle sub-trapezoidal. Elytral suture with contiguous moderate punctation; odd interstriae shortened, well defined basally. Prosternal process narrow and setose. Abdominal ventrites with posterior carinate margin. Aedeagus subparallel, anterior phallobase narrower than posterior one, sub-trapezoidal with fine sides, almost triangular; median lobe somewhat elongate; in lateral view posterior phallobase convex, parameres slightly concave. Females with less conspicuous supra-antennal projection, apically rounded with a somewhat strong, perpendicular carina. Pronotal groove strongly excavated, extended anteriorly interrupting, at least partially the dorsal portion of pronotal tubercle, anterior portion of pronotum with a fine declivity.

Description Male. ***Size*****:** *Total length*. 15-21.1 mm. *Total width.* 5-10 mm. ***Colour*****:** dorsally with brown to dark-red tones, some specimens with somewhat black colouration. ***Head:*** shape transverse, strongly emarginate anteriorly; surface with moderate to large, dense punctation; frons slightly excavated. Antenna with six lamellae; supra-antennal projection with rounded to somewhat truncate apex, also with a subconical non-conspicuous carina. Mandibles with rounded but acute apex; external face with large punctures and decumbent to strongly curved setae; median portion expanded, producing a narrow dorsal surface; inner surface finely punctate, apparently smooth with slightly curved setae mostly distributed at apex, not forming a conspicuous tuft; Gamma tooth subconical with rounded apex, projected to median axis of body, located medially, almost opposite to Beta lobe; Beta lobe wide, sub-trapezoidal, externally projected; Alpha median tooth directed upwards, trapezoidal. ***Pronotum:*** Pronotal tubercle covering first half of head; discal groove complete, shallow; surface with large to moderate, dense punctures; anterior and posterior angles rounded. ***Elytra:*** scutellar shield exposed, only with few large to somewhat coarse punctures along anterior margin, slightly carinate posteriorly; elytral humeri not striate, with few fine punctures, also with a tooth-like projection extended laterally; interstrial costae, with moderate to large punctation; epipleuron flat becoming somewhat concave posteriorly, carinate, complete to apex and gradually narrowed, with large to coarse punctures and decumbent to erect setae, densely distributed proximally becoming contiguous distally. ***Venter:*** Prosternum carinate along anterior and posterior margins, with a continuous line of appressed; surface with coarse to large punctures and appressed setae, becoming longer over anterior portion of prosternal process; prosternal process narrow, convex, not carinate at anterior portion, expanded posteriorly with a somewhat carinate apex. Mesoventrite slightly convex, with coarse to large punctures, posterior portion with decumbent to appressed setae. Metaventrite convex, extended distally producing a sub-trapezoidal carina; discrimen absent; surface with moderate punctures along disc, becoming larger along lateral and posterior margins with variable size of strongly curved setae. Abdominal ventrites carinate along anterior margins; surface with fine and dense to contiguous punctation, with decumbent setae along lateral portions and posterior margin at ventrite V. ***Genitalia*****:** Aedeagus symmetric, subparallel, with a somewhat rounded anterior margin. Phallobase sub-triangular. Parameres with almost straight sides, rounded to somewhat truncate apex, slightly concave along dorsal portion. Median lobe enlarged basally, in lateral view convex, with a strongly curved, three-lobed apex, also with some spicules present apically. Dorsal cross-bar "V" shaped, with a strong anterior emargination, and laterally enlarged.

Females: ***Size*****:** *Total length*. 13-16 mm. *Total width.* 5-6 mm. ***Head:*** Dorsally more exposed than males head, not strongly emarginate, dorsally exposed, frons slightly excavated, excavation extended to vertex producing a concave region; supra-antennal projection with conspicuous subconical carinae. Surface with coarse and dense punctation with erect to suberect setae. Mandibles symmetric, apically rounded but acute, in dorsal view almost straight, with a concave dorsal portion, lacking preapical teeth. Basally distinctly enlarged when compared with other species females. External face with coarse to large punctures continuous to dense with erect setae; internally with few large to somewhat coarse punctures and erect to slightly curved setae. ***Pronotum:*** pronotal tubercle transverse, strongly reduced; discal groove stronger and wider anteriorly. ***Venter:*** prosternal process somewhat conspicuous. ***Genitalia:*** Styli sub-oblong, divergent; apex acute, internally forming an oblique angle, with conspicuous setae. Gonocoxites distally elongate with subparallel sides; proximally abruptly narrowed, producing a slender structure. Lateral paraprocts C-Shaped, rounded and enlarged proximally, forming a capitate apex.

Distribution: Northeast Brazil – Parana Forest Province (Morrone 2022).

Remarks: the original description of *Psilodon xerophilicum* was based on two females from Encruzilhada municipality in the State of Bahia (Brazil), and the male was unknown. Here we describe for the first time male specimens from different localities in the State of Bahia. According to our observations *P. xerophilicum* shows similar morphological traits to other Brazilian *Psilodon* males, such as the absence of apical tuft of setae at mandibles, well defined dorsal face at base of mandibles, the reduction in supra-antennal carinae and less strong punctation. Females are close to males except for the presence of conspicuous carinae at supra-antennal projections. Martínez & Reyes-Castillo (1985) defined *P. xerophilicum* as a close species to *P. westwodii*, maybe due to the strong punctation and conspicuous carinae of females, nevertheless if males from both species are compared, the divergence between these taxa is clear.

Psilodon gilberti **Boucher, 1993**

Figure 9.

Examined material: Bolivia Nor. Yungas. Caravani-Coroico. Xi.2009. 1.800 m. B. Cavelius leg. 1♂ (CERPE)

Diagnosis: Females unknown. Males dark-red to somewhat brown. Head partially concealed by pronotum. Mandibles upwards directed, with a conspicuous tuft at apex, also with long yellowish setae along ventral portion of internal face, apex concave. Antennal club with seven lamellae. Pronotal tubercle narrow and convex, not contiguous with discal groove, separated by a fine declivity. Elytral humeri with a tooth-like projection. Meso and metatibiae serrate, with strong teeth and expanded apex. Aedeagus and median lobe distinctly elongate, somewhat slender; in lateral view with concave shape.

Description Male. *Size*: *Total length*. 13 mm. *Total width.* 5 mm. ***Colour*:** Body dark-red with brownish tones; ventrally with brighter tones close to median axis. ***Head:*** concealed, partially covered by pronotum; surface with moderate to large punctures, and erect to slightly curved setae. Antennae with seven lamellae; supra-antennal projection with a subconical carina. Mandibles with somewhat acuminate apex; external face finely punctate, with few curved setae along dorsal portion, also with some decumbent inconspicuous setae at base; inner face with moderate punctation and more conspicuous setae; setae decumbent to slightly curved at apex; apically with a tuft of conspicuous setae; base of mandibles expanded, producing a dorso-lateral surface with moderate punctation and suberect setae. Gamma tooth located medially, between Beta lobe and Alpha tooth, with sub-trapezoidal to somewhat triangular shape, projected medially; Beta lobe sub-triangular, reduced, located basally, somewhat projected externally; Alpha median tooth located apically, producing a concave region. ***Pronotum:*** shape convex, with two lateral constrictions; pronotal tubercle conspicuous; discal groove complete, shallow; surface with moderate to large punctures, densely to moderately distributed; anterior and posterior angles rounded. ***Elytra:*** scutellar shield exposed, with few moderate punctures, slightly carinate posteriorly; elytral humeri not striate, with fine to moderate punctures and a fine tooth-like projection extended laterally; interstrial costae, with moderate punctation and fine setae; epipleuron somewhat concave, carinate and complete to apex, with large to somewhat coarse and contiguous punctures, also with erect to decumbent setae, mainly distributed apically. ***Legs:*** Protibiae dorsally carinate, serrate, with several teeth increasing in size distally, also with tooth-like projections between teeth; external and internal face with decumbent setae, also with curved setae at apex. Mesotibiae with yellowish decumbent to slightly curved setae, external face with several tooth-like projections and at least three strong teeth, increasing in size distally, stronger teeth with bifurcate apex, resembling two merged teeth; apex expanded with several tooth-like projections and two subequal apical spur. Metatibiae as mesotibiae except for the shorter anterior apical spur ***Venter:*** Prosternum carinate along anterior margin with a continuous line of yellowish appressed setae; posteriorly somewhat carinate; surface with few coarse punctures, and strongly curved to appressed setae; prosternal process narrow and convex, with two longitudinal inconspicuous carinae at anterior portion, also with coarse and dense to contiguous punctation. Mesoventrite convex with coarse to large punctures, densely distributed with yellowish appressed setae. Metaventrite convex, with a sub-triangular region extended distally, discimen absent; surface with moderate to large punctures, medially densely distributed, becoming moderate to sparse laterally. Abdominal ventrites carinate along posterior margins, with fine and contiguous punctures over anterior portions of all ventrites and moderate, densely distributed ones along posterior margins, also with yellowish erect setae along posterior margin of ventrite V. ***Genitalia*:** Aedeagus symmetric, with proximal apex truncate. Phallobase sub-triangular with concave sides. Parameres with slightly convex sides, rounded at apex and somewhat concave in lateral view. Median lobe finely enlarged at base, with truncate apex. Dorsal cross bar "V" shaped with a capitate projection at posterior margin.

Distribution: Bolivia, Northern Yungas Province (Morrone 2022).

Remarks: *P. gilberti* was the third species described for the Andes and the only one distributed along the Yungas. Even though it shares several morphological traits with the Andean species, as is the tuft of setae at mandibles, other traits such as body punctation, pronotal tubercle shape and humeral tooth-like projections suggest a close relation between *P. gilberti* and Brazilian *Psilodon*. Another interesting feature is the antennal club with seven lamellae, being *P. gilberti* the only member of the genus that presents it, a trait which is only shared with the Australian species of *Syndesus*.

Psilodon paschoali Pardo-Locarno & Ríos-Málaver, 2011

Figure 10.

Examined Material: VENEZUELA: Altos de Pipe, 12.viii.2011, 1650m, C. Ríos-Málaver leg. 1♂ (CERPE); Miranda, Oripoto, v.2004, 1400 m D. Garcia col.

Diagnosis: Males mainly black with brownish and reddish tones. Mandibles with somewhat acuminate apex, showing a shape closer to Brazilian species. Supra-antennal projection with a reduced carina. Pronotum with moderate to large punctation and a discreet pronotal tubercle. Elytral humeri with tooth-like projections, also with an almost smooth scutellar shield. Aedeagus with almost subparallel sides; median lobe basally enlarged; dorsa cross-bar somewhat "V" shaped, with a wide posterior margin, producing a trapezoidal shape with lateral portions.

Description Male. ***Size*****:** *Total length.* 14.1-14.4 mm *Total width.* 6.45-7.01 mm ***Colour*****:** dorsally black with reddish to brownish tones, sometimes entirely brown to dark-red. Ventrally brown with dark-red tones, metaventrite dark-red with blackish highly distributed fine spots. ***Head:*** surface with coarse to large punctation, dense to contiguous; dorsally somewhat concealed, partially covered by pronotum. Antennae with six lamellae; supra-antennal projection finely carinate. Mandibles with rounded to almost acuminate apex; external face with large to moderate punctures and decumbent to strongly curved setae, mainly distributed medially and close to base; inner face excavated at base; surface finely punctate, apparently smooth, with slightly curved to erect setae, mainly distributed apically; basal dorsal surface with contiguous and coarse punctation, also with curved setae; Gamma tooth located medially, opposite to Beta lobe, shape subconical, almost directed upwards, rounded to somewhat truncate apically; Beta lobe sub-trapezoidal, narrow, slightly projected laterally; Alpha median tooth directed upwards , almost truncate at apex, with large punctures and somewhat erect setae. ***Pronotum:*** lateral portion with two somewhat constricted spots; anterior margin projected with a conspicuous pronotal tubercle, covering head medially; discal groove complete, deeper and wider medially; surface with large to coarse punctures, densely to moderately distributed; anterior and posterior angles rounded. ***Elytra:*** scutellar shield exposed, with large to somewhat coarse punctures; elytral humeri not striate with fine to moderate punctures, also with a tooth-like projection; interstrial costae with moderate punctation, moderately to sparsely distributed; epipleuron concave, carinate and complete to apex, with large to somewhat coarse punctures at proximal portion, becoming moderate to fine distally, dense to contiguous, also with appressed setae, mainly at base, becoming curved to suberect along epipelural carina. ***Legs:*** Protibiae somewhat carinate at base, serrate, with several teeth increasing in size distally, also with tooth-like projections between strong teeth. External and internal face with curved and suberect setae. Mesotibiae with yellowish suberect and slightly curved setae along entire surface, external face serrate, with several tooth-like projections, also with two or three strong setose teeth, increasing in size distally; apex enlarged with several tooth-like projections and two subequal apical spur. Metatibiae with suberect to erect setae, externally serrate with several, subequal tooth-like projections, also with a row with at least three strong and setose teeth, increasing in size distally; apex enlarged with conspicuous setae and two apical spur, being the anterior one shorter. ***Venter*:** Prosternum carinate along anterior and posterior margins, both margins with a continuous line of appressed setae; surface with coarse, densely distributed punctures and appressed setae; prosternal process narrow and convex with few moderate to large punctures and appressed setae. Mesoventrite slightly convex, surface with large to coarse punctures, densely distributed, and strongly curved setae. Metaventrite convex, median surface glabrous, laterally with coarse punctures, and appressed setae, becoming slightly curved proximally; discrimen absent; posterior margin with a median projection, producing a strong declivity. Abdominal ventrites with fine punctures, dense to contiguous with few curved setae, posterior margin of all ventrites carinate medially; ventrite V with more conspicuous yellowish setae concentrated at apex. ***Genitalia***: Aedeagus symmetric. Sides subparallel, only slightly enlarged medially. Phallobase elongate, with a truncate to slightly rounded proximal apex; posterior phallobase with slightly concave sides; phallobase constriction reduced. Parameres with straight sides, in lateral view, ventral margin somewhat convex, dorsally slightly concave apically. Median lobe enlarged basally, narrowed from median portion to apex, not distinctly elongate. Dorsal cross bar "V" shaped, median portion wide and truncate.

Distribution: Colombia "Cordillera Oriental" and Northern Venezuela – Magdalena and Venezuela provinces (Morrone 2022).

Remarks: *Psilodon paschoali* is the second species described for Colombia, registered for the "Cordillera Oriental", now we extend its distribution to Venezuela, specifically to "Altos de Pipe" a mount that belongs to a series of peaks called "Altos Mirandinos" located at the "Cordillera de la Costa". Even though this species was originally described for northern Andes several characteristics such as the narrowed apex of mandibles, absence of the apical conspicuous tuft of setae, tooth shape and orientation, body surface and elytral humeri with tooth-like projections suggest a closer relation with Brazilian *Psilodon* than with the Andean species. We did not have access to the type material or high quality photographs because the Holotype is deposited in a private collection but recently, with the help of Cristobal Ríos-Málaver, who collected another specimen close to the type locality at Cerro de la Uchata, Galán, Santander (Colombia), we were able to confirm that the Venezuelan specimens are correctly identified as *P. paschoali*. Jiménez-Asúa & Martínez (1963) mention a male specimen of *P. schuberti* collected in August 1941 at the

"Macizo del Niguatá" in Venezuela. This locality is close to the collection places of both specimens studied in this work, suggesting that this could be one of the first records ever made of *P. paschoali*.

Psilodon luki **(Onore, Bartolozzi, and Zilioli, 2011) (*Syndesus*)**

Figure 11.

Examined material: Holotype (examined by photographs) labelled: Tandayapa (2100m), Pichincha province, Ecuador, ii.2010, G. Onore Leg. (MZUF, collection number 15105). Paratypes labelled as Holotype 1♂1♀ (CERPE).

Diagnosis: Males mainly black with dark-red tones. Supra-antennal projections strongly carinate. Mandibles with a concave apex, Alpha tooth located distally with somewhat acuminate apex; Gamma tooth distinct and slender, directed upwards, merged with Beta lobe reducing the dorsal surface of mandibles, that is present in most of *Psilodon* species. Pronotum with coarse and contiguous to dense punctation; discal groove deep, reaching pronotal process base; disc with four excavated spots and two lateral fine constrictions. Elytal humeri without tooth-like projection, with a strongly punctate surface and distinct interstrial costae. Females slightly larger than males, mostly as males except for a less emarginate and more exposed head; supra-antennal projection with rounded apex, carina conspicuous, subconical, directed upwards but finely projected medially. Anterior margin of pronotum less projected, with a reduced pronotal tubercle.

Description Paratype Male. ***Size***: *Total length*. 16.1-16.93 *Total width.* 5.9-6.34 mm. ***Colour***: dorsally entirely black, ventrally black with some dark-red reflections mainly at coxae and base of legs. ***Head:*** surface with large to somewhat coarse punctures; median portion concealed, covered by anterior portion of pronotum. Antennae with six lamellae; supra-antennal projections with subconical carinae. Mandibles with acute but rounded apex; externally with moderate and dense punctures, also with slightly curved to decumbent setae mainly distributed at base; inner face with a setose, strong excavation at base, producing a distinct basal tooth, surface finely punctate, with a tuft of conspicuous erect to slightly curved setae at apex; basal portion expanded basally forming a distinctly narrow surface; Gamma tooth located medially, merged to Beta lobe, shape subconical, rounded at apex and projected internally; Beta lobe reduced, sub-triangular, projected laterally, rounded at apex; Alpha median tooth located at distal portion, close to apex producing a concave region. ***Pronotum:*** surface irregular; pronotal tubercle convex and conspicuous; discal groove almost complete, ending before posterior margin, dividing pronotum into two portions; surface with four excavated spots, also with moderate to large punctures, densely distributed at disc, becoming contiguous laterally; anterior and posterior angles rounded. ***Elytra:*** scutellar shield exposed, with few large to somewhat coarse punctures; elytral humeri not striate with fine to moderate punctures, with no tooth-like projection; interstrial costae, with moderate punctation; epipleuron flat at base becoming somewhat concave apically, carinate and complete to apex, with moderate, dense to contiguous punctures and decumbent setae, mainly distributed distally. ***Legs:*** Protibiae dorsally carinate, serrate, with several teeth increasing in size distally, all teeth joint by a smooth to somewhat serrate carina; external and internal face with decumbent to slightly curved setae. Mesotibiae with yellowish erect to decumbent setae along whole surface, external face with several tooth-like projections and strong teeth, increasing in size distally, each projection with one smooth setae, strong teeth containing two or more smooth setae; apex enlarged with several tooth-like projections and two subequal apical spur. Metatibiae with several decumbent to erect setae, serrate, similar to mesotibiae but presenting tooth-like projection of similar size; apex expanded with two apical spur, being the anterior one shorter. ***Venter*:** Prosternum carinate along anterior and posterior margins, also with a continuous line of appressed setae along both margins; surface with large to coarse punctures, dense, with strongly curved to appressed setae; prosternal process narrow and convex, anteriorly carinate, with moderate to large, contiguous punctures and appressed setae. Mesoventrite convex with large to coarse punctures, densely distributed with yellowish appressed setae. Metaventrite convex, slightly extended posteriorly with a median declivity at posterior margin; discrimen present as an incomplete and shallow groove; surface with moderate to large punctures, densely distributed with fine, strongly curved setae. Abdominal ventrites finely punctate, dense medially becoming contiguous laterally; posterior margin of all ventrites with a transverse carina along median portion, also with decumbent to appressed setae along posterior portion; ventrite V with erect conspicuous setae at apex. ***Genitalia*** Aedeagus symmetric, strongly pigmented, proximally almost trapezoidal with acute apex. Phallobase sub-triangular with slightly concave sides. Parameres with somewhat concave sides, in ventral view rounded at apex with a tooth-like projection, in lateral view concave, somewhat constricted dorsally. Median lobe enlarged at base and apex, laterally scleretized with rounded apex. Dorsal cross bar apparently “V” shaped.

Description Paratype Female: ***Size*:** *Total length*. 17.69 mm. *Total width.* 6.45 mm. ***Head:*** dorsal surface less concealed, less emarginate at anterior margin, medially excavated; carina at supra-antennal projection more conspicuous, subconical; surface with contiguous, coarse punctures, and curved to erect setae. Mandibles symmetric, with rounded but acute apex, almost straight, dorsally concave, also with a dorsal carina, expanded basally producing a tooth-like structure; surface of external and internal face with dense, large to somewhat coarse punctures and conspicuous slightly curved to erect setae. ***Pronotum:*** less projected anteriorly, with a reduced pronotal tubercle. ***Venter:*** with more conspicuous punctation, especially at metaventrite and abdominal ventrites. Metaventrite with an incomplete discrimen, present as a longitudinal carina instead of a groove. Abdominal ventrites with contiguous fine punctures along lateral portion of every ventrite, medially with moderate punctures and strongly curved seta, ventrite V with decumbent to appressed setae and a group of conspicuous erect setae at apex. ***Genitalia:*** Styli elongate, somewhat contiguous, with rounded apex, with an oblique angle at internal face, also with conspicuous setae. Gonocoxites distally elongate, with subparallel sides, contiguous, proximally abruptly narrowed.

Distribution: Northern Ecuador – Cauca Province (Morrone 2022).

Remarks: *Psilodon luki* is the second species described for Ecuador and shows the typical traits of the Andean *Psilodon*, as is the concave apex of mandibles and the conspicuous tuft of setae located distally. This species presents unique characteristics only shared with the other Ecuadorian species, *P. seguyi* as is the fusion of Beta and Gamma teeth, and the strong pronotal excavations. Male Aedeagus of *P. luki* is the most pigmented among the genus and is the only one that presents a highly distinct separation between the anterior and posterior phallobase, it also shows a somewhat rhomboid shape. Onore *et al*. (2011), in the original description recognize *Psilodon* as a synonym of the Australasian genus *Syndesus* MacLeay, 1819, following a classification historically used by several authors such as Benesh (1960); Maes (1992); Karjcick (2001, 2003); Holloway (2007). In spite of the high resemblance between *Syndesus* and *Psilodon*, considering both taxa as a single one, would ignore that Australasian and South American fauna got isolated around 65 mya (Late Cretaceous) (Grimaldi & Engel 2004). Here we follow the *sensu* proposed in Grossi & Aguiar (2014) where this taxon is included in *Psilodon*.

Psilodon buhrnheimi Grossi and Aguiar, 2014

Figures 12

Examined material: Holotype labelled: Brasil, Amazonas, Coari/Rio Urucu, próx. IMT-1,/ 4°49′33.00″S S\ 65°01′49″W,/ 24–25-ix-1995, 89 m, P.F./ Buhrnheim and N.O.Aguiar/ BLB [black light bulb] – Pennsylvania 1♂ (CZPB); Paratype labelled: Brasil, AM, Guajará,/Ramal do Gama km 12,/ 07°27′16″/72°38′56″,/06–19.xi.2006, tronco,/ F°. [Filho] F. F. Xavier leg. 1♂ (EPGC).

Additional material: BRAZIL: **RONDÔNIA:** Porto Velho. MUIE 9° 33´41.85´´S, 65°01´28 ´´W. 02.x.2004, Luminosa M.A.P.A. Silveia leg. 1♂(CERPE); **PARÁ:** Obidos, x.1938 1♂(MNRJ); **PERU**: **JUNIN:** Satipo, Río desconocido 1.2003, 1600 m. R.R. Koike col. 1♂(CERPE).

Diagnosis: Males with brownish to dark-red tones along body. Mandibles narrowed apically and directed upwards; Alpha tooth almost located medially; Gamma tooth opposite to Beta lobe. Supra-antennal projections finely carinate. Pronotum with moderate punctures, uniformly distributed; pronotal groove shallow with a reduced pronotal process. Elytral humeri with tooth-like projections, with almost complete interstriae to apex. Meso and Metatibiae with two to three strong teeth, enlarged apically. Aedeagus proximally truncate, wide, with strongly curved median lobe.

Description Holotype. ***Size:*** *Total length.* 13.49 - 16.53 mm. *Total width* 4.11 - 7.28 mm. ***Colour***: dorsal and ventral face dark-red with brownish tones. ***Head***: frontal surface somewhat excavated, with coarse punctures, dense to somewhat contiguous, also with erect to slightly curved setae. Antennae with six lamellae; supra-antennal projection slightly carinate, with almost truncate and setose apex, setae erect to slightly curved. Mandibles with rounded and acute apex; external face with moderate to large punctation, and strongly curved setae, mainly distributed at base; inner face mostly smooth, with large punctures at base, moderate at apex, also with suberect to slightly curved setae, basally somewhat excavated, producing a sub-triangular tooth; proximal dorsal surface with moderate punctation and erect setae; Gamma tooth located medially, subconical, with rounded apex, almost vertical, opposite to Beta lobe; Beta lobe somewhat reduced, sub-trapezoidal, extended along base; Alpha median tooth directed upwards, almost trapezoidal, internally with slightly curved setae. ***Pronotum:*** pronotal tubercle slightly convex; discal groove complete, shallow; surface with dense, coarse to somewhat large punctation. ***Elytra:*** scutellar shield exposed, almost smooth; elytral humeri not striate, with moderate punctures, also with a somewhat conspicuous tooth-like projection; interstrial costae with moderate to somewhat large punctures, sparse, except medially; elytral suture with contiguous and somewhat coarse punctures; epipleuron concave, carinate, complete to apex, with contiguous, large to coarse punctures and appressed to suberect setae, mainly distributed distally. ***Legs:*** protibiae somewhat carinate dorsally, serrate, with several teeth, increasing in size distally, also with tooth-like merged projections between teeth; external and internal face with suberect to curved setae. Mesotibiae with yellowish suberect to decumbent setae; external face serrate with few strong teeth and tooth-like projections, increasing in size distally; apex somewhat enlarged with several tooth-like projections and two subequal apical spur. Metatibiae as describe for mesotibiae, except for apical spur, being the anterior one shorter than the other. ***Venter:*** Prosternum carinate along anterior and posterior margins, with a continuous line of yellowish appressed setae; surface coarse, densely distributed punctures and appressed to strongly curved setae; prosternal process anteriorly carinate, narrow and convex with few contiguous, large to coarse punctation and strongly curved setae. Mesoventrite slightly convex, with dense, large to somewhat coarse punctures, and appressed to strongly curved setae. Metaventrite convex; surface with large to coarse punctation, sparsely to moderately distributed, medially finely punctate; discrimen absent, posterior margin slightly projected distally, producing a somewhat strong declivity. Abdominal ventrites finely punctate, punctures dense to contiguous with strongly curved setae, mostly distributed along posterior margins of ventrites I-IV; all ventrites with a median transverse carina; ventrite V with a group of conspicuous erect setae at apex. ***Genitalia*:** Aedeagus symmetric, strongly pigmented, proximally almost quadrate. Phallobase sub-triangular with almost straight sides. Parameres almost straight laterally, with rounded apex, dorsal portion in lateral view slightly concave. Median lobe enlarged at base, rounded but acute at apex, in lateral view concave. Dorsal cross bar "V" shaped, anterior portion projected medially.

Distribution: North Brazil and Central Peru - "Cordillera Central" – Madeira, Rondônia, and Yungas Provinces (Morrone 2022).

Remarks: As most Brazilian species *P. buhrnheimi* presents gradually narrowed mandibles with the Alpha tooth located medially, Gamma tooth and Beta lobe free; supra-antennal carinae less pronounced when compared with Andean species; pronotum without excavations or a strong punctation and elytral humeri with tooth-like projections. *P. buhrnheimi* represents the third Lucanidae genus recorded from the Amazonian region, and is the species with the widest geographical range, involving the states of Pará, Amazonas, Rondônia in Brazil, and Satipo province in Peru. The distribution of this species seems to be associated with the Amazon basin and part of its tributaries, as it follows the path of Satipo (Peru-Junín), Juruá (Brazil-AM), Urucu (Brazil-AM), Amazonas (Brazil-PA) and Madeira (Brazil-RO) rivers, reflecting a possible and strong relationship between this species and amazonian riparian forests.

Psilodon n. sp. 1 Cáceres & Grossi.

Figure 13.

Examined material: Holotype male labelled: Brasil, CE, Fortaleza**?**, Nativas. No more data available 1♂ (CERPE).

Diagnosis: Male specimen close to *Psilodon* n. sp. 6, small when compared with other Brazilian species of *Psilodon*. Head partially covered by pronotum, not covering frons; frons almost flat; supra-antennal projections with strongly reduced carinae. Mandibles basally expanded, producing a distinct dorsal surface, with Gamma tooth and Beta lobe opposite almost with same width and projected externally; Alpha tooth truncate, almost perpendicular. Pronotum anteriorly extended with a non-conspicuous pronotal tubercle. Mesotibiae with two rows of strong teeth, apically enlarged producing a tooth-like structure. Last tarsomeres of Meso and Metatibiae strongly convex, enlarged apically; apex with several constrictions producing a somewhat dentate surface. Aedeagus moderately elongate, almost with quadrate habitus.

Description Holotype Male. ***Size:*** *Total length.* 12.37 mm. *Total width* 5.70 mm. ***Colour*****:** Body with dark-red and brownish tones. ***Head*****:** shape transverse and emarginate; labrum elongate, somewhat convex, with rounded and setose apex; frons somewhat concave; surface with coarse, dense to contiguous punctation and curved setae. Antennae with six lamellae; supra-antennal projection with rounded apex, surface weakly carinate with almost erect setae, only slightly curved at apex. Mandibles with rounded apex, directed upwards; Alpha tooth truncate, almost perpendicular; Gamma tooth sub-triangular, opposite to Beta lobe; Beta lobe sub-trapezoidal, strongly punctate with curved conspicuous setae, distinctly projected externally. ***Pronotum*****:**

anterior margin projected anteriorly, covering median portion of head, almost reaching anterior margin; pronotal tubercle reduced. Surface almost uniformly punctate, punctures large, densely distributed; discal groove shallow with coarse punctation. ***Elytra*:** striae with coarse and dense punctation, interstrial costae weak. Elytral humeri with a tooth-like projection. Epipleuron concave with moderate to fine punctation, basally densely distributed, getting somewhat contiguous distally. ***Venter*:** Prosternum with coarse punctation, dense to contiguous, with conspicuous appressed setae; median portion carinate, prosternal process strongly punctate with well-defined margins and long setae. Mesoventrite convex, with coarse, densely distributed punctation, also with appressed smooth setae. Metaventrite strongly convex with large to coarse punctation; discrimen present as a shallow groove without a distinct suture. All abdominal ventrites, except V, with shagreened surface, and a distinct transverse carina along posterior margin, also with a line of strongly curved setae and large to somewhat coarse punctation; last ventrite entirely covered by coarse to moderate punctation, contiguous to dense with erect and conspicuous setae at posterior margin. ***Genitalia*:** Aedeagus symmetric, subparallel. Anterior phallobase with somewhat rounded apex, shape sub-trapezoidal. Posterior phallobase with slightly concave sides. Parameres with almost straight sides and rounded apex. Median lobe wide, almost entirely enlarged, only narrowed just before apex, in lateral view, with concave apex.

Epithet: The specific epithet alludes to the Jenipapo-Kanindé peoples from the state of Ceará in Brazil, an ethnicity that has its origins in the Payaku peoples, which inhabited the sublittoral region of the States of Rio Grande do Norte and Ceará during the 16th century, and whose extension was gradually reduced leading to their actual distribution at Aratuba and Canindé municipalities.

Distribution: Northeast Brazil – Caatinga province (Morrone 2022).

Remarks: *Psilodon* n. sp. 1 is the first species described for Northeast Brazil since *P. xerophilicum*. This species shows typical traits of Brazilian *Psilodon* species with a clear reduction in size when compared with the Southeast species, even when comparing it with small males. Besides size, other diagnostic traits are represented by the more exposed dorsal face of head, which is covered by the pronotal projection but not covered by the pronotal process that is reduced in this species, the well-defined meso and metatibial teeth, the irregular apex of last tarsomeres, and the distinct shape of aedeagus, seems to be important traits to distinguish *P.* n. sp. 1 from other Brazilian species.

***Psilodon* n. sp. 2 Cáceres & Grossi.**

Figure 14.

Examined material: Holotype male labelled: Brasil, GO, São João d´Aliança, 11.xi.1986, 14.7114°S, 47.5161°W, 1000m, R.R. Koike col. 1♂ (EPGC).

Diagnosis: Male dark-red to somewhat brown. Head almost entirely concealed medially, covered by pronotal projection and pronotal tubercle. Supra-antennal projection almost truncate, with reduced carinae, Mandibles strongly curved inwards at apex, with somewhat conspicuous setae; in lateral view slender; Beta lobe widely extended proximally along external face, with sub-trapezoidal shape; Gamma tooth located internally between Alpha and Beta lobe, somewhat constricted, producing a narrow sub-conical tooth; Alpha tooth located medially. Scutellar shield narrowed posteriorly, sub-triangular. Meso and Metatibiae with three to four strong teeth. Aedeagus subparallel, in lateral view almost straight, only slightly concave along parameres; Median lobe strongly curved apically, enlarged at base; dorsal cross bar strongly transverse.

Description Holotype Male. ***Size:*** *Total length.* 15.62 mm. *Total width* 5.25 mm. ***Colour*****:** dorsally dark-red with brownish to blackish tones, pronotum and legs with clearer tones. Ventrally dark-red with brownish tones. ***Head*****:** frontal surface excavated; with dense and coarse punctures, also with curved to suberect setae. Antennae with six lamellae; supra-antennal projection with rounded to almost truncate apex, and a wide sub-triangular carina, also with conspicuous curved setae covering supra-antennal surface. Mandibles with rounded apex, slightly curved and upwards directed; external face with moderate to large punctures and appressed to strongly curved setae; internal face almost smooth, with few large punctation and curved setae at apex, also with a strong excavation at base; Gamma tooth located medially, between Beta lobe and Alpha tooth, closer to Beta lobe, shape subconical with rounded apex, projected to internal axis; Beta lobe wide, almost trapezoidal, outwards directed; Alpha tooth located apically, subconical with rounded to somewhat truncate apex, directed upwards. ***Pronotum*****:** pronotal tubercle conspicuous, almost reaching anterior margin of head; discal groove complete, shallow; surface with densely distributed coarse to large punctures; anterior and posterior angles rounded. ***Elytra:*** scutellar shield exposed, somewhat convex, almost smooth, with few large punctures at anterior margin; elytral humeri not striate with fine and dense punctation, also with a tooth-like projection extended laterally; interstrial costae strong, complete or almost complete to apex, with moderate punctures; epipleuron flat to slightly concave, carinate and complete to apex, with contiguous moderate punctures, producing a somewhat wrinkled surface. ***Venter:*** Prosternum carinate along anterior and posterior margins, also with a continuous line of appressed setae; prosternal process narrow and convex, carinate, carina continuous with posterior margin, also with few large punctures and strongly curved setae. Mesoventrite somewhat convex, with large to coarse, dense punctures and strongly curved to decumbent setae. Metaventrite convex; surface with moderate to large, moderately to sparsely distributed and suberect to strongly curved setae; discrimen absent, but presenting a flattened median region, with an acuminate projection and a strong distal declivity. Abdominal ventrites with fine, contiguous punctures, medially with a transverse carina; all ventrites with strongly curved setae along posterior margins. ***Genitalia*:** Aedeagus symmetric, narrower proximally. Phallobase sub-triangular, somewhat slender with no constrictions at sides. Parameres with almost straight sides, with rounded to somewhat truncate apex, and finely punctate surface, in lateral view somewhat concave. Median lobe enlarged basally, rounded apically, and concave in lateral view. Dorsal cross bar transverse, and strongly narrowed.

Epithet: With this specific epithet, we would like to honour the life and work of Professor Germán Amat García (1960-2021), curator of the Entomological collection at The National Natural Sciences Institute of the "Universidad Nacional de Colombia", where he developed taxonomic and ecological studies focus on Passalid beetles and other Scarabaeoidea taxa. His work and great personality inspired an entire generation of Colombian naturalists, who hopefully will continue with his legacy by offering knowledge on Colombian and Latin American beetles.

Distribution: Central-West Brazil – Cerrado Province (Morrone 2022).

Remarks: *Psilodon* n. sp. 2 could be distinguished from other Brazilian species of *Psilodon* by the slender and strongly curved mandibles at apex, Gamma tooth located between Alpha tooth and Beta lobe, and the transverse and inconspicuous dorsal cross bar of aedeagus, which is distinctly different from other males that present "V" to somewhat "U" shaped and strongly sclerotized cross bars. *P.* n. sp. 2 is also the first species described from the Brazilian Cerrado, nevertheless, it is important to point out that the type locality is based at approximately 1064 m, suggesting the presence of habitats with higher humidity levels than most areas across Cerrado, as all species of *Psilodon* seems to be associated with medium to high humidity environments.

Psilodon n. sp. 3 Cáceres & Grossi.

Figure 15.

Examined material: Holotype male labelled: **BRAZIL: ESPIRITO SANTo:** Linhares, P.N. Soretama A: 650m 31.xii.1982 1♂ (EPGC).

Paratypes labelled: **BRAZIL: ESPIRITO SANTO: LINHARES:** Caliman Agricola S/A, Sede, 23.x.2003, Luz. P.C. Grossi Leg. 1♀ (CERPE); 11/12/99; 1♂ (CERPE); RFCVRD, Date. 24/11/89 JSS Col. 1♂(CERPE); same data except Date: 23.11.88 1♂(CERPE); RFCVD, 24.xi.1989, A: 700m JSS Leg. 1♂(CERPE); P.N. Soretama A: 650m F.Z.V. Mello Leg. 1♂(CERPE); **MINAS GERAIS:** Viçosa, Data 27/11/82. Col. Martins 1♂(CERPE); Manhu-Mirim, Col. J. Guerin. S. Paulo Brasil. 1♂ (CEAH).

Diagnosis: Species close to *Psilodon schuberti*. Males dark-red to somewhat brown, some specimens with fine carmine tones. Mandibles somewhat wide in lateral view, with acute but rounded apex; base of Gamma tooth located opposite to median portion of Beta lobe; Beta lobe distinct, in lateral view almost entirely extended through base. Head medially covered by pronotum; most specimens with a distinct projection and a conspicuous pronotal tubercle, reaching anterior margin of head. Discal groove of pronotum shallow in major males, stronger in small specimens; pronotal surface with almost uniformly distributed punctation, punctures coarse along median region, becoming large close to sides. Mesotibiae with two or more strong teeth, in major males with three strong ones with several tooth-like projections along whole surface. Metatibiae with two to three strong teeth. Ventrally with a strongly narrowed prosternal process; metaventrite convex but somewhat flattened at disc. Aedeagus moderately elongate, in lateral view slightly convex; median lobe enlarged basally. Females body with darker tones than males.

Mandibles subparallel, with concave dorsal face. Head dorsally exposed, supra-antennal projection strongly carinate. Pronotum less projected anteriorly than males, with a deeper discal groove, complete, sometimes dividing prosternal tubercle in two portions. Meso and Metatibiae with more conspicuous teeth.

Description Holotype Male: ***Size:*** *Total length.* 13.6 mm. *Total width*. 3.6 mm. ***Colour*****:** dorsally dark-red with brownish tones. Ventrally dark-red, with stronger brownish tones. ***Head:*** frontal surface excavated, with coarse punctures, densely distributed, and erect to slightly curved setae. Antennae with six lamellae; supra-antennal projection with rounded to somewhat truncate apex, slightly carinate, with erect to slightly curved setae. Mandibles with rounded but acute apex; external face with moderate to large punctures, also with appressed to decumbent setae; internal face basally excavated, surface mostly smooth and glabrous, apically with fine punctures and curved setae; basal dorsal face of mandibles coarse punctures and decumbent to slightly curved setae; Gamma tooth located medially, almost opposite to Beta lobe, shape subconical with rounded apex, directed to internal face; Beta lobe wide, almost trapezoidal, outwards directed; Alpha tooth subconical, rounded apically and slightly projected anteriorly. ***Pronotum*****:** shape convex, pronotal tubercle conspicuous, reaching anterior portion of head; discal groove complete, shallow; surface with large to coarse punctures, dense; anterior and posterior angles rounded. ***Elytra:*** scutellar shield exposed, slightly convex, posteriorly slightly carinate with few moderate to somewhat large punctures at anterior margin; elytral humeri not striate, finely punctate with a tooth-like projection, extended laterally; interstrial costae with fine to moderate punctures; epipleuron slightly concave, strongly carinate and complete to apex, with contiguous, and coarse punctures, producing a wrinkled surface at apex, also with appressed to slightly curved setae. ***Venter:*** Prosternum carinate along anterior and posterior margins, also with a continuous line of appressed setae along both margins; prosternal process narrow and convex, anteriorly carinate, with contiguous moderate to large punctures and strongly curved setae. Mesoventrite convex, mainly at anterior portion, becoming somewhat concave posteriorly, with coarse and dense punctures, also with strongly curved to decumbent setae. Metaventrite convex, surface with coarse punctation, dense with some smooth spots, medially with two lines of conspicuous, strongly curved setae, laterally with strongly curved to appressed setae; discrimen absent, instead with a flattened and glabrous region, projected posteriorly producing an acute and strong declivity. Abdominal ventrites with fine and contiguous punctures, also with few moderate punctures along posterior margin of every ventrite; posterior margins of ventrites with a transverse carina and strongly curved setae; ventrite V with a conspicuous group of yellowish setae at apex. ***Genitalia*****:** Aedeagus symmetric, narrower proximally. Phallobase with almost straight sides, narrowed only at apex. Parameres with almost straight sides and rounded apex, finely punctate distally, in lateral view somewhat concave and slightly excavated. Median lobe enlarged basally, rounded at apex with some spicules, in lateral view concave. Dorsal cross bar transverse, "V" shaped, mostly emarginate anteriorly, posterior margin slightly projected posteriorly.

Paratypes male: ***Size:*** *Total length:* 10.1-13 mm. *Total width.* 1.15-3.4 mm. As Holotype except for presenting a strong variation in size, representing small and medium size males, which is related with fine changes in general morphology, as is the case of a reduction in pronotal projection and tubercle. In minor males Gamma tooth is located closer to base, they also show a deeper discal groove at pronotum.

Paratype Female: ***Size*****:** *Total length*. 13 mm. *Total width.* 5 mm. ***Colour:*** dorsally black, legs dark-red with brownish tones, darker than males; ventrally dark-red with brownish and blackish tones, darker than males. ***Head:*** anterior margin less emarginate, dorsal surface more exposed;

labrum narrower than males, proximally internally projected, distally downwards directed, with convex and rounded apex, also with a tuft of setae; frons and vertex as males. Supra-antennal projection strongly carinate, carina subconical, with coarse punctures and erect to slightly curved setae. Mandibles symmetric, almost straight, with rounded and upwards directed apex; dorsally expanded producing a concave region with coarse and contiguous punctures; external margin with a narrow longitudinal carina from base to apex; external and internal surface with coarse and contiguous punctures, also with erect to slightly curved setae. ***Pronotum:*** as males except for a less projected anterior margin, pronotal tubercle reduced and transverse, medially interrupted by discal groove, also with stronger punctation. ***Venter:*** as males except for more conspicuous setae, also for a strongly elongate gula. Abdominal ventrites with stronger punctation, and less conspicuous posterior carinae. ***Genitalia:*** Styli elongate, not divergent, with conspicuous setae and acute apex, internally forming an oblique angle. Gonocoxites with sub-trapezoidal shape distally, also with subparallel sides, proximally slightly concave along external face, anteriorly abruptly narrowed, producing a slender projection. Lateral paraprocts only narrowed distally, with almost subparallel sides proximally, with rounded apex.

Epithet: The specific epithet alludes Professor Luciana Iannuzzi, curator at the Entomological collection of the “Universidade Federal de Pernambuco” based in Recife, Brazil, where she has been conducting different works involving Taxonomy and Ecology of Coleoptera taxa, specially with several genera of dung beetles. In recent years she has supervised more than 60 projects conducted at the Centre of Biological Sciences by undergraduate and graduate students, representing one of the most important women in science in North-East Brazil, who has offer important knowledge regarding Caatinga and Atlantic Forest beetles.

Distribution: South-East Brazil – Atlantic and Parana Forest provinces (Morrone 2022).

Remarks: *Psilodon* n. sp. 3 is the second species described for the Brazilian Atlantic Forest, mainly distributed along the state of Espirito Santo. *P. n.* sp. 3 shows strong similarities with *P. schuberti* and the remaining species described for this biome. Its high resemblance with *P. schuberti* and *Psilodon n. sp. 4* Cáceres & Grossi*,* both from the state of Rio de Janeiro, would be explained by their geographical proximity and the geological connections through the Mantiqueira province that extends across Espirito Santo, Minas Gerais, Rio de Janeiro and São Paulo states. *P.* n. sp. 3 can be distinguished by its darker body colour when compared with other Atlantic forest species, a fine reduction in male and female size; the absence of a fine preapical constriction at mandibles, position and extension of mandibular teeth; Meso and Metatibiae strong teeth; shape of the anterior margin of pahllobase; median lobe width and dorsal cross bar shape, showing in general terms a more elongate aedeagus when compared with *P. schuberti* and *P.n. sp. 4*.

***Psilodon n. sp. 4* Cáceres & Grossi.**

Figure 16.

Examined material: Holotype male labelled: **BRAZIL: RIO DE JANEIRO:** Macaé de Cima 02.i.2002, Altitude: 1600 m, Isabel Miller leg. 1♂ (EPGC).

Paratypes labelled: **BRAZIL: RIO DE JANEIRO**: Nova Friburgo, Macaé de Cima i.2002, 1400 m, I. Miller leg. 1♂ (EPGC); Petrópolis, Morim, Morro da Bandeira, 1600 m, Torres da Petrobras 02-10.ii.2010 1♂ (CERPE); Nova Friburgo, A: 1600 m, Cascatinha 1.ii.1999 E & P Grossi leg. 1♂ (CERPE);

Diagnosis: Males with strong purple and dark-red reflections along body. Size larger when compared with most Brazilian species. In lateral view mandibles somewhat slender; Alpha tooth located medially, with sub-triangular shape, projected anteriorly; Beta lobe inconspicuous; Gamma tooth opposite to Beta lobe with almost same width. Pronotal tubercle conspicuous covering median portion of dorsal face of head; pronotal disc with a well-defined groove, surface with sparse punctation and some lateral and dorsal, shallow excavations. Aedeagus robust, wide, in lateral view dorsal face strongly convex; median lobe distinctly enlarged basally and somewhat concave apically.

Description Holotype Male. ***Size:*** *Total length.* 14.53 mm. *Total width. 6.*34 mm. ***Colour*****:** dorsally dark-purple with reddish tones, legs with dark-red tones, almost black; ventrally dark-red with blackish tones. ***Head*** frons excavated, with a concave spot continuous with vertex; dorsal surface concealed, partially covered by pronotum, with coarse and dense punctures, also with erect and slightly curved setae. Antennae with six lamellae; supra-antennal projection slightly carinate with rounded to somewhat truncate apex. Mandibles with rounded and acute apex; external face with moderate to large punctures and strongly curved setae; internal face mostly smooth with few curved setae at apex; dorsal face at base with large and dense punctures, also with suberect setae; Gamma tooth located medially, rounded at apex with a cylindrical to sub-conical shape, projected to internal face, opposite to Beta lobe; Beta lobe inconspicuous, somewhat trapezoidal, extended along basal portion of external margin; Alpha tooth sub-triangular, with rounded apex, antero-dorsally projected directed. ***Pronotum*****:** pronotal tubercle distinct, covering median portion of head, not reaching anterior margin; discal groove complete, stronger at anterior portion; surface with large to coarse punctures, densely to moderately distributed. ***Elytra:*** scutellar shield exposed, almost smooth with few contiguous large punctures, slightly carinate along posterior margin; elytral humeri no striate with large to somewhat coarse punctation and a tooth-like projection extended laterally; interstrial costae with moderate to large punctures; epipleuron slightly concave, carinate and complete to apex, with contiguous coarse punctures and suberect setae. ***Venter:*** Prosternum carinate along anterior and posterior margins, also with a continuous line of appressed setae along both margins; surface with coarse punctures, densely distributed with appressed to decumbent setae; prosternal process narrow and convex, with a lateral carina, anterior portion distinctly convex, posteriorly carinate, with few large to coarse punctures and appressed setae. Mesoventrite slightly convex, with large to somewhat coarse, dense punctation and decumbent to appressed setae, mainly distributed posteriorly. Metaventrite convex, medially flattened; surface with large to coarse punctures, laterally with conspicuous, strongly curved setae, disc glabrous; discrimen as a shallow and incomplete groove; posterior margin projected distally with a strong declivity. Abdominal ventrites with fine and contiguous punctures, covering whole surface, posterior margin with moderate to large punctures and conspicuous strongly curved setae, almost with a transverse carina along margin. ***Genitalia*:** Aedeagus symmetric. Anterior phallobase spatulate, concave apically; posterior phallobase with almost straight sides, narrowing proximally. Parameres with almost straight sides, also with a finely punctate, rounded to somewhat convex apex, in lateral view, dorsal margin somewhat concave. Median lobe enlarged basally, rounded to somewhat lobed at apex, finely punctate distally and concave in lateral view. Dorsal cross bar "V" shaped and wide.

Paratypes males: *Total length.* 12.67-13.28 mm. *Total width.* 5.53-5.59 mm. as Holotype, almost of the same size, with fine differences at pronotal surface, presenting deeper excavations on dorsal and lateral portions.

Epithet: The specific epithet alludes to the Private Reserve (Reserva Particular do Patrimônio Natural – RPPN) "Fazenda Bacchus" based in Nova Friburgo municipality in the state of Rio de Janeiro, where these specimens were collected. The RPPN bacchus has an extension of 101 ha representing an important area of Atlantic Forest that has been preserved for more than 40 years. With this epithet, we would like to honour the work of Isabel and David Miller, original owners of the area that dedicated so many years to protecting part of this important and unique ecosystem.

Distribution: South East Brazil – Atlantic Province (Morrone 2014).

Remarks: Species very close to *P. schuberti*, distinguished by presenting stronger purple reflections and dark-red tones along entire body; larger size of males; slenderer mandibles; Alpha tooth narrower and projected anteriorly; apex of mandibles without preapical constriction; Beta lobe extended through base of mandibles; dorsal portion of pronotal process convex, and a more robust aedeagus. The strong resemblance between *P. schuberti* and *P.* n. sp. 4 could be explained by the similar distribution of both taxa, which are sympatric in some localities in the state of Rio de Janeiro. Even though both species almost share the same distribution, most of the altitudinal records for *P.* n. sp. 4 are higher than those recorded for *P. schuberti*, influencing the speciation process. While looking for information regarding Holotypes of *P. schuberti* and *P. brasiliense*, an associate professional from the Museum of Natural History at Oxford University stated that besides *P. schuberti* female and the male of *P. brasielense*, there was another male deposited in the collection which was distinctly larger than the other ones, unfortunately, we were not able to examine this male in order to determine if it belonged in fact to *P. schuberti* or it was a *P.* n. sp. 4 characterised by its size.

***Psilodon* n. sp. 5 Cáceres & Grossi.**

Figure 17.

Examined material: Holotype male labelled: Brasil, Santa Catarina, Itapema, i.1993, Col. J. Carlos. 1♂ (CERPE).

Paratypes labelled. **BRAZIL: SANTA CATARINA:** Hansa xii.1939 / Psilodon schuberti (Perty) ♀ P. Pereira det. 1♀ (MNRJ); Hansa, xii.1939 / Hexaphylum schuberti / Psilodon schuberti (Perty) ♂ P. Pereira det. 1♂ (MNRJ); Brasil, SC, Porto Belo, 28.ii.1961 1♂ (MZUEFS); Itapema, i.1994, Col. J. Carlos 1♂ (AMBC). **PARANA:** Olho d´Agua, Ponta Grossa, v.1943 / Hexaphylum schuberti (Perty) ♂ P. Pereira det. 1♂ (MNRJ); **SÃO PAULO:** Botucatu, São Paulo – Brasil, 23.i.1976, Mantovani col. 1♂ (CERPE). **RIO GRANDE DO SUL:** S.F. Paula, 19.2.1941 1♂(MCN); Idem except, 6.2.1944 1♂ (MCN); Handwritten label, text unclear 1♂ (MCN); S. Leopoldo 1♀ (MCN). **PARAGUAY:** Pto. Bertoni, Col. Bertoni / Psilodon schuberti Pty, AW.B.d., Hexaphyllum Gray. / MNHP A.W. Bertoni N – 93 Garcete rev. 1♂ (MNHNP).

Diagnosis: Males and females distinctly larger than other *Psilodon* species (in most specimens), with reddish tones along body. Mandibles robust, with rounded to somewhat truncate apex; Alpha tooth sub-trapezoidal, almost perpendicular; Gamma tooth opposite to Beta lobe with sub-conical shape; Beta lobe wide, robust, with sub-trapezoidal shape; supra-antennal projection carinate. Pronotal tubercle distinct, in lateral view with sub-trapezoidal shape; surface sparsely punctate; discal groove, somewhat deep. Prosternal process, wide, strongly carinate when compared with other species of *Psilodon*; Metaventrite with conspicuously setose disc.

Description Holotype Male. ***Size:*** *Total length.* 18 mm. *Total width.* 5 mm. ***Colour*****:** dorsally dark-red with brownish tones; ventrally as dorsal surface, with clearer tones. ***Head*****:** frons excavated, producing a concave continuous region with vertex; dorsal surface concealed, partially covered by a projection of pronotum, with coarse and dense punctures and slightly curved setae.

Antennae with six lamellae; supra-antennal projection with rounded to almost truncate apex, with a discreet subconical carina, distal portion with moderate punctures and slightly curved setae. Mandibles with rounded apex, somewhat acute; external face with moderate to large punctures, proximally with strongly curved setae; internal face almost smooth, slightly excavated at base with few moderate punctures, at apex moderately punctate with slightly curved setae; dorsal face at base with coarse punctation and decumbent to strongly curved setae; Gamma tooth located medially, with rounded apex, projected medially, opposite to anterior end of Beta lobe; Beta lobe almost trapezoidal, projected laterally; Alpha tooth located at apical region, shape sub-trapezoidal and upwards directed. ***Pronotum*****:** pronotal tubercle distinct, covering head medially but not reaching anterior portion; discal groove complete, wide; surface with coarse to large, densely distributed punctures. ***Elytra:*** scutellar shield exposed, with few coarse punctures, posterior margin slightly carinate; elytral humeri with a striate portion, also with fine punctation and a tooth-like projection extended laterally; interstrial costae with fine to moderate punctures; epipleuron slightly concave, carinate and complete to apex, proximally with dense, large to coarse punctures, becoming contiguous distally, producing a somewhat wrinkled surface, with strongly curved setae. ***Legs:*** Protibiae dorsally carinate, serrate, with several teeth increasing in size distally, almost of the same size, with several contiguous tooth-like projections; surface with suberect to decumbent setae. Mesotibiae with decumbent to erect setae, with an external line of somewhat strong teeth, internally with several tooth-like projections, both teeth and projections with a setose invagination; apex enlarged with few tooth-like projections and two subequal spur. Metatibiae as described for mesotibiae except for not presenting tooth-like projections at apex and two apical spurs, being the posterior one longer. ***Venter:*** Prosternum carinate along anterior and posterior margins, also with a continuous line of appressed setae along both margins; surface with coarse punctures, densely distributed with appressed setae; medially with two weak oblique carinae, apparently continuous with coxal transverse carinae; prosternal process narrow and convex, laterally carinate, with few large punctures and appressed setae. Mesoventrite slightly convex, with coarse, densely distributed punctation, anteriorly with short setae, becoming longer posteriorly, varying from decumbent to strongly curved. Metaventrite convex, medially flattened and glabrous; surface with moderate to coarse punctures, mainly distributed laterally and appressed conspicuous setae; discrimen present as a shallow groove, producing a declivity. Abdominal ventrites with fine contiguous punctures, covering most of surface, also with some moderate punctures along posterior margins; posterior margin of all ventrites entirely carinate, somewhat reduced at ventrite V, also with appressed to decumbent setae. ***Genitalia*:** Aedeagus symmetric. Anterior phallobase expanded, sub-triangular, with truncate apex; posterior phallobase with almost straight sides, slightly constricted medially. Parameres with almost straight sides, rounded at apex, surface finely punctate; in lateral view, dorsal portion slightly convex. Median lobe basally enlarged, rounded to somewhat lobed at apex, with fine punctation laterally, concave in lateral view. Dorsal cross bar "V" shaped, anteriorly strongly emarginate with two antero-lateral truncate projections.

Paratype males: *Total length*. 16.9-17.8 mm. *Total width*: 4.9-6.1 mm. Most paratypes of similar size, except one specimen from Ponta Grossa (PN), and another one from Puerto Bertoni in Paraguay. Size reduction is represented by a more acute apex of mandibles, and narrower Alpha tooth, also reducing extension of Gamma tooth and Beta lobe. Supra-antennal projection with reduced carina in small males.

Paratypes Female: ***Size*:** *Total length*.13.1-16.1 mm. *Total width.* 4.1-5 mm. ***Head:*** almost as large as males head, dorsal surface more exposed, due to reduction in pronotal tubercle; surface with more conspicuous punctation than males, punctures coarse and dense, with erect to slightly curved setae. Mandibles symmetric, almost straight, apex upwards directed and somewhat truncate; enlarged producing a dorsal surface; external margin with a narrow longitudinal carina from base to apex, resembling a laminar tooth; internal ventral portion with a weak carina, similar to the dorsal one; external surface with coarse and contiguous punctures, also with conspicuous curved to erect setae, inner face with few moderate punctures, with erect to appressed setae; dorsal face with contiguous coarse punctures and conspicuous erect setae. ***Pronotum:*** as males except for a less projected anterior margin, pronotal tubercle slightly reduced and somewhat transverse instead of perpendicular, also medially interrupted by discal groove; surface with more conspicuous punctation. ***Legs:*** as males, except for less pronounced teeth. ***Venter:*** as males, but showing a considerable reduction in several structures such as, mentum, also with narrow prosternum and mesoventrite; metaventrite convex as males, but somewhat elongate, with acute anterior angles; abdominal ventrites with fine and contiguous punctation, and more conspicuous setae, covering posterior portions of every ventrite, and the entire surface of ventrite V. ***Genitalia:*** Styli sub-oblong, extremely divergent; internal face of apex forming an oblique angle, apex almost truncate, with conspicuous setae. Gonocoxites distinctly projected anteriorly, with sub-trapezoidal shape, laterally convex, anterior portion abruptly narrowed.

Epithet: The specific epithet aims to honour the life and work of Jose Antonio Vanin (1948-2020), one of the most important Brazilian entomologists, who worked at the University of São Paulo, where he also was the director of its Museum of Zoology for more than 50 years. Most of current Brazilian professors and researchers dedicated to the study of insects were influenced in direct or indirect ways by Vanin´s works and teaching. He was one of the first researchers applying phylogenetic methods in Brazil, described 123 new species offering a significant contribution to Neotropical weevils, and contributed to the knowledge of immature stages of several beetle species.

Distribution: South Brazil - Parana Forest, Araucaria Forest and Atlantic Forest provinces (Morrone 2022).

Remarks: *Psilodon* n. sp. 5 is the species with the southernmost distribution record in South America. In Jiménez-Asúa & Martínez (1963) there is a mention of *P. schuberti*, as a species from Southern Brazil distributed in the states of Paraná and Santa Catarina; in their work they extend its distribution to the Province of Misiones in North-East Argentina represented by one male and one female collected in October 1953. This locality, actually corresponds to the distribution of *P.* n. sp. 5 and is continuous with Santa Catarina, Paraná and Paraguay records. In the original description of *P. xerophilicum*, Martínez & Reyes-Castillo (1985) discuss that there were specimens from North East Argentina deposited in their collections identified as *P. schuberti*, probably referring to this couple of a larger series of *P.* n. sp. 5.

***Psilodon* n. sp. 6 Cáceres & Grossi.**

Figure 18.

Examined material: Holotype male labelled: **BRAZIL: ALAGOAS:** Murici, v.1984 D.F. de Moraes Jr. 1♂ (MNRJ).

Diagnosis: Male of small size when compared with other *Psilodon* species. Body dark-red with brownish tones. Dorsal face of head more exposed than other *Psilodon* males, almost as exposed as in other species females. Supra-antennal projection rounded to somewhat truncate, finely carinate. In lateral view mandibles distinctly enlarged, robust; Alpha tooth sub-trapezoidal, finely projected anteriorly; Beta lobed entirely extended along base of mandibles; Gamma tooth almost with same extension of Beta lobe. In lateral view, pronotal tubercle somewhat conspicuous, convex to somewhat trapezoidal; discal groove shallow with contiguous punctation. Discirmen present as an incomplete, shallow groove, forming a sub-triangular spot posteriorly. Aedeagus distinctly slender, resembling to some extent, the *P. gilberti* one.

Holotype Male. ***Size:*** *Total length.* 12.92 mm. *Total width* 4.62 mm. ***Colour*:** dorsally dark-red with darker tones at head and pronotum; ventrally dark-red with brownish tones, darker than dorsal portion. ***Head*:** frons slightly excavated; dorsal face almost entirely exposed; surface with large to somewhat coarse punctation, also with erect to slightly curved setae. Antennae with six lamellae; supra-antennal projection with rounded to almost truncate apex, weakly carinate, with somewhat conspicuous setae, mainly distributed apically. Mandibles with rounded apex; external face with moderate to large punctures and suberect setae, mainly distributed at base; internal face basally excavated, surface almost smooth, finely punctate with strongly curved setae at apex, base of mandibles expanded, with large to somewhat coarse punctures and strongly curved setae; Gamma tooth located medially, with rounded apex, shape subconical, projected to internal axis, opposite to Beta lobe; Beta lobe almost trapezoidal, projected laterally; Alpha tooth located apically, sub-conical, rounded at apex and directed upwards. ***Pronotum*:** pronotal tubercle conspicuous, only covering posterior portion of head medially; discal groove almost complete, shallow and wide with contiguous punctation; surface with moderate to somewhat large, densely distributed punctures; anterior and posterior angles rounded. ***Elytra:*** scutellar shield exposed, with few moderate punctures, almost smooth, posterior margin slightly carinate; elytral humeri no striate with fine and dense punctation, also with a tooth-like projection extended laterally; interstrial costae finely punctate; epipleuron slightly concave, carinate and complete to apex, with large to coarse, contiguous punctures, distally producing a somewhat wrinkled surface with strongly curved setae. ***Legs:*** Protibiae dorsally carinate, serrate, with several teeth, increasing in size distally, also with several contiguous tooth-like projections between teeth; surface with decumbent to erect setae. Mesotibiae with decumbent to erect setae, with an external line of strong teeth, increasing in size distally, also with several tooth-like projections, all associated with simple setae; apex enlarged with several tooth-like projections and two subequal spur. Metatibiae as described for mesotibiae except for presenting less distinct tooth-like projections, instead with contiguous coarse punctation, apex enlarged without projections, with two apical spurs, being the posterior one longer. ***Venter:*** Prosternum carinate along anterior and posterior margins, also with a continuous line of appressed setae along both margins; surface with large to coarse punctures, densely distributed with appressed to strongly curved setae; prosternal process narrow and convex, continuous with posterior margin carina, also with few moderate punctures and appressed setae; procoxae with a proximal oblique carina and a surface with contiguous fine and coarse punctures, also with appressed to strongly curved setae. Mesoventrite slightly convex, with coarse, densely distributed punctation, with shorter setae along anterior portion, becoming longer posteriorly varying from decumbent to strongly curved. Metaventrite convex, medially flattened and glabrous, projected posteriorly with a strong declivity; discrimen present as a shallow groove; lateral portions with two spots with moderate, densely distributed punctures, and decumbent to appressed setae. Abdominal ventrites with fine and dense punctures, covering most of surface, also with some moderate punctures along posterior margins; posterior margin of all ventrites carinate, carina almost covering whole margin accompanied by few decumbent to strongly curved setae. Ventrite V with densely to contiguously distributed punctures, also with appressed to decumbent setae at sides and apex. ***Genitalia*:** Aedeagus symmetric, strongly elongate. Anterior phallobase acute, with rounded apex; posterior phallobase with almost straight sides, constricted medially. Parameres with almost straight sides, rounded at apex, surface finely punctate at apex; in lateral view, concave. Median lobe basally enlarged, rounded to somewhat lobed at apex, elongate, convex in lateral view. Dorsal cross bar “V” shaped.

Epithet: This specific epithet aims to honour friendship and brotherhood, alluding to Mr. Demis Vermelho Gomes, an IT professional whose support was a fundamental part of developing this work.

Distribution: North-East Brazil – Atlantic provinces (Morrone 2022).

Remarks: *Psilodon* n. sp. 6 is the sixth species distributed along the Atlantic Forest, being this, the only one with records in the northern portion of this biogeographical province. Although it is possible to perceive the resemblance between this species and the others from the Atlantic Forest, *P.* n. sp. 6 is characterized by its small size, less concealed head, the incomplete shallow groove at metaventrite and its typical narrow aedeagus, suggesting a stronger divergence process between the northern portion of Atlantic forest and the ones distributed through southern territories. These differences could be related to the interruption of this continuous biome, caused by the São Francisco river mouth, and differences between geological structures between Mantiqueira province (South-East Brazil) and the Borborema plateau (North-East Brazil). Recently we identified a *Psilodon* male for a group of researchers from the “Universidade de Pernambuco” (UPE), collected in Pernambuco which presumably belongs to *P.* n. sp. 6, unfortunately we were only able to determine until the genus level through photos (photo available at http://www.portal.zoo.bio.br/media1327).

Description of a new Syndesinae genus for South America

N. gen. 1 Cáceres & Grossi.

Type species: N. gen. 1 n. sp. 7 Cáceres & Grossi.

Diagnosis: Body colour entirely black. Head transverse and emarginate, labrum concealed from dorsal view. Gula strongly transverse. Antennae with seven lamellae, proximal lamellae slightly reduced. Mandibles with truncate apex; Alpha and Gamma teeth merged and located medially, projected internally; Beta lobe conspicuous. Pronotal shaped convex, with a strong declivity at anterior portion; pronotal tubercle dorsally conspicuous but somewhat reduced in lateral view; discal groove strong. Scutellar shield with punctate surface, cordiform; elytral humeri with weak tooth-like projections; striae strongly punctate, with one interstrial costae for two striae; interstrial joint obsolete. Legs with distinctly strong teeth; profemora distinctly robust. Genital capsule elongate. Aedeagi symmetric, subparallel and somewhat narrowed; median lobe enlarged basally, getting slender apically.

Description Male. ***Size:*** *Total length.* 11.9 mm. *Total width*. 2.0 mm. ***Colour*:** dorsally mostly black with dark-red to brownish tones; ventral face dark-red with brownish tones. ***Head*:** shape transverse, slightly emarginate; labrum wide, proximally excavated with truncate and slightly convex apex; posterior portion somewhat concealed, covered by anterior projection of pronotum; anterior margin shagreened, glabrous. Mentum sub-trapezoidal, not excavated, with two weak lobes at apex, anterior margin slightly emarginate, with few fine punctures and erect setae. Gula convex, sub-trapezoidal, almost entirely carinate, carina almost smooth with few fine punctures, surface mostly glabrous, anterior margin not carinate, with dense, moderate punctures, and erect setae. Gena with coarse punctures and yellowish appressed setae. Antennae with seven lamellae; supra-antennal projection with rounded apex, surface carinate. Eyes distinctly conspicuous; interocular distance 2.0 times longer than sides. Mandibles symmetric, slightly curved inwards;

apex truncate; Gamma tooth located close to apex, merged with Alpha tooth, shape sub-triangular, with rounded and slightly carinate apex, inwards directed; Beta lobe located basally, with rounded to somewhat truncate apex, directed upwards; Alpha tooth continuous with apex, producing a concave region, also with acute and rounded apex. ***Pronotum*****:** shape convex, anterior margin projected anteriorly, with a convex pronotal tubercle; discal groove complete; surface with strong punctation; antero-lateral angles concave; anterior and posterior angles rounded; in lateral view, anterior angles reaching posterior portion of eyes; lateral pronotal carina present, complete and continuous with anterior and posterior margins, scalloped with fine setae. ***Elytra*****:** scutellar shield exposed, with convex surface, and coarse punctation; elytral humeri not striate with fine punctures and a fine tooth-like projection; each elytra with 10 striae; each stria with coarse, densely distributed punctures; also with one complete interstrial costae for two striae; epipleuron somewhat flattened, carinate and complete to apex, distally enlarged; epipleural carina strong and somewhat wide, with strong punctation; elytral declivity with a narrow, convex interstrial joint. ***Legs:*** Protibiae dorsally carinate, serrate, with several teeth increasing in size distally, external and internal face with strongly curved to decumbent setae. Mesotibiae with yellowish suberect setae; externally serrate with a line of strong teeth, increasing in size distally, also with several tooth-like projections, irregularly distributed along whole surface; apex enlarged with several tooth-like projections and two subequal apical spur. Metatibiae as described for mesotibiae. ***Venter:*** Prosternum carinate along anterior and posterior margins, also with a continuous line of yellowish appressed setae; prosternal process narrow and convex, with conspicuous curved setae and few moderate punctures. Mesoventrite almost flat, with coarse and densely distributed punctures and yellowish appressed setae, being more distinct over median portion; shorter when compared with other species of the genus. Metaventrite convex; surface with moderate to large, densely distributed punctures, also with conspicuous appressed setae covering almost whole surface; posterior margin with a truncate declivity; discrimen present as a shallow groove, disc flattened to somewhat excavated posteriorly. Abdominal ventrites with fine contiguous punctures and appressed setae covering most surface, also with some moderate punctures along posterior portion of every ventrite; all ventrites with a conspicuous transverse median carina at posterior margin. ***Genitalia*:** Aedeagus symmetric. Phallobase sub-triangular, somewhat slender with almost straight sides. Parameres almost straight laterally, with acute to somewhat rounded apex, in dorsal view concave apically. Median lobe enlarged at base with acuminate and concave apex. Dorsal cross bar almost triangular with truncate ends.

Epithet: The specific epithet for this genus alludes to Ms Beverly Anne Holloway, who is probably the first woman in history to study lucanid beetles. She was contemporary with important taxonomists, who also contributed to the knowledge of Lucanidae, as is the case of Bernard Benesh (1891–1964), Robert Didier (1885–1977) and Eugène Séguy (1890–1985), all of them well-known for the production of some of the most important catalogues of World Lucanidae, but she was the first one developing strict morphological studies from a phylogenetic perspective. Even though she was mainly focused on New Zealand and Australian taxa, her works represent the principal scientific references exclusively dedicated to stag beetles of the 20th century. Her last published work in 2007 about Lucanidae of New Zealand summarizes most of her contributions and it still is our mandatory reference for starting every new project.

Distribution: Venezuela and Trinidad and Tobago.

Remarks: N. gen. 1 Cáceres & Grossi, 2022 is the third genus described within Syndesini and the second one with records in the Neotropical region. The information on this taxon is scarce, as is the case of most South American lucanid beetles, for which we basically only have morphological and distributional data, lacking knowledge regarding life history and evolutionary history. To our knowledge, only two male specimens have ever been collected. The amber fossil, *Syndesus ambericus* Woodruff (2009), which we do not believe to belong in *Syndesus*, could be the most closely related to this new genus instead of actual *Syndesus* species. According to its age (20.43 to 13.65 Ma) and some characteristics as body size, antennae with seven lamellae, the apparent presence of the Alpha tooth and Beta lobe on the mandibles, a reduction in pronotal tubercle, and the strong punctation along the entire body allow us to hypothesise this relation.

N. gen. 1 n. sp. 7 Cáceres & Grossi.

Figure 19.

Examined material: Holoytpe male labelled: Venezuela, Monagas State 10°10.332´N, 63°33.315 ´W, 1110 m, Guachero Cave N.P. 20-21.vii.2010 Holzenthal, Thomson, Cressa, UV lights; VZ10-07-21-02B 1♂ (UMSP).

Paratype male labelled: Trinidad and Tobago, “Handwriting”: ?, 50. / k. ɓưƌƌepa /?Hexaphyllum 1♂(ZIN).

Diagnosis: Body colour entirely black. Head slightly emarginate; labrum somewhat exposed in dorsal view. Antennae non-geniculate with seven lamellae. Anterior portion of supra-antennal projection concave, getting convex laterally. Alpha and Gamma tooth merged with a sub-conical Beta lobe. Head and pronotal surface with coarse and dense punctation, stronger along pronotal anterior declivity. Discal groove of pronotum strong and complete, interrupting posterior portion of tubercle. Elytra strongly punctate with one complete interstrial costae for two striae. Prosternum with coarse punctation; prosternal process narrow and convex. Protrochanters conspicuously exposed. Aedeagus symmetric, moderately elongate with subparallel sides.

Description Holotype Male. ***Size:*** *Total length.* 11.9 mm. *Total width*. 2.0 mm. ***Colour*****:** dorsally mostly black with dark-red to brownish tones; ventral face dark-red with brownish tones. ***Head*****:** shape transverse, emarginate; labrum wide, with a proximal excavation producing a concave surface; apex truncate; frons surface with two shallow excavations and a somewhat convex median line; vertex concealed, covered by a portion of pronotum; surface with large to coarse punctures and erect to slightly curved setae; anterior margin shagreened, glabrous, and somewhat carinate. Antennae with seven lamellae; supra-antennal projection with rounded apex, also with a distinct, subc-onical carina upwards directed. Mandibles symmetric, slightly curved inwards; apex truncate; external face with moderate to large punctures, also with few, strongly curved setae, mainly distributed at base; inner face with moderate to somewhat large punctation and erect setae distributed along entire surface; Gamma tooth located close to apex, merged with Alpha tooth, shape sub-triangular, with rounded and slightly carinate apex, inwards directed; Beta lobe located basally, with rounded to somewhat truncate apex, directed upwards; Alpha tooth continuous with apex, producing a concave region, also with acute and rounded apex. ***Pronotum*****:** shape convex, anterior margin projected anteriorly, with a convex vertical carina; discal groove complete; surface with densely distributed, coarse punctures; antero-lateral angles concave; in lateral view, anterior angles reaching posterior portion of eyes; lateral pronotal carina present, complete and continuous with anterior and posterior margins, scalloped with fine setae. ***Elytra:*** scutellar shield exposed, with convex surface, and shape semicircular, with few coarse punctures; elytral humeri not striate with fine punctures and a fine tooth-like projection; interstrial costae with fine, densely to moderately distributed punctures; epipleuron somewhat flat, carinate and complete to apex, with large to somewhat coarse punctures, dense proximally, becoming contiguous apically, with strongly curved to suberect setae; distal portion enlarged; epipleural carina strong and somewhat wide, with coarse, dense to contiguous punctures and decumbent to strongly curved setae. ***Legs:***

Protibiae dorsally carinate, serrate, with several teeth increasing in size distally, external and internal face with strongly curved to decumbent setae. Mesotibiae with yellowish suberect setae; externally serrate with a line of strong teeth, increasing in size distally, also with several tooth-like projections, irregularly distributed along whole surface; apex enlarged with several tooth-like projections and two subequal apical spur. Metatibiae as described for mesotibiae ***Venter:*** Prosternum carinate along anterior and posterior margins, also with a continuous line of yellowish appressed setae; prosternal process narrow and convex, with conspicuous curved setae and few moderate punctures. Mesoventrite almost flat, with coarse and densely distributed punctures and yellowish appressed setae, being more distinct over median portion; shorter when compared with other species of the genus. Metaventrite convex; surface with moderate to large, densely distributed punctures, also with conspicuous appressed setae covering almost whole surface; posterior margin with a truncate declivity; discrimen present as a shallow groove, wider posteriorly. Abdominal ventrites with fine contiguous punctures and appressed setae covering most surface, also with some moderate punctures along posterior portion of every ventrite. ***Genitalia*****:** Aedeagus symmetric, narrower proximally. Phallobase sub-triangular, somewhat slender with almost straight sides. Parameres almost straight laterally, with acute to somewhat rounded apex, in dorsal view with concave apical portion. Median lobe enlarged basally with acuminate and concave apex. Dorsal cross bar almost triangular with truncate ends, finely emarginate at anterior margin, narrow.

Paratype variation: Male of not determined size. As holotype with a less abrupt declivity at anterior portion of pronotum, also with less pronounced antero-lateral concavities along antero-lateral portion of pronotum.

Epithet: Nature is our object of study, but its essence is pure poetry, which constantly communicates with us, even though we do not always understand its words. Gladys Vargas, a Colombian mother, learned how to talk to a unique beetle the day that his son, Elvis Luis Vargas, was kidnapped and murdered by a paramilitary group near the Venezuelan border. His body was never recovered as is the case of at least 560 victims whose bodies were burned in crematorium ovens owned by this group. While waiting for his son, ignoring that he was no longer alive as she knew him, that beetle flew close to her ears and she understood that Luis had turned into that six-legged organism. This epithet aims to honour Luis' life, a life that was taken by the Colombian conflict, it also intends to recognize the huge effort that his mother has been doing in the fight for justice and to keep Luis' memory alive. N. gen. 1 n. sp. 7 is a small tribute to all the lives that stop beating as a consequence of the violence and became immortal through the memories of their families. Today we believe that Luis is more than alive, flying as one of the most remarkable stag beetles we have ever known.

"La naturaleza es nuestro objeto de estudio pero su esencia es pura poesía que constantemente se comunica con nosotros, aunque no entendamos sus palabras. Gladys Vargas, una madre colombiana, aprendió como hablar con un escarabajo especial el día en que su hijo, Elvis Luis Vargas, fue secuestrado y asesinado por un grupo paramilitar en la frontera colombo-venezolana. Su cuerpo nunca fue recuperado, como es el caso de por lo menos 560 víctimas cuyos cuerpos fueron quemados en hornos crematorios, propiedad de este grupo. Mientras esperaba por su hijo, ignorando que él no estaba vivo como ella lo conocía, aquel escarabajo voló cerca de sus oídos y así, entendió que Luis se había convertido en un organismo de seis patas. Este epíteto busca honrar la vida de Luis, una vida que fue tomada por el conflicto colombiano, también pretende reconocer el gran esfuerzo que su madre ha hecho en la lucha por la Justicia y por

mantener el recuerdo de Luis vivo. N. gen. 1 n. sp. 7 *es un pequeño tributo a todas las vidas que pararon de latir como consecuencia de la violencia y se tornaron inmortales a través de los recuerdos de sus familiares. Hoy creemos que Luis está más que vivo volando como uno de los ciervos volantes más extraordiarios que hemos conocido."*

Distribution: North-East Venezuela and Trinidad and Tobago – Venezuelan and Trinidad Province (Morrone 2022).

Remarks: N. gen. 1 n. sp. 7 is the only known species of this genus. Although it is possible to identify some shared traits with *Psilodon* and *Syndesus* species, *H.* n. sp. 7 shows exclusive characteristics, including the position of Alpha and Gamma teeth of the mandibles which are merged, truncate apex of mandibles, labrum truncate, less emarginate head, less conspicuous eyes, stronger punctation along whole body, specially at pronotum.

Track analysis

Due to the lack of ecological information on *Psilodon* species, we conducted a track analysis including all genera of South American plants in the order Fagales as a strong relation has been documented between *Syndesus* species in Australia and the southern beeches (Notophagaceae: *Nothofagus*). Given the restricted distribution of *Nothofagus* in South America (only Chile and Argentina), we extended the analysis to other genera of Fagales with distributional records in lower latitudes.

Through the Track Analysis (Figure 21), we recovered five individual tracks corresponding to the Fagales genera *Casuarina*, extending through Chacoan and Parana dominions in Brazil and South Brazilian and Pacific dominions across Tropical Andes; *Nothofagus* (two different individual tracks), restricted to the Andean region; *Quercus*, covering a short portion of Andean region in

Argentina, extending through southern region of Chacoan dominion in Argentina and Brazil, also crossing South Brazilian and Pacific dominions along Tropical Andes; the last individual track was recovered for *Castanea*, being the only one crossing the Chacoan, Parana, South-Eastern Amazonian, South Brazilian, Boreal Brazilian, ending at Colombian Eastern cordillera at Pacific dominion; this track extends across Atlantic Forest, Cerrado, Amazon and a portion of Montane ecosystems.

We also recovered three generalized tracks, the first one conformed by *Casuarina*-*Trigonobalanus*, which showed a main pattern across Tropical Andes with two branches, the first one extending through southern portion of Chacoan and Parana dominions, and the second one entering South Brazilian and South-Eastern Amazonian dominions from Andean slopes. The second generalized track conformed by *Alfaroa*-*Alnus*-*Juglans*-*Morella*-*Trigonobalanus*-*Quercus*, presents a similar pattern across the Andes, sharing the branch that extends from Andean slopes through South Brazilian and South-Eastern Amazonian dominions. The last generalized track recovered, composed by *Carya*-*Casuarina*, restricted to Parana dominion across Araucaria forest and southern regions of Atlantic forest provinces.

It was not possible to recover generalised tracks for *Psilodon* or *N. gen. 1* species (Figure 21) instead, we obtained one individual track for *Psilodon* and another one for *N. gen. 1*. There is a high overlap between the individual track for *Psilodon* and the generalised tracks for Fagales, and the individual track recovered for *Casuarina*. The individual track for *N. gen. 1* was restricted to the Venezuelan and Trinidad provinces and did not present overlapp with Fagales tracks.

We obtained individual tracks for *P.* n. sp. 5, *P. schuberti*, *P.* n. sp. 3, *P. xerophilicum*, *P.* n. sp. 6 (considering the Pernambuco collection data), *P. burmheimi*, *P. westwoodii*, and *P. paschoali*, with the Brazilian species extending through more than one biogeographic province (including *P. paschoali*), and *P. westwoodii* restricted to the Magdalena province in Colombia.

Discussion:

Psilodon is revised here for the first time. With our results we restrict its distribution to South America forming two groups, one represented by nine species (of which six are new) distributed in Brazil, and the other one represented by five species from the Tropical Andes (see Figure 20 for distribution map). With this revision we offer taxonomic support for *Psilodon,* considering it as a distinct genus, separated from *Syndesus*, which along with *N. gen. 1* **New Genus**, now conform the tribe Syndesini. The morphology of *N. gen. 1* seems to be the most divergent, being *H.* n. sp. 7 closer to the *S. ambericus* fossil described by Woodruff (2009), with *Psilodon* and *Syndesus* highly resemblant.

With two groups of *Psilodon* species, one from the Andes, which converges with the *N. gen. 1* distribution, and other mainly distributed along the Atlantic Forest in Brazil, the speciation processes of these taxa would respond to two main patterns. Andean species would respond to allopatric events caused by Pleistocene temperature oscillations of the Andean highlands, which were represented by dispersal events followed by strong isolations (Hazzi *et al*. 2018). This, in addition to the high levels of endemism across the Andes, would explain the high morphological divergence within the Andean *Psilodon* species and the unique morphology of *N. gen. 1.*

The second pattern, represented in the Atlantic Forest in Brazil, where all *Psilodon* species are highly resemblant. The speciation processes across this biogeographic province, and probably across the Parana dominion, would be explained by sympatric speciation processes (Gastauer *et al*. 2015), in a major degree than the one across the Andes. This could be due to the extension of ancient geological formations such as the Borborema plateau, the Mantiqueira province and the Parana plateau.

Considering the morphological resemblance among the Atlantic Forest species it is possible to identify three geographical groups which share some traits. In the North *P.* n. sp. 6 is the most divergent one, with very different male aedeagi characterised by its narrow shape. Going south, it is possible to recognize a highly resemblant group formed by *P. xerophilicum* (State of Bahia), *P.* n. sp. 3 (State of Espirito Santo), *P. schuberti* and *P.* n. sp. 4 (State of Rio de Janeiro), being these two the most resemblant ones. In the end, *P.* n. sp. 5 is the species with the southernmost distribution records of the genus, extending from the State of São Paulo to North East Argentina, with a morphology easily distinguished from the other species by its characteristic apical curvature of male mandibles and larger specimens.

The morphological divergence among the Atlantic Forest species could be related to the centres of endemism across the province, identified in the State of Pernambuco, State of Bahia and the "Serra do Mar" in South East Brazil (da Silva *et al*. 2004; Carnaval *et* al. 2009; Batalha-Filho & Miyaki 2011). Carnaval & Moritz (2008) also found evidence of another centre for butterflies taxa across South Brazil, which also could be related to the morphological divergences found in our study.

The remaining three species, *P.* n. sp. 1, *P.* n. sp. 2 and *P. buhrnheimi* seem to support the biogeographic hypotheses of the recurrent connections between the Atlantic Forest and the Amazon, which have been widely documented for several organisms (Sobral-Souza *et al*. 2015; Thomé *et al*. 2016; Ledo & Colli 2017; Devecchi *et al*. 2020). The individual track (Figure 21) of *Psilodon* shows these connections, represented by a median point with *P.* n. sp. 2, the only species from the Cerrado, continuing to the Amazonian region, where *P. buhrnheimi* presents a wide distributional range, from the North Bank of the Amazon to the South Bank, even extending beyond Brazil, and showing a distribution point from the Satipó province in Peru.

The distribution of these species is probably supported by the sclerophyll woodlands, and even with a distribution across the Amazonian region, some of the records coincide with several Amazonic savanna spots that reflects the biogeographic connections mentioned above, which would be offering similar habitats as the ones present in Australia and New Caledonia, where *Syndesus* species can be found.

Psilodon kanynde is the only species from the Caatinga province, which would be the only evidence represented by a lucanid species of the connections between the Eastern Brazil and the Northernmost portion of the Amazonian region, and despite its proximity to xerophytic habitats, it is probable that this species is actually distributed across high elevation ecosystems, suitable for its development. On the opposite site of this hypothetical biogeographic connection we find *P. paschoali*, which was originally described for Colombia, but we extend here its distribution to Northern Venezuela. This species represents a particular case, as despite its proximity to the Tropical Andes, it presents a morphology closer to all Brazilian species, suggesting a stronger phylogenetic relationship which supports the existence of the Northern routes of biotic interchange from the Atlantic rainforest.

In the absence of more data, it is difficult to provide insights regarding the evolutionary history of *N. gen. 1* but, with the existence of a well-preserved fossil from Hispaniola, the idea of finding answers to these questions will probably be found across the Antillean subregion.

Gondwanan origin of Psilodon and N. gen. 1

Besides the high morphological resemblance between all Syndesini genera, the disjunct distribution of these taxa suggests an influence of the migratory movements between the Australasian region and South America on the divergence processes of the tribe. The migration of the ancestral forms of the Syndesini genera may have occurred across the circum-Antarctic track (Lawver & Gahagan 2003; Moreira-MuñozCantrill 2018). Despite the lack of phylogenetic hypotheses to perform biogeographic analyses to offer more robust conclusions, the association between Gondwanan tectonics and the origin of different South American beetle taxa is widely supported, with several examples of austral disjuncts for Adephaga and Polyphaga (Kuschel 1995; Kuschel & Lawrence 1991; Chani-Posse 2013; Sota *et al*. 2021).

For the specific case of South American lucanid beetles, Kim & Farrell (2015) provided the only molecular phylogeny available for the entire family. With their results the Gondwanan origin of several Neotropical genera such as *Casignetus* MacLeay, 1819 (Lucaninae: Casignetini); *Chiasognathus* Stephens, 1831 Lucaninae: Chiasognathini; *Streptocerus* Dejean, 1833; *Sphaenognathus* Buquet, 1838 (Lucaninae: Chiasognathini) was supported. Previous work by Paulsen (2013), showed similar results for the origin of the austral genus *Hilophyllus* Paulsen & Mondaca, 2006 (Aesalinae: Ceratognathini). Unfortunately, none of the Syndesini genera have been included in these kinds of analyses, however, the highly convergent morphology of *Syndesus*, *Psilodon*, and *N. gen. 1*, along with their distributional patterns, represent strong evidence for similar biogeographic processes which should be tested in the future using molecular tools.

Panbiogeographic analysis for Psilodon and N. gen. 1 and its association with Fagales plants

Without molecular or ecological data it is difficult to provide precise interpretations regarding the species distribution of *Psilodon* and *N. gen. 1*. Nevertheless it is possible to propose some hypotheses for these questions.

The southernmost distribution records for the South American Syndesini are from Northern Argentina, but given the under-representation of this taxon among entomological collections, and the difficulty in finding alive specimens in the field, the possibility of a non-recorded wider distribution in Southern South America is high.

If southern populations of *Psilodon* or *N. gen. 1* actually exist, they would represent the remnants of the first species that migrated across the *Nothofagus* southern temperate forests of the circum-Antarctic track. These forests were well established when the Gondwanan rifting began around 140 MYA (Moreira-Muñoz 2011; Hill & Khan 2022), constituting the main ecological association that allowed the geo-dispersal of Australasian taxa to South America, and still, fosters several lucanid genera such as *Erichius* Maes, 1992 (Roig-Juñent *et al*. 2004) (Lucaninae: Sclerostomini), *Hilophyllus* Paulsen & Mondaca 2006 (Tello 2020) and *Apterodorcus* Arrow, 1943 (Mondaca & Paulsen 2008) (Lucaninae: Sclerostomini).

Despite that there is no evidence of association between South American Syndesini and southern beeches, there are records of this relationship with *Syndesus* species in Australia and New Caledonia (Batolozzi *et al*. 2017), allowing us to expect similar relations in the Neotropical region. *Nothofagus* species are restricted to the southern portion of South America (see Figure 21 Individual tracks *Nothofagus* 1 and 2), however, there are records in lower latitudes for other Fagales (southern beeches Order) species across South America, which besides the biogeographic processes discussed above, could explain the current distribution of *Psilodon* and *N. gen. 1* species.

The generalised tracks obtained through our panbiogeographic analysis, including the records of the South American Fagales genera *Quercus* (oaks), *Alfaroa* (campano), *Alnus* (black alder), *Castanea* (American chestnut), *Carya* (Hickory), *Casuarina* (sheoaks), *Juglans* (Andean walnut), *Morella* (Wax myrtle) and *Trigonobalanus* (purple oak), showed to be highly congruent with the individual tracks of *Psilodon.*

The main generalised track composed by *Alfaroa*-*Alnus*-*Juglans*-*Morella*-*Trigonobalanus*-*Quercus* extends across the South American Transition Zone (Morrone 2014) and the adjacent provinces where the Andean species of *Psilodon* and *N. gen. 1* are distributed.

The second generalised track is constituted by *Casuarina*-*Trigonobalanus*, which besides extending across the Andes, shows a connection with southern Brazil, crossing through the Pampa province, and enters to the Araucaria Forest province, where *P.* n. sp. 5 is widely distributed.

As complementary tracks, the *Carya*-*Casuarina* and *Casuarina* tracks showed to be highly resemblant to the tracks of all *Psilodon* species. The *Carya* genus track coincides with the distributional data of *P.* n. sp. 5, *P. schuberti* and *P.* n. sp. 4. The *Casuarina* individual track is the only one extended towards the north, even reaching the distribution record of *P.* n. sp. 1, however *Casuarina* was introduced to the Americas, so any interpretation regarding the association between the *Psilodon* species and these plants should be careful.

The remaining species *P.* n. sp. 2 and *P. buhrnheimi* would be related with the *Castanea* track, which, besides a portion of the *Casuarina,* is the only one crossing the Cerrado province, entering the Amazon. In addition to these tracks, the projection from the Andes towards southwestern Brazil, represented by the *Trigonobalanus* genus suggests another association that would be complementary to the ones recovered for the Amazonic and Cerrado species of *Psilodon.*

Even though these associations are still hypothetical, the distribution of most Lucanidae along high elevation ecosystems, usually characterised by high humidity and low temperatures, only leads to the conclusion of strong evolutionary relations between temperate and sclerophyll forests, where Fagales and other plant taxa would be fostering *Psilodon* populations. Unfortunately none of the obtained tracks showed to be related with *N. gen. 1* distributional data.

The need for further studies involving the life history of these lucanids is extremely important, and now, with the proposition of the hypothetical relationships between the plant genera mentioned above, we expect to guide future fieldwork focusing on sampling *Psilodon* and other lucanid species in habitats where fagales plants are dominant, as has been reported in other regions that *Alnus*, *Castanea*, *Casuarina*, *Juglans Quercus* (Avgin & Thomaes 2014; Maynard 2019; Scaccini 2022) hosting several species of *Lucanus*, *Platycerus* and *Lissotes.*

Acknowledgments

We would like to thank all collection curators who share material and photographs in order to conduct this study. Thanks to Jennifer C. Giron and Juan Jose Morrone for the considerations on this manuscript. In last we would like to thank the "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior" – CAPES for the Doctoral Scholarship of the Academic Excellence Programme PROEX, which made possible the conduction of this work.

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Appendix II – List of Figures

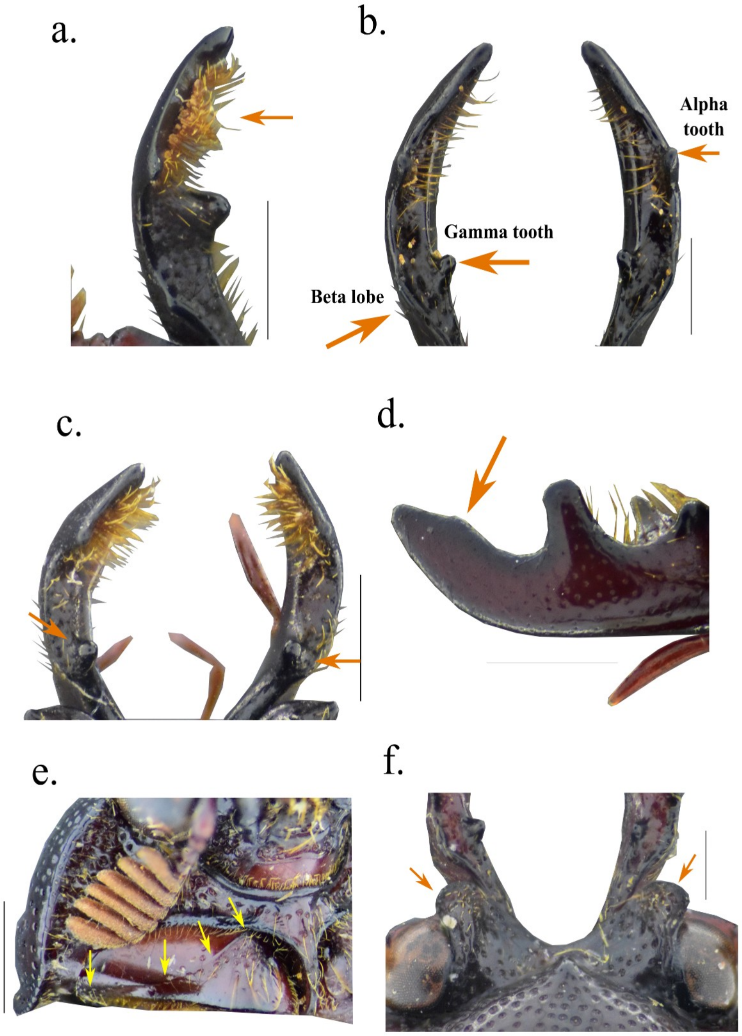
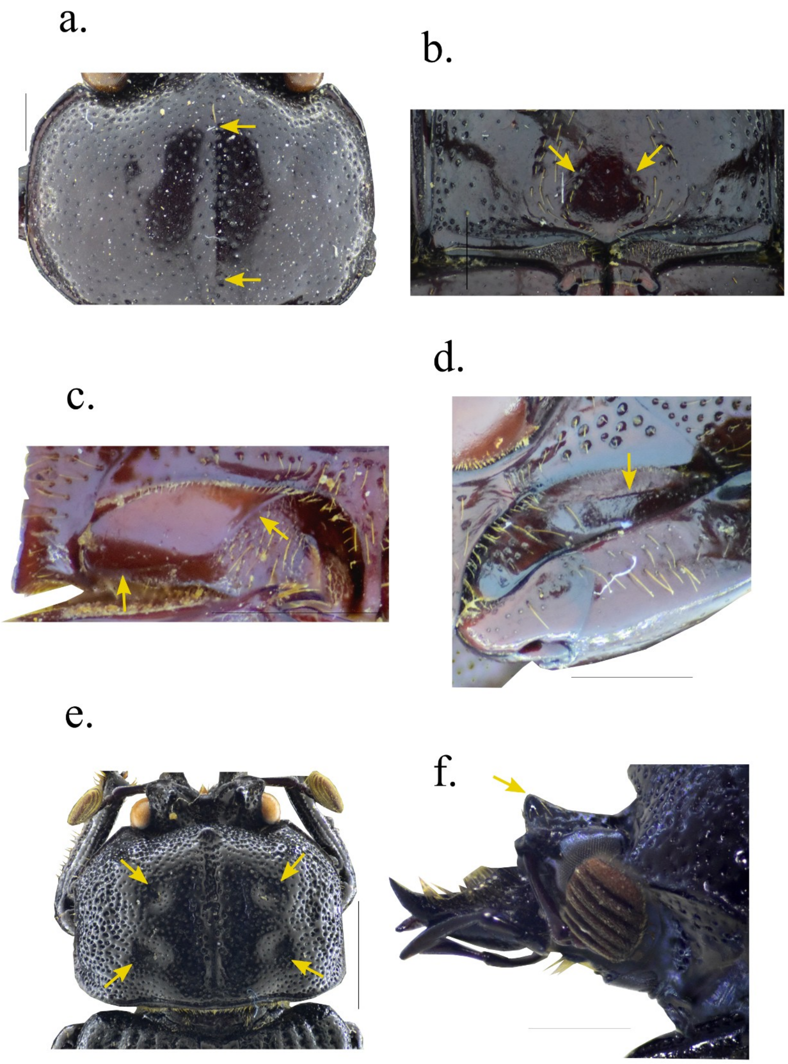


Figure 1. a. *P. gilberti* apical tuft of male left mandible. **b.** *P.* n. sp. 4 **new species** Alpha, Gamma and Beta teeth of male mandibles. **c.** *P. seguyi* male mandibles with Gamma tooth and Beta lobe merged. **d.** *P. schuberti* preapical tooth-like projection of male mandibles. **e.** *P.* n. sp. 1 **new species** procoxal carina medially interrupted. **f.** *P. buhrnheimi* supra-antennal projection with truncate apex. Scale bars 1 mm.



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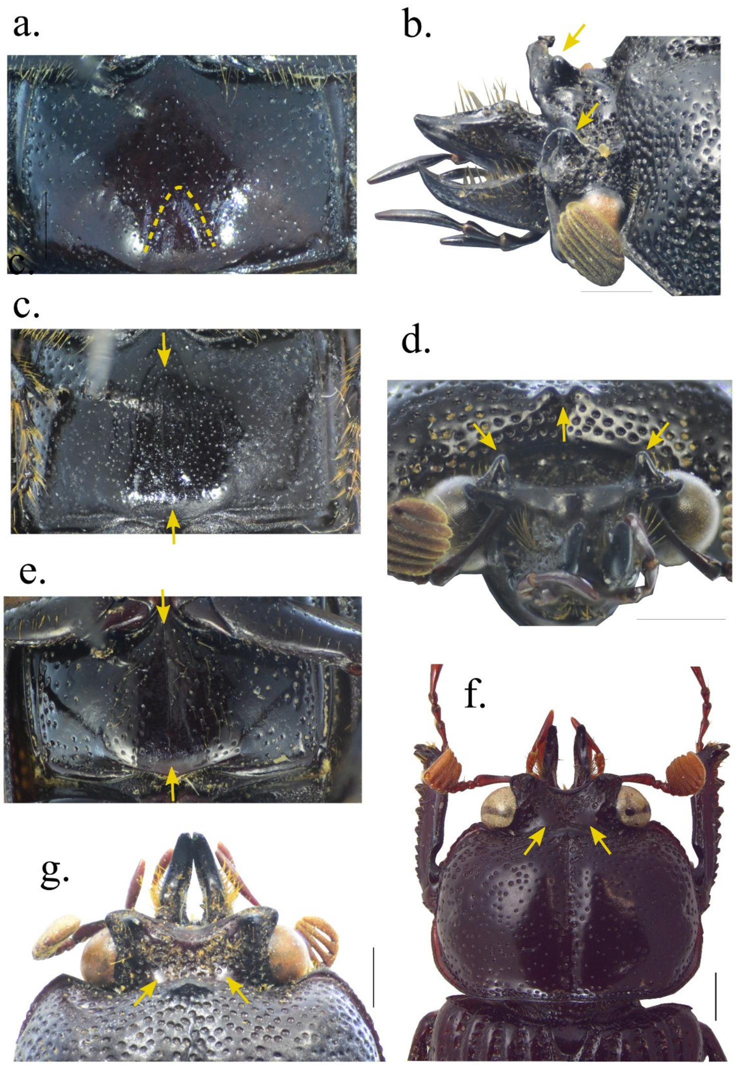

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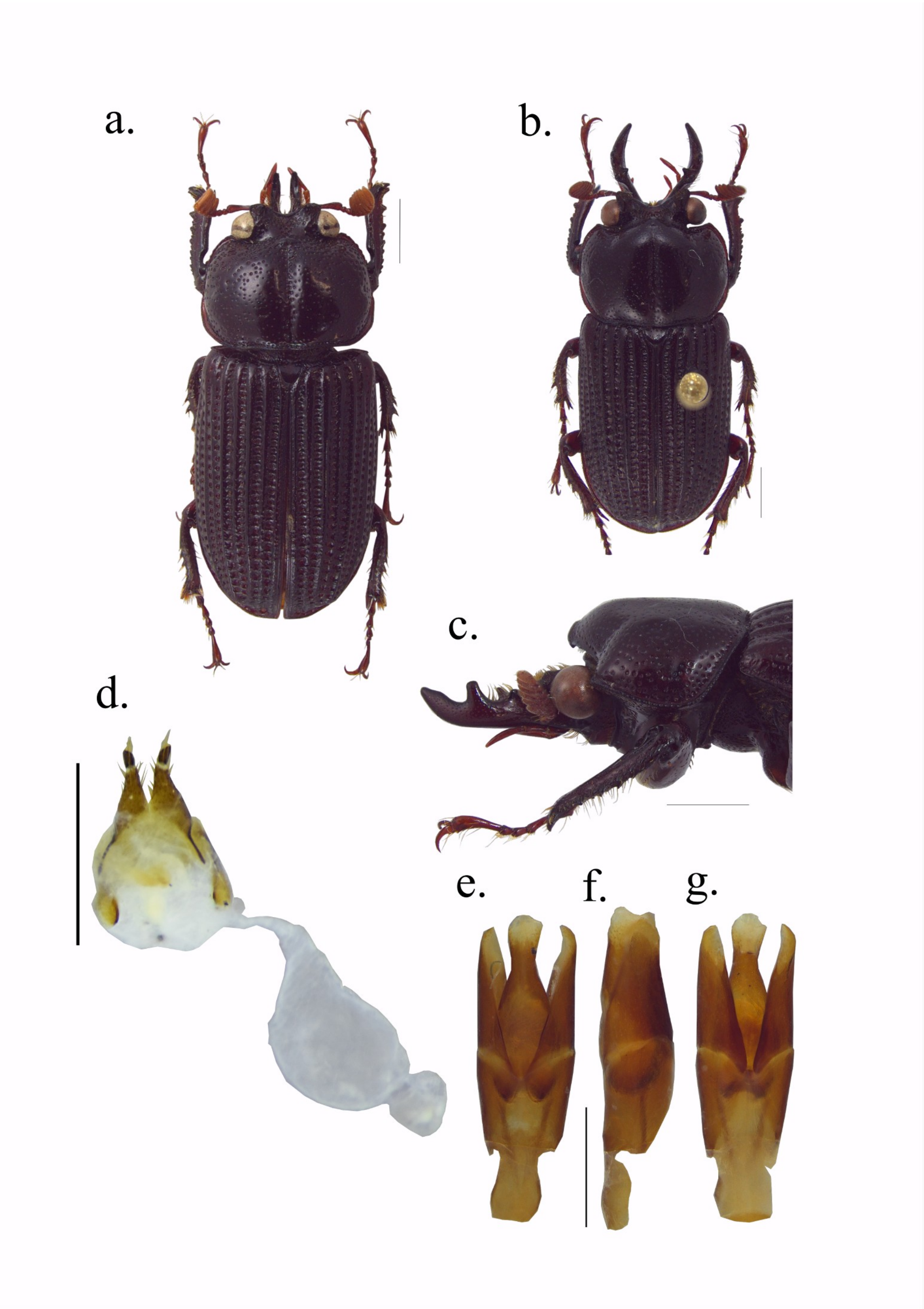

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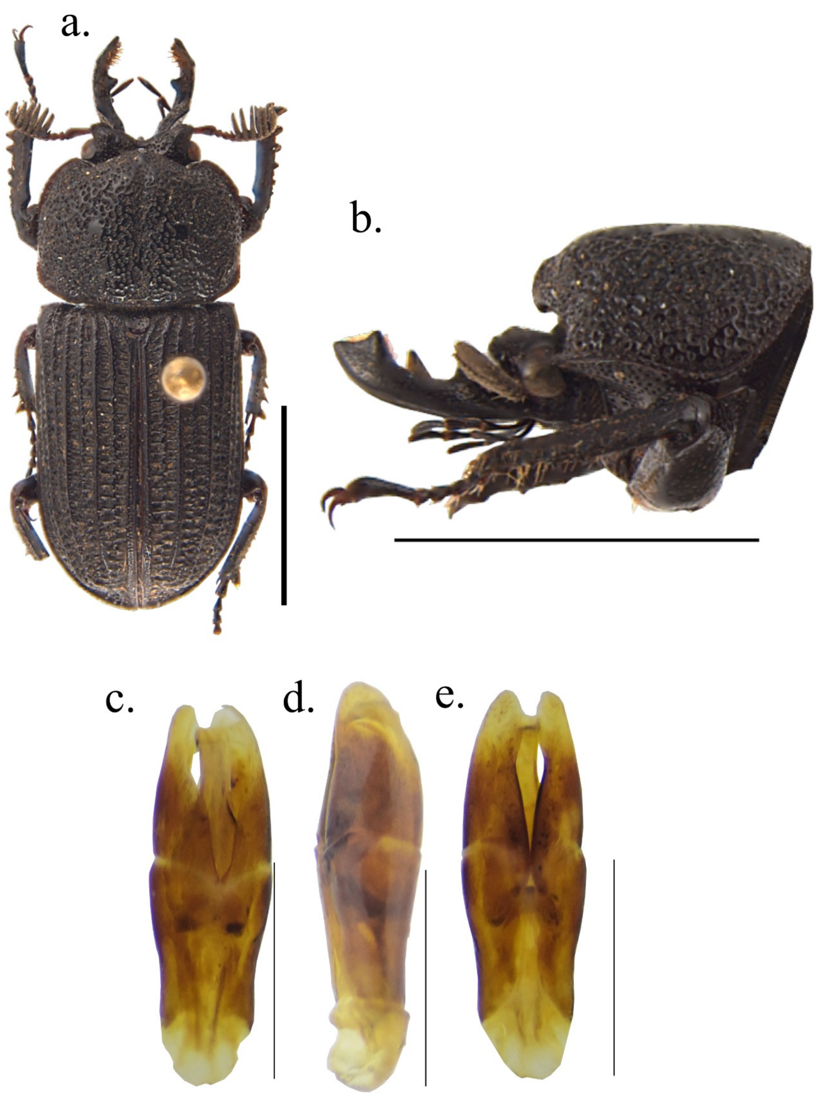

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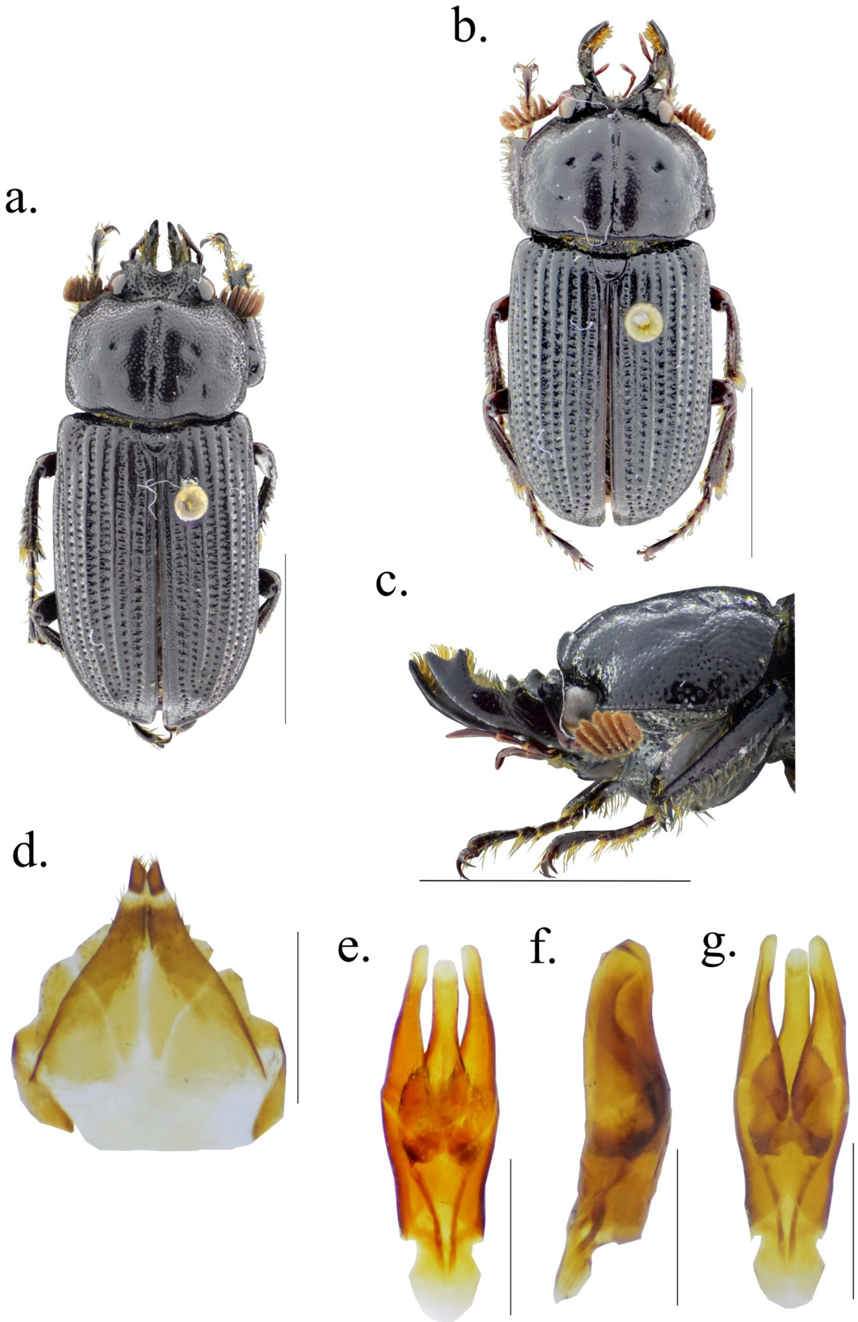

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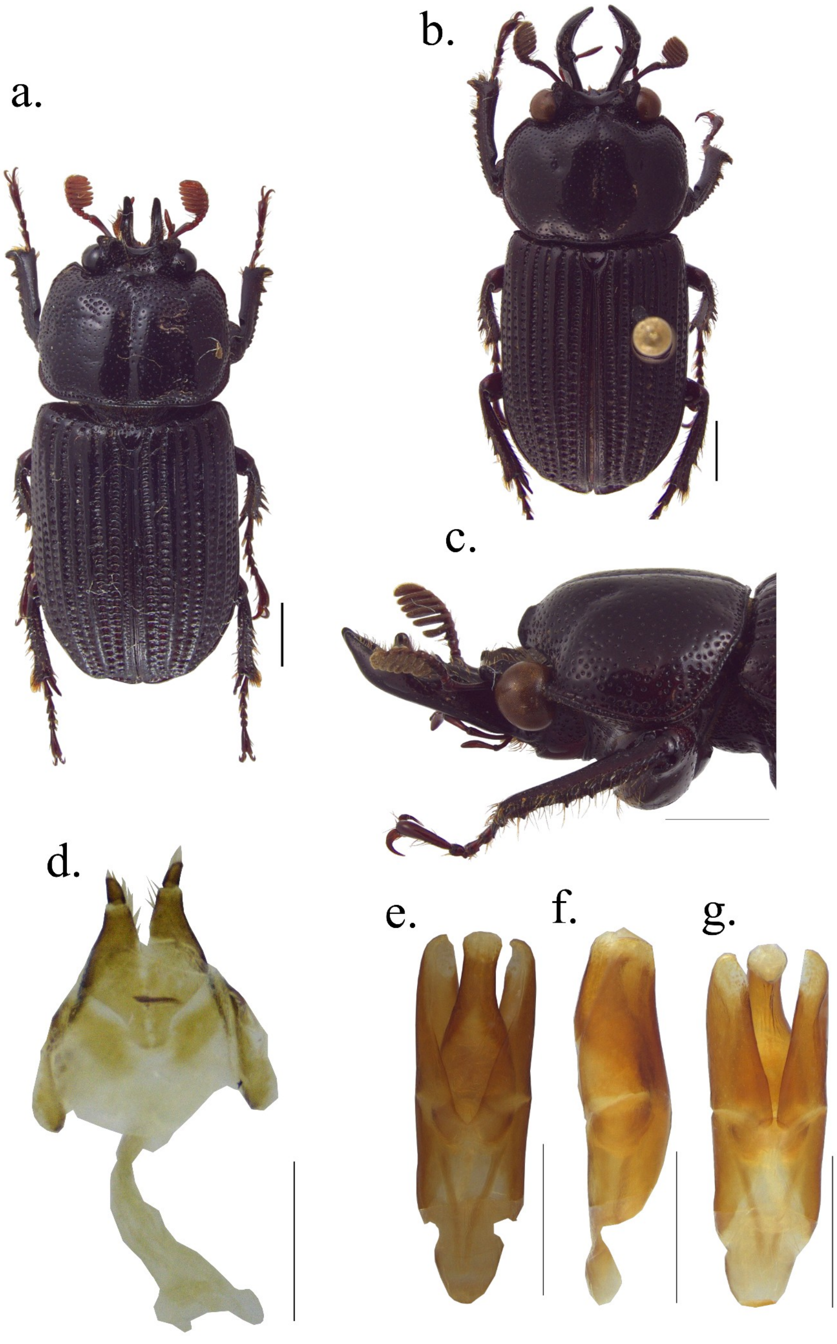

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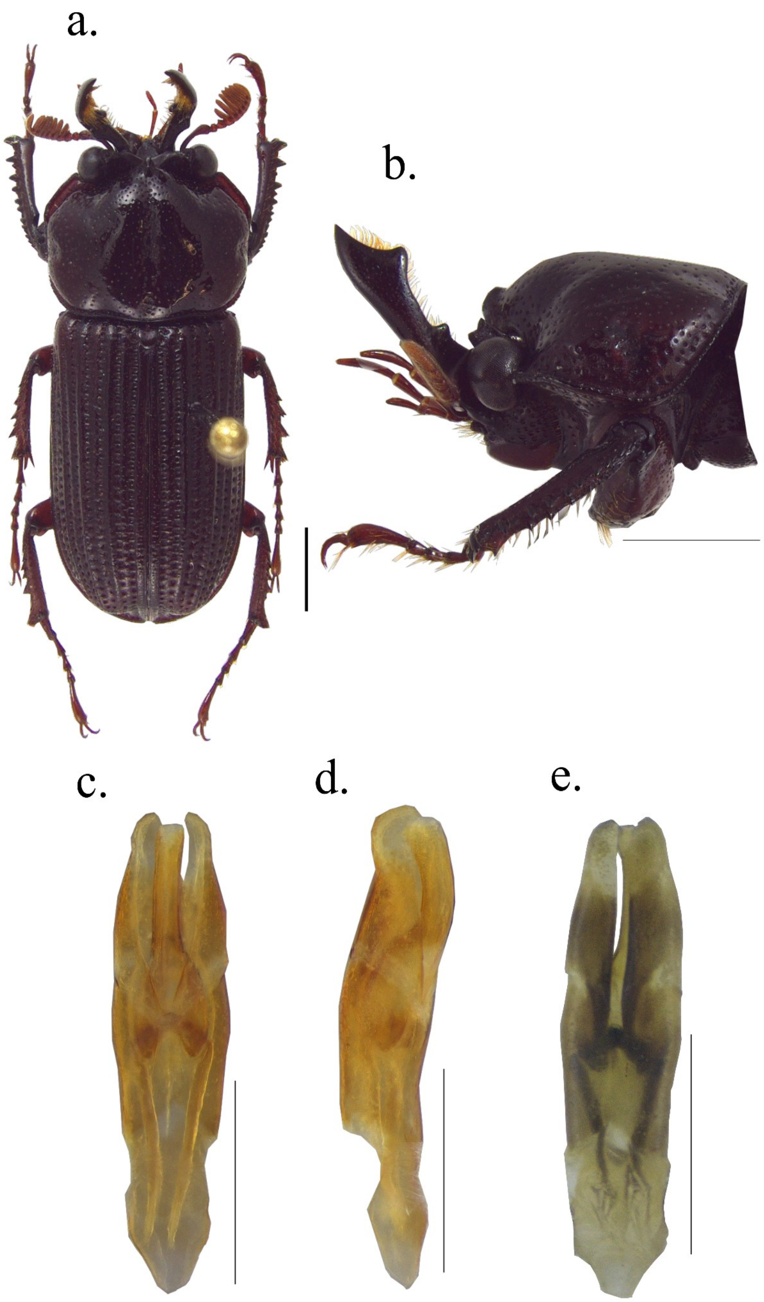

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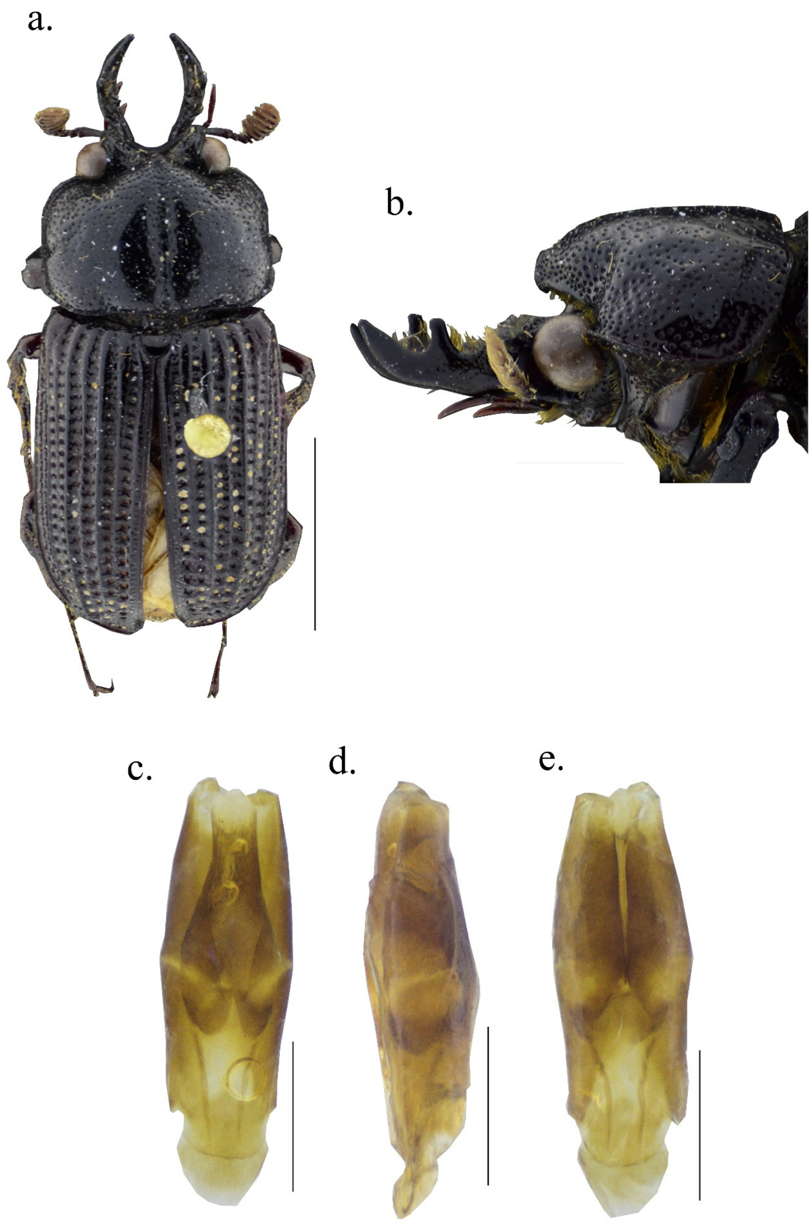

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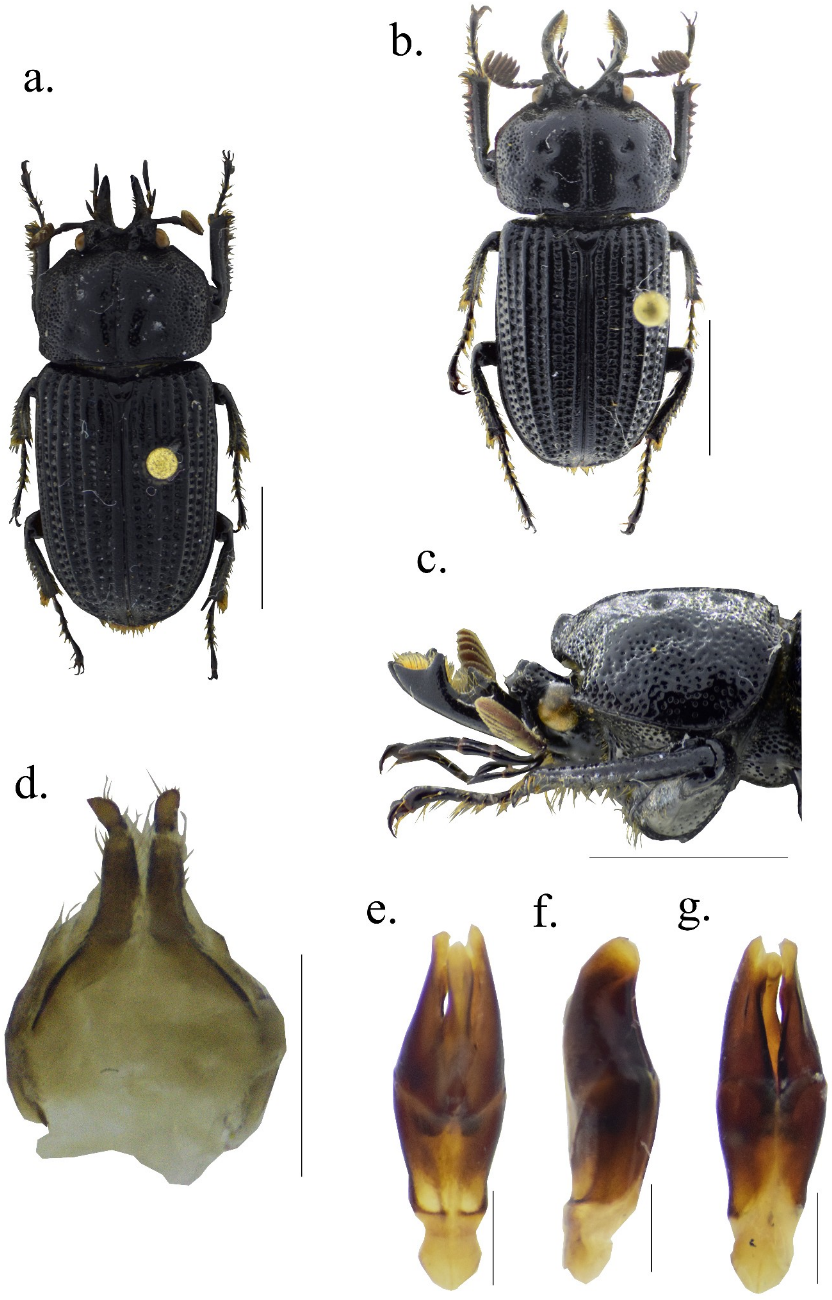

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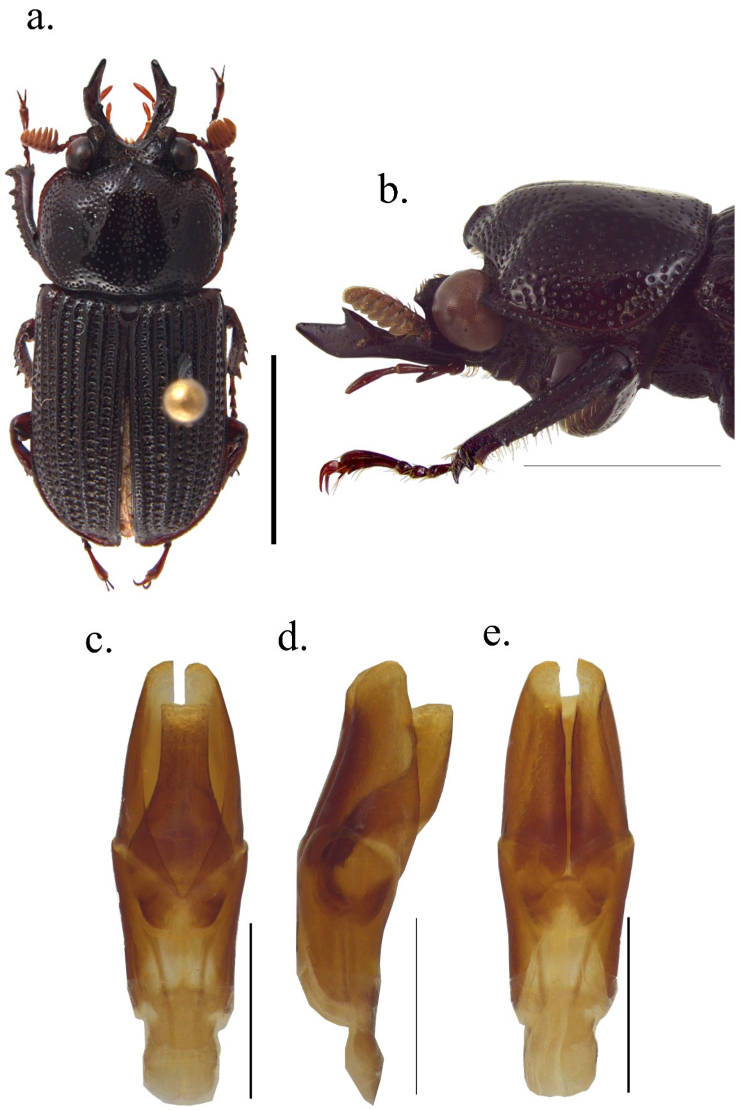

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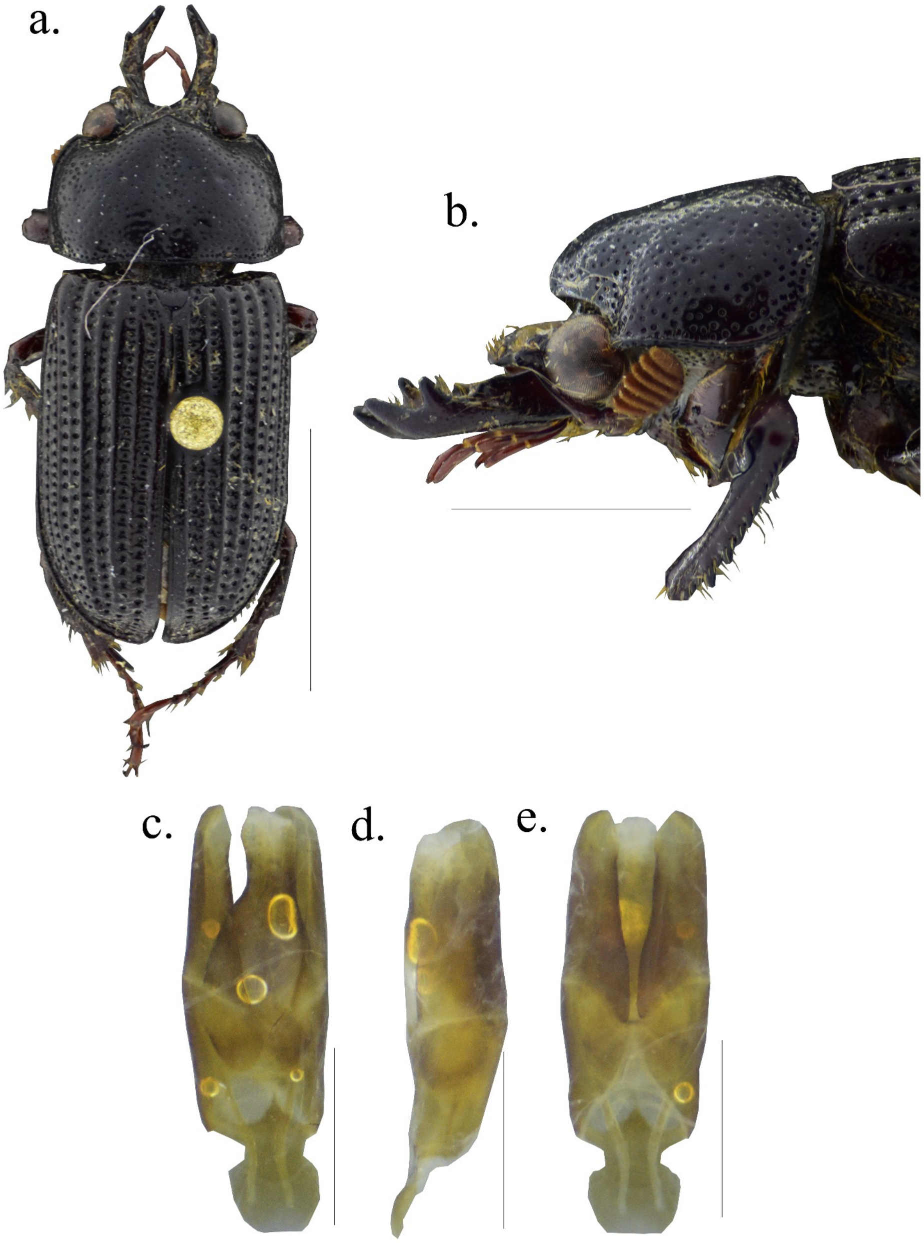

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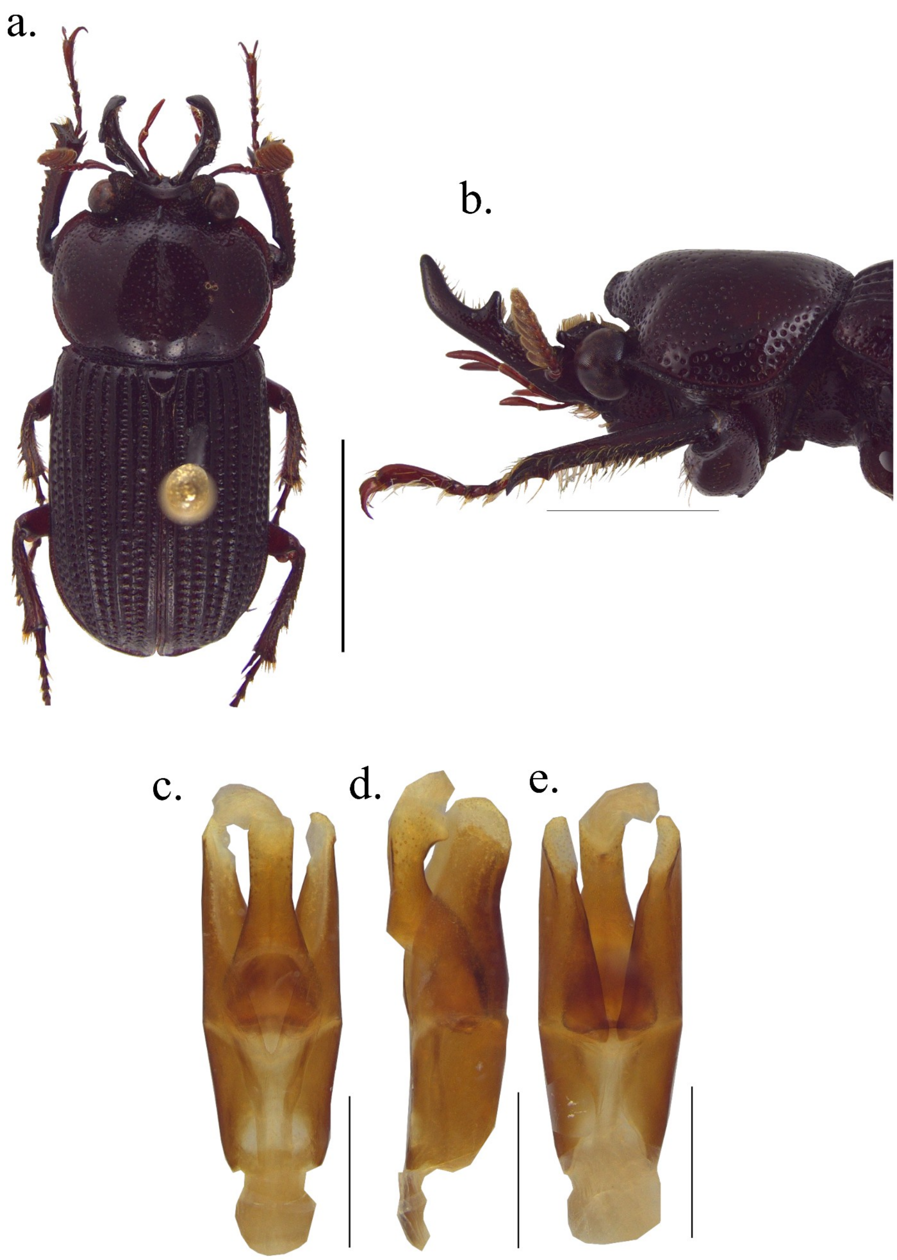

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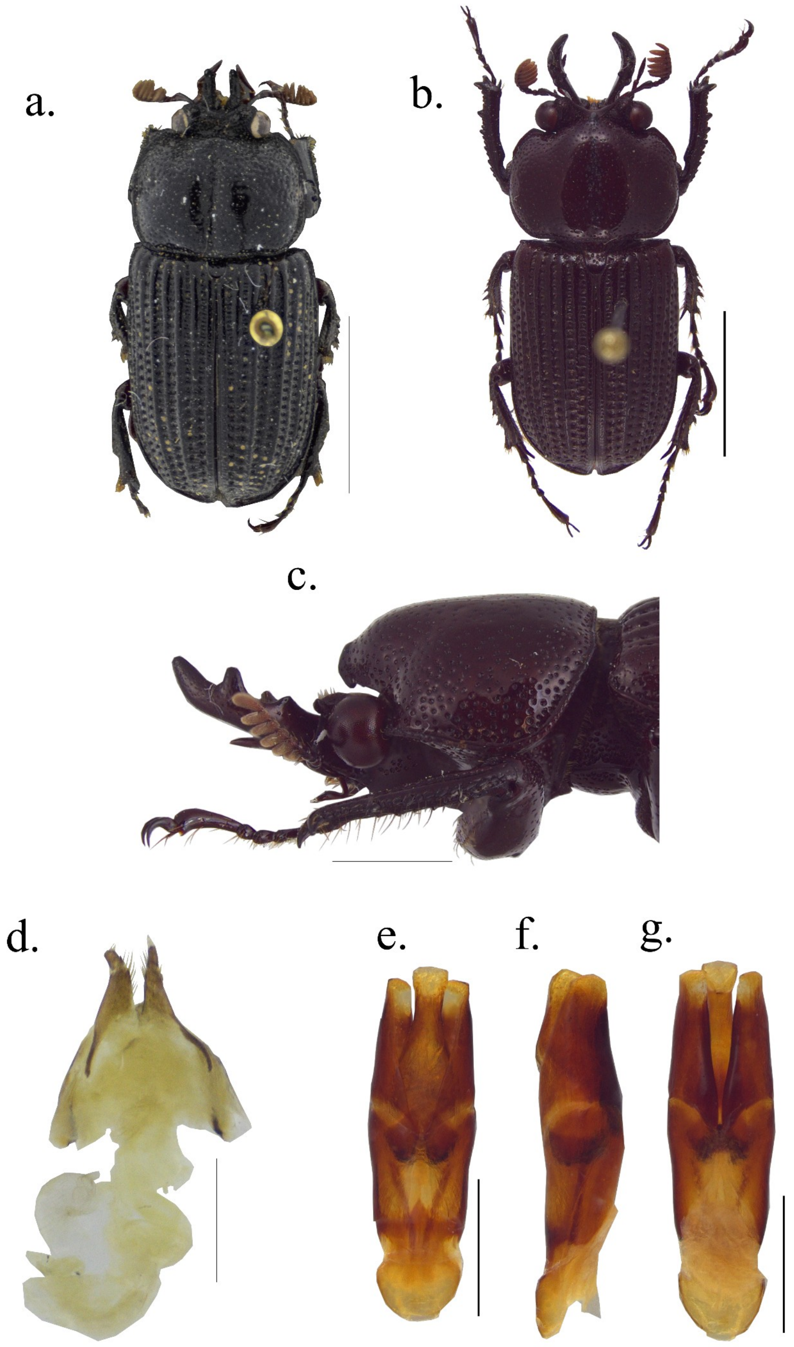

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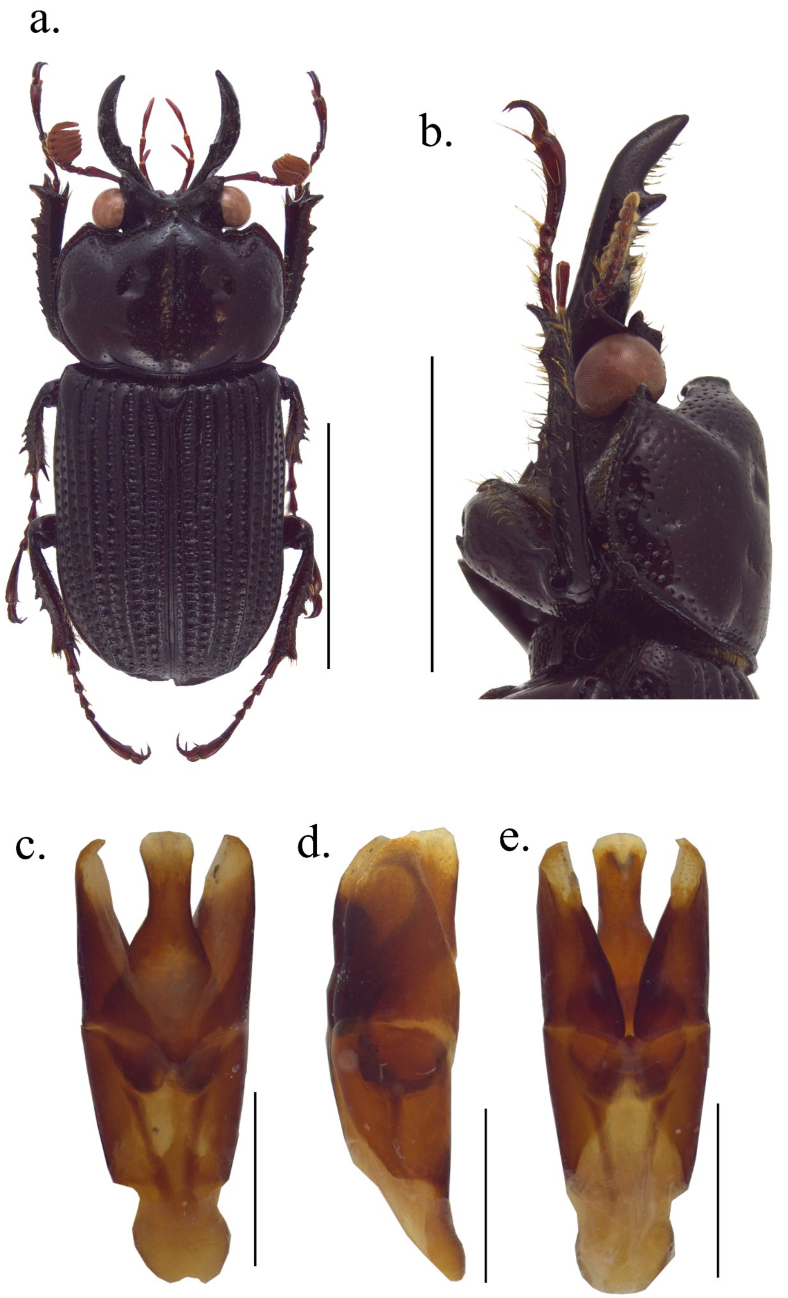

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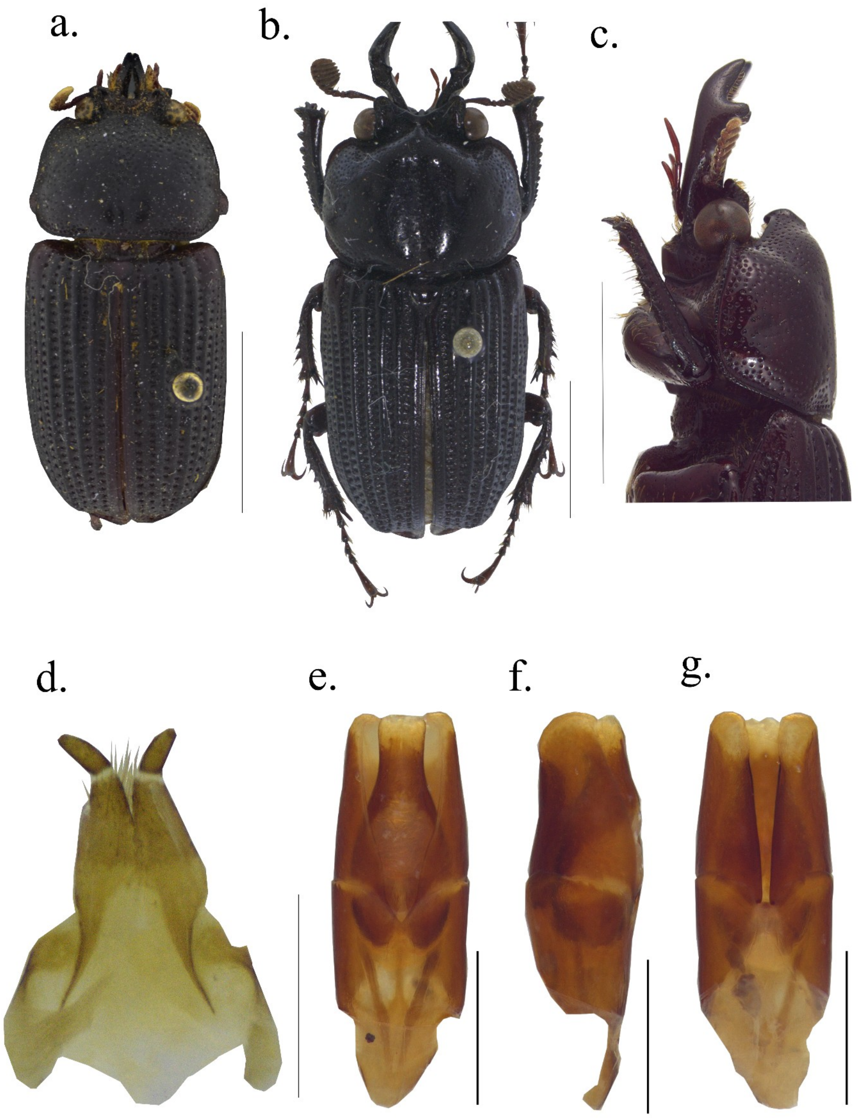

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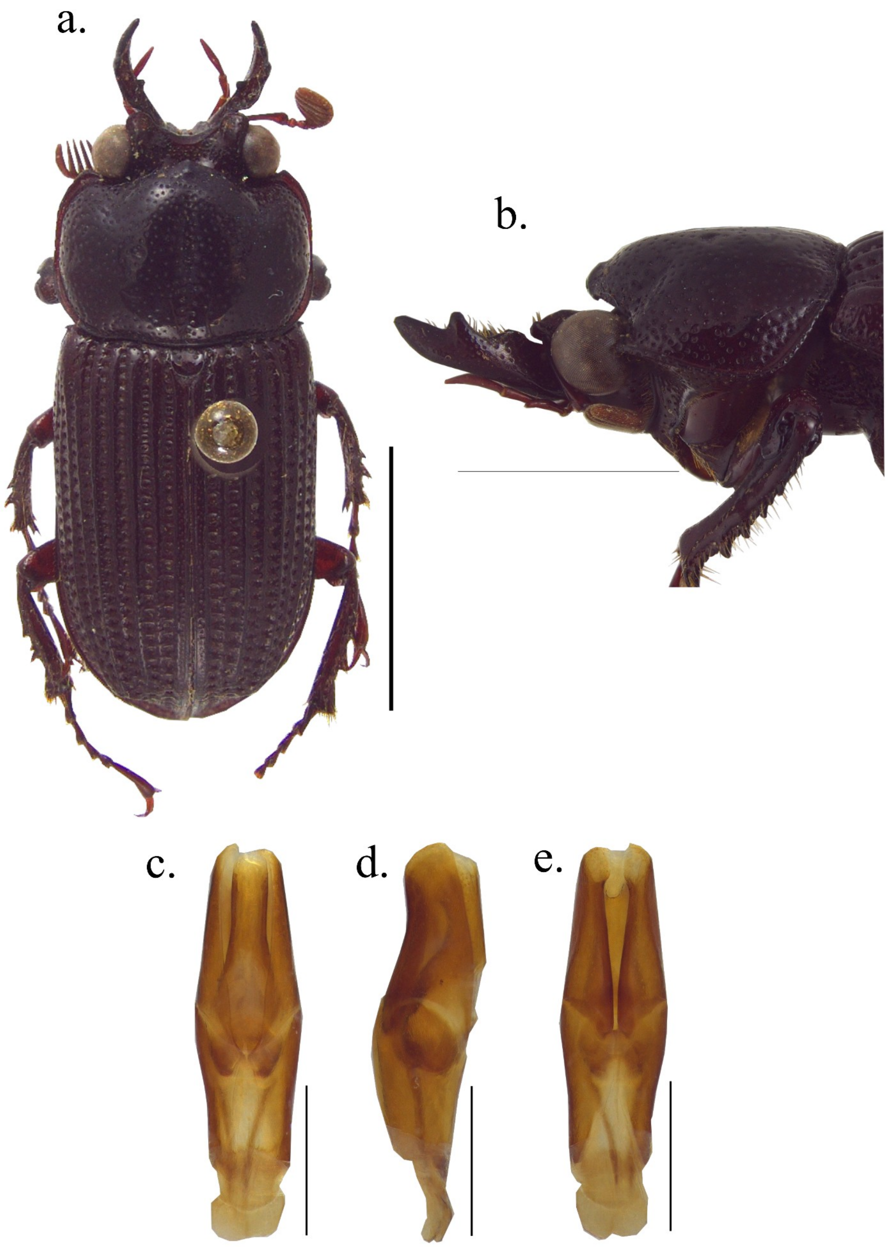

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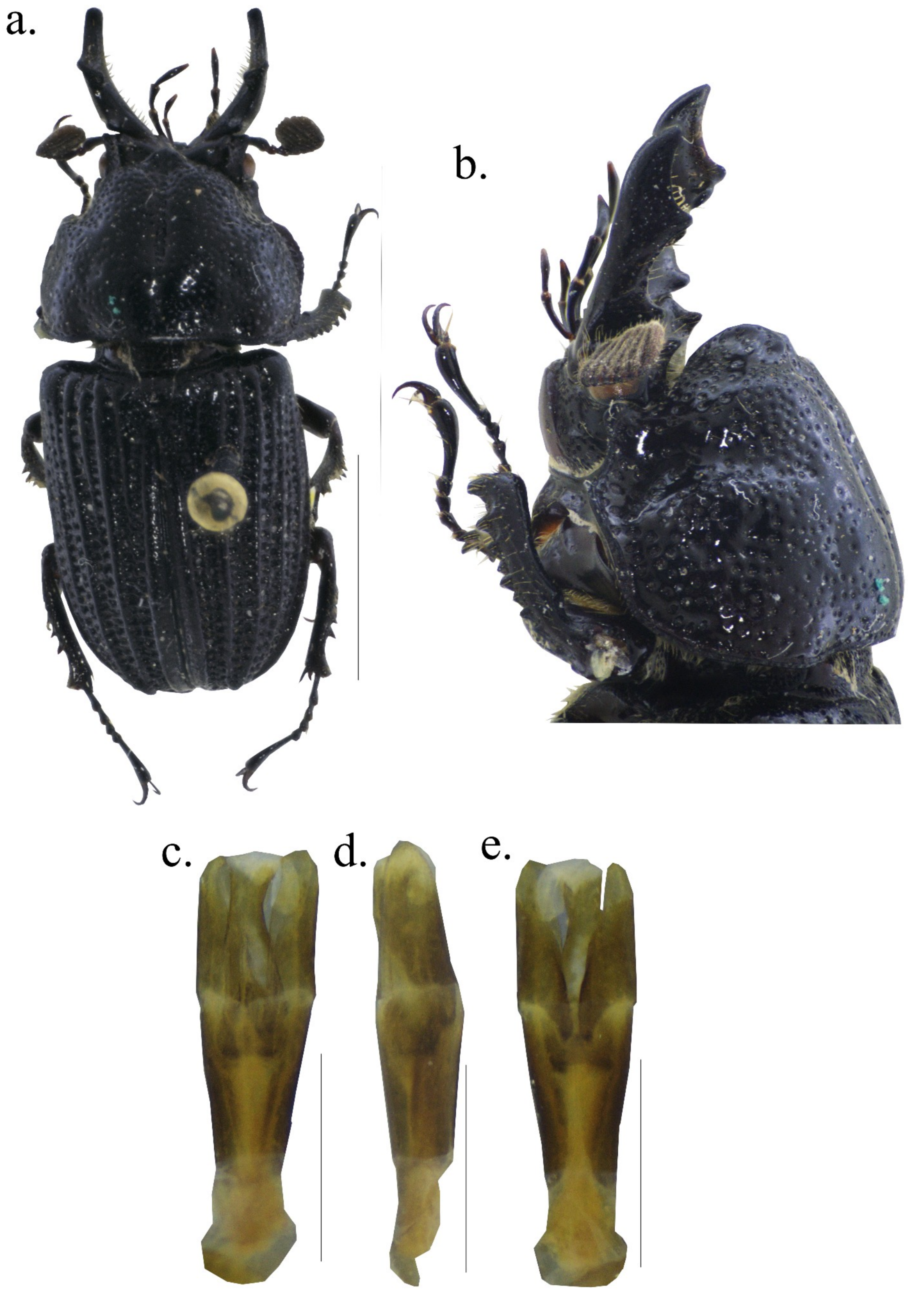

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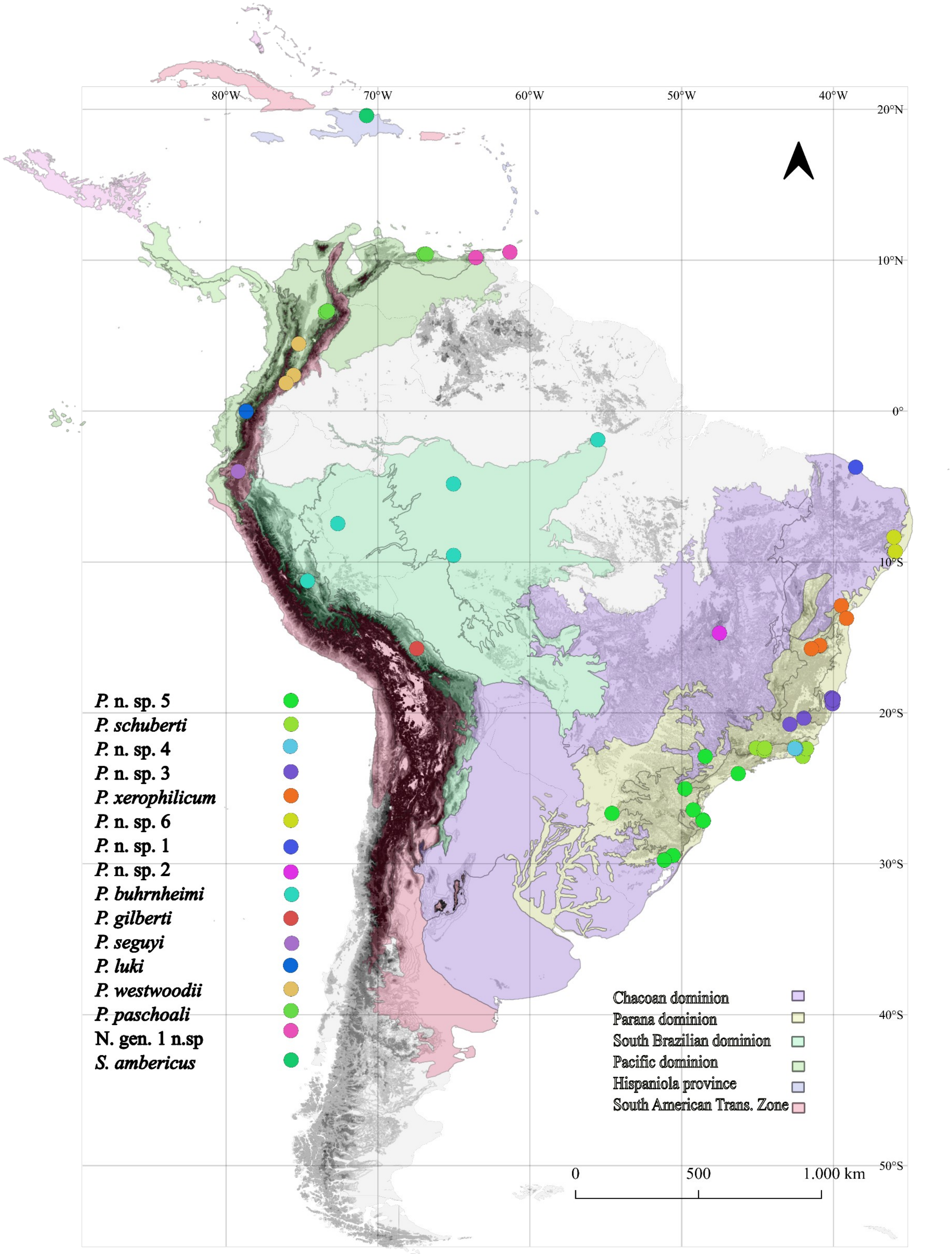

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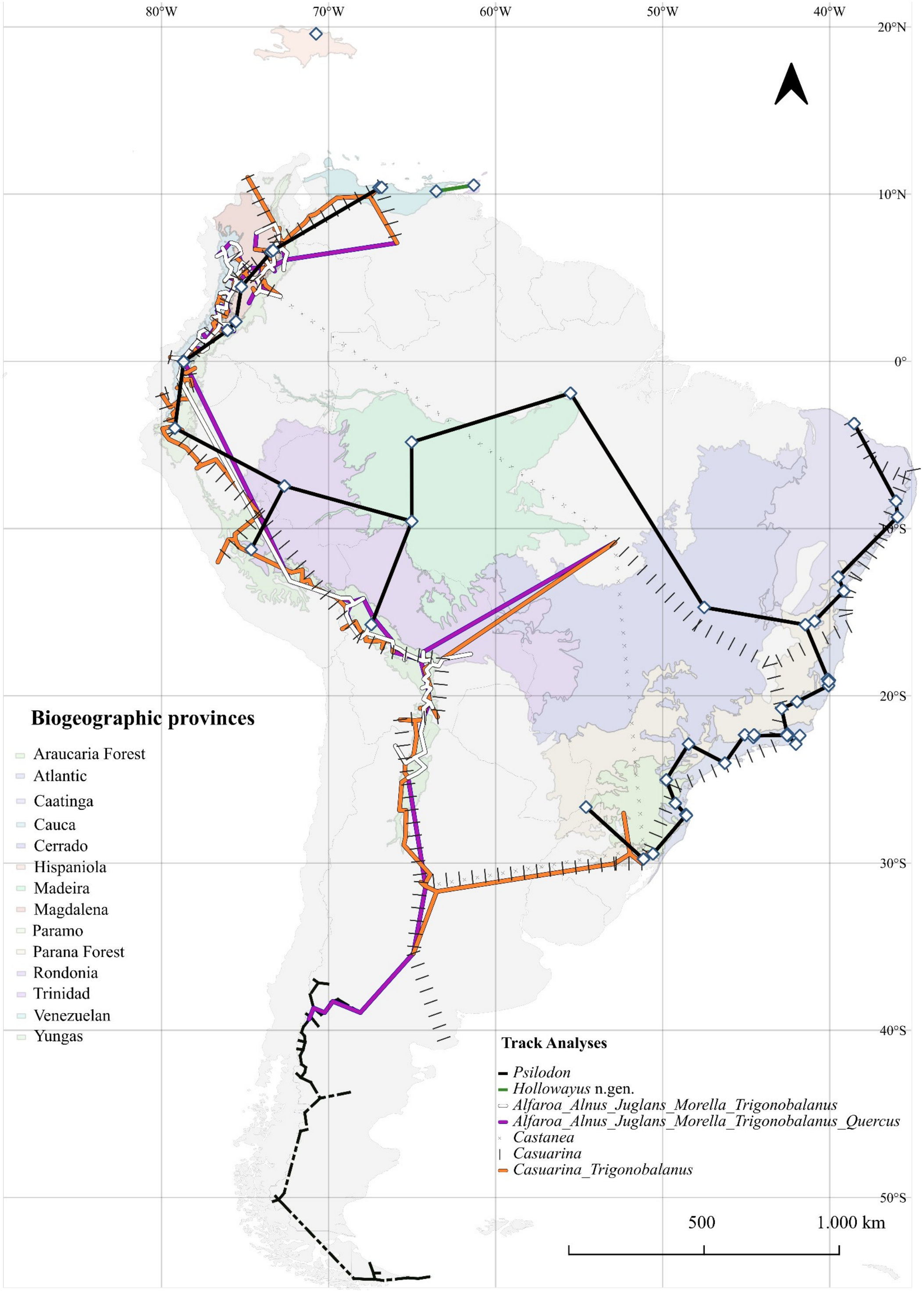

Figure 21. Track analysis for plant genera of Fagales with occurrence in South America and both South American Syndesini genera.

CAPÍTULO 4

MORPHOLOGY REVEALS THE POLYPHYLY OF SYNDESINAE MACLEAY, 1819 (COLEOPTERA: LUCANIDAE)

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[1] **Cáceres, J.S.D. & P.C. Grossi.** Morphology reveals the polyphyly of Syndesinae MacLeay, 1819 (Coleoptera: Lucanidae). Zoologischer Anzeiger

Morphology reveals the polyphyly of Syndesinae MacLeay, 1819 (Coleoptera: Lucanidae)

Juan Sebastián D. Cáceres & Paschoal C. Grossi.

Abstract.

The monophyly of Syndesinae MacLeay, 1819 is tested for the first time including all genera. By the analysis of 18 Syndesinae taxa and six more used as outgroups we obtained 87 morphological characters, which through the performance of parsimony and bayesian inference, failed to support the monophyly of Syndesinae, recovering it as a polyphyletic group. Both bootstrap and bayesian support suggest the existence of independent lineages for *Sinodendron* Hellwig, 1782 and *Ceruchus* MacLeay, 1819, with this, the re-evaluation of the validity of Sinodendrinae and Ceruchinae should be considered. A highly supported clade conformed by *Syndesus* MacLeay, 1819, *Psilodon* Perty, 1830, and a new South American genus led us to propose to resume the original *sensu* proposed for Syndesinae, restricting it to the Australasiatic and South American taxa. We also provide evidence for the Gondwanan origin of this subfamily and the validity of *Syndesus* and *Psilodon* as individual genera. Our results represent an important step for the reduction of the significant gaps that still persist in regard to Lucanidae classification.

Key words: Stag beetles, new genus, Neotropical region, Australasian region.

Introduction

Stag beetles (Lucanidae Latreille, 1804) are a small family in Scarabaeoidea represented by approximately 1500 species in 115 genera (Bouchard *et al*. 2017). According to the *sensu* proposed in Holloway (1960; 1968; 1969; 1972; 2007) Lucanidae is composed of 4 subfamilies, a classification that is broadly accepted nowadays.

Most of the described species belong in Lucaninae Latreille, 1804 with around 1200 species (Holloway 2007). The other subfamilies are the less diversified ones, Aesalinae MacLeay, 1819 comprises around 55 species classified in 7 genera (Holloway 2007); Lampriminae MacLeay, 1819 is the smallest one with five genera and about 11 species only distributed in Australia, New Guinea, New Zealand and Southern South America (Holloway 2007; Paulsen 2010); in last, Syndesinae MacLeay, 1819 with approximately 30 species and four genera, *Sinodendron* Hellwig, 1792 and *Ceruchus* MacLeay, 1819, both restricted to the Holarctic region (Howden & Lawrence 1974); *Syndesus* MacLeay, 1819, considered here as an exclusive genus from Australia, New Caledonia and New Zealand; and *Psilodon* Perty, 1830, from South America, treated by several authors as a synonym of *Syndesus* (Benesh 1960; Maes 1992; Krajcik 2001; Krajcik 2003; Holloway 2007; Onore, Bartolozzi & Zilioli 2011).

The monophyly of Lucanidae has been widely discussed and supported by different phylogenies, as is the case of Iablokoff-Khnzorian (1977) that supports the strong relationship between Lucanidae, Passalidae and Pleocomidae; Howden (1982), recovered the stag beetles as sister group of Passalidae; Lawrence & Newton (1982) described the strong phylogenetic relation between Lucanidae, Passalidae, Trogidae and Pleocomidae; Scholtz (1990) that summarized the use of different characters in Scarabaeoidea phylogenetics and also reinforced the idea of Lucanidae as one of the basal lineages of scarab beetles.

d´Hotman & Scholtz (1990) who used male genitalic structures to infer the internal relationships of different families in Scarabaeoidea established in the case of Lucanidae, Aesalinae as the basal subfamily and Lampriminae as sister group of *Sinodendrinae* (only including *Sinodendron*), and the most derived clade conformed by *Ceruchus* and Lucaninae. Here it is important to point out that neither *Syndesus* nor *Psilodon* were included in the analysis. This study was probably based on the initial observations made by Sharp & Muir (1912), Holloway (1960), Holloway (1968) and Holloway (1972) that proposed the use of four subfamilies in Lucanidae and Diphyllostomatidae as a separated family.

With these taxonomic bases, Browne & Scholtz (1995) using hindwings characters confirmed the existence of a clade composed of Diphyllostomatidae and Lucanidae, both as sister group of Passalidae. With this work, morphology-based phylogenies involving Lucanidae were abandoned for several years and only were resumed until Lawrence *et al*. (2011) published a new morphological phylogeny of Coleoptera which supported the findings of Browne & Scholtz (1995).

After the works made in the early 90s, the use of molecular tools allowed the analysis of big datasets for the construction of a new type of phylogenies of Coleoptera and Scarabaeoidea. One of the first examples is Smith *et al*. (2006) who published a preliminary phylogeny of Scarabaeoidea, supported once again the monophyly of Lucanidae, considering the four subfamilies previously proposed in Holloway (1968) and *Diphyllostoma* as members of the same taxon.

Posterior molecular phylogenies for scarab beetles and Coleoptera were published by Ahrens *et al*. (2014); Gunter *et al*. (2016); Zhang *et al*. (2018) and Cai *et al*. (2022), which continue recognizing the monophyly of Lucanidae, nevertheless, the internal relationships of Lucanidae and its relation with other basal families of Scarabaeoidea have not been clarified, hindering the use of a well-supported consensus of Lucanidae classification at subfamily and tribal level, observation that was formerly made by Holloway (2007), who proposed to maintain the use of four subfamilies and abandon the use of tribes until new taxonomic revisions and phylogenies of the less studied taxa of Lucanidae were made.

Some specific works on systematics have been conducted with Lucanidae, as is the case of Ratcliffe (1984), who conducted phylogenetic analysis considering Penichrolucaninae Arrow, 1950 as another subfamily (now placed in Lucaninae), where he supported the monophyly of the taxon, including one clade composed of *Penichrolucanus* Deyrolle, 1863 and *Brasilucanus* Vulcano & Pereira, 1961. Hosoya & Araya (2005) reconstructed the phylogeny of Japanese Stag Beetles and failed to support monophyly at the subfamily level. Paulsen (2013) described a new genus of Aesalinae for the Neotropical region and offered the first molecular phylogeny exclusively dedicated to a subfamily of Lucanidae; in this work, he recovered Aesalinae as a monophyletic group. Lucaninae was recovered as another clade and Syndesinae + Lampriminae with a low number of terminals formed another one.

Finally, Kim & Farrell (2015) is probably one of the most important recent works of Lucanidae. They recovered a relatively complete phylogeny for the family, and although their focus was Lucaninae, they offered some interesting insights regarding the other subfamilies as well as the Gondwanan origins of the Neotropical genus *Casignetus*. These authors supported the monophyly of Lucanidae, Lucaninae and Lampriminae, but Aesalinae and Syndesinae were recovered as polyphyletic groups, probably due to the low representation of terminals among these subfamilies; they also failed to recover most tribes as monophyletic groups.

With this, it is possible to perceive that even though Lucanidae is widely known by taxonomists and amateur collectors, there are still huge gaps regarding the classification within the family (Smith 2006), which considerably limit the understanding of evolutionary relationships in most Stag Beetles taxa. As was discussed above, the monophyly of the family is strongly supported, and after Paulsen (2013) Aesalinae can be considered a natural group as well. In Kim & Farrell (2015) Lampriminae appears to be somewhat resolved, at least at the Subfamily level, but in the case of Syndesinae there are still doubts about its monophyly, the classification at the tribal level and even at generic classification.

In order to fill the gaps in Syndesinae classification we conducted a phylogenetic study based on several morphological characters, aiming in the first place to test the monophyly of the subfamily, secondly to test the existence of the tribes Sinodendrini Mulsant, 1842; Ceruchini Jacquelin du Val, 1859; and Syndesini MacLeay, 1819. This is also the first time that the Australian genus *Syndesus* and *Psilodon* from South America are included in a phylogenetic analysis, as previous works only included *Sindendron* and *Ceruchus* as Syndesinae representatives.

Materials and Methods

Specimens examined

All pinned specimens and photographs were obtained from the following collections.

CEMT	Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso. Brazil, Mato Grosso, Cuiabá.

CERPE	Coleção Entomológica da Universidade Federal Rural de Pernambuco. Brazil, Pernambuco, Recife.
CZPB	Coleção Zoológica Paulo Buhrnheim, UFAM, Brazil, Amazonas, Manaus Brazil.
EPGC	Everardo and Paschoal Grossi Collection. Brazil, Rio de Janeiro, Nova Friburgo.
HEC	Hope Entomological Collections, Oxford University Museum of Natural History. UK, Oxford.
MNHN	Muséum national d'Histoire naturelle. France, Paris.
MNRJ	Museu Nacional Rio de Janeiro. Brazil, Rio de Janeiro.
MZUEFS	Museu de Zoologia Universidade Estadual de Feira de Santana. Brazil, Bahia, Feira de Santana.
NZAC	New Zealand Arthropod Collection. New Zealand, Auckland.
UMSP	University of Minnesota – Saint Paul Insect Collection. United States, Minnesota, St. Paul.
ZIN	Zoological Institute of Russian Academy of Sciences. Russia, St. Petersburg.

Character analysis

Morphological characters were analysed using a stereomicroscope Zeiss stemi 508 at 0.63 to 0.50x. External traits were observed from pinned specimens, obtaining complementary information from high-quality photographs provided by the MNHN and NZAC collections. Internal structures such as mouthparts, thoracic structures, male and female genitalia were observed through the dissection of several specimens following the protocol proposed by Grossi & Aguiar (2014). Microscopic images were obtained using a MEV TESCAN-VEGA3 following the protocols proposed in Harrison 2012.

Phylogenetic analysis

Characters from all Syndesinae genera (*Sinodendron* Hellwig, 1792; *Ceruchus* MacLeay, 1819; *Syndesus* MacLeay, 1819 and *Psilodon* Perty, 1830) were included in the analysis, additionally there were included as outgroups, one species of Diphyllostomatidae, two from Aesalinae, one Lampriminae and two Lucaninae. Outgroups were chosen in order to represent all Lucanidae subfamilies according to the *sensu* proposed by Holloway (2007). All discrete characters were added to a Matrix built using the Mesquite software 3.51 V. (Maddison & Maddison 2018).

The final matrix was analysed under parsimony using TNT v.1.5 (Goloboff *et al*. 2008). Under parsimony it was used implied weighting, using k=7.5 as this value showed to maximize tree stability (Mirande 2009). Branch supports were calculated using standard bootstrapping (Goloboff *et al*. 2003). Searches for optimal trees and bootstrap used 1000 replicates of random addition sequences with TBR branch swapping. Under Bayesian inference trees were obtained using the Markov K-States (Mk) model, which is based on the same assumptions of the simple Jukes-Cantor model for molecular sequence evolution (Jukes & Cantor 1969), and it is applied for morphological data in BEAST 2.7.3 software (Bouckaert *et al*. 2022). The consensus tree obtained from Bayesian inference was edited using FigTree v.1.4.4. All characters from the parsimony analyses were mapped using Winclada (Nixon 2022), tracing its history and calculating tree statistics.

Results

Characters

We were able to score 86 morphological characters in total for 18 species of Syndesinae, representing all three genera currently position in this subfamily, being two from *Sinodendron*, three from *Ceruchus,* four from *Syndesus*, and 8 from *Psilodon*. We also included an undetermined species which resulted in the proposition of a new genus (see chapter 3). 48 characters were binary and 38 multistate. Discussions on reconstructions consider only Bayesian, and Parsinomy-based tree topologies.

Discrete characters

0. Sexual dimorphism (binary, L=1; CI=100; RI=100)

(0) Obsolete

(1) Evident

Sexual dimorphism characterisation

1. Sexual dimorphism in Females head shape (binary, L=2; CI=50; RI=85)

(0) Shape of head highly resemblant to males

(1) Shape of head distinctly different from males

Note: Reduction in size produces changes in females heads, reducing some conspicuous characteristics as is the frontal horn in *Sinodendron* males. Other changes are related to a reduction in the degree of the anterior emargination in *Ceruchus* specimens. Heads in *Syndesus* and Psilodon are highly resemblant, event though the size of females heads are finely larger than males.

Body general appearance

2. Body shape (binary, L=3; CI=33, RI=66)

(0) Flattened (=weakly convex)

(1) Convex

3. Body vestiture appearance (binary, L=1; CI=100; RI=100)

(0) Conspicuous

(1) Inconspicuous

4. Body, dorsal surface, vestiture type (multistate, L=2; CI=100; RI=100)

(0) Squamose, fan-shaped

(1) Simple setae

(2) Dendritic setae

Head

5. Eyes margin (multistate, L=2; CI=100; RI=100)

(0) Entire

(1) Posteriorly interrupted by pronotal antero-lateral angles

(2) Interrupted by ocular canthus.

6. Eye size: Eye diameter / Body length ratio (multistate, L=4; CI=50; RI=75)

(0) 0.0676-0.09

(1) 0.046-0.0675

(2) 0.0225-0.045

7. Interocular distance (mm) (multistate, L=5; CI=100; RI=100)

(0) 0.71-0.83

(1) 1-1.47

(2) 1.6-1.7

(3) 1.96-2.40

(4) 3.1-4.2

(5) 6.3-12

8. Eyes diameter (binary, L=2; CI=50; RI=85)

(0) Longer than vertex and frons length together

(1) Shorter than vertex and frons length together

9. Temporal process (binary L=2; CI=50; RI=80)

(0) Absent

(1) Present

10. Temporal process when present (binary, L=2; CI=50; RI=66). Not applicable when C9=0

(0) Exposed

(1) Concealed by pronotum

11. Antennae: Lamellar vestiture (binary, L=4; CI=25; RI=50)

(0) Entirely tomentose (dorsal and ventral surface covered by setae)

(1) Partially tomentose (with one or more glabrous areas)

12. Apical lamellae shape (binary, L=3; CI=33; RI=66)

(0) Different from proximal lamellae (Figure 1b, d.)

(1) Subequal (Figure 1a, c.)

13. Pedicel insertion (multistate, L=3; CI=66; RI=80)

(0) Non-geniculate (Figure 1b, c.)

(1) Partially geniculate (Figure 1a.)

(2) Geniculate (Figure 1d.)

14. Number of lamellae (multistate, L=4; CI=75; RI=90)

(0) Three

(1) Seven

(2) Six

(3) Four

15. Pre-apical lamellar shape (multistate, L=2; CI=100; RI=100)

(0) Dorsally flattened

(1) Sub-cylindrical

(2) Dorso ventrally flattened

16. Scape length (binary, L=1)

(0) Shortened (shorter than as frontal and vertex length together

(1) Distinctly elongate (almost as frontal and vertex length together)

17. Anterior margin of head (binary, L=1; CI=100; RI=100)

(0) Not emarginate

(1) Emarginate

18. Head visibility (binary, CI=100; RI=100)

(0) Entirely exposed

(1) Partially concealed (by pronotum)

19. Frontal surface (multistate, L=5; CI=40; RI=25)

(0) Finely to strongly excavated

(1) Convex

(2) Flat

20. Head sides (binary, L=1; CI=100; RI=100)

(0) With well-defined punctation

(1) With contiguous strong punctation forming a waved surface (Figure 1e.)

21. Head, dorsal surface vestiture (binary, L=1; CI=100; RI=100)

(0) Setose

(1) Glabrous (=apparently glabrous)

22. Intermandibular projection (clypeus in part) direction (multistate, L=4; CI=75; RI=83)

(0) Dorso-ventrally projected, reaching ventral face of mandibles (Figure 1f.)

(1) Anteriorly projected

(2) Tranverse, not projected between mandibles (Figure 2a.)

(3) Dorso-ventrally projected, not reaching ventral face of mandibles (Figure 3b.)

Note: Holloway (2007) proposed the use of this trait. The definition of the Clypeus is unclear within Lucanidae, however, the intermandibular projection seems to represent a portion of this structure, which according to our results is fused to labrum in *Syndesus*, *Psilodon* and the new Syndesini genus. For the case of *Ceruchus* the intermandibular is strongly shortened, and as is the case of *Sinidendron*, it is not fused to labrum. Holloway (2007) also stated that the remaining portion of clypues would be merged with the frons.

23. Frontal horn (binary, L=1; CI=100; RI=100)

(0) Absent

(1) Present

24. Labrum (binary, L=3; CI=33; RI=75)

(0) Distinct

(1) Indistinct (merged with intermandibular projection)

Note: Labrum is present as a separate structure within *Ceruchus* and *Sinodendron*. *Syndesus, Psilodon* and the New Genus is merged with the intermadibular projection, and even though it is not distinct, is possible to observe changes along the surface, producing convex or finely excavate areas at the apex that could be considered the labrum.

25. Labrum distinct (binary, L=2; CI=50; RI=0). Not applicable when C24=1.

(0) Separated from clypeus (intermandibular projection) by a carina

(1) Free, entirely separated from clypeus.

26. Labral direction (binary, L=3; CI=33; RI=71)

(0) Dorso-ventrally directed

(1) Antero-ventrally directed

27. Labral visibility (binary, L=3; CI=33; RI=33

(0) Dorsally concealed

(1) Dorsally visible

28. Labral vestiture (binary, L=2; CI=50; RI=80)

(0) Entirely or almost entirely covered by setae

(1) Setae restricted to apex

29. Labral shape (multistate, L=5; CI=60; RI=75)

(0) Sub-trapezoidal

(1) Quadrate and flattened (Figure 2c.)

(2) Sub-triangular with rounded apex (Figure 1f.)

(3) Sub-triangular with truncate apex (Figure 2d.)

30. Maxillary palp length (multistate, L=5; CI=40; RI=62)

(0) Second palpomere shorter than fourth

(1) Second palpomere as long as fourth

(2) Second Palpomere longer than fourth

31. Number of labial palpomeres (binary, L=1)

(0) Four

(1) Three

32. Mandible visibility (binary, L=1; CI=100; RI=100)

(0) Dorsally visible

(1) Concealed

33. Mandibular apex direction (multistate, L=5; CI=40; RI=62)

(0) Directed upwards

(1) Directed anteriorly

(2) Directed downwards

34. Mandibles when closed (binary, L=2; CI=50; RI=88)

(0) Apex of both mandibles visible

(1) Apex of left mandible covering the one of the right one

35. Mandibular apex position (multistate, L=3; CI=66; RI=83)

(0) Apex of both mandibles never in contact

(1) Apex of both mandibles interlocking

(2) Apex of both mandibles in contact but never interlocking

36. Mandibles Beta lobe and Gamma tooth (multistate, L=4; CI=100; RI=100)

(0) Absent

(1) Only gamma tooth present (in this case present as a laminar tooth)

(2) Beta lobe and Gamma tooth merged

(3) Beta lobe and Gamma tooth distinct ("free")

(4) Gamma tooth merged with Alpha tooth-like

Note: The use of Alpha and Gamma tooth, and Beta lobe was proposed by Didier (1929). The Alpha tooth is located externally and normally close to apex, in Syndesus species it is often located medially. The Gamma tooth is located internally, present as a laminar to sub-conical tooth, varying in position and sometimes covering the internal face from base to apex. The Beta lobe is a reduced tooth located at the base of the external face of mandibles.

37. Mandibular internal surface vestiture (multistate, L=6; CI=83; RI=92)

(0) With not uniformly distributed conspicuous setae

(1) With a line of conspicuous setae extended from base to apex, not densely distributed

(2) With conspicuous setae extended from base to apex, densely distributed

(3) With a conspicuous tuft of setae at apex

(4) With inconspicuous sparsely distributed setae

(5) Glabrous

Thorax

Pronotum

38. Pronotal anterior margin 1 (multistate, L=3; CI=66; RI=87)

(0) Without emarginations

(1) With two emarginations located anteriorly

(2) With two antero-lateral emarginations

39. Pronotal anterior margin 2 (multistate, L=3; CI=66; RI=87)

(0) Entirely carinate

(1) Not carinate

(2) Partially carinate, with a median interruption

40. Pronotal anterior region direction (binary, L=2; CI=50; RI=87)

(0) Not projected (=finely projected) anteriorly

(1) Distinctly projected anteriorly

41. Pronotal anterior region shape (binary, L=1; CI=100; RI=100)

(0) Without a declivity

(1) With a strong declivity projected anteriorly

42. Pronotal tubercle (multistate, L=2; CI=100; RI=100)

(0) Absent

(1) Present, with a basal constriction

(2) Present, not constricted basally

43. Pronotal lateral margins (binary, L=3; CI=33; RI=33)

(0) Smooth

(1) Scalloped

44. Pronotal antero-lateral angles (binary, L=3; CI=33; RI=77)

(0) Forming a convex margin

(1) Forming an almost straight margin

45. Pronotal antero-lateral angles direction (binary, L=1)

(0) Not projected anteriorly

(1) Projected anteriorly

46. Pronotal antero-lateral angles length (binary, L=2; CI=50; RI=87)

(0) Not reaching eyes

(1) Reaching eyes

47. Pronotal sides (binary, L=3; CI=33; RI=66)

(0) Flattened

(1) Not flattened

48. Pronotal surface (multistate, L=3; CI=66; RI=50)

(0) Without excavations

(1) With two excavations

(2) With four well-defined excavations

Meso and Metanotum

49. Elytral striae (multistate, L=3; CI=66; RI=88)

(0) Irregularly aligned (=with few vaguely defined rows) (Figure 4a, b.)

(1) Regularly or almost regularly aligned

(2) With well define striae (Figure 4c.)

50. Elytra, number of intercostal striae (binary, L=3; CI=33; RI=50). Not applicable when C49=0; 1.

(0) One striae

(1) Two striae

51. Elytral punctation appearance (multistate, L=3; CI=66; RI=80)

(0) Minute, not visible under optic microscopy

(1) Visible under optic microscopy but inconspicuous

(2) Visible and conspicuous

52. Punctation surface (binary, L=2; CI=50; RI=83)

(0) Non polygonal

(1) Polygonal (Figure 3a.)

53. Wing venation (multistate, L=4; CI=50; RI=66)

(0) Only RA4 present

(1) RA4+RP1 present

(2) RA4 and RP1 distinct

54. Elytral punctation shape (multistate, L=4; CI=50; RI=60)

(0) Circular

(1) Oval

(2) Polygonal

55. Elytral setae type (multistate, L=5; CI=80; RI=87)

(0) Smooth (Figure 3a.)

(1) Barbed (Figure 3b.)

(2) Incised barbed (Figure 3c,d.)

(3) Scale with undivided ribs

(4) Dendritic

56. Elytral punctation – Point of origin of setae (binary, L=2; CI=50; RI=87)

(0) Centre

(1) Anterior portion

57. Elytral punctation size, according to Paulsen (2005) (multistate, L=3; CI=66; RI=80)

(0) Fine

(1) Large

(2) Coarse

58. Elytral humeri (binary, L=2; CI=50; RI=75)

(0) Without tooth-like projections

(1) With a tooth-like projection

59. Interstrial joint (binary, L=1; CI=100; RI=100)

(0) Absent

(1) Present

60. Epipleural direction (multistate, L=7; CI=28; RI=37)

(0) Entirely (=almost) projected externally

(1) Projected externally only at base

(2) Projected externally except at apex

61. Metanotum, alacrista direction (binary, L=2; CI=50; RI=50)

(0) Subparallel (Figure 4d.)

(1) Diverging anteriorly (Figure 4e.)

Legs

62. Tarsomeres length (binary, L=1)

(0) All tarsomeres elongate, almost as long as tibia and femur together

(1) Less than femur and tibia together

63. Meso and Metatibial apex (multistate, L=3; CI=66; RI=50)

(0) Both apex enlarged

(1) With the same width (=finely enlarged apically)

(2) Only metatibial apex enlarged, also showing a conspicuous processes

Body ventral portion

Head

64. Gula shape (binary, L=2; CI=50; RI=80)

(0) Strongly convex and conspicuous

(1) Flattened

Thorax

65. Prosternal process width (binary, L=3; CI=33; RI=71)

(0) Extremely narrowed, allowing procoxal contact

(1) Somewhat wide, separating procoxae

66. Metaventrital discrimen (multistate, L=4; CI=50; RI=66)

(0) Absent

(1) Present, incomplete

(2) Present, incomplete

67. Metaventrital convexity (multistate, L=4; CI=50; RI=81)

(0) Smooth

(1) With a shallow discrimen

(2) With a carinate discrimen

Females

Head

68. Mandibles (binary, L=1; CI=100; RI=100)

(0) With distinct teeth

(1) Without distinct teeth

69. Head visibility (dorsal) (binary, L=1; CI=100; RI=100)

(0) Exposed

(1) Partially concealed

70. Antennal shape (binary, L=2; CI=50; RI=80)

(0) Equal to males

(1) Different from males

Thorax

71. Pronotal disc (multistate, L=3; CI=66; RI=83)

(0) Without carina or groove

(1) With a longitudinal carina

(2) With a shallow to strong groove

Genitalic structures Males and Females

Female genitalia

72. Styli (binary, L=2; CI=50; RI=0)

(0) Absent

(1) present

73. Styli shape (multistate, L=2; CI=100; RI=100). Not applicable when C72=0

(0) Sub-oblong

(1) Sub-trapezoidal

(2) Sub-conical

74. Gonocoxites – Shape (multistate, L=7; CI=100; RI=100)

(0) Distally with an external concavity, proximally with an internal one

(1) Only with an internal concavity along the distal half

(2) With almost straight sides (=distally with a fine concavity)

(3) Sub-trapezoidal, internally slightly convex at base

(4) Internally with a fine concavity extended from base to apex

(5) External face forming a right angle distally

(6) Strongly convexity

(7) Strongly narrowed proximally

75. Lateral paraprocts shape (multistate, L=6; CI=100; RI=100)

(0) Straight (=slightly convex) and slender

(1) Sub-oblong, flattned

(2) Shortened, strongly curved proximally

(3) “C” shaped, bulbous at both ends

(4) Almost straight, proximally enlarged

(5) Proximally straight, becoming convex distally

(6) Almost straight, enlarged distally

Male genitalia

76. Aedeagus – Struts (binary, L=1; CI=100; RI=100)

(0) Absent

(1) Present

77. Dorsal cross-bar (binary, L=2; CI=50; RI=87)

(0) Absent

(1) Present

Note: Holloway (2007) stated that Syndesinae taxa, at least *Syndesus* lacked a dorsal crossbar, but we were able to identify this structure not only in *Syndesus* species but also in *Psilodon. Sinodendron* and *Ceruchus* also presented this structure, characteristic that was also noted by d'Hotman & Scholtz (1990). Shape variation within this structure seems to be a good diagnostic trait at species level.

78. Dorsal cross-bar shape (multistate, L=4; CI=75; RI=0)

(0) "V" shaped

(1) Transverse bar shaped

(2) "H" to "X" shape

(3) "U" shape

79. Aedeagus symmetry (binary, L=1)

(0) Asymmetric

(1) Symmetric

80. Width/Length ratio (multistate, L=5; CI=60; RI=75)

(0) 0.3 times wider

(1) 0.4 times wider

(2) 0.2 times wider

(3) 0.5 times wider

81. Parameres length (multistate, L=3; CI=66; RI=75)

(0) As long (=almost) as phallobase

(1) Strongly reduced, at least five times shorter than phallobase

(2) Longer than phallobase

82. Parameres and phallobase (binary, L=1; CI=100; RI=100)

(0) Separated from phallobase

(1) Continuous with phallobase

83. Genital capsule symmetry (binary, L=2; CI=50; RI=0)

(0) Asymmetric

(1) Symmetric

84. Internal sac (binary, L=2; CI=50; RI=50)

(0) Permanently everted

(1) Eversible

85. Parameres extension (binary, L=3; CI=33; RI=33)

(0) Extended beyond median lobe apex

(1) Ending before or at median lobe apex

86. Median lobe appearance (multistate, L=7; CI=85; RI=75)

(0) Narrow, of uniform width

(1) Sub-triangular, gradually and uniformly narrowed distally

(2) Sub-cylindrical

(3) Bulbous basally, narrowing distally

(4) Bulbous at base and abruptly narrowed distally

(5) Medially constricted

(6) Sub-oblong

Trees

Under the parsimony search the values of *k* with a mean distortion of 94.8 or above resulted in the same most parsimonious tree (Figure 7), corresponding to a value of *k* of 7.5. The selected tree presented a length of 241, a consistency index of 63 and a retention index of 80.

Parsimony and Bayesian inference (Figure 6) recovered Syndesinae MacLeay, 1819 as a polyphyletic group, recovering three different clades, the first one with 100% bootstrap and posterior probability support represented by *Sinodendron cylindricum* (Linnaeus, 1758) and *Sinodendron rugosum* Mannerheim, 1843. The second one, with a 99% (bootstrap) and 100% (posterior probability), containing, *Ceruchus chrysomelinus* (Hochenwarth, 1785), *Cercuhus punctatus* LeConte, 1869, and *Ceruchus piceus* (Weber, 1801). The last clade, consisting on *Syndesus* MacLeay, 1819*, Psilodon* Perty, 1830*,* and a new South American genus, showed a 100% support (bootstrap and posterior probability), with several internal nodes with a low bootstrap support (under 51%). In contrast, the Bayesian inference supported two principal clades, one containing the Australasian *Syndesus* species (from Australia and New Caledonia), with a support of 88%, and the other, represented by the South American genus *Psilodon*, and a new genus from Venezuela and Trinidad and Tobago. The South American clade showed a low support of 39%, but the internal node, including *Psilodon* with a 72% support, originated two well-supported clades, one restricted to the Andes, containing *Psilodon gilberti* Boucher, 1993, *Psilodon seguyi* Didier, 1929 and *Psilodon luki* (Onore, Bartolozzi & Zillioli, 2011), and the other containing the Brazilian and Colombian species with a posterior probability support of 95%.

Discussions

According to the *sensu* proposed by Holloway (1968), Syndesinae is composed of four genera, two from the holarctic realm, *Sinodendron* and *Ceruchus*, one Australasiatic, *Syndesus,* and one Neotropical, *Psilodon*. Although in her works on Lucanidae, B. Holloway proposed several phylogenetic hypotheses based on comparative morphology, she never performed a cladistic analysis. The lack of this approach led her in some cases, to relate different taxa considering few characteristics. This seems to be the case of Syndesinae, which only included *Syndesus* and *Psilodon* (=*Hexaphyllum*) (van Roon 1910; Didier & Seguyi 1953; Benesh 1960), but based on several characteristics of the eyes, mouthparts and male genitalic structures, she added *Sinodendron* and *Ceruchus* to the subfamily (Holloway 1968).

Before that, *Sinodendron* was included in a separated subfamily, Sinodendrinae Lacordaire, 1856, and *Ceruchus*, was included in Ceruchini Jacquelin du Val, 1859, which was posteriorly included as a tribe in Aesalinae (van Roon 1910; Didier & Seguyi 1953; Benesh 1960), or in an independent subfamily, Ceruchinae Mawa, 1934.

The *sensu* Holloway (1968) was adopted by posterior authors, and is still widely accepted, however, there are few examples of scientific works containing phylogenetic discussions that consider all Syndesinae taxa. Some of this examples are Scholtz (1990) and Nel & Scholtz (1990) who discussed the phylogenetic relationships within Lucanidae, considering all Syndesinae genera but, once again, lacked a cladistic analysis.

Only d'Hotman & Scholtz (1990) conducted a phylogenetic analysis, and despite of considering the four Syndesinae genera in their discussion, they only included *Sinodendron* and *Ceruchus* in their analysis. Their phylogeny recovered Aesalinae as the basal group, and a clade including Lampriminae, *Sinodendron*, *Ceruchus* and Lucaninae as the derived taxa. The most derived clade included *Sinodendron* as sister group of the *Ceruchus*-Lucaninae clade, showing a similar topology to the one obtained by us, recovering *Sinodendron* (100% bootstrap and Bayesian inference support) and *Ceruchus* in separated groups, being *Ceruchus* closely related with Lucaninae. Recent genomic studies (Chen *et al*. 2019; Chen *et al*. 2020; Lee *et al*. 2020; Zhai *et al*. 2020) support these observations, but only by the addition of the South American and Australasiatic genera is now possible to confirm that Syndesinae, according to Holloway (1968) does not represent a natural group.

Recovering Syndesinae as a polyphyletic group, previous classifications proposed for the subfamily which only included *Syndesus* and *Psilodon* should be resumed. Furthermore, the validity of Sinodendrinae and Ceruchinae must be re-evaluated, as we consider there is enough recent evidence to reinstate the use of this subfamilies, and should not be considered as tribes of Syndesinae anymore.

We obtained a strong support for the Syndesinae clade (100% of support) composed by *Psilodon* and *Syndesus*, with this we proposed the restriction of the subfamily for these genera, considering now the following synapomorphies as the diagnostic traits for Syndesinae: Eyes posteriorly interrupted by pronotal anteo-lateral angles; shape of lamellae dorso-ventraly flatetened; males and females head partially concealed by pronotum; pronotal tubercle present without basal constrictions; Gamma tooth present in male mandibles; elytral setae barbed; interstrial joint present. Female mandible without distinct teeth; lateral paraprocts of female genitalia “C” shaped.

Besides the possibility of resuming the original *sensu* proposed for this subfamily (van Roon 1910; Didier & Seguyi 1953; Benesh 1960), we also provide evidence for defining the limits between *Syndesus* and *Psilodon*, which still lack a general consensus, but now it possible to support the classification accepted by several authors (Didier & Seguyi 1953; Holloway 1968, 1997; Howden & Lawrence 1974; Martínez & Reyes-Castillo 1985; Boucher 1993; Ratcliffe (2002); Pardo-Locarno & Ríos-Málaver 2011; Grossi & Aguiar 2014).

In last, our phylogeny has some biogeographic implications, the first one, regarding the disjunct distribution of *Syndesus* and *Psilodon,* which suggested a Gondwanan origin for both taxa, now has a cladistic support. Additionally, we recovered a basal South American lineage conformed by a new genus from Venezuela and Trinidad and Tobago, and two *Psilodon* lineages, one represented by the Brazilian and Northern Andes species, and other including the Tropical Andes species from Bolivia and Ecuador, which reflects a least three biogeographic patterns that should be the subject of future studies using molecular data.

Our results represent one important step in order to reduce the significant gaps regarding Lucanidae classification. By defining the limits of Syndesinae the following steps shopuld be focused on the study of *Ceruchus* and *Sinodendron* species, using a larger taxon sampling and, if possible, integrating molecular and morphological data.

Acknowledgments

We would like to thank all collection curators who share material and photographs in order to conduct this study. We thank all the personnel from the CENAPESq-UFRPE for allowing us to use their facilities in oirder to obtain the MEV photographs. We also thank the "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior" – CAPES for the Doctoral Scholarship of the Academic Excellence Programme PROEX, which made possible the conduction of this work.

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Appendix III – Character Matrix

Table 1. Matrix with 87 morphological characters and 24 taxa used for the cladistic analyses.

Characteres/Taxa	0	1	2	3	4	5	6	7	8	9	10
D. linsleyi	0	0	0	0	1	0	0	0	0	0	-
A. scarabaeoides	0	?	1	0	0	0	1	1	0	0	-
H. argentinensis	0	0	0	0	0	0	1	1	0	0	-
L. aurata	1	1	1	1	1	0	2	4	1	1	0
S. rugosum	1	1	1	1	1	0	2	2	1	1	1
S. cylindricum	1	1	1	1	1	0	2	2	1	1	1
C. chrysomelinus	1	1	0	1	1	0	2	4	1	0	-
C. punctatus	1	1	0	1	1	0	2	4	1	0	-
C. piceus	1	1	0	1	1	0	2	4	1	0	-
S. cornutus	1	0	1	1	1	1	0	3	0	1	1
S. macleay	1	0	1	1	1	1	0	3	0	1	1
S. cancellatus	1	0	1	1	1	1	0	3	0	1	1
S. punctatus	1	0	1	1	1	1	0	3	0	1	1
P. xerophilicum	1	0	1	1	1	1	0	3	0	1	1
P. buhrnheimi	1	0	1	1	1	1	0	3	0	1	1
P. paschoali	1	0	1	1	1	1	0	3	0	1	1
P. gilberti	1	0	1	1	1	1	0	3	0	1	1
P. aequinoctiale	1	0	1	1	1	1	0	3	0	1	1
P. luki	1	0	1	1	1	1	0	3	0	1	1
P. seguyi	1	0	1	1	1	1	0	3	0	1	1
P. schuberti	1	0	1	1	1	1	0	3	0	1	1
N. gen 1	1	0	1	1	1	1	0	3	0	1	0
L. femoratus	1	1	0	1	2	2	1	5	1	1	0
L. cervus	1	1	0	1	1	2	1	5	1	1	0

Characteres/Taxa	11	12	13	14	15	16	17	18	19	20
D. linsleyi	0	0	0	0	0	0	0	0	0	0
A. scarabaeoides	1	0	0	0	0	1	0	0	0	0
H. argentinensis	0	1	0	0	1	1	0	0	2	0
L. aurata	0	1	0	0	0	1	1	0	0	0
S. rugosum	1	1	1	0	0	1	0	0	1	0

S. cylindricum	1	1	1	0	0	1	0	0	1	0
C. chrysomelinus	1	0	1	0	0	1	1	0	0	1
C. punctatus	1	0	1	0	0	1	1	0	0	1
C. piceus	1	0	1	0	0	1	1	0	1	1
S. cornutus	0	1	0	1	2	1	1	1	0	0
S. macleay	0	1	0	1	2	1	1	1	0	0
S. cancellatus	0	1	0	2	2	1	1	1	0	0
S. punctatus	0	1	0	2	2	1	1	1	0	0
P. xerophilicum	0	1	0	2	2	1	1	1	0	0
P. buhrnheimi	0	1	0	2	2	1	1	1	0	0
P. paschoali	0	1	0	2	2	1	1	1	0	0
P. gilberti	0	1	0	1	2	1	1	1	0	0
P. aequinoctiale	0	1	0	2	2	1	1	1	0	0
P. luki	0	1	0	2	2	1	1	1	0	0
P. seguyi	0	1	0	2	2	1	1	1	0	0
P. schuberti	0	1	0	2	2	1	1	1	0	0
N. gen. 1	0	1	0	1	2	1	1	1	0	0
L. femoratus	1	0	2	0	0	1	1	0	1	0
L. cervus	0	0	2	3	0	1	1	0	2	0

Characteres/Taxa	21	22	23	24	25	26	27	28	29	30
D. linsleyi	0	0	0	0	0	0	0	0	0	0
A. scarabaeoides	0	1	0	0	1	1	1	0	1	0
H. argentinensis	0	1	0	0	1	1	1	0	1	0
L. aurata	0	3	0	1	-	1	1	1	0	2
S. rugosum	0	2	1	0	1	1	0	0	0	1
S. cylindricum	0	2	1	0	1	1	0	0	0	1
C. chrysomelinus	1	3	0	0	1	1	1	1	1	2
C. punctatus	1	3	0	0	1	1	1	1	1	2
C. piceus	1	3	0	0	1	1	1	1	1	2
S. cornutus	0	0	0	1	-	0	1	1	2	1
S. macleay	0	0	0	1	-	0	1	1	2	1
S. cancellatus	0	0	0	1	-	0	1	1	2	1
S. punctatus	0	0	0	1	-	0	1	1	2	1
P. xerophilicum	0	0	0	1	-	0	1	1	2	2
P. buhrnheimi	0	0	0	1	-	0	1	1	2	2
P. paschoali	0	0	0	1	-	0	1	1	2	2
P. gilberti	0	0	0	1	-	0	1	1	2	2
P. aequinoctiale	0	0	0	1	-	0	1	1	2	2
P. luki	0	0	0	1	-	0	1	1	2	2
P. seguyi	0	0	0	1	-	0	1	1	2	2
P. schuberti	0	0	0	1	-	0	1	1	2	2
N. gen. 1	0	0	0	1	-	0	1	1	3	2
L. femoratus	1	3	0	1	-	0	1	0	2	1

L. cervus	1	0	0	0	0	0	0	1	0	2

Characteres/Taxa	31	32	33	34	35	36	37	38	39	40
D. linsleyi	0	0	0	0	0	0	0	0	0	0
A. scarabaeoides	1	0	1	1	1	0	0	0	1	0
H. argentinensis	1	0	1	1	1	0	0	0	1	0
L. aurata	1	0	0	1	2	0	2	0	0	0
S. rugosum	1	1	1	1	1	0	0	0	0	1
S. cylindricum	1	1	1	1	1	0	0	0	0	1
C. chrysomelinus	1	0	2	1	1	0	1	0	0	0
C. punctatus	1	0	2	1	1	0	1	0	0	0
C. piceus	1	0	2	1	1	0	1	0	0	0
S. cornutus	1	0	0	0	2	1	4	1	2	1
S. macleay	1	0	0	0	2	1	4	1	2	1
S. cancellatus	1	0	1	0	2	1	1	1	2	1
S. punctatus	1	0	0	0	2	1	1	1	2	1
P. xerophilicum	1	0	0	0	2	3	4	1	2	1
P. buhrnheimi	1	0	0	0	2	3	4	1	2	1
P. paschoali	1	0	0	0	2	3	4	1	2	1
P. gilberti	1	0	0	0	2	3	3	1	2	1
P. aequinoctiale	1	0	0	0	2	3	3	1	2	1
P. luki	1	0	0	0	2	2	3	1	2	1
P. seguyi	1	0	0	0	2	2	3	1	2	1
P. schuberti	1	0	0	0	2	3	4	1	2	1
N. gen. 1	1	0	0	0	2	4	1	2	2	1
L. femoratus	1	0	1	1	2	0	5	1	2	0
L. cervus	1	0	2	1	2	0	5	1	0	0

Characteres/Taxa	41	42	43	44	45	46	47	48	49	50	51	52	53	54
D. linsleyi	0	0	0	0	0	0	0	0	0	-	1	?	0	0
A. scarabaeoides	0	0	1	0	1	0	0	0	0	-	2	1	1	1
H. argentinensis	0	0	1	0	1	0	0	0	0	-	2	1	0	1
L. aurata	0	0	0	0	1	0	1	0	2	-	0	1	2	2
S. rugosum	1	1	1	0	1	1	1	0	0	-	2	1	1	0
S. cylindricum	1	1	1	0	1	1	1	0	0	-	2	1	1	0
C. chrysomelinus	0	0	1	1	1	0	0	0	0	-	1	0	1	1
C. punctatus	0	0	1	1	1	0	0	0	0	-	1	0	1	1
C. piceus	0	0	1	1	1	0	0	0	0	-	1	0	1	1
S. cornutus	0	2	1	0	1	1	1	0	1	0	2	0	2	0
S. macleay	0	2	1	0	1	1	1	0	1	0	2	0	2	0
S. cancellatus	0	2	1	1	1	1	1	1	1	1	2	0	2	0

S. punctatus	0	2	1	1	1	1	1	0	1	1	2	0	2	0
P. xerophilicum	0	2	1	0	1	1	1	1	1	0	2	0	2	0
P. buhrnheimi	0	2	1	0	1	1	1	0	1	0	2	0	2	0
P. paschoali	0	2	1	0	1	1	1	0	1	0	2	0	2	0
P. gilberti	0	2	1	1	1	1	1	0	1	1	2	0	2	0
P. aequinoctiale	0	2	1	0	1	1	1	0	1	0	2	0	2	0
P. luki	0	2	1	1	1	1	1	2	1	1	2	0	2	0
P. seguyi	0	2	1	1	1	1	1	2	1	0	2	0	2	0
P. schuberti	0	2	1	0	1	1	1	0	1	0	2	0	2	0
N. gen. 1	0	2	1	0	1	1	1	0	1	1	2	0	?	0
L. femoratus	0	0	0	1	1	0	0	0	2	-	1	1	2	0
L. cervus	0	0	0	1	1	0	1	0	2	-	1	1	2	2

Characteres/Taxa	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
D. linsleyi	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
A. scarabaeoides	3	1	2	0	0	1	?	1	0	1	1	0	0	?	?
H. argentinensis	3	1	2	0	0	2	?	1	1	0	0	1	0	0	0
L. aurata	0	0	0	1	0	2	?	1	1	0	0	2	0	0	0
S. rugosum	0	0	2	1	0	0	0	1	2	0	0	0	1	0	0
S. cylindricum	0	0	2	1	0	0	0	1	2	0	0	0	1	0	0
C. chrysomelinus	2	0	1	1	0	2	1	1	0	1	0	1	0	0	0
C. punctatus	2	0	1	1	0	2	1	1	0	1	0	1	0	0	0
C. piceus	2	0	1	1	0	0	1	1	0	1	0	1	0	0	0
S. cornutus	1	1	2	1	1	2	1	1	0	0	1	0	0	1	1
S. macleay	1	1	2	1	1	2	1	1	0	0	1	0	0	1	?
S. cancellatus	1	1	2	1	1	2	1	1	0	0	1	0	1	1	1
S. punctatus	1	1	2	1	1	0	1	1	0	0	1	0	1	1	?
P. xerophilicum	2	1	2	1	1	0	1	1	0	0	1	0	1	1	1
P. buhrnheimi	2	1	2	1	1	0	1	1	0	0	1	0	1	?	?
P. paschoali	2	1	2	1	1	0	1	1	0	0	1	0	1	1	1
P. gilberti	2	1	2	1	1	0	1	1	0	0	1	0	2	?	?
P. aequinoctiale	2	1	2	1	1	0	1	1	0	0	1	0	1	1	1
P. luki	2	1	2	0	1	0	1	1	0	0	1	0	2	1	1
P. seguyi	2	1	2	0	1	0	1	1	0	0	1	0	1	1	1
P. schuberti	2	1	2	1	1	0	1	1	0	0	1	0	1	1	1
N. gen. 1	?	1	2	1	1	0	?	1	0	0	1	1	1	?	?
L. femoratus	4	0	0	1	0	2	?	1	0	1	1	2	0	0	0
L. cervus	0	0	0	1	0	1	0	1	0	1	1	2	0	0	0

Characteres/Taxa	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86
D. linsleyi	?	?	0	-	0	-	0	0	-	0	-	1	0	0	0	0	0
A. scarabaeoides	?	?	1	0	2	0	0	0	-	1	0	2	1	0	1	1	2
H. argentinensis	1	0	1	0	5	0	0	0	-	1	1	2	1	1	1	1	3

L. aurata	1	0	?	1	1	0	1	0	-	1	0	1	0	1	1	0	1
S. rugosum	0	1	1	2	3	1	1	0	-	1	1	1	0	1	1	0	1
S. cylindricum	0	1	1	2	3	1	1	0	-	1	1	1	0	1	1	0	1
C. chrysomelinus	1	0	1	1	4	2	1	0	-	1	1	0	0	1	1	1	3
C. punctatus	1	0	1	1	4	2	1	0	-	1	1	0	0	1	1	1	3
C. piceus	1	0	1	1	4	2	1	0	-	1	1	0	0	1	1	1	3
S. cornutus	1	2	1	2	7	3	1	1	0	1	1	0	0	1	1	1	3
S. macleay	?	?	?	?	?	?	1	1	?	1	1	0	0	1	1	1	?
S. cancellatus	1	2	1	2	?	?	1	1	3	1	0	0	0	1	1	1	3
S. punctatus	?	?	?	?	?	?	1	1	?	1	0	0	0	1	1	1	?
P. xerophilicum	0	2	1	2	7	4	1	1	0	1	0	0	0	1	1	1	3
P. buhrnheimi	?	?	1	2	7	?	1	1	0	1	0	0	0	1	1	1	3
P. paschoali	?	?	1	2	7	?	1	1	0	1	2	0	0	1	1	1	3
P. gilberti	?	?	1	2	7	?	1	1	0	1	0	0	0	1	1	1	4
P. aequinoctiale	?	?	1	2	7	?	1	1	3	1	0	0	0	1	1	1	3
P. luki	0	2	1	2	7	5	1	1	0	1	0	0	0	1	1	1	4
P. seguyi	0	2	1	2	7	3	1	1	0	1	0	0	0	1	1	1	4
P. schuberti	0	2	1	2	7	4	1	1	0	1	0	0	0	1	1	1	3
N. gen. 1	?	?	?	?	?	?	1	1	0	1	0	0	0	1	1	1	3
L. femoratus	1	0	1	1	6	0	1	1	1	1	3	0	0	1	0	1	5
L. cervus	1	2	0	-	?	6	1	1	2	1	3	0	0	1	0	1	6

Appendix III – List of Figures

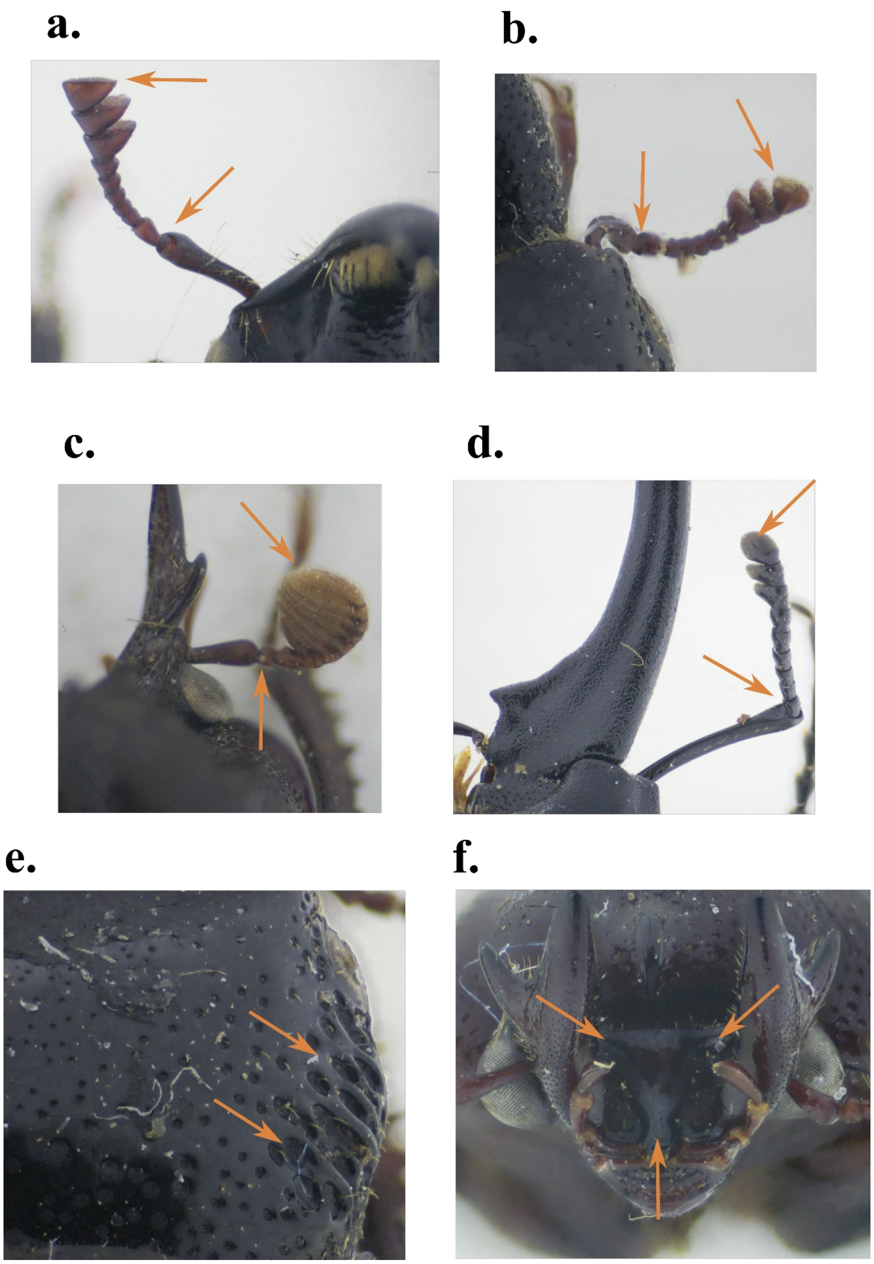

Figure 1. **a.** *S. rugosum* left antennae. **b.** *C. chrysomelinius* right antennae. **c.** *S. cornutus* right antennae. **d.** *L. femoratus* right antennae. **e.** *C. chrysomelinius* lateral portion of male head. **f.** *S. cornutus* male intermandibular projection.

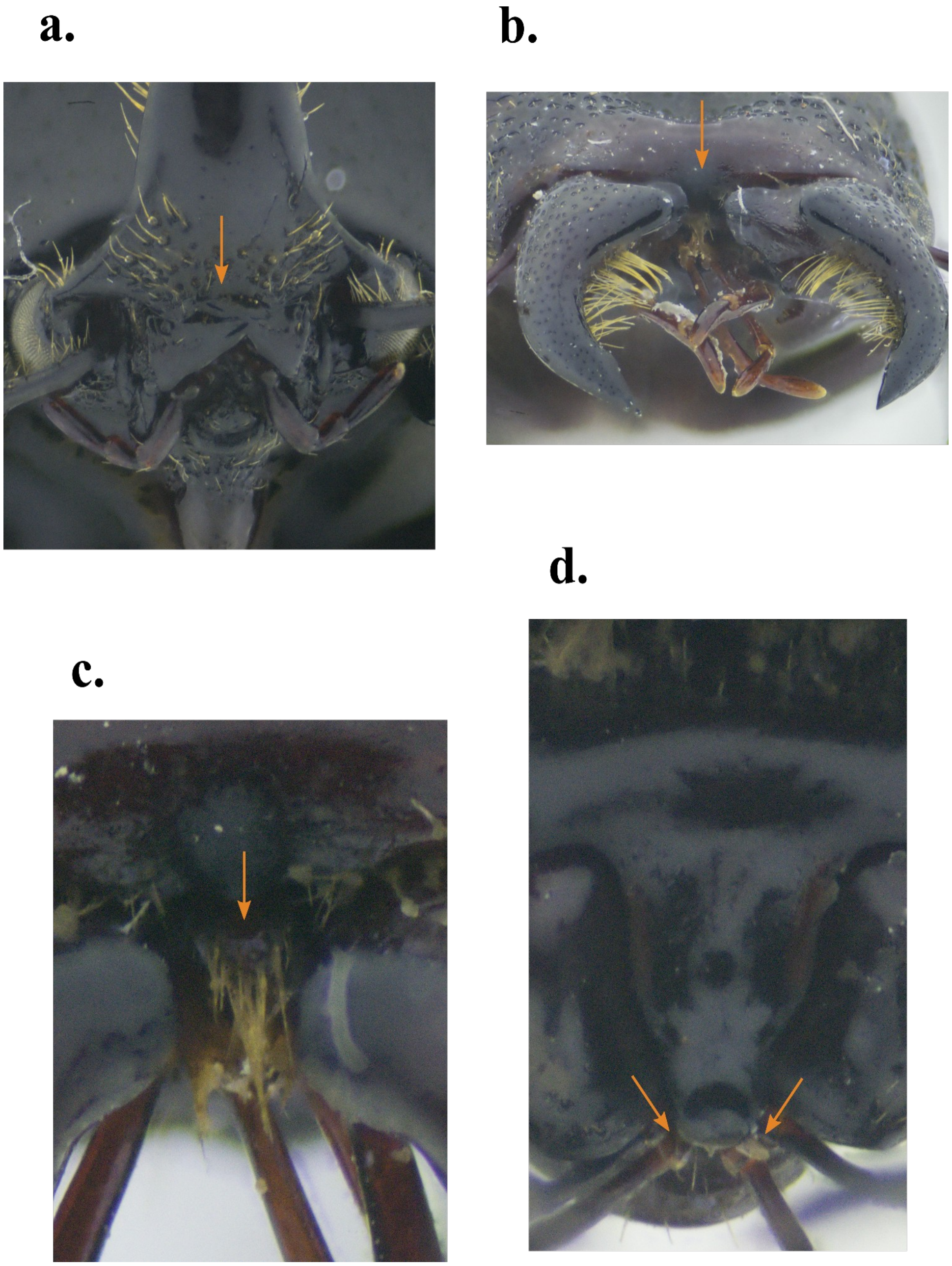

Figure 2. a. ***S.*** *rugosum* intermandibular projection. **b.** *C. chrysomelinius* intermandibular projection. **c.** *C. chrysomelinius* labrum. **d.** *S. cornutus* labrum.

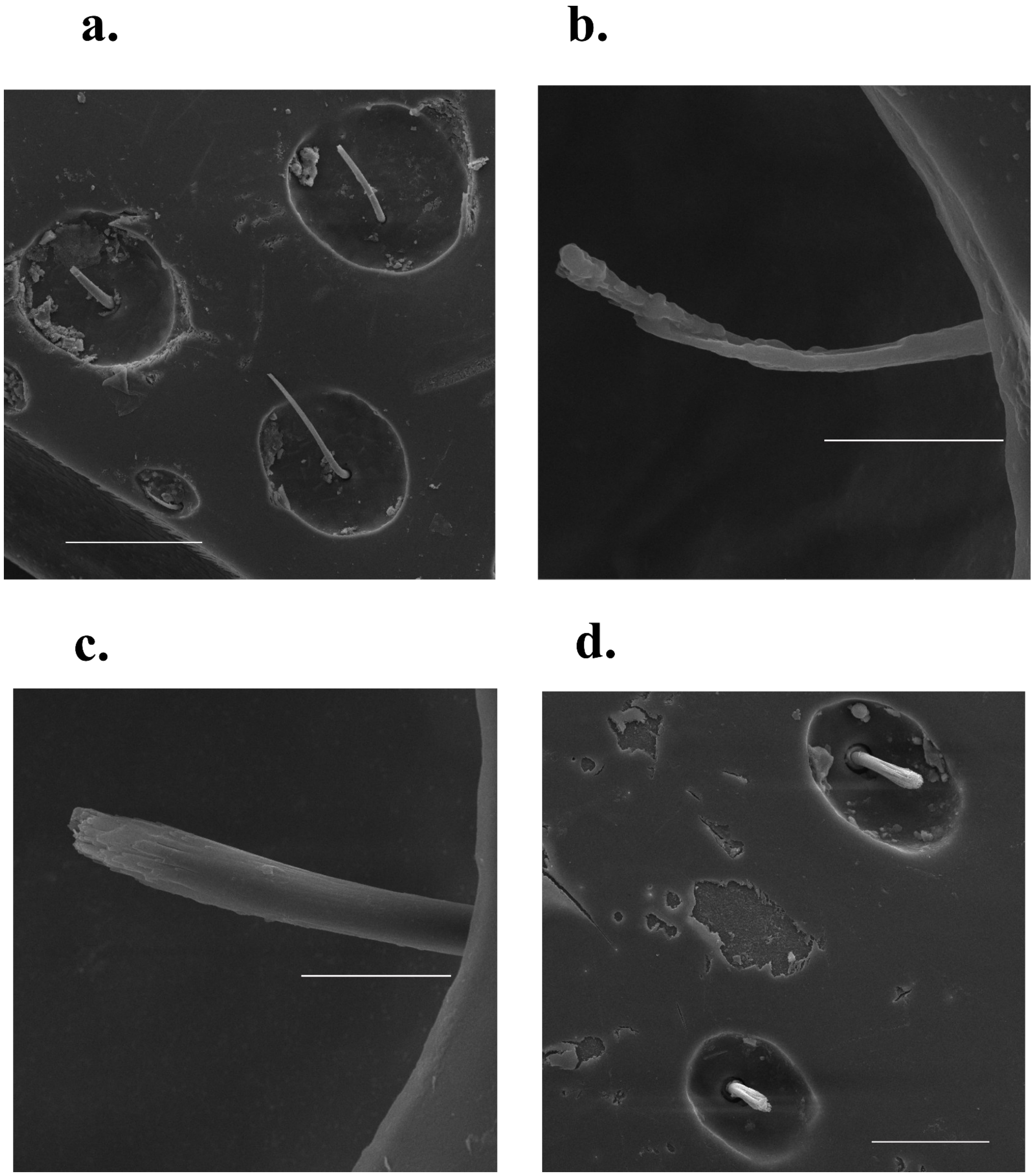

Figure 3. a. *S. rugosum* elytral smooth setae. Note the polygonal surface in the pit. Scale bar 50 µm **b.** *S. cornutus* elytral barbed setae. Scale bar 5µm. **c.** *P. schuberti* elytral barbed incised setaed. Scale bar 10 µm. **d.** *C. chrysomelinius* elytral barbed incised setae. Scale bar

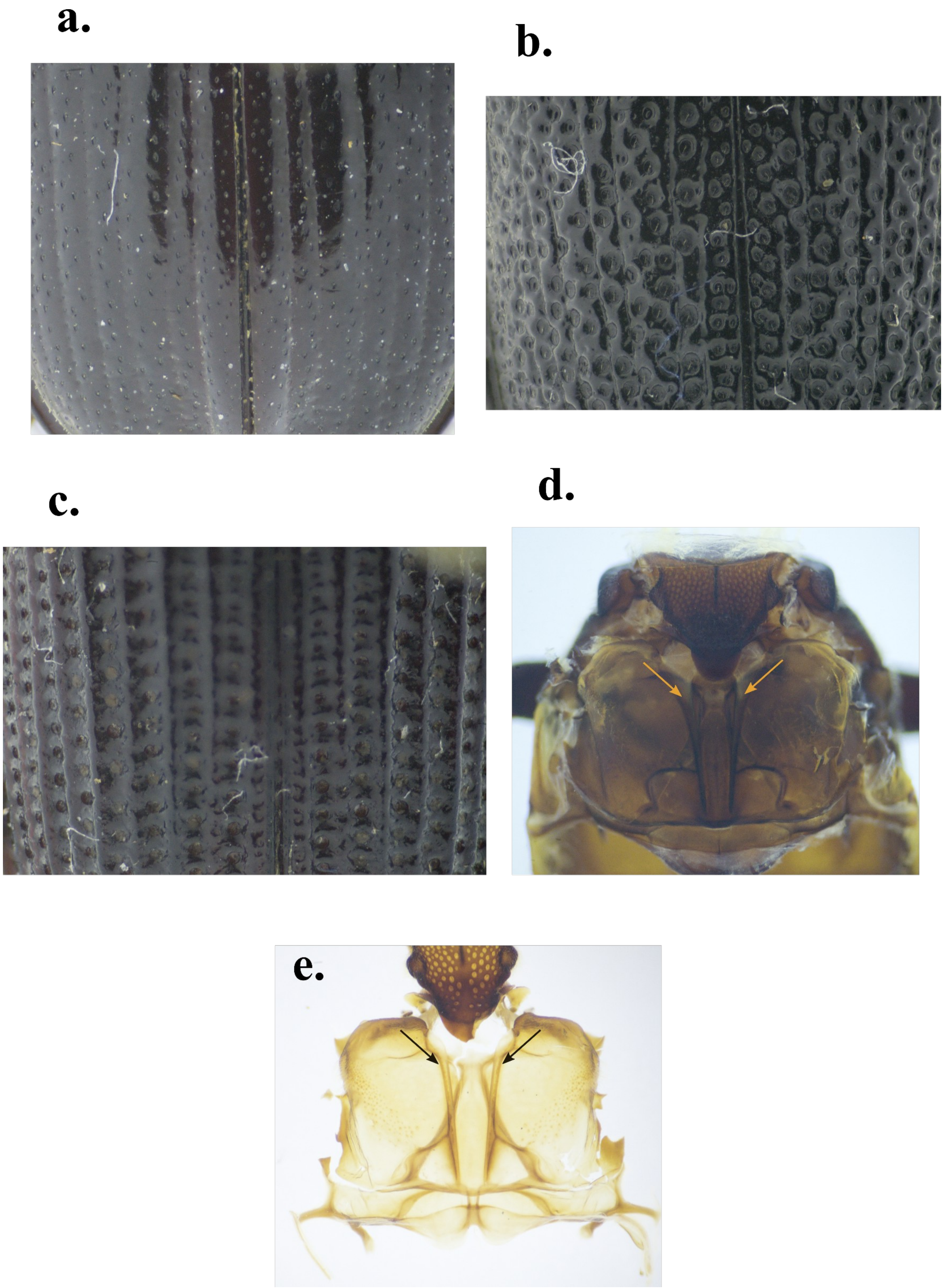

Figure 4. a. *C. piceus* elytral surface. **b.** *S. rugosum* elytral surface. **c.** ***S****. cornutus* elytral surface. **d.** *S. rugosum* metanotum. **e.** *S. cornutus* metanotum.

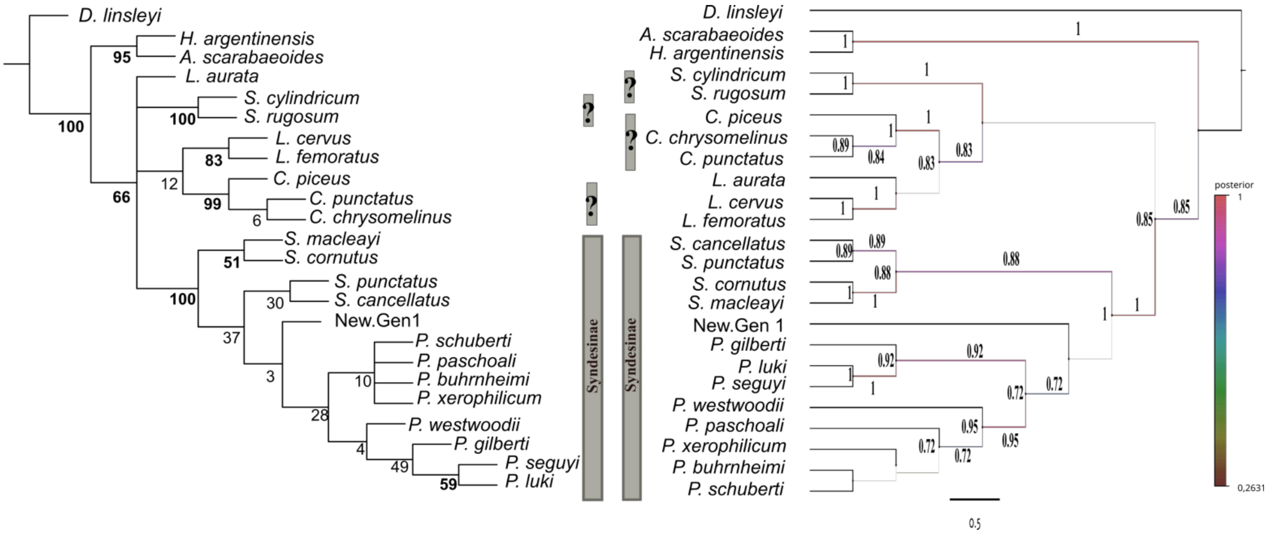

Figure 5. Phylogeny of Syndesinae MacLeay, 1819, including outgroups. **Left,** Parsimony tree with traditional bootstrapping. Bold font indicates values equal or above 50%. **Rigth,** Bayesian tree with posterior probabilities as branch and node support. Only support values above 50% are shown. **?** Symbol refers to the remaining clades of Syndesinae *sensu* Holloway (1968) which needs a taxonomic re-evaluation.

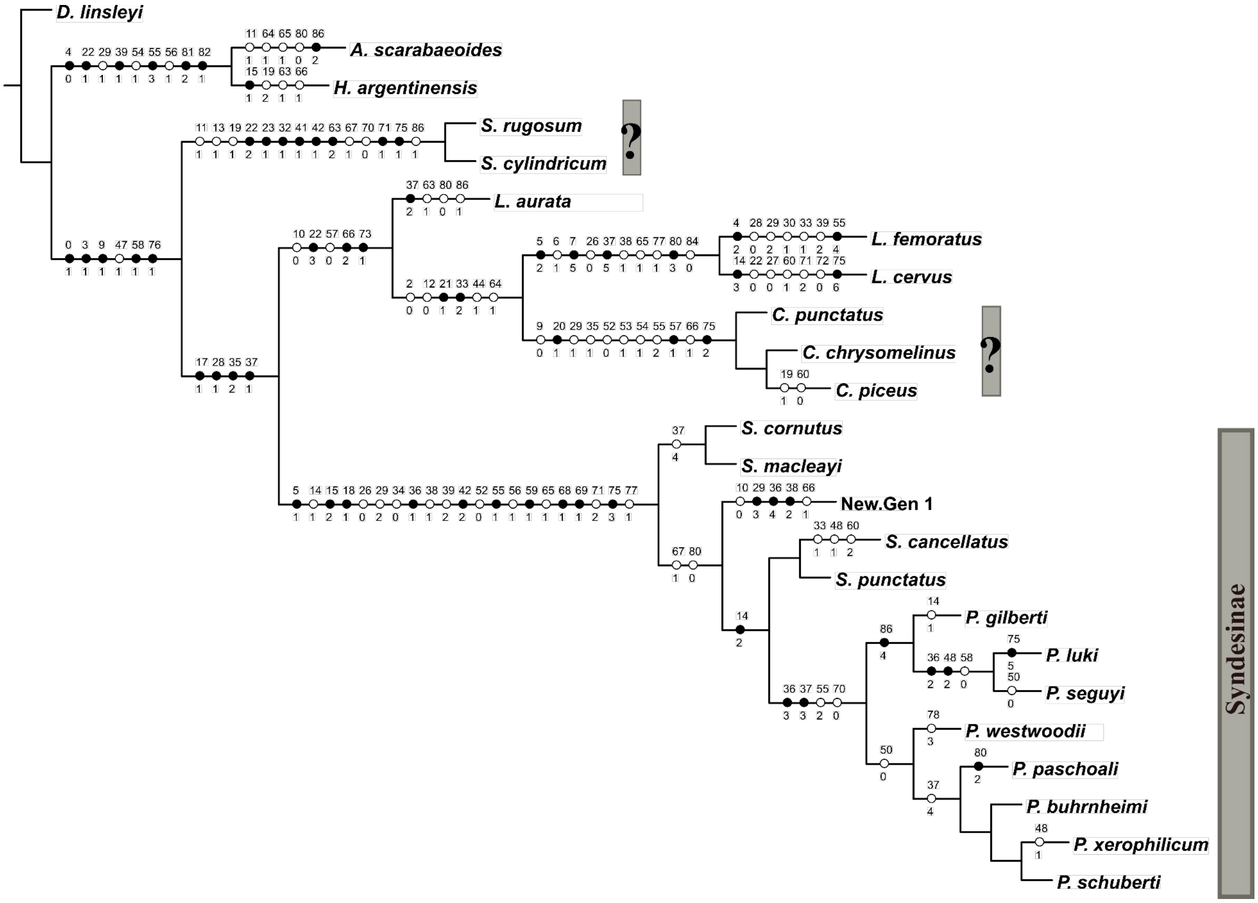

Figure 6. Morphological character reconstruction on the parsimony tree obtained under traditional search using implied weight (*k*=7.5).

CAPÍTULO 4

FINAL CONSIDERATIONS

By applying an integrative approach using comparative morphology techniques, geometric morphometrics and phylogenetic methodologies we provide new information that contributes to the reduction of some of the significant gaps in regard to Lucanidae classification. We support the existence of Syndesinae as a natural group in respect to the *sensu* proposed before Holloway (1968), separating *Sinodendron* and *Ceruchus* from this taxon. We also offer taxonomic, systematic and distributional data to validate the existence of three genera in Syndesinae, defining the limits between *Syndesus* and *Psilodon*.

With this work we expect to contribute different types of data to help the scarab researcher to work on a wider consensus regarding one of the less studied subfamilies within Lucanidae, considering now as natural groups the subfamilies Aesalinae, Lampriminae, Syndesinae (restricted to the Australasiatic and Neotropical taxa) and Lucaninae, pending a more profound study study to evaluate the validity of Sinodendrinae and Ceruchinae as subfamilies of the Stag beetles.

There is still need to conduct molecular and biogeographical analysis with larger taxa samplings in order to offer new insights related to the evolutionary history of world Lucanidae, and helping to resolve the enormous classification problems that still persist, especially at the suprageneric level.