SISTEMÁTICA DO GÊNERO *Enema* HOPE, 1837 (COLEOPTERA: MELOLONTHIDAE: DYNASTINAE: ORYCTINI) E REVISÃO TAXONÔMICA DE *Enema endymion* CHEVROLAT, 1843

por

ADRIANA ANDRADE MOTA

(Sob Orientação do Professor Paschoal Coelho Grossi - UFRPE)

RESUMO

Oryctini Mulsant, 1842 incluído em Dynastinae com 26 gêneros e 230 espécies a nível mundial. Com sete gêneros com registros de ocorrência para o Brasil, totalizando 45 espécies reportadas. O gênero *Enema* Hope, 1837 pertence a essa tribo e atualmente possui duas espécies, *E. pan* (Fabricius, 1775) com ampla distribuição do México à Argentina e *E. endymion* Chevrolat, 1843, presente na América Central e norte da América do Sul. A taxonomia deste gênero permaneceu mais de 40 anos sem nenhuma atualização, e ele nunca foi analisado filogeneticamente. O objetivo deste trabalho foi verificar os sinônimos da espécie *E. endymion* através dos tipos primários disponíveis, além de analisar filogeneticamente o gênero. Para isso foi realizado o empréstimo de material de outras coleções, nos quais tiveram sua morfologia externa e terminálias de machos e fêmeas, analisadas e fotografadas, mapas de distribuição das espécies também foi fornecido. Após a revisão taxonômica se constatou diferença morfológica dentro da população nomeada como *E. endymion*. O sinônimo *E. gibbicollis* Sternberg, 1908 foi revalidado, com caracteres diagnósticos e novos dados de distribuição, essa espécie ocorre da Amazônia Brasileira e Suriname. Além da designação de dois Lectótipos. Uma espécie nova foi descrita, *Enema* sp.1 sp.nov. com ocorrência para o nordeste do Brasil. A análise cladística confirmou o gênero como monofilético. Dessa forma, esse estudo contribui com o conhecimento das relações

filogenéticas de *Enema*, chave de identificação, atualiza os limites de distribuição das espécies e pode ser utilizado como aporte para conservação deste táxon.

PALAVRAS-CHAVE: Floresta Atlântica, Floresta Amazônica, Diversidade, Região Neotropical, Besouros rinoceronte, Sistemática Filogenética, Taxonomia, Distribuição geográfica.

SYSTEMATIC OF THE GENUS *Enema* HOPE, 1837 (COLEOPTERA: MELOLONTHIDAE: DYNASTINAE: ORYCTINI) AND TAXONOMIC REVISION OF *Enema endymion* CHEVROLAT, 1843

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ADRIANA ANDRADE MOTA

(Under the supervision Professor Paschoal Coelho Grossi – UFRPE)

ABSTRACT

Oryctini *Mulsant*, 1842, belonging to Dynastinae includes 26 genera and 230 species in the world. Among these genera, seven have occurrence records for Brazil with a total of 45 species reported. The genus *Enema* Hope, 1837 belongs to this tribe and currently includes two species, *E. pan* (Fabricius, 1775) with a distribution from Mexico to Argentina and *E. endymion* Chevrolat, 1843, occuring in Central America and northern South America. The taxonomy of the genus remained more than 40 years without any updates, and it was never analyzed phylogenetically. The objective of this work was to verify the synonyms through the avaible types and to analyzing the genus phylogenetically. Thence, material from other collections was loaned, the external morphology and terminalia of the specimes were analyzed and photographed, species distribution maps were also provided. After the taxonomic review, a morphological difference was found within the population named *E. endymion*, which was considered to be only the population occurring in Central America. The synonym *E. gibbicollis* Sternberg, 1908 was revalidated, diagnostic characters and new distribution data were provided This species occur in Brazilian amazon and Suriname. c. A new species was described, *Enema* sp.1 sp .nov with occurrence for northeastern Brazil. Cladistic analysis confirmed the genus as monophyletic. Thus,

this study contributed to the knowledge of the phylogenetic relationships of *Enema*, provided an identification key, updated the limits of species distribution and can be used as a contribution to the conservation of this taxon.

KEY WORDS: Atlantic Forest, Amazon Forest, Diversity, Neotropical Region, Rhinoceros beetles, Phylogenetic systematics

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“Things do not change because time passes,

but because we women are committed to changing them.”

Nancy Hopkins

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Nomenclatura

Previsto no Código Internacional de Nomenclatura Zoológica (ICZN, 2000, cap. 3, art. 8), a nomenclatura dos táxons proposta nessa dissertação não é considerada válida enquanto não for publicada em periódicos científicos.

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CAPÍTULO 1

INTRODUÇÃO

Coleoptera é um dos maiores táxon em Metazoa e a maior ordem dentro em Insecta, com aproximadamente 395 mil espécies descritas, cerca de 2 % das espécies conhecidas (Slipinski *et al*. 2011; Zhang 2018). Seus representantes são cosmopolitas, ocorrem em quase todos os ecossistemas terrestres e invadiram habitats aquáticos pelo menos dez vezes, como larvas, adultos ou ambos (Beutel 1995). Além disso, apresentam uma grande variedade de hábitos alimentares, morfologia e comportamentos e são facilmente reconhecidos, na maioria das espécies, pelas suas asas anteriores enrijecidas, os élitros (Rafael *et al.* 2012). Coleoptera é dividida em quatro subordens viventes, Archostemata, Myxophaga, Adephaga e Polyphaga, esta última com 24 superfamílias atuais, distribuídas ainda em séries: Staphyliniformia, Scarabaeiformia, Elateriformia, Derodontiformia, Bostrichiformia e Cucujiformia (Bouchard *et al.* 2011).

Scarabaeoidea Latreille, 1802 (Coleoptera, Polyphaga, Scarabaeiformia), tem seu monofiletismo sustentado por caracteres morfológicos de larvas e adultos, o formato larval em C conhecido como larva do tipo escarabeiforme, antenas lameladas e geralmente tíbias anteriores denteadas (Lawrence *et al*. 2011) e caracteres moleculares (Ahrens *et al.* 2014, Gunter *et al.* 2016, Sípek *et al*. 2016). Scarabaeoidea é formada por aproximadamente 35 mil espécies descritas, podendo haver, efetivamente, 50 mil no total (Jameson & Ratcliffe 2002, Scholtz & Grebennikov 2005), presente em todos os ambientes terrestres, com comportamentos alimentares muito diversificados (Slipinski *et al.* 2011).

A classificação seguida neste trabalho é a proposta por Bouchard *et al.* (2011), com modificação de Cherman & Morón (2014), na qual Melolonthidade Leach, 1819 é elevado a nível de família, subdividida em três subfamílias: Melolonthinae Samouelle, 1819, Rutelinae MacLeay, 1819 e Dynastinae MacLeay, 1819. Esta última possui aproximadamente 1.600 espécies descritas

no mundo (Ratcliffe *et al.* 2020), podendo chegar a 2.000 espécies (Endrödi 1985; Ratcliffe, 2003; Gasca-Álvarez & Amat-García 2010). O Brasil é o país com a maior riqueza de espécies, contando com cerca de 400, distribuídas em 53 gêneros (Grossi & Vaz-de-Mello 2019). Estas caracterizam-se por possuírem mandíbulas frequentemente expostas em vista dorsal, labro coberto pelo clípeo, antenas com nove ou dez antenômeros, escutelo visível, região posterior do pronoto e élitros semelhantes em largura, pronoto convexo com variações que podem ir de cornos diminutos a prolongamentos que alcançam a altura dos chifres, élitros nunca encurtados porém com pigídio exposto, processo prosternal entre os trocânteres anteriores arredondado, cilíndrico ou triangular, ápice do último ventrito abdominal no macho emarginado e na fêmea arredondado e ápice da metatíbia com dois esporões (Endrödi 1985).

Dynastinae é dividida em oito tribos: Dynastini, Phileurini, Oryctoderini, Hexodontini, Agaeocephalini, Cyclocephalini, Oryctini e Pentodontini. Destas, 6 ocorrem na região Neotropical. Dentre elas, destaca-se Oryctini Mulsant, 1842, com 26 gêneros e 230 espécies reportadas em âmbito mundial (Gasca-Alvárez *et al.* 2008). Para o Brasil, reportam-se 7 gêneros e 47 espécies (Grossi & Duarte 2020). A maior diversidade dessa tribo encontra-se na região Neotropical (Endrodi 1985). As espécies pertencentes a ela são, em geral, robustas com lados convexos, quase paralelos, clípeo emarginado ou bidentado com coloração de marrom a negra, mandíbulas largas e visíveis, protíbia tridentada ou quadridentada, ápice das tíbias posteriores com dentes, processo prosternal alongado ou encurtado, e os élitros podem ser estriados ou não (Endrödi 1985). Algumas espécies de Oryctini apresentam crescimento alométrico de seus chifres, uma vez que a forma e o tamanho dos chifres, em machos pertencentes às mesmas espécies, podem variar consideravelmente (Figura 14ABC) (Gasca-Álvarez & Ratcliffe 2011). O desenvolvimento dos chifres e o tamanho do corpo podem estar atrelados às condições nutricionais das larvas (Ratcliffe 2003). A história natural desse grupo ainda é pouco relatada. Sabe-se que os adultos têm hábitos

noturnos e, durante o dia, não são vistos (Ratcliffe 2003). Algumas espécies apresentam associação com ninhos de formigas. As fêmeas de *Coelosis biloba* (Linnaeus, 1767) foram reportadas ovopositando nos ninhos de *Atta sexden*s (Linnaeus, 1758) (Ratcliffe 2003), *A. cephalotes* (Linnaeus 1758) e *A. mexicana* (Smith, 1858) (Bruch 1917, Navarrete-Heredia 2001, Pardo-Locarno *et al.* 2006). A alimentação das larvas de *Coelosis* é baseada em matéria orgânica e fungos e o seu desenvolvimento acontece nas câmaras dos formigueiros. *Strategus aloeus* (Linnaeus, 1758), em sua forma adulta, também foi encontrado em depósitos de detritos dos ninhos de *A. mexicana*, no México (Deloya, 1988), e *A. columbica* (Guérin-Meneville, 1844), na Colômbia (Neita *et al*. 2006).

De forma geral, as espécies dessa tribo se alimentam de matéria orgânica em decomposição, frutos doces apodrecidos ou caules. Estas já foram avistadas em cana-de-açúcar (Ratcliffe 2003) e também nas raízes de várias espécies de palmeiras (Cockerell 1946; Gonçalves 1946; Vayssiere 1965; Bodkin 1919). Algumas espécies de Oryctini causam danos econômicos, sendo as mais danosas as que se alimentam de palmeiras, em especial, algumas espécies do gênero *Strategus* kirby, 1828. Sabe-se que a fêmeas deste gênero realizam a ovoposição em cascas de árvores e a larva se alimenta de troncos, de dentro para fora, e, após um período, o tronco oco se rompe, causando a morte da árvore (Endrödi 1985; Lourencao *et al*. 1999). Larvas de *Strategus aloeus* são devastadoras de raízes e mudas de coqueiros, assim como algumas espécies de Bromeliaceae (Costa-Lima, 1953) e também *Mangifera indica* (Bodkin, 1919). Os imaturos já foram encontrados no solo, forrageando em busca de matéria orgânica, resíduos vegetais, formigueiros ou até mesmo dentro de troncos e raízes apodrecidas (Morón 1997).

Já foram reportadas algumas espécies causando danos em cana-de-açúcar e também no milho, em que machos de *Podishnus agenor* (Olivier, 1789) constroem galerias nos caules de cana-de-açúcar, liberando hormônios com intuito de atrair fêmeas (Morón, 1997). Ainda ao se tratar

dessa espécie, na Colômbia, esta foi registrada causando danos a plantações de *Brassica oleracea var*. *capitata*, *B. oleracea* var. *botrynus*, *Cocos nucifera*, *Elaeis guineensis*, *Solanum tuberosum* e *Annona squamosa* (Restrepo-Giraldo & Lopez-Avila 2000). *Enema pan* Hope foi reportado em associação com espécies de Bambusoideae, no Sudoeste da Bacia Amazônica, onde os adultos foram vistos se alimentando de seiva de bambu triturado e também cavando longos túneis subterrâneos na base de seus caules (Jacobs *et al*. 2012).

A tribo Oryctini passou por algumas mudanças de categorias taxonômicas nos últimos anos. Mulsant (1842) chamava de Oryctésiens os besouros escaravelhos lamelicórnios, que se caracterizavam por possuírem prosterno coberto de cerdas, antenas com dez antenômeros, e mandíbulas projetadas lateralmente. Posteriormente, Burmeister (1847) usou o nome Oryctidae para se referir a tribo que foi usado como nome válido até hoje, esse nome foi amplamente usado por diversos autores como Lacordaire (1856), LeConte & Horn (1883), Bates (1888), Casey (1915) e Arrow (1937). Bates (1888), em contrapartida usava "Pentodontinae" para um determinado grupo de gêneros da América Central. Mulsant (1842) classificou os pentodontíneos como um grupo pertencente a Oryctines. No entanto Arrow (1937), Blackwelder (1944), Saylor (1946a, b) e Arnett (1968) não seguiram essa classificação e, em face do exposto, incluíram os pentodontines dentro dos Oryctini. Por fim, Oryctini foi definido por Endrödi (1966, 1985) que também restabeleceu o uso de Pentodontini. As duas tribos são separadas pela tíbia posterior com borda truncada e quase lisa no ápice em Petondontini e em Oryctini por uma borda dentada e fortemente crenulada no ápice da tíbia posterior (Ratcliffe 2003).

Alguns gêneros de Oryctini apresentam ampla área de ocorrência da América Central até o Brasil, os quais são: *Coelosis* Hope, 1837, *Heterogomphus* Burmeister, 1847, *Gibboryctes* Endrödi, 1974, *Megaceras* Hope, 1837, *Podischnus* Burmeister, 1847, *Strategus* Kirby, 1828, e *Enema* Hope, 1837.

Quanto a *Coelosis* Hope, 1837, com oito espécies descritas (Schoolmeesters 2019), apesar de ocorrer na América Central, a maior parte de suas espécies ocorrem no Brasil. A última revisão taxonômica foi realizada por Iannuzzi & Marinoni (1995), e a última espécie descrita foi *Coelosis (Eucoelosis) wayuorum*, por Neita-Moreno *et al*. (2018), com ocorrência para a Colômbia. Uma descrição para a espécie *C. biloba* (Linaeus, 1767) foi realizada por Pardo-Locarno *et al*. (2006).

Quanto a *Heterogomphus* Burmeister, 1847, com 47 espécies (Schoolmeesters, 2019), apenas seis espécies foram descritas depois de Endrodi (1985) (Dechambre 1986, 1998; Ratcliffe 2006; Dupuis & Dechambre 2008, Dupuis *et al*. 2012), sendo que a espécie *Heterogomphus effeminatus* Ratcliffe, 2006 não é válida (Dupuis *et al*. 2012). Amplamente distribuída da América Central ao sul do Brasil, com muitas espécies endêmicas reportadas para o Brasil e para o Peru. As revisões disponíveis foram a de Endrodi (1985), e também a revisão do grupo de *H. pauson* (Perty, 1830), de Dupuis & Dechambre (2008), porém carece de revisão taxonômica. De acordo com Ratcliffe (2006), esse grupo manifesta barreiras taxonômicas consistentes, pois há muita similaridade morfológica entres as espécies do gênero. Pouco se conhece da biologia e do ciclo de vida, com exceção de algumas espécies que exibem descrição de larvas e pupas, como *H. dilaticollis* Burmeister, apenas descrição de larvas (Neita-Moreno & Orozco 2009), *H. chevrolati* Burmeister, 1847 (Ratcliffe 2003).

Gibboryctes Endrödi, 1974: atualmente com três espécies devidamente descritas, foi recentemente revisado por Costa *et al*. (2020). Espécies desse gênero já foram coletadas dentro de cupinzeiros no sul do Brasil (Grossi *et al*. 2011; Costa *et al*. 2020).

Megaceras Hope, 1837: das 21 espécies (Schoolmeesters, 2019), que ocorrem integralmente na América do Sul, somente duas alcançam o Norte até Guatemala, Honduras e Nicarágua (Ratcliffe & Cave 2006; Ratcliffe *et al*. 2013). O gênero nunca foi revisado. Recentemente

Ratcliffe & Saltin (2021) descreveram *Megaceras sarecagem,* uma nova espécie reportada para o Peru.

Podischnus Burmeister, 1847: com cinco espécies descritas, sendo que as duas foram descritas recentemente por Duarte & Grossi (2020). *P. agenor* (Olivier, 1789) é a única espécie com distribuição na América Central, *P. oberthuri* Sternberg, 1907 reportado para Equador, Bolívia e Paraguai, *P. sexdentatus* (Taschenberg, 1970) para Colômbia, Peru e Brasil (Gasca-Alvarez & Ratcliffe, 2011), e as outras espécies ocorrem no norte do Brasil (Duarte & Grossi 2020). Sua história natural foi pouco explorada, com registros apenas de Eberhard (1979) e Neita-Moreno & Orozco (2009), que descreveram estágios imaturos.

Strategus Kirby, 1828: com 36 espécies (Schoolmasters, 2019), a última revisão foi realizada por Ratcliffe (1976). A história natural e a descrição de imaturos são conhecidas nesse gênero devido a sua grande importância econômica. Espécies com descrições de imaturos: *S. aloeus* (Linnaeus, 1758) (Dugès 1876), *S. antaeus* (Drury, 1773) e *S. splendens* (Palisot de Beauvois, 1809) (Ritcher 1966), *S. fascinus* Burmeister, 1847 (Neita & Ratcliffe 2009), *S. longichomperus* Ratcliffe, 1976 (Morón & Ratcliffe 1990), *S. mormon* Burmeister, 1847 (Morón & Ratcliffe 1990), *S. surinamensis hirtus* Sternberg, 1910 (Costa *et al*. 1988) e *S. syphax* (Fabricius, 1775) (Ratcliffe & Chalumeau 1980).

O gênero *Enema* Hope, 1837, foco deste trabalho, atualmente inclui duas espécies: *E. pan* (Fabricius, 1775) e *E. endymion* Chevrolat, 1843, ambas com ampla distribuição neotropical. *E. pan* é reportada para a América Central e do Sul, enquanto *E. endymion* reportada para a América Central e o norte da América do Sul (Gasca-Alvárez *et al.* 2008). Este gênero *Enema* Hope, 1837 nunca foi revisado, além das descrições originais são apresentadas apenas descrição de larvas de *E. endymion* (Ratcliffe 2003) e aspectos biológicos e comportamento de *E. pan* (Puker *et al.* 2011). Acredita-se que *E. pan* possa estar restrita a áreas florestadas, enquanto *E. endymion* possa ser

coletada em áreas de florestas e arbustivas, sendo frequentemente atraída por armadilhas luminosas, especialmente em períodos chuvosos (Ratcliffe 2003).

O primeiro registro do nome 'Enema' foi exibido em Marcgrave (1648), em seu livro *Historia Naturalis Brasiliae*. Esse autor fez os primeiros registros da fauna e da flora do nordeste brasileiro e se apropriou do termo indígena Enena, aquele que era usado para chamar os besouros que ali se encontravam; traduzindo esse termo para o português, seria Escaravelhos. Em 1787, Fabricius, descreve as espécies com os nomes *Scarabaeus enema.* Hope (1837), na descrição do gênero *Enema*, afirmou que o autor Kirby se apropriou do nome *Enema* de Fabricius (1787) e o aplicou ao tipo do gênero *Infundibilum*. Muitos autores, em suas descrições, usam o nome ''Kirby ou Kirby-Hope'' devido à identificação de espécimes oriundas da coleção de Hope (Hope, 1837). Nesses relatos também afirmou que Lacordaire foi o primeiro a registrar que as fêmeas de *Enema* assim como os machos possuíam chifres.

Antes do nome Enema ser considerado válido, Dejean (1833) listou *Hoplites* como gênero que era composto por três táxons neotropicais *Hoplites enema, H. pan,* reportado para o Brasil, e *H. lupercus* reportado para o México. Nenhuma descrição e espécie-tipo foi localizada. Quatro anos depois, em seu catálogo, Dejean traz *H. paniscus e H. endymion*, com registros para Guiana e e México, respectivamente (Dejean, 1837). Posteriormente, considerada sinônimo sênior do gênero *Enema* descrita por Hope (1837), no qual considera *Enema* como nome válido por ser sinônimo júnior de *Hoplites*, com *Geotrupes pan* Fabricius, 1775 como espécie-tipo. Scudder (1882) listou todos os gêneros nomeados *Hoplites* em sua lista suplementar, e dentre eles, havia indivíduos de filos distintos, incluindo o Coleoptera, que foi o descrito por Dejean (1833). Prell (1936) afirma que o nome usado por Dejean nunca entrou em uso geral, argumentando que *Hoplites* Hubber, 1816 foi o primeiro a ser publicado. Portanto, o nome já disponível a ser usado deveria ser *Enema*, descrito por Hope (1837), e outrora usado informalmente por Kirby. Contudo, *Enema*, a despeito

de sua condição de sinônimo júnior, é o nome válido do gênero porque *Hoplites* Dejean, 1833 foi suspenso em relação ao Princípio de Prioridade e ao Princípio de Homonímia pela Comissão Internacional de Nomenclatura Zoológica (Bousquet & Bouchard 2013).

Enema endymion foi descrito por Chevrolat (1843), na mesma publicação, descreveu *Enema lupercus*, que, pela descrição, claramente se tratava de um exemplar da espécie *Enema pan*. Burmeister (1847) aplica o nome erroneamente, considerando que *E. lupercus* Chevrolat seria, na verdade, composto por exemplares pequenos ('*Var. minor*') de *E. endymion* e não uma espécie separada e descreve *Enema paniscus* Burmeister, 1847, reportada para o interior da Guiana e da Colômbia. Lacordaire (1856) concorda com a validade de *E. paniscus* e reforça que *E. lupercus* seriam exemplares menores de *E. endymion*. Reich (1859), por outro lado, defende que *E. endymion* e *E. lupercus* seriam espécies distintas. Bates (1888) sinonimizou *E. lupercus* com *E. endymion*, o que foi, mais tarde, seguido por Heyne & Taschenberg (1907). Por fim, Stenberg (1908) descreveu *Enema gibbicollis* Sternberg, 1909, com Suriname sendo a localidade-tipo.

Arrow (1937) listou, em seu catálogo, o gênero com duas espécies: *Enema pan* (Fabricius, 1775) e *Enema endymion* Chevrolat, 1843, assim como Blackwelder (1944). Arrow (1937) reportou as seguintes localidades para *Enema pan:* México, Nicarágua, Costa Rica, Colômbia, Peru, Brasil e Paraguai, e para *E. endymion:* México, Nicarágua, Panamá, Colômbia, Venezuela e Guiana. Blackwelder (1944), acrescentou a Argentina na distribuição de *E. pan,* enquanto para *E. endymion* adicionou Honduras, Guatemala e Costa Rica.

Endrödi (1976), em uma das suas principais publicações na tribo Oryctini, seguiu Arrow (1937) e Blackwelder (1944), definindo uma lista de sinônimos para as duas espécies. *Enema pan* com sete sinônimos. Três foram estabelecidos ainda no século XVIII por Fabricius (1775, 1781): *Scarabaeus chorinaeus* Fabricius, 1775, *S. quadrispinosus* Fabricius, 1781 e *S. enema* Fabricius, 1787. Os outros sinônimos junior de *E. pan* são: *S. aeneas* Kirby 1818, *S. titornus* Perty, 1830, *E.*

lupercus Chevrolat, 1843 e *E. infundibulum* Burmeister, 1847. Para *E. endymion*, foram listados três sinônimos: *E. lupercus* Burmeister, 1847, *E. paniscus* Burmeister, 1847 e *E. gibbicollis* Sternberg, 1908.

Ratcliffe (2003) chama atenção para a má aplicação por parte de Burmeister (1847) do nome *E. lupercus* de Chevrolat (1843), pois ele usou o nome que Chevrolat atribuiu a um exemplar que é sinônimo de *E. pan*. Concordando com Endrödi (1975), também considerou *Hoplites* inválido por ser um *nomen oblitum*, enquanto *Enema* seria válido por ser um *nomen protectum.*

Oryctini não apresenta hipóteses de relacionamento entre as espécies, com exceção de alguns trabalhos, como em Bitar & Morón (2014), que, em sua análise cladística, recuperou *Xyloryctes* Hope, 1837 como monofilético, usando *Enema pan* como um dos terminais do grupo externo.

Basset *et al*. (2022) definiram grupos funcionais dentro da subfamília Dynastinae e usaram dados moleculares na construção de uma hipótese filogenética. A amostragem foi feita com espécies que ocorrem no Panamá. Os próprios autores afirmam que os grupos funcionais podem se estender para outras espécies de Dynastinae neotropicais de outras localidades, também pela potencialidade de dispersão desses indivíduos. Ainda neste trabalho, na árvore que mostrava a relação dos grupos funcionais *Enema*, este se encontra parafilético, diferente do resultado da análise filogenética com dados moleculares, o qual tem alto suporte (bootstrap support >70%) para o clado monofilético *Enema* com dois terminais, compostos por *E.pan* e *E.endymion*. O autor afirma que, apesar de uma hipótese filogenética bem suportada, tribos e muitos gêneros se mostram parafiléticos, necessitando de uma reconstrução filogenética robusta para Dynastinae.

Enema endymion nunca havia passado por revisão taxonômica com exame de material tipo e exemplares depositados em coleções brasileiras, e por atestar uma variação morfológica dentro da população e a separação geográfica das espécies, aqui foi proposta uma validação de sinônimo, a designação de dois Lectótipos, uma descrição de uma espécie nova, a chave de identificação para o

gênero e um mapa de distribuição. Todos as espécimes-tipos depositadas em museus na Europa foram examinadas por fotografias. O tipo *Enema lupercus* Burmeister, 1847, atestado como perdido em Endrodi (1976), não foi, de fato, encontrado, afirmando-se o desaparecimento deste. Para mais, foi feita uma análise cladística de *Enema*, para testar uma hipótese de monofilia, usando uma matriz com caracteres morfológicos adaptada com base em Bitar e Morón (2014).

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CAPÍTULO 2

Phylogenetics of the genus *Enema* Hope, 1875 (Coleoptera: Melolonthidae: Dynastinae: Oryctini) and taxonomic revision of *Enema endymion*, Chevrolat, 1843

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Abstrat

Enema Hope, 1837 is one of the thirteen Neotropical genera within the Oryctini and prior to this study had two species. They are: *E. pan* (Fabricius, 1775) with a wide distribution from Mexico to Argentina and *E. endymion* Chevrolat, 1843, present in Central America. This work aimed to verify synonyms through primary type specimens available in collections and also to test the monophyly of the genus based on a matrix with data from morphological characters. The study material was borrowed from collections, and external structures of adults, males and females, and terminalia were compared. After taxonomic revision, a morphological difference was found within one population of *E. endymion*, which was considered only the population that occurs in Central America, the synonym *E. gibicollis* Sternberg, 1908 was revalidated with occurrence for the Brazilian Amazon. Besides the designation of two lectotypes for *E. endymion* and *E. gibbicollis*. Additionally, a new species was described for the Pernambuco Center of Endemism in northeastern Brazil. Cladistic analysis recovered the genus as monophyletic. Finally, photographs and distribution maps with updated new records were provided.

KEY WORDS: Atlantic Forest, Amazon Forest, Neotropical Region, Rhinoceros beetles, New species.

Resumo

Enema Hope, 1837 é um dos treze gêneros Neotropicais dentro de Oryctini e antes da realização deste trabalho possuía duas espécies. São elas: *E. pan* (Fabricius, 1775) com ampla distribuição do México à Argentina e *E. endymion* Chevrolat, 1843, presente na América Central. Este trabalho buscou verificar os sinônimos através dos espécimes de tipos primários disponíveis em coleções e também se testou a monofilia do gênero com base em uma matriz com dados advindos de caracteres morfológicos. O material de estudo foi emprestado de coleções, e usou-se estruturas externas de adultos, machos e fêmeas, e terminálias foram comparadas. Após a revisão taxonômica, uma diferença morfológica foi encontrada dentro de uma população de *E. endymion*, que foi considerada apenas a população que ocorre na América Central, o sinônimo *E. gibicollis* Sternberg, 1908 foi revalidado com ocorrência para Amazônia brasileira. Além da designação de dois Lectótipos para *E. endymion* e *E. gibbicollis.* Adicionalmente uma nova espécie foi descrita para o Centro de endemismo de Pernambuco, no Nordeste do Brasil. A análise cladística recuperou o gênero como monofilético. E por fim foram fornecidas fotografias e mapas de distribuição com atualização de novos registros.

Palavras-chave: Mata Atlântica, Floresta Amazônica, Região Neotropical, Besouro rinoceronte, Novas espécies.

Introduction

The genus *Enema* Hope, 1837 is here revised for the first time. The name first appereared in the literature that this name appeared was in Marcgrave's (1648) section of the book *Historia Naturalis Brasiliae*. There, the author presented the first records of the fauna and flora of the Brazilian northeast, including that of the beetle known to the Tupi-speaking indigenous populations of the region as enena*,* their word for 'scarab'. The second time was by Fabricius (1787), when he described the species with the *names Scarabaeus enema*. Hope (1837), in his description of the genus *Enema*, stated that the author Kirby took the specific name *enema* from Fabricius (1787), and applied it to the type of the genus *Infundibilum*. Many authors in their descriptions use the name "Kirby or Kirby-Hope" due to the identification of specimens from the Hope collection (Hope 1837). In these reports, he claimed that Lacordaire was the first to record that *Enema* females also had horns. But three years before this publication, Dejean (1833) listed *Hoplites*, as a genus that was composed of three Neotropical species *Hoplites enema*, *H. pan*, reported from Brazil and *H. lupercus* reported from Mexico, neither description and type species were located. Four years later, his catalog included *H. paniscus* and *H. endymion*, with localities in Cayenne and Mexico, respectively (Dejean 1837). Later, considered a senior synonym of the genus *Enema* described by Hope (1837), in which he considers *Enema* as a valid name because it is a junior synonym of *Hoplites*, with *Geotrupes pan* Fabricius, 1775 as the type species. Scudder (1882) listed all the genera named *Hoplites* in his supplementary list, among which were individuals of different phyla, including that of Coleoptera which was described by Dejean (1833). Prell (1936) claims that the name used by Dejean never came into general use, arguing that *Hoplites* Hubber, 1816 was the first to be published. Therefore, the readily available name to be used should be *Enema* described by Hope (1837) and formerly used informally by Kirby.

However, *Enema*, despite its status as a junior synonym, is the valid name of the genus because *Hoplites* Dejean, 1833 was suspended regarding the Principle of Priority and the Principle of Homonymy by the International Commission on Zoological Nomenclature (Bousquet & Bouchard 2013).

Enema endymion was described by Chevrolat (1843), who in the same publication describes *Enema lupercus*, which from the description clearly was a specimen of the *Enema pan* species. Burmeister (1847) misapplies the name, considering that *E. lupercus* Chevrolat would actually be composed of small specimens ('Var. minor') of *E. endymion* and not a separate species, and describes *Enema paniscus* Burmeister, 1847 reported to the interior of Guyana and Colombia. Lacordaire (1856) agrees with the validity of *E. paniscus* and reinforces that *E. lupercus* would be smaller specimens of *E. endymion*. Reich (1859), on the other hand, argues that *E. endymion* and *E. lupercus* are distinct species. Bates (1888) synonymized *E. lupercus* with *E. endymion*, which was later followed by Heyne & Taschenberg (1907). And the last author to describe a species for this genus was Stenberg (1908) who described *Enema gibbicollis* Sternberg, 1909 with the type locality reported for Suriname was the latest species described of the genera.

Arrow (1937) listed two species of Enema in his catalog: *E. pan* (Fabricius, 1775) and *E. endymion* Chevrolat, 1843 as well as Blackwelder (1944). Arrow (1937) reported the following localities for *Enema pan*: Mexico, Nicaragua, Costa Rica, Colombia, Peru, Brazil and Paraguay, and for *E. endymion*, Mexico, Nicaragua, Panama, Colombia, Venezuela and Guyana. Blackwelder (1944), for *E. pan*, reported the same localities but added Argentina to the distribution, while for *E. endymion* he added Honduras, Guatemala and Costa Rica.

Endrödi (1975), in one of his main publications on the Oryctini tribe, defined a list of synonyms for both species in agreement with Arrow (1937) and Blackwelder (1944). *Enema pan* with seven synonyms, three already established in the 18th century by Fabricius (1775, 1781):

Scarabaeus chorinaeus Fabricius, 1775, *S. quadrispinosus* Fabricius, 1781 and *S. enema* Fabricius, 1787. The other junior synonyms of *E. pan* are: *S. aeneas* Kirby 1818, *S. titornus* Perty, 1830, *E. lupercus* Chevrolat, 1843 and *E. infundibulum* Burmeister, 1847. For *E. endymion*, he listed three synonyms: *E. lupercus* Burmeister, 1847, *E. paniscus* Burmeister, 1847 and *E. gibbicollis* Sternberg, 1908.

Ratcliffe (2003) recognized to the misapplication of the name *E. lupercus* Chevrolat (1843) by Burmeister (1847), as he used the name that Chevrolat attributed to an specimen that belongs to *E.pan*. Agreed with Endrödi (1975) about considering *Hoplites* invalid for being a *nomen oblitum*, while *Enema* would be valid for being a *nomen protectum*.

Currently, the moment, there are no hypotheses of a phylogenetic relationship within the Oryctini tribe, except for of the review and phylogeny of the genus *Xyloryctes* Hope, 1837 carried out by Bitar & Morón (2014), which used the terminal *Enema pan* in its outgroup. Recently Basset et al. (2022) defined functional groups for the species of Dynastinae, which occur in Panama and also a phylogenetic analysis with molecular data that has as monophyletic clade the species *Enema pan* and *Enema endymion*.

The aim of the present work was to review *Enema endymion* and test the monophyly of the genus. Based on the results of the taxonomic review, it was verified the validation of a synonym, the designation of two lectotypes and the description of a new species reported from Brazil. Additionally, we present a key to the species of the genus and update the known distribution map of the *Enema endymion* species group. After cladistic analysis, the monophyly of the genus was recovered.

Material and methods

The study was carried out at the Insect Taxonomy Laboratory of the Fitossanidade sector at the Federal Rural University of Pernambuco, Brazil.

Examined collections: 84 specimens deposited in the following collections were examined: CEUPE (Coleção Entomológica da Universidade de Pernambuco, Instituto de Ciências Biológicas, Universidade de Pernambuco, Recife, Brazil (Dra. Rita de Cássia de Moura); CEMT – Setor de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil (Dr. Fernando Zagury Vaz-de-Mello); CEMABC – Coleção Científica Entomológica Dr. Mário Bezerra de Carvalho, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil (Dra. Luci Duarte da Rosa Borges Regis); CERPE - Coleção Entomológica da Universidade Federal Rural de Pernambuco Recife, Brazil (Dr. Paschoal Coelho Grossi); DZUP – Coleção Entomológica Pe. Jesus Santiago Moure, Curitiba, Paraná; Brazil (Dra. Lúcia Massutti Almeida); EPGC – Coleção privada de Everardo e Paschoal Grossi, Nova Friburgo, Rio de Janeiro, Brazil (Everardo Grossi); MNHN – Muséum national d'Histoire naturelle, Paris, França (Dr.Antoine Mantilleri); MNRJ – Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Dra. Marcela Monné); MPEG – Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (Dr. Orlando Tobias Silveira); MLUH – Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle, Germany (Dr. Hendrik Muller); MFNB– Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany (Dr. Johannes Frisch); MZUSP – Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Dra. Sônia Cassari); INPA–Instituto Nacional de Pesquisas da Amazônia, Coleção Sistemática da Entomologia, Manaus, Brasil (Dr. Márcio de Oliveira); IAVH- Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogota, Colombia (Dr. Jhon Neita Moreno).

Morphological study: The specimens examined were adult males and females threaded and stored dry. Mouthparts and male genitalia were studied for all species. For dissection, the material was placed in mineral warm water (between 80°C and 90°C) for five minutes to soften the structures. The specimens were then dissected using a scalpel and a pin attached to a stick. For the mouthparts, the basal part of the mentum was cut and then pulled upwards, then the mandibles were removed using a pin by forcing backwards, the maxillae were released after this process and the labrum was carefully removed with the tip of the scalpel. For the male genitalia, the elytra were opened by the fingers and the membrane above the sternum was opened with the scalpel. Then they were glued to on cardboard following Ohaus (1934), they were taken to a lab oven (40ºC) for five to eight days and pinned below the specimen.

Identification and terminology: The identification of the material analyzed was based on the original descriptions and the terminology used according to Endrodi (1985), Ratcliffe (2003), Snodgrass (1993), Lawrence et al. (2011) for morphology in general, for oral apparatus Nel & Scholtz (1990) and Hotman & Scholtz (1990) for the genitalia.

Photographs and distribution maps: The images of the specimens were taken with a Zeiss Stemi 508 Doc stereomicroscope coupled with a Nikon D7500 digital camera. Afterwards these images were stacked using Helicon Focus version 5.3, resulting a single combined focus image. The images were edited in Adobe Photoshop CC 2018 version, with lighting and contrast corrections following the guide by Bevilaqua (2020). The distribution map was made with the QGis 3.20.0 RC software.

Cladistic analysis with morphological data: The in-group was composed by four terminals, all species belonging to the genus *Enema*. The outgroup was composed of seven

terminals, one species from the Rutelinae subfamily: *Chrysina macropus* (Francillon, 1795), and the remaining from the Dynastinae subfamily *Megasoma (Megasoma) hyperion*, Prandi et al., 2020 (Dynastini) and all other representatives of the Oryctini tribe, they are: *Megaceras morpheus* Burmeister, 1847, *Coelosis biloba* (Linnaeus, 1767), *Podischnus agenor* (Olivier, 1789), *Xyloryctes jamaicensis* (Drury, 1773), and *Heterogomphus telamon* (Burmeister, 1847). Some of them were selected according to the phylogeny of Bittar and Morón (2014),. The characters were derived from the adult morphology of males and females and for terminalia only the male morphology was inserted. Character construction was performed according to Sereno (2007) in the WINCLADA program, version 1.00.08 (Nixon, 2002). For non-applied characters, '-' was used, for non-observed characters, '?' was used. Subsequently, the matrix was saved in the 'ss' format to be exported to the TNT program, version 1.5, where the analyzes were performed (Goloboff et al. 2008b). The rooting of the analyzes was performed in the terminal *Chrysina macrocopus*, as it is the most distant from the group of interest. To find the most parsimonious trees, all the analyzes carried out followed the parameters: Analyze > "traditional search"; "max. tree" = 99,999; "random seed" = 1; "number of additional sequences" = 1,000; "tree to save per replication" = 1000, for "tree bisection reconnection" (TBR) as branch permutation algorithm. For the stability of the branches, the Bremer Support (Bremer 1994) was used, and for the analysis of equal weighting, the absolute support was selected, and for the implicit weighting, the relative support was used.

In comparing the retrieved trees, the consistency (CI) and retention (RI) indices were retrieved, and a strict consensus tree was constructed. The analyzes were performed with equal weights and with implicit weighing using the concavity constant k= 3,000 (Goloboff et al. 2008a). For the analysis with implicit weights, weights are assigned to the characters against homoplasy (Goloboff 1993). The appropriate value of the constant k for the dataset used in this study was

calculated using the TNT script "setk.run" developed by Salvador Arias (Golobof et al. 2008a). The script calculated a value of *k*= 3.000 for the data set used here. For the figures, the representation of black circles was used for synapomorphies and white circles for homoplasies.

Results and discussion

Enema Hope, 1837

Type-species: *Scarabaeus pan* Fabricius, 1775 (original designation).

Enema Hope 1837: 83 (*nomen protectum*); Burmeister, 1847: 233 (Redescription); Lacordaire, 1856: 439; Endrodi, 1976: 60 (Monograph); Sternberg, 1908: 27 (Redescription); Ratcliffe, 2002: 33 (Catalogue); Ratcliffe, 2003: 295 (Catalogue); Ratcliffe, 2006: 246 (Catalogue); Ratcliffe, 2013: 366 (Catalogue); Ratcliffe, 2020: 27 (Catalogue); Gasca-Alvarez et al., 2008: 11 (Catalogue); Gasca-Álvarez & Ratcliffe, 2011: 25 (Checklist);

Hoplites Dejean 1833: 150 (*nomen oblitum*) (citation in catalogue); Dejean 1837: 167 (*nomen oblitum*) (citation in catalogue); Scudder 1882: 153 (citation in catalogue); Prell, 1936: 149 (Note); Bousquet & Bouchard, 2013: 36;

Diagnosis: Body flattened dorsoventrally, mandibles bidentate, directed upwards in dorsal view, frontoclypeal suture suture at the base of eyes, ocular canthus subtriagular, horn occupying most of the head, present in both sexes with variable sizes, usually with elongated projections in the pronotum, elytral epipleura directed upwards, propigydium with stridulatory apparatus.

Enema and morphologically similar genera: Females of the genus *Dichodontus* Burmeister, 1847 also have horns. However, the species of this genus do not have a Neotropical distribution.

Redescription: Size: 45 length x 25 width mm; Color: Black, brown or reddish brown; *Head:* horn present in both sexes, which may or may not exceed the anterior region of the pronotum; *Clypeus:* emarginate, bifurcated, two teeth, parallel or oblique slightly curved upwards (Figure 8A), surface covered by wrinkles or pits; *Ocular canthus:* subtriangular, covered by deep punctures or rugopunctures that may or may not be spaced apart, setae at the apex present or absent; *Labrum:* with bristle brush, punctuated in longitudinal rows, parallel or not; central region always glabrous, sides with bristles or occasionally glabrous (Figure 3GH); *Mandibles:* bidentate, punctuations and bristle brush on the ventral part (Figure 3A); *Maxillae:* galea with two to four teeth, if the fourth tooth is present very small, with variation in its position, surface of the lacinia with rugose area and punctuations (Figure 3DE); *Labium:* fused to the mentum, subtriangular, wider or narrower at the base, or rounded, surface with rugopunctures or punctuations, apex curved or straight, central part from concave to straight, glabrous or punctuated; *Antenne*: with ten articles, first antennomere with arrowed punctuations;

Pronotum: posterior part often elevated, ranging from two short gibbons or bifurcated extensions of the same height as the horns of the head, anterior part generally concave and glabrous, most of the surface covered by rugopunctures, in females the median region excavated, which can be slightly or deep, covered by punctures on its surface and on the sides covered by rugopunctures, the posterior part with two rough gibbons (Figure 1,7,13 and 22);

Elytra: enlarged, moderately convex, with elytral sutures present, laterals bending upwards, with deep or moderate punctures (Figure 7); *Stridulatory aparatus:* present in propygid; *Scutellum:* visible, with punctures that may be juxtaposed or spaced out;

Ventral region of thorax: Hypomere: punctuated with bristles with setae or not, never glabrous (Figure 4A, 10A, 16A); *Prosternum:* Anteriorly sulcated, median region glabrous or with setae and the excavated base that can be smooth to rugose (Figure 2E, 8E, 14E); *Prosternal process:* short, not extending beyond the middle of the prototrochanter (Figure 2E, 14E); *Mesosternum:* rugose or punctuated over the entire surface (Figure 2F, 8F, 14F); *Metaventrite:* rugose, punctuated and with setae at the base or over the entire surface; *Mesoepisternum:* rugose, punctuated or ocellated over the entire surface; *Mesoventrite:* elongated with ocellated punctuations; *Metaepisternum*: subtriangular with punctuations or rugopunctures with or without setae; *Epipleura:* partially visible in lateral view, with arrowed punctuations, margin usually strongly marked, sulcated or not (Figure 4B, 10B, 16B);

Legs: coxae with rugopunctate or ocellated punctures, anterior tibiae with four teeth, five tarsomeres, the first with a unilateral extension and the last twice as long as the last three separated, surface with punctures; *Procoxae:* anterior region usually with ocellate punctures; *Profemur:* In ventral view, three rows of parallel bristles between the bristles, the surface is glabrous. Trochanter divided by a sulcus with a row of bristles parallel to the carina. *Protibia:* with four tibial teeth, the first two being closer together than the others, and the last often small; *Protarsi:* Five tarsomeres, the first four semi-equal, the last twice as long as the others, two tarsal claws facing inwards; *Mesotibia*: with two lateral truncations with bristles, dorsal view: presence of two truncated transverse carinae with bristles, surface rugopunctate. Apex of tibia expanded to form a spine. Presence of two tibial spine, the one on the end longer than the one on the inside.

Abdomen: Ventrites: five visible segments, usually the first with a sulcus in the median region, often with a row of bristles at the base of each segment, surface with subtle or deep punctations (Figure 4CD, 10CD, 16CD); *Propygidium:* with rugose region for stridulation; with the presence of bristles or not; *Pygidium:* convex, with punctures or rugopunctations with or without bristles; *Edeago:* symmetrical parameters, with variation in width and fit of the base (Figure 5 AB, 11AB, 17AB).

Female: Pronotum with depresion, horn smaller, body ventrally flatter (Figure 6A, 12A, 18A);

Geographical Distribution: Central America and South America.

***Enema endymion* Chevrolat, 1843**

Enema endymion Chevrolat 1843: 29 (Original description); Reiche 1859:17 (Nota); Burmeister 1847:236 (Desciption); Bates 1888:329 (Redesciption); Heyne-Taschenberg 1907:96 (Note); Sternberg 1908: 24 (Original description); Endrödi 1975: 63 (Monography); Ratcliffe, 2002: 33 (Catalogue); Ratcliffe, 2003: 296; Gasca, 2005:312 (Checklist); Ratcliffe, 2006: 247 (Catalogue); Ratcliffe, 2013:367 (Catalogue); Ratcliffe, 2020: 28 (Catalogue);

Diagnosis: Smaller in size compared to the other species of the genus, reddish brown, frontal surface of the horn rugose, lateral of the pronotum with four angles, the two in the apex ones being more rounded and smaller than those at the base which are more angular and open. Epipleuron marginate, wider at the apex and sulcated from the mesosternal region to the base, narrowed at the height of the metacoxa, from the median region to the base, completely visible in lateral view. Elytra without elytral striae. Hypomere concave at posterior region, base with triangular extension formed by a sulcus a carenate region.

Redescription: *Male:* Size: 36.8mm/34.93mm x 19.15mm/19.02mm; Coloration: Reddish-brown, elytra lighter than the pronotum (Figure 1A). *Head:* horn often the same size as the width of the head, acuminate, facing backwards with excavations from the base to the region close to the apex, more subtle on the sides and at the apex (Figure 2C); Frontal surface of the horn rugopunctate, sides with ocellated punctuations, base of the horns laterally almost smooth, with only fine punctuations (Figure 2B); Frons: rungopunctured surface; *Vertex:* with juxtaposed ocellate punctuation that begins and ends at the apex of the eyes, with a band of dense bristles in the median region; *Clypeus:* subtrapezoidal (Figure 2A), sides strongly contracted before the apex forming a concavity with ocellate punctuations in lateral view (Figure 2B), apex widely emarginated (Figure 2C); Dorsal surface of clypeus scored. *Ocular canthus:* subtriangular, transverse, densely punctuated (Figure 2C); Frontoclypeal suture emarginate above the corner of the eye, sulcated below the horn; *Labrum:* Dorsally transverse with a dense brush of bristles, transversely arranged emerging from ocellate points at apex. Ventral anterior surface with long bristles emerging from ocellated punctures (Figure 3 GH); *Mandibles:* bidentate, apical tooth wider. *Dorsal:* Flat bristles forming a continuous brush, surface covered by ocellated punctures; Concave internal lobe; *Ventral:* diagonal band of defined punctuations that meet the mesal bristles (Figure 3ABC); *Maxillae:* Galea with teeth varying in number, with none, one very long apical or three teeth in ventral view (one elongated apical, one subapical). Ventral surface densely covered with bristles. Maxillary palps II and IV clearly longer than the others, sensory area of palpomere IV oval, elongated, confined to (restricted) basal half (Figure 3DE). *Mentum: Ventral:* Subtriangular, surrounded by bristles, sides densely covered with deep punctures, disc region with a convexity in apical half, apex rounded slightly backwards; *Labium*: fused to the mentum with Palpomere II shorter than the others and covered by bristles (Figure 3F). *Antennae:* scape forming a sphere in the basal region, being more elongated in the apex, with elongated bristles in the lateral

part. Pedicel narrow at the base and more rounded at the apex. Three flat semi-uniform articles and two laminated articles projecting three lamellae.

Pronotum: Apex of the pronotum with four angles, the central two more rounded and smaller than those at the extremity which are more angulated. The external angulated region is narrower than the base of the posterior angles of the pronotum; External angle of the pronotum does not exceed the basal half of the eyes (Figure 1A); Pronotum margin line is formed by a very expressive marking, flattened and darker than the rest of the pronotum, the lateral margin from the apex to the base is continuous (Figure 1C). Higher part of the pronotum without area rugose, just weakly punctuated (Figure 2A). Laterals of the pronotum punctuated throughout the entire lateral extension, except on the sides adjacent to the edge (Figure 2D). Rugopunctate anterobasal region (Figure 1C). The posterior part of the pronotum next to the scutellum is curved (Figure 1A). Back part forming an angle on each side with the side and base.

Elytra: reddish, elytral suture present and excavated, wavy (Figure 1A), surface glabrous, laterally with alternately excavated ocellate punctuations (Figure 1C); Angle of the anterior region deep below the humeral carina; two oblique sulcus adjacent to the scutellum, lateral margin marginated and directed upwards; Humeral knobs with a sequence of rugose area to the edge of the elytra; *Stridulatory apparatus*: triangular, forming a callus with interrupted parallel microstructures;

Scutellum: glabrous margin, rough, punctured surface (Figure 1A);

Ventral of the thorax: Hypomere: presence of defined ocellate punctures spaced apart, anterior region with longitudinal sulcus (Figure A); *Prosternum:* margin marked with bristles, furrow parallel below margin; The side of the prosternum next to the hypomere forming a fovea,

followed by two more foveas in the anterior part of the sulcus parallel to the margin, median region with defined ocellate punctures. Higher basal region covered by carinated lines (Figure 2E); *Prosternal process:* triangular, laminar, small rounded at the ocellated apex with the presence of bristles (Figure 2E). *Mesosternum:* With ocellated punctuations, posterior part marginated and darker at the base with weakly punctuations (Figure 1B); *Mesoepisternum:* anterior region with defined ocellated punctures, smooth surface; *Mesoventrite:* surface covered by rounded punctures. *Metaventrite:* black metasternal line, differing from the dominant color. Bristles present in the anterior and posterior part, median surface covered by punctuations, spaced and unequal ocellated punctures on the sides (Figure 2F); *Metaepisternum:* Elongated and narrow forming an angle at the base, with setigerous ocelli. *Metaepimeron:* triangular covered by rugopunctation, basal region rounded forming a tubercle; *Epipleura:* Marginate, wider and concave at the apex, and sulcated towards at the base, narrowed at the height of the metacoxa, median region at the base completely visible in lateral view (Figure 4B);

Legs: Procoxae: transverse carina at the apex dividing the coxae. Apex rugose with bristles, middle region glabrous; *Profemur:* In ventral view, three inner bristles, one in the middle and two at the external. Trochanter divided by a sulcus with an opening of bristles parallel to the carina. *Protibiae:* in ventral view, longitudinal carina with perforations, region of the teeth frequently roughened with bristles on the margin, opposite region glabrous; *Dorsal view*: four unequal teeth, the two closest at the apex, the last small than others. Row of setigerous ocellate punctures in the median region, region of the teeth rugopunctate, presence of curved and acuminate tibial spine; *Protarsi:* tibial spin reaching second tarsomere, five tarsomeres, first four semi-equal, last twice as long as others. Equal tarsal claws with punctures at the base. Presence of shortened and set tibial spine; *Mesocoxae:* apex covered by ocellate punctuations, generally setae, base with punctuations

with bristles; *Mesotibia:* dorsal view: presence of two truncated transverse carina with bristles, surface rugose; apex of tibia expanded; Presence of two tibials spines, the one on the end longer than the one on the inside; tibial spine more elongated, not surpassing the second tarsomere. Row of bristles opposite the transverse carina. *Mesotarsus:* Five tarsomeres, all truncated and setae, the first with an external extension and the next three of the same size, and the last twice the size of the previous ones. Presence of semi-parallel claws, ventrally furrowed and with a round, arrowed tibial spine. *Metatibia:* longer than the mesotibiae, but with the same pattern of bristles and punctuations. Tarsi and claws same as mesotarsus.

Abdomen: Ventrite I truncated and marginated, in dorsal view with concavity for the metacoxae, triangular apex covered by bristles, ventrite II with a parallel sulcus in the median region, ventrite III the same size as ventrite II, ventrite IV and V larger than the previous ones, ventrites with the same punctuation pattern: laterals rugopunctate and with bristles and median region with subtle punctuations, connective membrane wider medially and narrower at the ends, ventrite VI with subtle punctuations with a row of bristles at the base (Figure 4C); *Propygidium:* stridulatory apparatus present, triangular with microsculptures in the median region, lateral surface rugopunctate; *Pygidium:* concave, apex rugopunctate, median region with spaced punctuations; *Aedeagus:* symmetrical parameters wider at the apex than at the base, curvature in the median region of the phallobase with a rounded elevation, in lateral view with a teeth (Figure 5 AB); Spiculum gastrale: Y-shaped, base of lateral branches with undulation, main branch longitudinally sulcated, with the same size from base to apex (Figure 5C);

Female: Similar to males, as follows; Pronotum much rougher than in males, with presence of wrinkles on the sides and in the median frontal region more concave than in males; elytra darker and brighter (Figure 6A); Last abdominal ventrite wider than in males, with excavated punctions;

Ventrite VI rounded with transverse line of punctures with serdas, overlapping gonocoxites with bristles at the apex (Figure 6 DC).

Variation: pronotum darker than elytra and opaque; Elytra with punctation marked on the sides; elytra may be more shortened and flattened; Shortened horn.

Geographic distribution: **Mexico**: Campeche, Chiapas, Hidalgo, Oaxaca, Tuxla, Puebla, Quintana Roo, San Luis Potosi, Tabasco, Tamaulipas, Veracruz; **Guatemala:** Alta Verapaz, Baja Verapaz, Escuintlas, Huehuetenango, Jutiapa, Petén, Quetzaltenango, San Marcos, Santa Rosa, Zacapa; Quiché; **Belize:** Cayo, Stann Creek, Toledo; **Costa Rica:** Alajuela, Cartago, Guanacaste, Heredia, Puntarenas, São José; **Panama:** Chiquiri, Herrera; **El salvador:** Ahuachapán, Cuscatlán, La libertad, San Salvador, Santa Ana, Sonsonate; **Honduras:** Atlántida, Choluteca, Comayagua, Copán, Cortés, El paraíso, Francisco Morazán, Olancho, Santa Bárbara; **Nicaragua:** Carazo, Chinadega, Chontales, Estelí, Jinotega, Léon, Managua, Raa Norte; **Guyana; Venezuela:** Cuyagua; **Colombia; Peru; Paraguay**; **Brazil:** Roraima, Pará.

Type material:

Lectotypes (hereby designated): *Enema endymion* Chevrolat, 1843; (1 ♂) MNHN. EC 4410 – MNHN: ’Syntipe’ (red label), ‘Enema endymion Chev._Mexique; Scarab.Titan St. Enema Lupercus Chevr. Ex- Musae A. Sallé 1897;

Additional material examined

27 specimens 12 ♂ 17 ♀); Muséum Paris 1952 coll. R. Oberthur; ‘Syntype (red label)’; EC 4411 – MNHN, ‘Ex- Musae A. Sallé 1897; Muséum Paris 1952 coll. R. Oberthur, Syntype (red label)’; ♀ EC 4412 – MNHN ‘Ex- Musae A. Sallé 1897; Muséum Paris 1952 coll. R. Oberthur,

Syntype (red label)'. *Enema paniscus* Burmeister, 1847; 'Lectotypus Enema paniscus Burm. Zool. Inst. Halle; México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♀ [dissected] E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♂ [dissected] E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♂ [dissected] E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♀ [dissected] E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♂ [dissected] E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♂ [dissected] E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♀ E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♀ E&P.Grossi); México: Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♀ E&P.Grossi); Chiapas: Ocozocuautla, 01-18.vi.1897, 800m, B.C.Ratcliffe (1♀ E&P.Grossi); México: Chiapas: Ocozocuautla, 23.v.1982, 800m, luz flúor, R.Novelo (1♀ E&P.Grossi); México: Chiapas: Ocozocuautla, 23.v.1982, 800m, luz flúor, R.Novelo (1♀ E&P.Grossi); México: Chiapas: Ocozocuautla, 23.v.1982, 800m, luz flúor, R.Novelo (1♀ E&P.Grossi); México: Oaxaca, (1♀ DZUP); México: Tuxla: Guitessa, vi.2004, F.Nicolalde, (1♂ CERPE); México: Chipas: Ocosingo, 9.vi.2010, L.Cervantes & D.Brzoska, km20 desv a San Quintin (1♂ CEMT); Guatemala: Guiché: Env. D' llom, 03. vi. 2008, 100m, J. Touroult (1♀ [dissected] CERPE); Venezuela: Cuyagua, 22. vii. 2005, D. G. Fagre (1♀ [dissecado] CERPE); (1♀ [no data] CERPE); Colômbia: Magdalena, San Pedro, Hierbabuena, 10.895134ºN, 999611ºW, 2104msnm, 08-May-2016, captura manual, BHM, I. Mendoza- Pérez (1 ♂ IAVH); Colômbia, 11. 019 (2 ♀ MZUSP); Colômbia, 11. 019 (1♂ MZUSP); Brasil: Roraima, Caracaraí, PN Viruá, 1º29'23. 3"N, 61º00'08. 7W19. iv. 2015, J. A. Rafaael, R. A. Heleodoro, D. M. M. Mendes, D. W. A. Marques & C. Maldaner, Arm. Luz (1♀ CERPE); Brasil: Pará, Benevides, 9. xii. 1989, Hélio (1♀ MPEG);

Comments: In its original description, Chevrolat did not designate a holotype, the possible *Enema endymion* type material was deposited at the MNHN (Figure 19). After examining it through photographs previously available on the MNHN website, and comparing it with the examined material, we see that *Enema endymion* is the species that occurs in Central America, and northern South America. In the present work. It is we examined a specimen from Roraima (Brazil). Based on the non-type specimens from MPEG, we confirm that *E.endymion* also occurs in the Amazon Forest, as stated previously by Gasca-Alvarez et al. (2008).

Enema endymion primary type bears a label written "Enema lupercus Chevr." and "Scarab. Titan St". The latter is a current synonym of *Enema pan*, which can confirm that this label is just an identification that is now found to be mistaken. The type of *Enema paniscus* Burmeister, 1847 deposited at MLUH (Figure 20) was examined and confirmed that it is a specimen of *Enema endymion* Chevrolat, 1843. The type of the synonym *Enema lupercus* Burmeister, 1847 was not located, as reported by Endrodi (1976). We searched for this specimen at the MLUH, we only found the type specimens of *E. paniscus* as mentioned above, as well as *Enema infundibulum* Burmeister, 1847 a current synonym of *E. pan,* also confirmed by photographs. This species differs from the other synonyms and from the new species in the color, as they are redder than the others, are smaller and less robust, and have a sulcus in the epipleura. Therefore, the lectotype is designated here in from MNHN original series of syntypes.

***Enema gibbicollis* Sternberg, 1908** rev. stat.

Enema endymion Chevrolat 1843: 29 (Original description); Reich 1859:17 (Nota); Burmeister 1847:236 (Desciption); Bates 1888:329 (Redesciption); Heyne-Taschenberg 1907:96

(Note); Sternberg 1908: 24 (Original description); Endrödi 1975: 63 (Monography); Ratcliffe, 2002: 33 (Catalogue); Ratcliffe, 2003: 296; Gasca, 2005:312 (Checklist); Ratcliffe, 2006: 247 (Catalogue); Ratcliffe, 2013:367 (Catalogue); Ratcliffe, 2020: 28 (Catalogue).

Diagnosis: Predominantly black, more robust than the other species; Dorsal surface of horn with ocellate punctuations; Lateral of the pronotum with four angles, the two central ones being more angular than those at the extremity which are more rounded, two tubercles very apparent at the apex of the pronotum. Epipleura without median sulcus, and without margin; Elytra with elytral striae; Two sulcus excavated at the apex of the pronotum perpendicular to the scutellum; The ventral surface of the body is covered with tiny ppunctuations;

Redescription: Male: Size: 46.8mm/44.58mm x 25.1mm/24.85mm; *Coloration:* predominantly black. *Head:* with horn often the same size as the width of the head (Figure 8A), broadly at the base, surface with adjacent ocellate punctures, interspersed with weakly punctures, rounded at apex; *Clypeus:* subtrapezoidal, sides strongly contracted before the apex forming an extensive concavity over the entire surface, with rounded ponctures often adjacent (Figure 8C); *Ocular canthus:* subtriangular, transverse, densely punctuated (Figure 8C); Frontoclypeal suture sulcated above the ocular canthus and below the horn; *Vertex:* surface punctuated with bristle brush at apex; *Frons:* Punctuated surface, diminished and juxtaposed punctuations;

Labrum: Dorsal: transverse with definite punctations visible below bristle brush, transversely arranged from ocellate punctures at apex. Ventral anterior surface with long bristles emerging from ocellated punctures (Figure 9 GH);

Mandibles: bidentate, apical tooth wider. Dorsal: Mesal bristles forming a continuous brush, Surface covered by eyespots; concave inner lobe; *Ventral:* diagonal stripe of arrowed punctuations that next to the mesal bristles (Figure 9ABC); *Maxillae:* four teeth on the galea, the extremity being twice as large as the other two which are equal in size and shape, and the last very shortened; Maxillary palp with cylindrical sensory area, not exceeding the median region (Figure DE); *Mentum:* subtriangular, margin covered by excavated punctures with long setae passing from the median region, median region with ocellate punctures smaller than the medians, apex facing backwards (Figure 9F); *Labium:* fused to the mentum, sulcated dorsolaterally, glabrous in the median region with punctuated and arrowed sides; *Antennae:* scape forming a sphere in the basal region, being more elongated in the apex, with elongated bristles in the lateral part. Pedicel narrow at the base and more rounded at the apex. Three flat semi-uniform articles and two laminated articles projecting three lamellae;

Pronotum: The entire surface is micro punctuated (Figure 8D), the apex of the pronotum with four angles, the central two rounded and smaller than those at the base, which are more angulated at the apex (Figure 7A). The external angulated region is narrower than the base of the posterior angles of the pronotum; External angle of the pronotum exceeds the basal half of the eyes; The entire edge of the pronotum is formed by a very expressive marking, flattened and slightly sulcated, the lateral margin has an angle before reaching the base (Figure 7C). Central part of the pronotum with ocellate punctuations interspersed with tiny punctuations in the highest part, with pronotal striae extending from the median base to the apex; Sides of the pronotum slightly sulcated (Figure 7C); The posterior part of the pronotum next to the scutellum is curved (Figure 7A).

Elytra: black, elytral suture present (Figure 7A), laterally with ocellate punctures sequentially in rows (Figure 7C), anterior region angle excaveted below the humeral carina, weakly marked; two oblique sulcus adjacent to the scutellum, lateral margin marginated and facing upwards, slightly furrowed; Basal region rugopunctate just after the apical knob (Figure 7A); Stridultory apparatus: forming a callus with interrupted parallel microstructures;

Scutellum: margin glabrous, surface rugose;

Ventral to thorax: Hypomere: surface covered by ocellate punctuations separated by one time their diameter, interspersed by punctuations throughout the surface (Figure 10A); *Prosternum:* margin marked with bristles, sulcus parallel below the margin; The lateral prosternum next to the hypomere forming a fovea, followed by two more foveas in the anterior part of the sulcus parallel to the margin, median region with setigerous ocellate puntures. Base rugopunctate that follow the margin (Figure 8E). *Prosternal process:* Triangular, laminar, small rounded at the apex with the presence of bristles. *Mesosternum:* surface covered by perforated punctures, in the anterior region very marked, generally with bristles, and in the posterior region with perforated ocelli, smaller than the anterior ones (Figure 7B); *Metaventrite:* surface punctate, in the anterior region very marked, usually with bristles, and in the posterior region with tiny punctures (Figure 8F); *Mesoepisternum:* margin marked carinated, surface with ocellate punctures. *Mesoventrite:* elongated with excavated ocellate punctures, anterobasal region with a depression; *Metaepisternum:* elongated with ocelli arrowed over the entire surface; *Metaepimer:* surface rugose; *Epipleura:* wider and rounded at the apex, short parallel row of setae, carina on the inside, laterally visible, median region to the base completely visible in lateral view;

Legs: Procoxae: surface ocellated; *Profemur:* region of the femoral trochanter covered at the base by ocellate punctuations, three parallel rows of bristles, surface covered by punctuations; *Protibia:* ventral view with three rows of bristles, the median being composed of setae rugopunctate; *Protarsus:* five tarsomeres, the first being almost the same size as the other three, semi-unequal tarsal claws, with a spine rounded and arrowed at the apex; *Mesocoxa:* surface rugopunctate; *Mesofemur:* Surface slightly punctuated, three parallel rows of bristles, the middle one with bristles emerging from a carina, and the others with ocleate punctuations; *Mesotibia:* surface covered by ocellated punctuations, with extension at the apex of the tibia, presence of two tibial spines; *Mesotarsi:* five tasomeres, the first with a unilateral extension, and the last of the same size as the other three. With semi-uniform tarsal claws and a rounded, setated tibial spine; *Metacoxa:* surface covered by ocellated and setae punctuations; *Metafemur:* With four rows of bristles, surface covered by punctures varying with ocellate punctures *Metatibia:* same as the mesotibiae; *Metatarsals:* same as mesotarsals;

Abdomen: ventrite*s:* ventrite I truncated and marginated, in dorsal view with concavity for metacoxae, apex triangular with arrowed punctuations restricted to margin, laterals marginalized, ventrite II with a parallel sulcus in the median region, ventrite III the same size as ventrite II , ventrite IV and V larger in width than the anterior ones, ventrites with the same punctuation pattern; laterals with juxtaposed and ocellated punctuations and median region with ocellate punctuations on the upper margin and at the base with ocellate punctuations alternating with subtle punctuations medially, connective membrane wider medially and narrower at the ends, ventriteVI with subtle punctation with a row punctate at the base and surface covered by ocellate punctures (Figure 10A); *Propygidium:* stridulatory apparatus present, triangular with microsculptures in the median region, lateral surface rugopunctate, setted; *Pygidium:* concave, apex and sides

rugopunctate, median region with ocellate punctuations; *Aedeagus:* apex of the parameters smaller in size than the base, tooth close to the base in lateral view, with a fovea above the tooth in the paramere, lateral apex of the phallobase forming a slightly rounded angle (Figure 11AB); *Spiculum gastrale:* Lateral branches straight at the base, main branch wider at the apex and flattened from the median region to the apex (Figure 11C).

Female: Similar to males, more robust and rounded body, differing in the following aspects; The pronotum is much rougher than in males, and with the presence of rugose surface on the sides and in the median frontal region, it is more concave than in males; darker and brighter elytra; Last ventrite wider than in males, with strong and setae punctuations; Hypogyid rounded with a transverse line of pits with setae (Figure 12AB). Parallel gonocoxites, with bristles at the apex (Figure 12C); *Variation:* The pronotum may be narrower on the sides and with a greater elevation in the region of the gibbons; The horn can vary in size, being longer and acuminate.

Geographical Distribution: Suriname, Brazil: Amazonas, Pará, Roraima.

Type material:

Lectotype (hereby designated): ‘Enema gibbicollis Sternberg ♂ - type (red)- Suriname x coll. Fruhstorfer (white)’;

Additional material examined

9 exemplare (6♂3♀); Brasil: Amazonas, Manaus, 02°35'21"S, 60°06'55"W, 16-19. vii.2004, J.A.Rafael, C.S.Motta, F.F.Xavier F°, J.M.F. Ribeiro & S. Trovisco, lencol: luz mista e BLB 40mts altura, ZF2 Km-14, Torre, (1♂ [dissecado] E&P.Grossi); Brasil: Amazonas, Manaus, 02°35'21"S, 60°06'55"W, 16-19. vii.2004, J.A.Rafael, C.S.Motta, F.F.Xavier F°, J.M.F. Ribeiro & S. Trovisco,

lencol: luz mista e BLB 40mts altura, ZF2 Km-14, Torre, (1♂ [dissecado] E&P.Grossi); Brasil: Amazonas, Manaus, 02°35'21"S, 60°06'55"W, 16-19. vii.2004, J.A.Rafael, C.S.Motta, F.F.Xavier F°, J.M.F. Ribeiro & S. Trovisco, lencol: luz mista e BLB 40mts altura, ZF2 Km-14, Torre, (1♀ [dissecado] E&P.Grossi); Brasil: Amazonas, Manaus, 02°35'21"S, 60°06'55"W, 16-19. vii.2004, J.A.Rafael, C.S.Motta, F.F.Xavier F°, J.M.F. Ribeiro & S. Trovisco, lencol: luz mista e BLB 40mts altura, ZF2 Km-14, Torre, (1♀ E&P.Grossi); Brasil: Amazonas, Manaus, 02°35'21"S, 60°06'55"W, 16-19. vii.2004, J.A.Rafael, C.S.Motta, F.F.Xavier F°, J.M.F. Ribeiro & S. Trovisco, lencol: luz mista e BLB 40mts altura, ZF2 Km-14, Torre, (1♀ E&P.Grossi); Brasil: Amazonas, Manaus, 02°35'21"S, 60°06'55"W, 13-16.ix.2004, F.F.Xavier F°, A.R.Ururahy, F.Godoi, & S.Troviso, lencol: lencol: luz mista e BLB 30 mts altura, ZF2 Km-14, Torre, (1♂ [dissecado] E&P.Grossi); Brasil: Carlos boi, Rio Negro de Juarete, ii.1935 (1♂ MNRJ [dissecado]); Brasil: Carlos boi, Rio Negro de Juarete, ii.1935 (1♂ MNRJ [dissecado]); Brasil: Roraima, Tepequém, SESC, 3º44'45"N, 61º43'40"W, 29. iii. 2016, D. Takya, F. F. Xavier, A. Santos, Arm. Luz (1♂ CERPE);

Comments: Enema gibbicollis was described based on two male specimens from Surinam, and deposited in the ZMHB (Figure 21), but was not designated holotype by the author. The images provided of a specimen with dissected aedeagus is one of the syntypes due to the labels, and the second specimen had only a label giving the locality: Surinam. Not checking if it is the other type of the described species. Therefore, the lectotype is designated here in from MNHN original series of syntypes.

***Enema* sp. 1, Mota, Grossi & Vaz-de-Mello, 2023 sp. nov.**

Diagnosis: Black in color, less robust than the other species; Head with horn cut at the apex which may vary, surface ocellated, separated by a distance one to three times the size of the ocellus; Pronotum flattened rugopunctate covering the entire lateral side; Apex of the epipleura the same size as the width of the median region, without sulcus; Hypomere: extremely concave anterior region, with subtriangular basal extension with a carina that forms the lateral one;

Description: *Male*: *Size:* 37.00mm / 38.67mm x 15.72mm / 13.80mm; Coloring: Black

Head: With triangular horn occupying most of the head, which may vary from acuminate to well-rounded and short; *Clypeus:* partially straight, with ocellate punctuations (Figure 14C) , frontoclypeal suture slightly marginated (Figure 14A); *Frons:* surface covered by ocelli; *Vertex:* region with ocellated punctuations and bristle brush in the apical median region; *Ocular canthus:* surface with deep punctures, usually with tiny setae (Figure 14BC); *Labrum:* ventrally with the apical half with rows of punctates with setae, base without punctates and with a longitudinal sulcus (Figure 15F); *Mandibles:* bidentate, apical tooth broadly. *Dorsal:* Mesal bristles forming a continuous brush, surface covered by ocellate punctures; concave inner lobe; *Ventral:* diagonal stripe with punctuations next to mesal bristles (Figure ABC); *Maxillae:* two pointed teeth and two tiny tubercles on the galea or with three teeth, one apical and the other parallel, maxillary palp with an oval sensory area close to the base (Figure DE); *Mentum:* Ventral: Subtriangular, surrounded by bristles, sides densely covered by deep punctures, disc region with a convexity in apical half, apex rounded slightly backwards (Figure 15F); *Labium:* fused to the mentum, furrowed dorsolaterally, glabrous in the median region with punctuated and arrowed sides;

Antennae: scape forming a sphere in the basal region, being more elongated in the apex, with elongated bristles in the lateral part. Pedicel narrow at the base and more rounded at the apex. Three flat semi-uniform articles and two laminated articles projecting three lamellae;

Pronotum; Apex of the pronotum with four angles, the central two being rounded and smaller than those at the extremity which are more angulated at the apex. The external angulated region is narrower than the base of the posterior angles of the pronotum; External angle of the pronotum does not exceed the basal half of the eyes (Figure 13A); The entire edge of the pronotum is formed by a very expressive marking, flattened and darker than the rest of the pronotum, the lateral margin has an angle before reaching the base (Figure 13C). Central part of the pronotum with ocellated punctures in the upper part (Figure 14A), with pronotal striae extending medially and laterally (Figure 14F); Sides of pronotum slightly sulcated; The posterior part of the pronotum next to the scutellum is curved (Figure 13A).

Elytra: black, elytral suture present, laterally with ocellate punctures excavated sequentially in alternating rows with sulcus, surface punctures separated up to six times their diameter, angle of anterior region excavated below humeral carina, which is faintly marked; two oblique furrows adjacent to the scutellum, lateral margin marginated and directed upwards furrowed, flatter in height on the humerus, slightly sulcated; Basal region with a sequence of parallel rugose just after the apical callus (Figure 13A); Stridulatory apparatus: forming callus with interrupted parallel microstructures;

Scutellum: margin glabrous, surface rugopunctate;

Ventral the thorax: Hypomere: surface covered by arrowed eyespots separated at least at a distance of three times their diameter (Figure 16A); Prosternum: margin marked with bristles, furrow excavated parallel below the margin; The side of the prosternum meets the hypomere forming a fovea, followed by two more foveas in the anterior part of the sulcus parallel to the margin, median region with setigerous eyespots. Base with rugopunctation that follow the margin (Figure 14E); *Prosternal process:* Triangular, small rounded at the ocellated apex with the presence of bristles (Figure 14E). *Mesosternum:* surface covered by ocelli that are seta or not, partially separated at the base and very close together at the apex (Figure 13B). *Metaventrite:* presence of ocellated punctuations on the side of the apex, which can be ocelated, coalescent or reduced to half, parallel sulcus in the median region, concavity in the apex, serdas in the apex (Figure 14F). *Mesoepisternum:* marked margin separated by a sulcus at the height of the mesosternum, surface with ocellate punctuations; *Mesoventrium:* margin marked, surface ocellate punctures; *Metaepisternum*: elongated, surface with ocellate punctuations set apart by once its own diameter. *Metaepimeron:* triangular, surface rough and with bristles, basal region rounded forming a tubercle;

Epipleura: wider and rounded at the apex, short parallel row of serdas, carina on the inside, laterally visible, median region to the base completely visible in lateral view (Figure 16B);

Legs: Procoxae: Transverse carina at the apex dividing the coxae. Upper part rugopunctate with bristles, middle region glabrous and base rugose; *Profemur:* three parallel rows of ocelatte punctate extending to the trochanteric region; *Protibiae:* ventral view with row of arrowed ridges, and surface rugopunctate; *Protarsi:* five tarsomeres, the last three times the size of the last two, tarsal claws present, tibial spine goes beyond the second tarsomere; apex covered by ocellate punctuations, usually setated, smooth median region, base with bristle punctuations; *Mesofemur:*

three parallel rows of bristles, two at the apex and the other in the middle; *Mesotibia:* dorsal view: presence of two truncated transverse carinae with bristles, surface rugose; apex of tibia expanded to form a spine. Presence of two tibial spines, the one on the end longer than the one on the inside; tibial spine more elongated, not surpassing the second tarsomere. Row of bristles opposite the transverse carinae; *Mesofemur:* In ventral view, three inner bristles, one in the middle and two at the apex, between the dense bristles and the surface of the glabrous base. Trochanter divided by a groove with an opening of bristles parallel to the carinae; *Mesotarsus:* five tasomeres, the first with a unilateral extension, and the last of the same size as the other three. With semi-parallel tarsal claws. *Metacoxa:* line of ocellated punctuations, sulcated line near the base. Metafemur: surface covered by widely spaced punctures; *Metatibia*: rugopunctate and spaced punctures;

Abdomen: ventrite I truncated and marginated at the apex, in dorsal view with concavity for the metacoxae, apex triangular with arrowed punctuations at the apex, ventriteII with a parallel sulcus in the median region, ventrite III the same size as ventrite II, ventriteIV and V larger in width than the anterior ones, ventrites with the same punctuation pattern: laterals with rugopunctate and arrowed punctuations and median region rugopunctate on the upper margin, median region with subtle punctuations and at the base with ocellate punctate punctuations, wider connective membrane medially and narrower at the base, ventrite VI rugopunctate surface with a row of punctures at the base (Figure 16C); *Propygidium:* stridulatory apparatus present, triangular with microsculptures in the median region, lateral surface rough-punctured with arrowheads; *Pigidium:* concave, apex and sides rugopunctate, median region with ocellate punctuations;

Female: Horn more rounded at the apex, pronotum rugopunctate excavated, pronotum flattened, on both sides and in the posterior median region smooth surface with punctuations (Figure 18A); Overlapping gonocoxites, setae at apex (Figure 18C);

Etymology: In honor of Josival Francisco Araújo, nicknamed Josi, who collected specimens of the type series.

Type locality: Professor João Vasconcelos Sobrinho Municipal Natural Park, Serra Dos Cavalos, Caruaru, Pernambuco, Brazil.

Geographical Distribution: Brazil: Rio Grande do Norte, Paraíba, Pernambuco, Alagoas.

Holotype: Brasil: Pernambuco, Caruaru, Serra dos Cavalos, 8º21'47.94"S 36º02'09.66"W, 07-10. iv. 2022, J. F. Araujo (1♂[dissected] CERPE).

Paratypes: 39 (20 ♂ e 19♀); Brasil: Pernambuco, Serra dos Cavalos, 8. 3633S, 36. 0360W, 07-10. iv. 2022, J. F. Araujo (3 ♂ CERPE); Brasil: Pernambuco, Serra dos Cavalos, 8º21'47.94"S 36º02'09.66"W, 07-10. iv. 2022, J. F. Araujo (2 ♂ CEUPE); Brasil: Pernambuco, Serra dos Cavalos, 8º21'47.94"S 36º02'09.66"W, 07-10. iv. 2022, J. F. Araujo (1♂ MNRJ); Brasil: Pernambuco, Serra dos Cavalos, 8º21'47.94"S 36º02'09.66"W, 07-10. iv. 2022, J. F. Araujo (1♂ MZUSP); Brasil: Pernambuco, Serra dos Cavalos, 8º21'47.94"S 36º02'09.66"W, 07-10. iv. 2022, J. F. Araujo (1♂ CEMT); Pernambuco, Camaragibe, Aldeia, 7. 929S, 35. 038W, 01-28. ii. 2019, PE 027, Km 14, 140m (1♂ CERPE); Pernambuco, Vitória de Santo Antão, 28 28. xi. 2018, A. Diana (1♂ CERPE); Pernambuco, Garanhuns (1♀ CEUPE); Alagoas, Ibateguara, Aquidabã-II, 16. iii. 2008, fezes, B. K. C. Filgueiras (3♂ CERPE); Alagoas, Ibateguara, 08.iii.2008, B.K.C. Filgueiras (1♂ E&PG) Alagoas, Ibateguara, 4.ii.2011, L.Pordeus (1♂ CERPE); Alagoas, Rio Largo, 23.iv.2015, C.G.Santos (1♂ UFAL); Alagoas, coleção didática UFAL, sem dados (6♀ 3 ♂ UFAL); Alagoas, Rio largo, 19.iii.2019, manual, A.T.Lima (1♂ UFAL); Alagoas, Rio largo, 19.iii.2010, manual, R.Sousa (1♂ UFAL); Alagoas, Rio largo, 15.ix.2018, C.S.Peixoto (1♂ UFAL); Alagoas, Rio largo, 11-12.2018, M.V.P.Silva(1♂ UFAL); Alagoas, Igaci, 17.ii.2019, Manual, I.B.Santos

(1♂ UFAL); Alagoas, Maceio, 25.vi.2019, M.V.P.Silva (1♂ UFAL); Alagoas, Maceió, 02.xi.2017, J.W.S.Nascimento (1♂ UFAL); Alagoas, Messias, 4.iii.2018, R.F.Silva (1♀ UFAL); Rio Grande do Norte, Natal, xii.1956, A.P.Magalhaes (2♂ MNRJ); Paraíba, João Pessoa, Campus UFPB, 01.xii.1979, J.Torreli (1♀ CERPE); Paraíba, João Pessoa, Campus UFPB, 05.ii.1977 (1♀ CERPE); Paraíba, João Pessoa, Campus UFPB, 10.viii.1980, J.Torreli (1♀ CERPE); Paraíba, João Pessoa, Campus UFPB, 14.ii.1977, G.Pekola (1♀ CERPE);

Comments: This species is distinguished from the others by the flattened and horizontal pronotum, with rounded sides, with rugose sides, its size is smaller than *E. gibbicollis*, they are black and shiny. This species is endemic to the Pernambuco Endemism Center, which includes all forests between the states of Rio Grande do Norte and Alagoas, located above the São Francisco River (Tabarelli et al. 2006; Prance 1982; Silva & Casteleti 2005). When compared to other regions of the Atlantic Forest, it is the most deforested and the least known and protected in conservation units (Silva & Tabarelli 2001). Currently, the remaining forest is represented only by archipelagos and small forest fragments in the midst of urban and agricultural matrices (Silva & Tabarelli 2000), consequently several endemic species are on the verge of global extinction (Brooks & Rylands 2003). This Center is one of the regions of more urgency for environmental conservation efforts (Rodrigues et al. 2004; Paglia et al. 2004). Possibly *Enema* sp.1 sp. nov. is in some degree of threat of extinction. The specimens collected in the Serra dos Cavalos in Pernambuco, were collected in the morning, most of them dead on a trail on the banks of the dams, apparently attracted by the reflections of the moon in the water, which appears to have been a flock, all individuals were males.

Identification Key

1 Males with pronotal prolongation exceeding the height of the pronotum (Figure 22C). *Enema pan* Hope, 1875

- No pronotal prolongation. 2

2 Reddish-brown coloration, epipleura sulcated and marginated, occurs in Central America to South America (Figure 1) . . . . *Enema endymion* Chevrolat, 1843

- Black coloration, epipleura without sulcus and margin, occurs in South America (Figure 16B) 3

3 Predominantly black, robust, apex of pronotum with two gibbons, tiny punctuations distributed throughout the body, occurrence Suriname, Amazonas, Roraima, Pará (Figure 7) . . . . *Enema gibbicollis* (Sternberg, 1908)

- Black, which may vary to dark brown, not robust, apex of pronotum without two gibbons, flattened pronotum, lateral sides of the pronotum rugopunctate, it occurs in northeastern Brazil from Rio Grande do Norte to Alagoas (Figure 13). . . . . .*Enema* sp.1 Mota, Grossi & Vaz-de-Mello, 2023

Delimitation of characters

The matrix includes 46 characters for the 11 terminal taxa. Of the total characters, 41 are binary and 5 are multistate. Below follows the list of characters and their states presented in the cladistic analysis. The CI and RI indices are included for each character. The proportion of characters examined was: Head (41,3%; 19 characters), Pronotum (8,6%; four characters), Elytra (13,0%; six characters), Prosternum (6,5%; three characters), Hippomere (2,1%; one character), Protíbia (6,5%; three characters), Mesotibia (2,1%; one character), Metatarsomere (2,1%; one character), Propygideus (2,1%; one character), Aedeagus (10,8%; five characters).

Head (characters 1-19)

1. Clypeus, anterior margin, shape: (0) Straight (Figure 14BC); (1) Sinuated (Figure 2BC). CI: 0.25, RI: 0.00.
2. Clypeus, anterior region, sulcus: (0) Absent; (1) Present (Figure 2B). CI: 0.33, RI: 0.33.
3. Horn, size of the horn in relation to the head: (0) Smaller than the width of the head (Figure 2C); (1) Equal to the width of the head (2) Twice the width of the head (Figure 22). CI: 0.66, RI: 0.50.
4. Horn, surface, form of punctuation: (0) Ocellated surface (Figure 8C); (1) Rugged punctured surface (Figure 2C); (2) Smooth surface. Character dependent character 3. CI: 1.00, RI: 1.00.
5. Horn, height in lateral view,higher than the margin of the pronotum: (0) Absent (Fig. 2AC); (1) Present (Figure 22). CI: 0.33, RI: 0.33.
6. Horn, denticle on anterior part: (0) Absent (Figure 2B); (1) Present (Figure 22C). CI: 0.33, RI: 0.33.

7. Horn in females: (0) absent; (1) present (Figure 6;12;13). CI: 1.00, RI: 1.00.
8. Tubercle in females mid-region: (0) Absent; (1) Present. CI: 0.50, RI: 0.75.
9. Front, surface punctures: (0) Absent; (1) Present. CI: 0.33, RI: 0.33.
10. Front, punctuations, shape: (0) Ocellate; (1) Rugopunctada. CI: 0.25, RI: 0.25.
11. Vertex, surface punctuations: (0) Absent; (1) Present. CI: 0.50, RI: 0.66.
12. Vertex, form of punctuation (0) Ocellated juxtaposition; (1) Ocellata separated by the size of two ocelli. Character dependent on character 11, state 1. CI: 0.33, RI: 0.00.
13. Mouthparts, labrum, anterior border in ventral view: (0) Absent; (1) Present (Figure 2B;8B;14B;22C). CI: 0.50, RI: 0.33.
14. Mouthparts, mentum, basal disc, shape: (0) Flat; (1) Convex (Figure 15F); (2) Excavated (Figure 9F). CI: 0.66, RI: 0.50.
15. Mouthparts, mentum, surface, excavated punctations: (0) At apex; (1) On the sides (Figure 3F; 9F;15E); (2) On the surface. CI: 0.66, RI: 0.50.
16. Mouthparts apex of mentum, shape: (0) Round or flat (1) Acuminate (Figure 3F; 9F;15E). CI: 0.50, RI: 0.50.
17. Ocular canthus, shape: (0) Rounded; (1) Subtriangular. CI: 1.00, RI: 1.00.
18. Frontoclypeal suture: (0) Absent; (1) Present (Figure 25). CI: 0.50, RI: 0.00.
19. Frontoclypeal suture, shape; (0) Sulcus (Figure 25A); (1) Carinae (Figure 25EF). Character dependent on state 18 state 1. CI: 0.25, RI: 0.00.

Pronotum (characters 20-24)

20. Lateral region in males, surface: (0) With punctations (Figure 14D); (1) Glabrous (Figure 2D). CI: 1.00, RI: 1.00.
21. Pronotal horn: (0) Absent (Figure 14A); (1) Present (Figure 22). CI: 0.33, RI: 0.50.

22. Pronotal horn, form; (0) Extended (Figure 22); (1) Bifurcated; Dependent on character 21 state1. CI: 0.50, RI: 0.00.
23. Posterior margin region: (0) Without sulcus; (1) With a horizontal sulcus above the margin. CI: 0.50, RI: 0.50.
24. Middle region flattened dorsoventrally; (0) Absent (Figure 1A); (1) Present (Figure 13A). CI: 0.50, RI: 0.00.

Elytra (caracteres 25-31)

25. Elytral striae, surface: (0) Absent (Figure 1A); (1) Present (Figure 22A). CI: 0.25, RI: 0.00.
26. Elytral suture: (0) Absent; (1) Present (Figure 1A). CI: 1.00, RI: 1.00.
27. Elytral suture, margin shape: (0) Straight (1) Curved. CI: 1.00, RI: 1.00.
28. Lateral edges, conformation: (0) Positioned downwards; (1) Positioned upwards (Figure 1A). CI: 0.66, RI: 0.00.
29. Epipleura in lateral view: (0) Not visible; (1) Partially visible (Figure 13C) (2) Completely visible. CI: 0.66, RI: 0.00.
30. Epileura, surface, medially sulcated: (0) Absent (Figure 10B) (1) Present (Figure 4B). CI: 0.50, RI: 0.00.
31. Epipleura, visibility: (0) Ventrally; (1) Laterally (Figure 1C;13C). CI: 0.50, RI: 0.66.

Prosternum (characters 32-34)

32. Prosternal process, length: (0) Long, reaching coxae; (1) Short, not reaching the coxae (Figure 2E). CI: 0.33, RI: 0.00.
33. Prosternal process, shape: (0) Columnar; (1) Laminar (Figure 2E). CI: 0.50, RI: 0.00.

34. Carina above procoxa: (0) Absent; (1) Present. CI: 0.50, RI: 0.75.

Hypomeron (Character 35)

35. Basal region: (0) Flat; (1) Excavated (Figure 4A;10A;16A). CI: 0.50, RI: 0.00.

Protibia (Characters 36-38)

36. Shape: (0) Straight; (1) Arched and curved. CI: 0.50, RI: 0.50.
37. Length of protibial spine: (0) Does not reach apex of second tarsomere; (1) Reaches or passes the apex of the second tarsomere. CI: 1.00, RI: 1.00.
38. Number of teeth on external edge: (0) three teeth; (1) four teeth. CI: 0.50, RI: 0.75.

Mesotibia (Character 39)

39. Shape: (0) Continuous throughout its length; (1) Expanded at apex. CI: 0.50, RI: 0.00.

Metatarsus (Character 40)

40. Basimetatarsomere, shape: (0) Cylindrical (1) Triangular. CI: 0.50, RI: 0.50.

Propygidium (Character 41)

41. Stridulatory apparatus in the medial region: (0) Absent; (1) Present. CI: 1.00, RI: 1.00.

Aedeagus (caracteres 42-46)

42. Parameres, apex: (0) Glabrous (Figure 5AB; 11AB; 17AB; 24AB); (1) with bristles. CI: 0.33, RI: 0.50.

43. Paramers, apical half: (0) parallel; (1) divergent (Figure 5AB; 11AB; 17AB); (2) Convergents. CI: 0.66, RI: 0.75.
44. Parameres, latero-basal tooth: (0) Absent; (1) Present (Figure 5B; 11B; 17B). CI: 0.50, RI: 0.75.
45. Spiculum gastrale, medial shaft sulcated: (0) Absent (Figure 5E); (1) Present (Figure 11E;17E). CI: 0.50, RI: 0.75.
46. Spiculum gastrale, base of lateral branches: (0) Continuous (Figure 5E); (1) Interrupted (Figure 11E;17E). CI: 0.25, RI: 0.00.

Cladistic analysis

For the analysis of equal weights (EW) of the characters through heuristic searches, four parsimonious trees were generated. The consensus tree has a step length of 118 (CI= 0.44 and RI= 0.44) (Figure 27), the calculation of the absolute Bremmer support was performed through suboptimal trees, represented in each clade in strict consensus. In the equal weights analysis the genus appears monophyletic, but there is a polytomy within the clade. Species have better resolution when characters were analyzed with implicit weighting, so we will only discuss the tree with implicit weighting (Figure 28).

Analysis with implicit weighting generated a cladogram with 109 steps length (CI= 0.47 and RI= 0.51). From the concavity constant *k*, with the recommendation of the "setk.run" script according to Salvador Arias (Goloboff et al., 2008a), the value of *k* indicated was 3.0000, in which the smaller this value, the greater the force against homoplasies (Goloboff, 1993; Goloboff et al., 2008a). To compare the results, different values of *k* were tested, with an interval of 1.0000-20.0000, to test the stability of the trees. No variations were obtained in these intervals, only for the fit values, ranging from 24.33 to 41.03, and with *k*= 3,000 the calculated fit was 34,000.

The genus *Enema* represents a monophyletic group (Figure 28), with well-supported branches (Bremer Support (SBR)=31, symmetric resampling (RS=70, bootstrap 69%) (Figure 29) separated by two synapomorphies (Figure 29): Horn in females (7:1) (Figure 6;8;18) and Lateral borders, conformation (28:1) (Figure 1A;7A;13A) and four homoplasies: Tubercle in females (8:0), Vertex, surface scores (11:1), (42:0) and (43:1).

On the clades topology outside *Enema*, comparing with the phylogeny results of Bitar & Morón (2014), the authors only provided bootstrap values for clade support. In this work we obtained node 5 formed by *Coelosis biloba* (Linnaeus, 1767) and *Podiscnus agenor* (Olivier, 1798), (SBR=23 and RS=40) (Figure 29), with the synapomorphies: Shape of the anterior margin of the clypeus (2:1), size of the horn in relation to the head (3:2), when comparing the bootstrap values, here 36%, different from the result of Bitar & Morón (2014) in which *Coelosis biloba* appears forming a clade with *Heterogomphus pehlkei*, Kolbe 1906, supported by 44% bootstrap. The *Heterogomphus* species used in this work was *H. telamon*, which in the phylogenetic tree obtained is a sister group of the genus *Enema* (SBR=24, RS=7, bootstrap=15%) and supported by 15% booststrap), with the synapomorphies: Elytral suture (26:1) and basitarsomere shape (40:1), previously in the Bitar & Morón (2014) the sister group of *Heterogomphus* is *Coelosis biloba* (Supported by 50% bootstrap). This divergence might be justified by the great species richness of the genus, which has never been revised. Regarding the genus *Megaceras*, it shared a node with the species of *Coelosis*, *Podischnus*, *Heterogomphus* and *Enema* in both works, with SBR=34, RS=67, bootstrap= 60% for this work and 44% for bootstrap in Bitar & Morón (2014). *Xyloryctes jamaicensis* is the sister group of all other Oryctini in both results.

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Tabel 1. Matrix of characters used in cladistic analysis of *Enema*.

Espécies	Caracteres																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Chrysina macropus	0	0	–	–	–	–	–	–	1	0	1	1	1	–	0	0	0	1	0	0	0	–	0
Megasoma hyperion	1	1	0	0	0	0	0	1	1	0	1	0	0	1	2	0	0	1	0	0	1	0	0
Megaceras morpheu	1	0	2	0	1	1	0	1	1	1	0	–	0	2	1	1	1	0	–	1	1	1	1
Coelosis biloba	1	1	1	2	1	1	0	0	0	1	0	–	1	0	2	1	1	0	–	1	1	1	0
Podischnus agenor	0	1	1	2	1	1	0	1	0	0	0	–	1	0	1	1	1	1	1	1	1	1	1
Xyloryctes jamaicensis	1	1	0	0	0	0	0	1	1	0	1	1	0	2	2	1	1	1	1	0	0	–	1
Heterogomphus telamon	1	0	0	0	0	0	0	1	0	1	0	–	1	0	1	1	1	1	0	1	1	1	1
Enema pan	0	0	2	0	1	1	1	0	0	1	1	0	1	2	1	1	1	1	0	1	1	0	1
Enema endymion	1	1	0	1	0	0	1	0	1	1	1	0	1	2	1	1	1	1	1	1	0	–	1
Enema gibicollis	1	1	0	0	0	0	1	0	1	0	1	0	1	2	1	1	1	1	1	1	0	–	1
Enema sp.1	0	1	0	1	0	0	1	0	1	0	1	1	1	1	1	1	1	1	0	1	0	1	1

Espécies	Caracteres																						
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	45	44	45	46
Chrysina macropus	1	1	0	–	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	2	0	0	0
Megasoma hyperion	0	0	0	–	0	1	0	0	1	1	0	1	0	0	0	1	0	0	1	2	1	0	1
Megaceras morpheu	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	1	1	0	1	2	0	1	1
Coelosis biloba	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	2	0	0	0
Podischnus agenor	0	0	1	0	0	2	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0	0	1
Xyloryctes jamaicensis	0	1	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	1	1	0	0	0
Heterogomphus telamon	0	1	1	1	0	1	0	0	0	0	0	1	1	1	1	1	0	1	1	2	1	1	1
Enema pan	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
Enema endymion	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1

Enema gibicollis	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
Enema sp.1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1

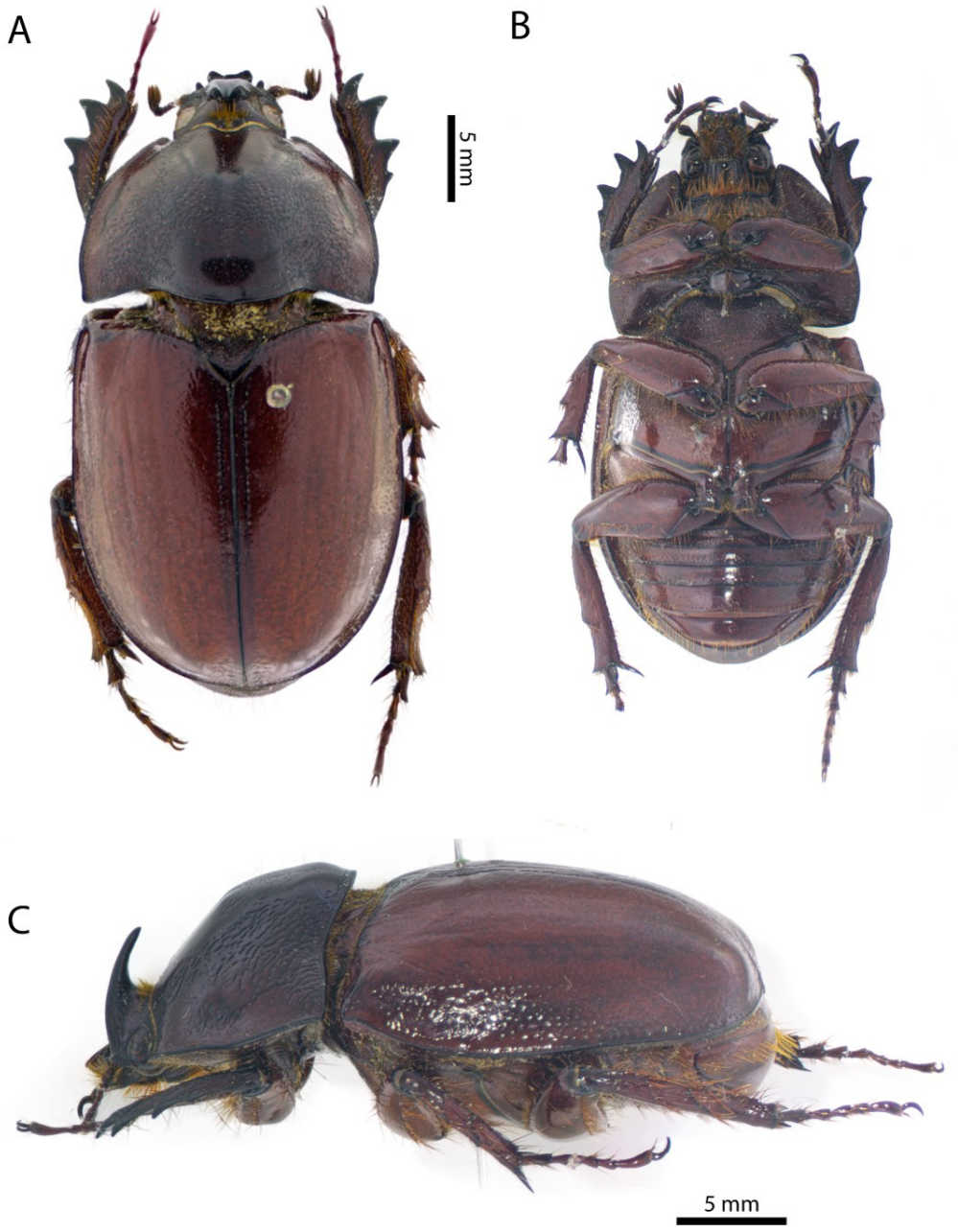

Figure 1. (A-C) Habitus de *Enema endymion* Chevrolat, 1843, male: A. Dorsal view; B. Ventral view; C. Side view. Scale: A-C: 5mm;

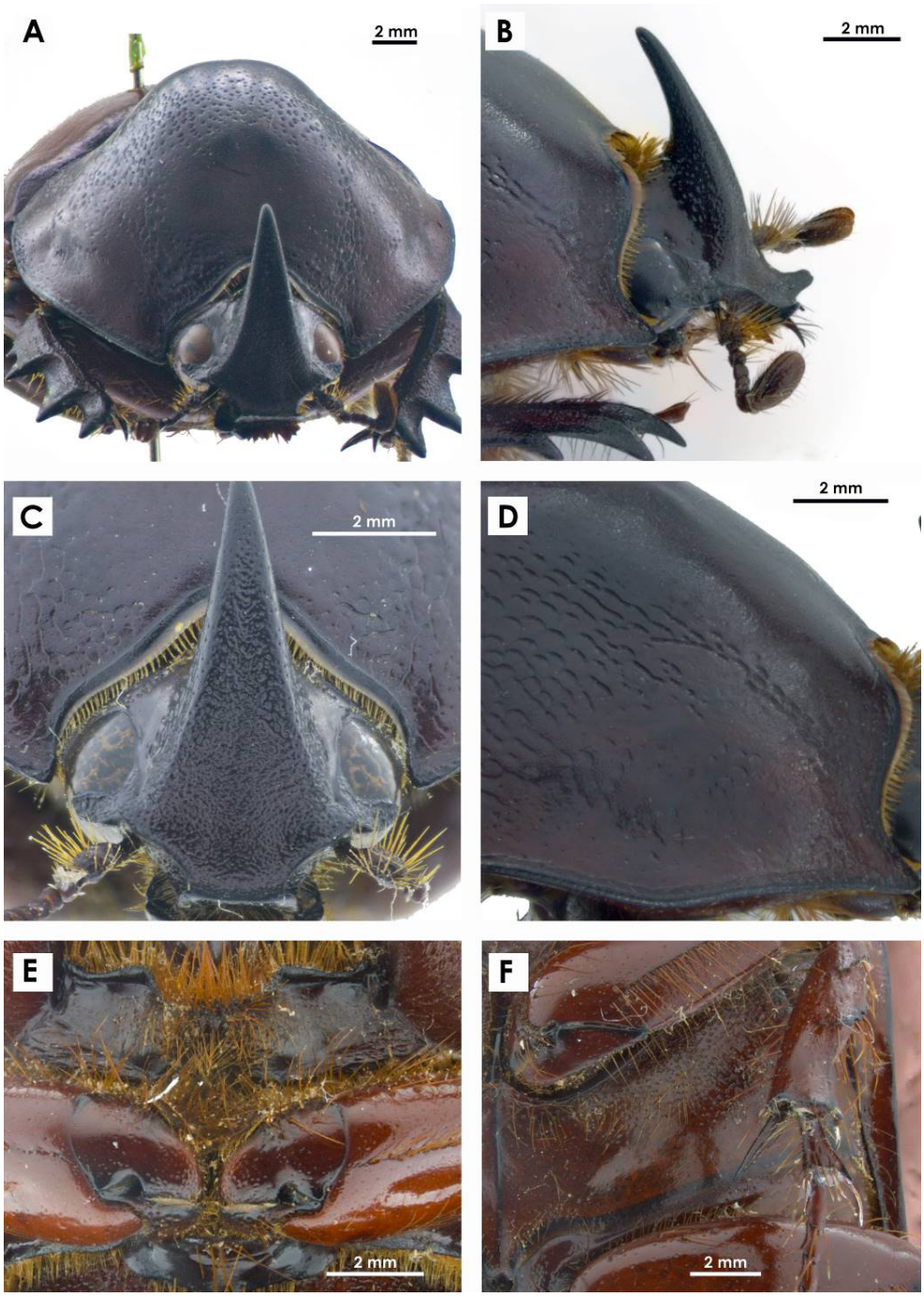

Figure 2. (A-F) Morphological structures of *Enema endymion* Chevrolat, 1843, male: A. Frontal view of horn and pronotum; B. Lateral view of the horn; C. Front view of the horn; D. Punctures on the side of the pronotum; E. Prosternum and prosternal process laminated and shortened; F. Mesosternum punctures. Scale: A-F: 2mm;

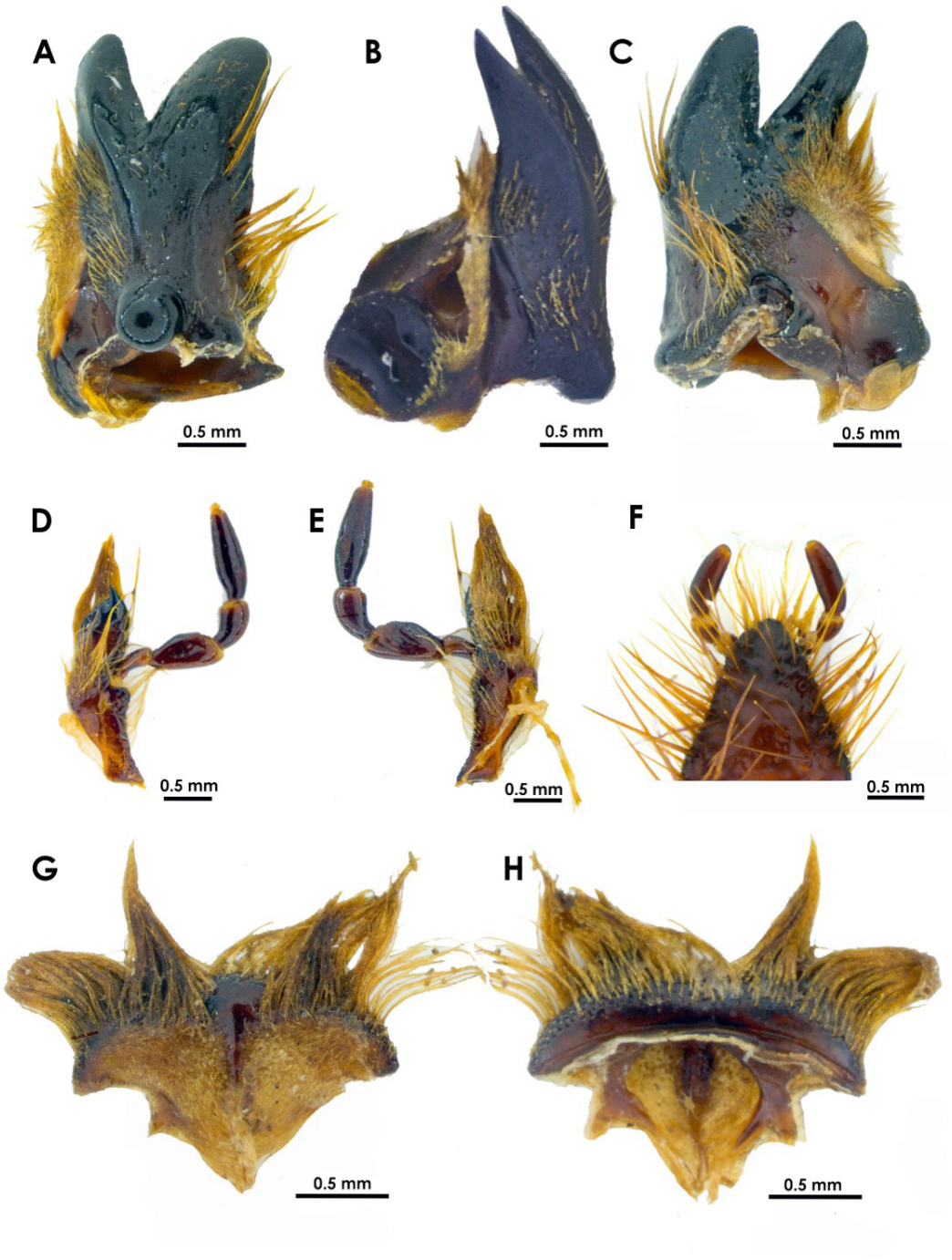

Figure 3. (A-H) Mouth parts of *Enema endymion* Chevrolat, 1843, male: A. Mandible, dorsal view; B. Mandible, lateral view; C. Mandible ventral view; D. Maxilla dorsal view; E. Maxilla dorsal view and palpomere IV with oval sensory area; F. Mentum ventral view; G. Labrus dorsal view; H. Labro ventral view. Scale: A-H: 0.5 mm;

Figure 4. (A-D) Ventral structures of *Enema endymion* Chevrolat, 1843: A. Hypomere surface; B. Sulcate and marginated epipleura; C. Male ventrites; D. Ventritos of the Female. Scale: A-D: 2mm;

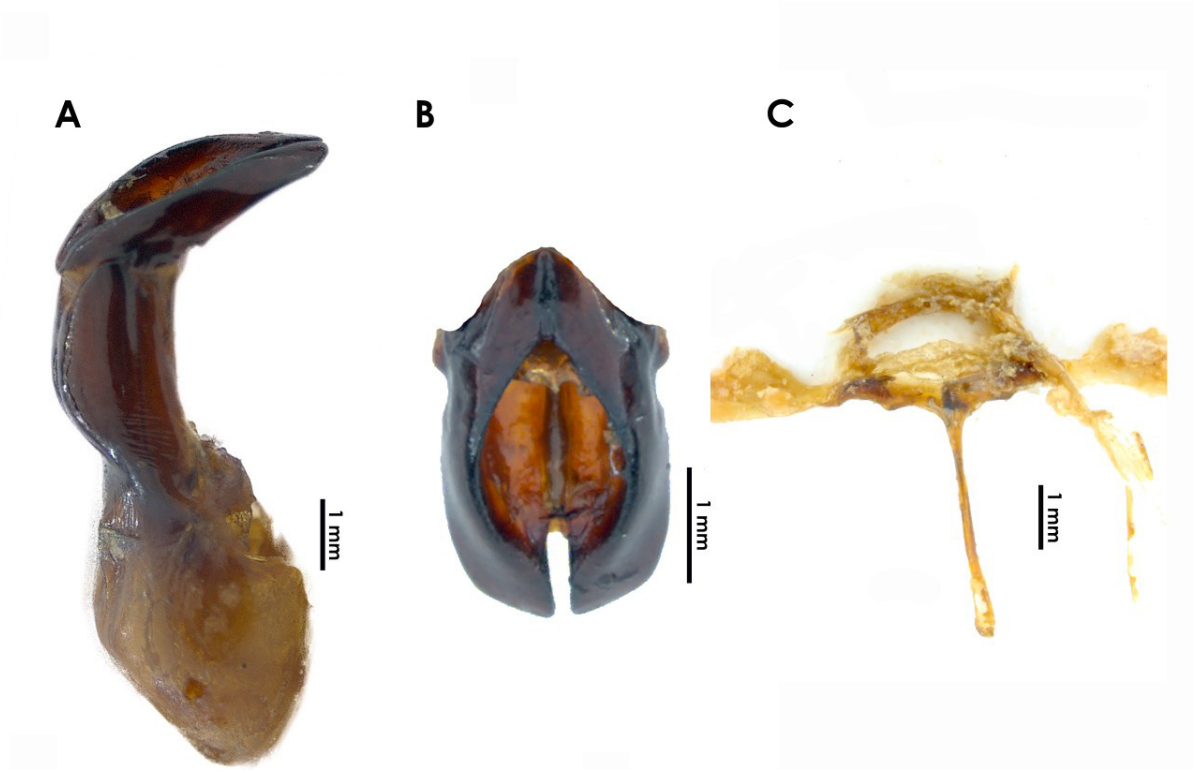

Figure 5. (A-C) Structures of terminalia, *Enema endymion* Chevrolat, 1843: A. Aedeagus lateral view; B. Parameros dorsal view; C. Spiculum gastrale. Scale: A-C: 1mm;

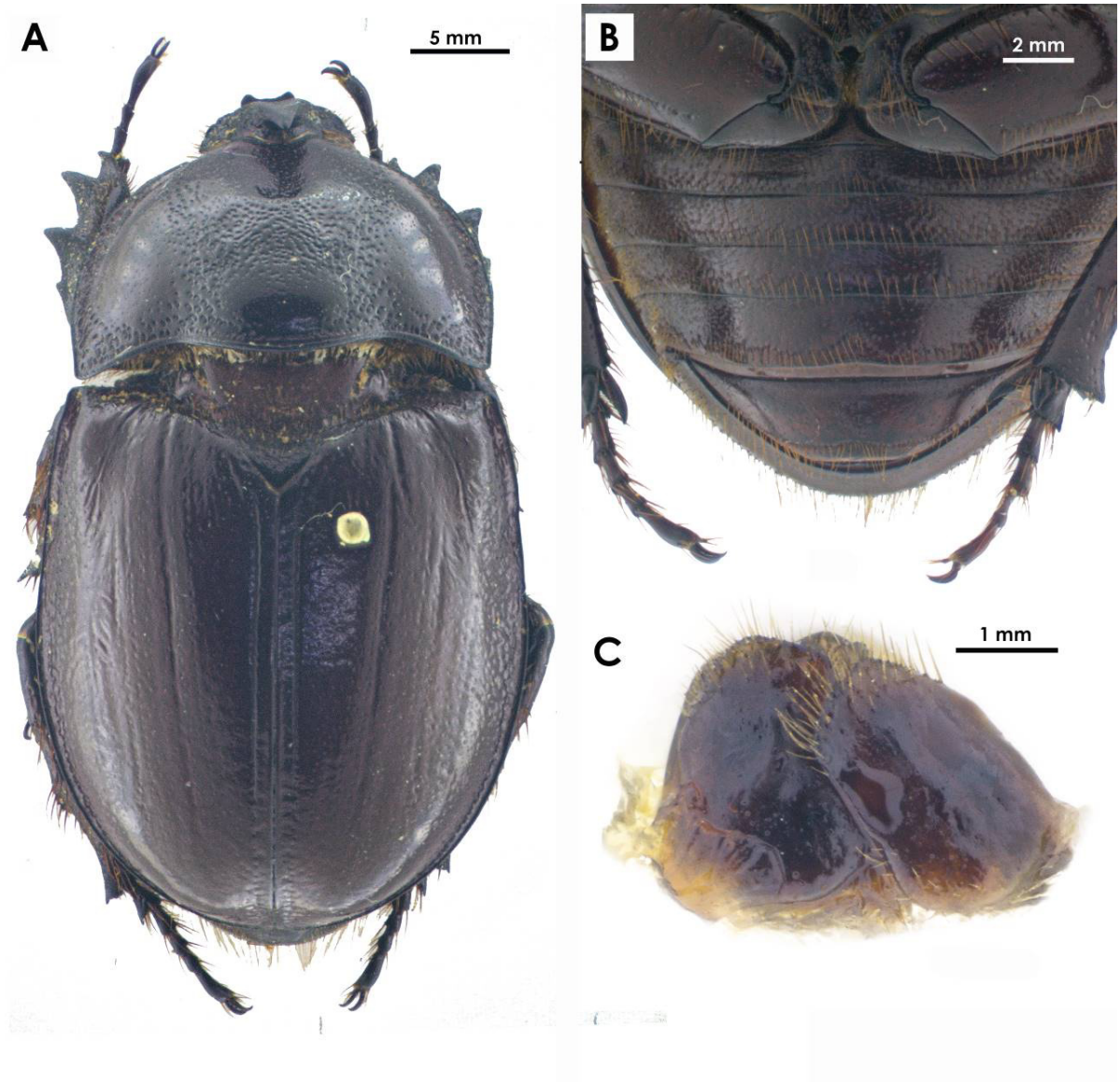

Figure 6. (A-C) Habitus *Enema endymion* Chevrolat, 1843, female: A. Dorsal view; B. Ventrites; C. Gonocoxites. Scale: A: 5mm; B: 2mm; C: 1mm;

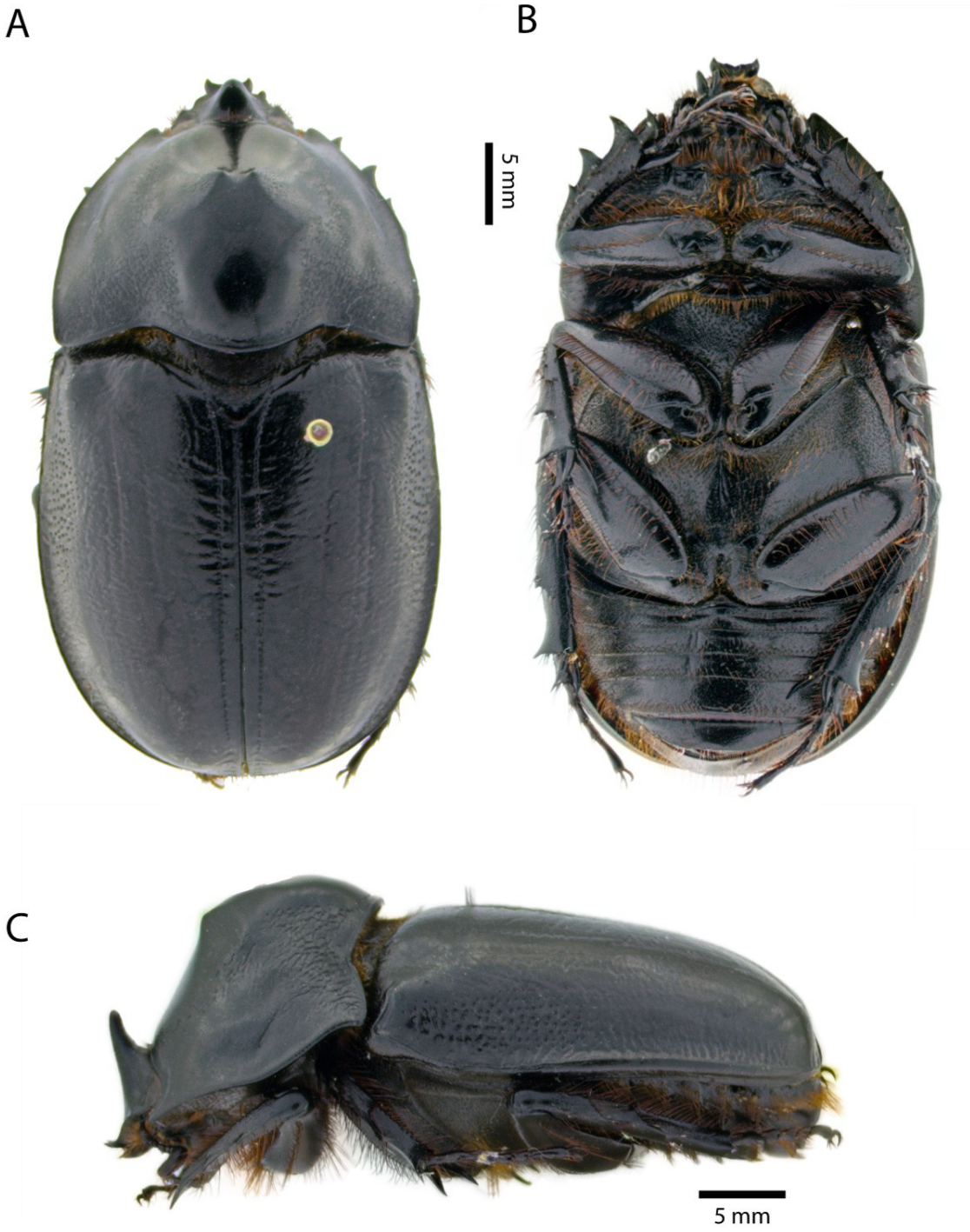

Figure 7. (A-C) Habitus de *Enema gibbicollis* Sternberg, 1908, male: A. Dorsal view; B. Ventral view; C. Side view. Scale: A-C: 5mm;

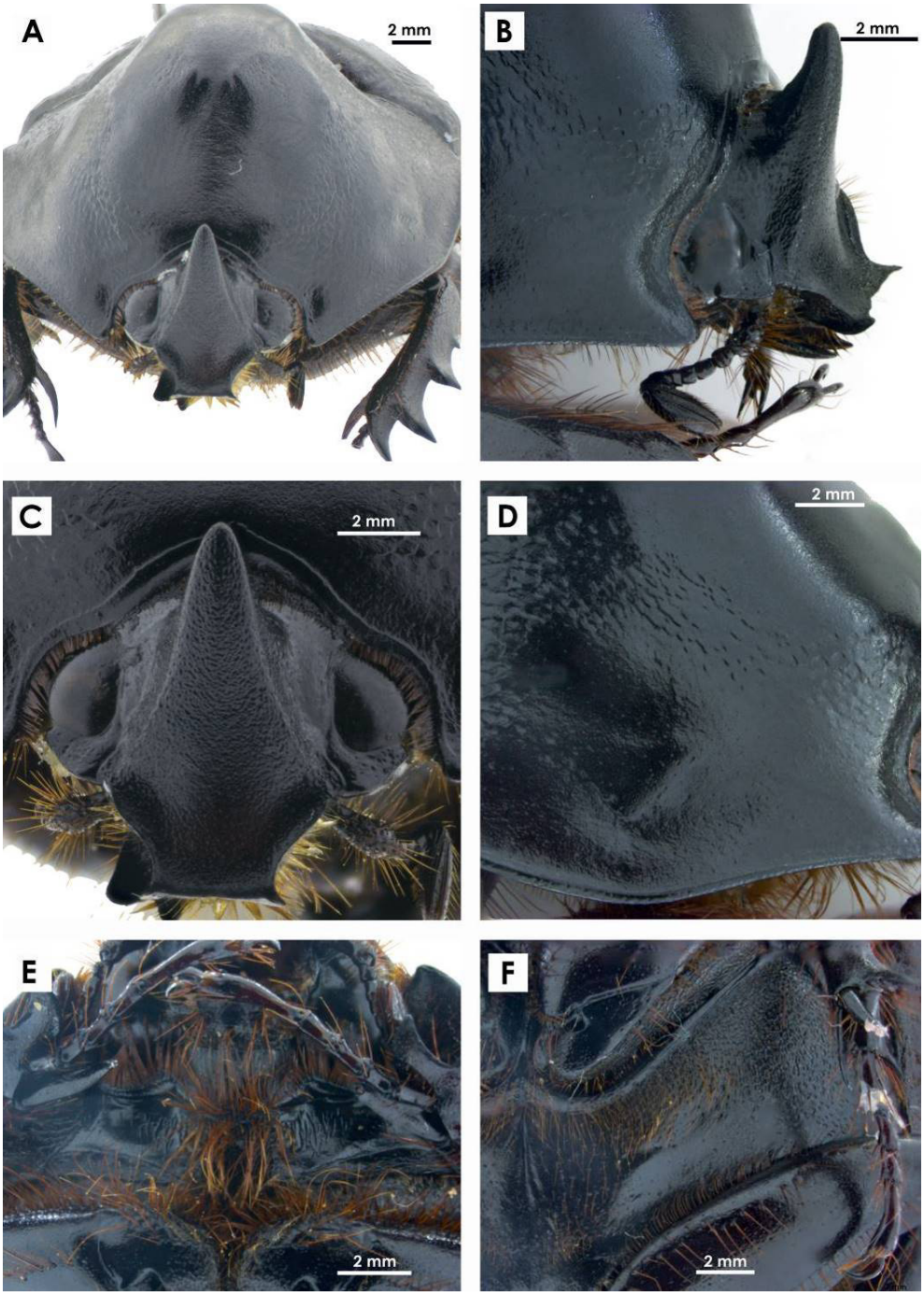

Figure 8. (A-F) Morphological structures of *Enema gibbicollis* Sternberg, 1908, male: A. Frontal view of horn and pronotum; B. Lateral view of the horn; C. Front view of the horn; D. Rupunctures on the side of the pronotum; E. Prosternum and prosternal process laminated and shortened; F. Mesosternum punctures. Scale: A-F: 2mm;

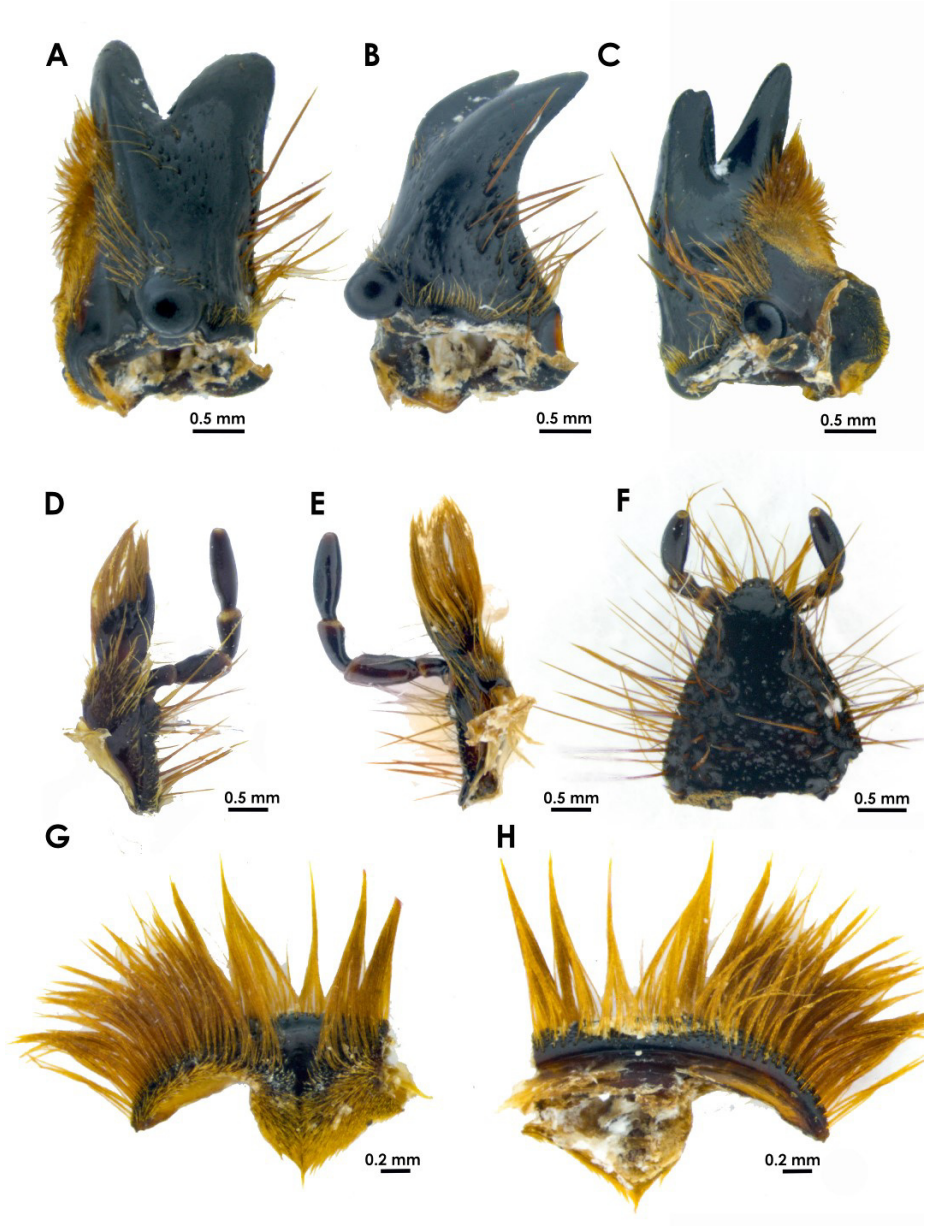

Figure 9. (A-H) Mouth parts of Enema gibbicollis Sternberg, 1908, male: A. Mandibula dorsal view; B. Mandible, lateral view; C. Mandible ventral view; D. Maxilla dorsal view; E. Maxilla dorsal view and palpomere IV with oval sensory area; F. Mentum ventral view; G. Labrus dorsal view; H. Labro ventral view. Scale: A-H: 0.5 mm;

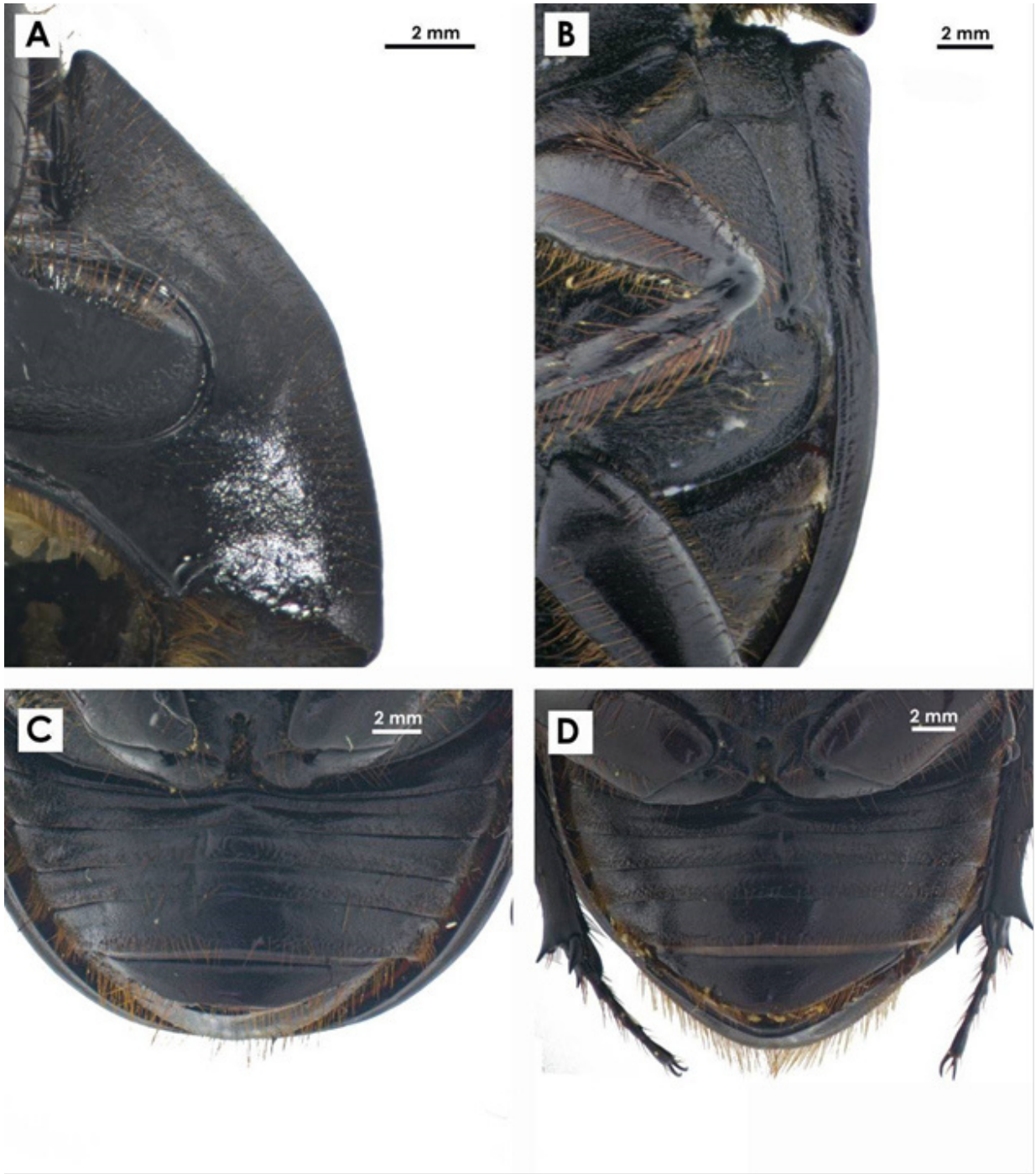

Figure 10. (A-D) Ventral structures of *Enema gibbicollis* Sternberg, 1908: A. Hypomere surface; B. Sulcate and marginated epipleura; C. Male ventrites; D. Ventritos of the Female. Scale: A-D: 2mm;

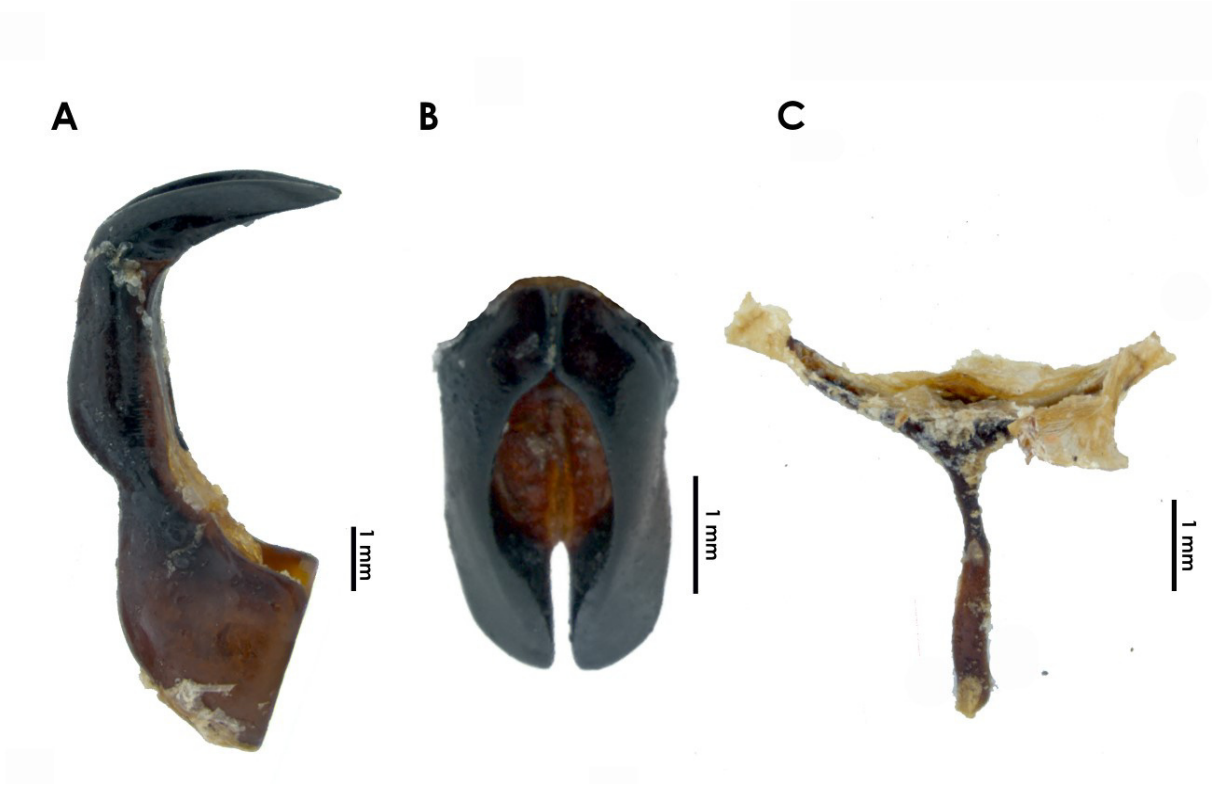

Figure 11. (A-C) Structures of terminalia, *Enema gibbicollis* Sternberg, 1908: A. Edeago lateral view; B. Parameros dorsal view; C. Spiculum gastrale. Scale: A-C: 1mm;

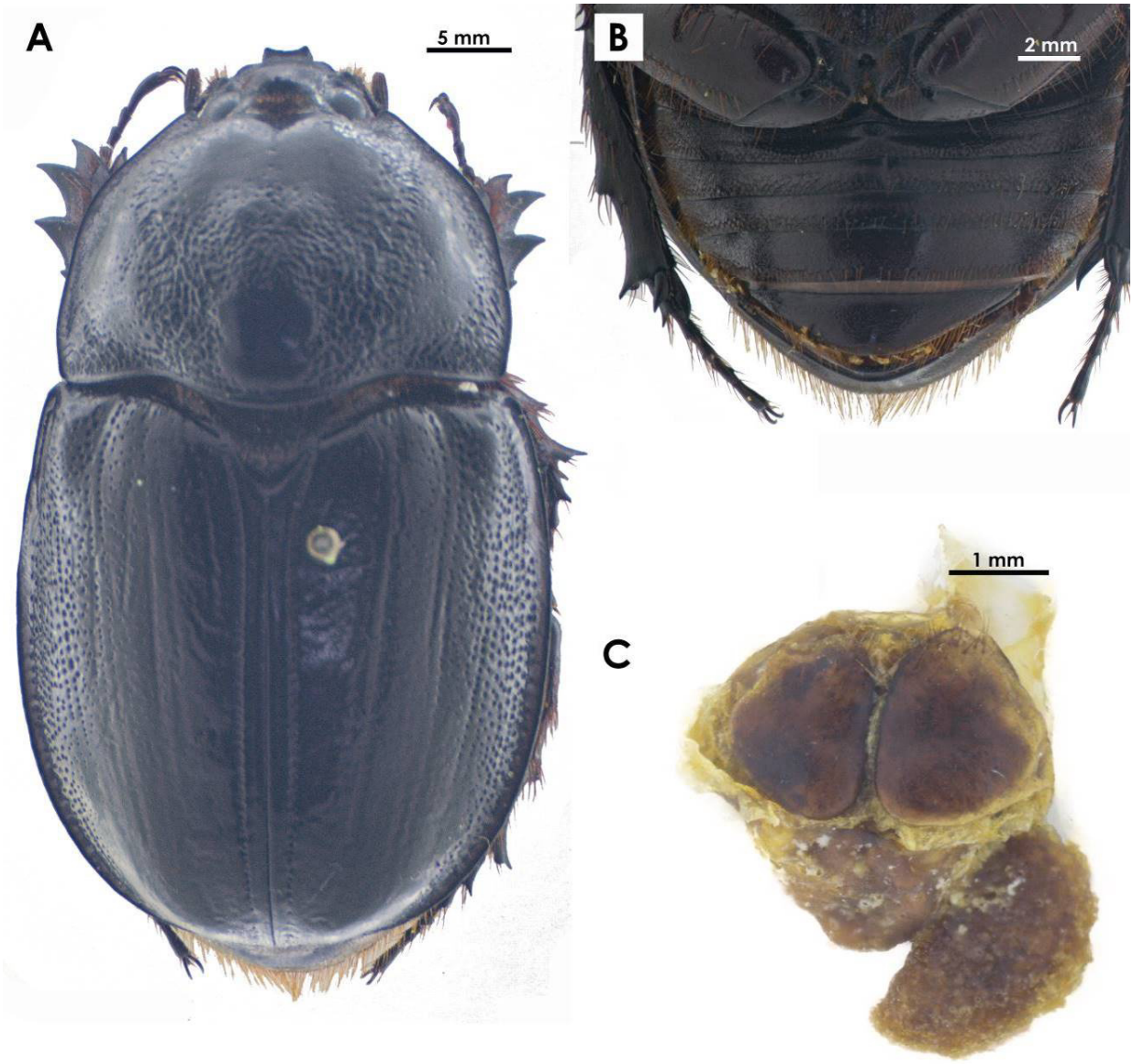

Figure 12. (A-C) Habitus Enema gibbicollis Sternberg, 1908: A. Dorsal view; B. Ventrites; C. Gonocoxites. Scale: A: 5mm; B: 2mm; C: 1mm

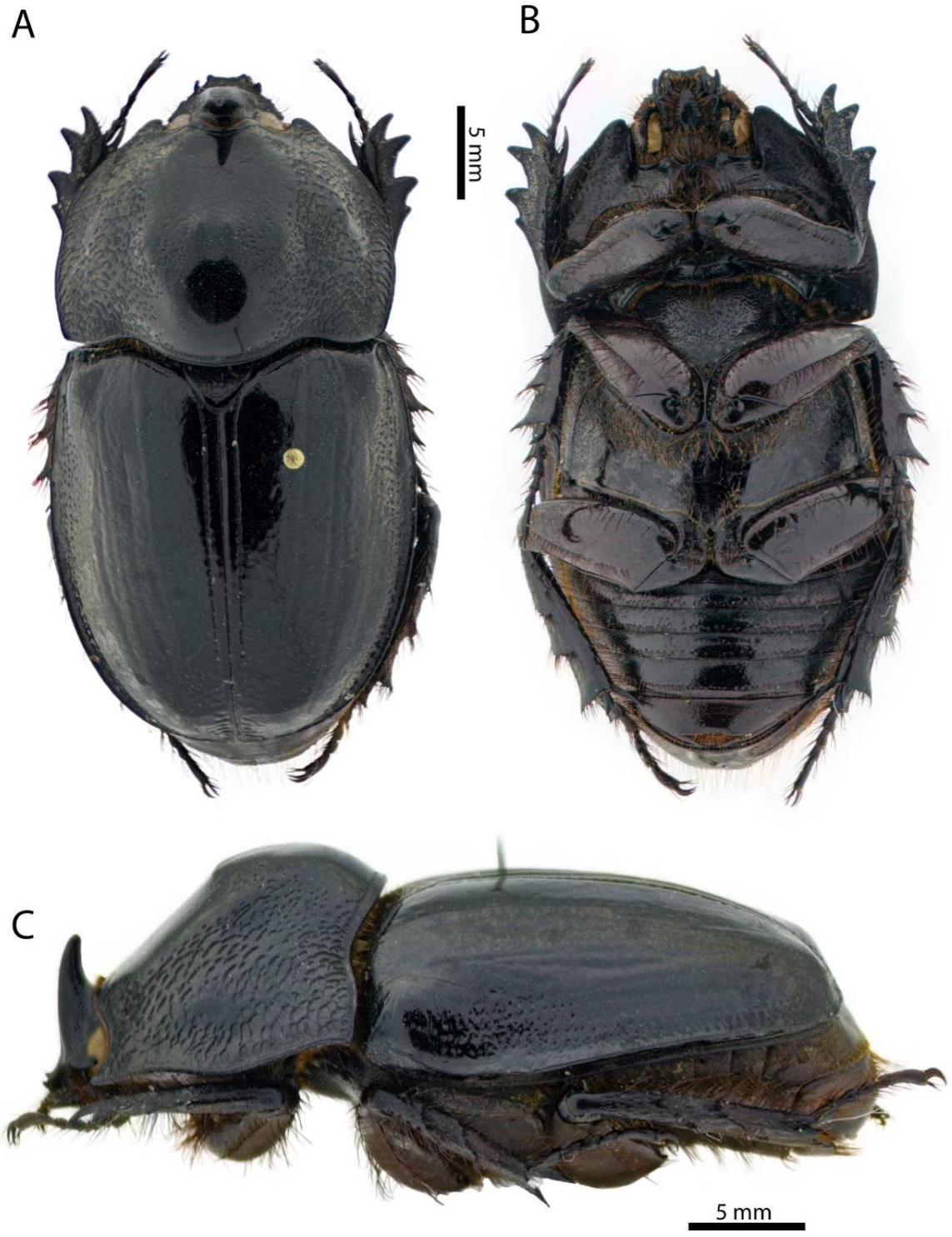

Figure 13. (A-C) Habitus de *Enema* sp.1 Mota, Grossi & Vaz-de-Mello, 2023 male: A. Dorsal view; B. Ventral view; C. Side view. Scale: A-C: 5mm;

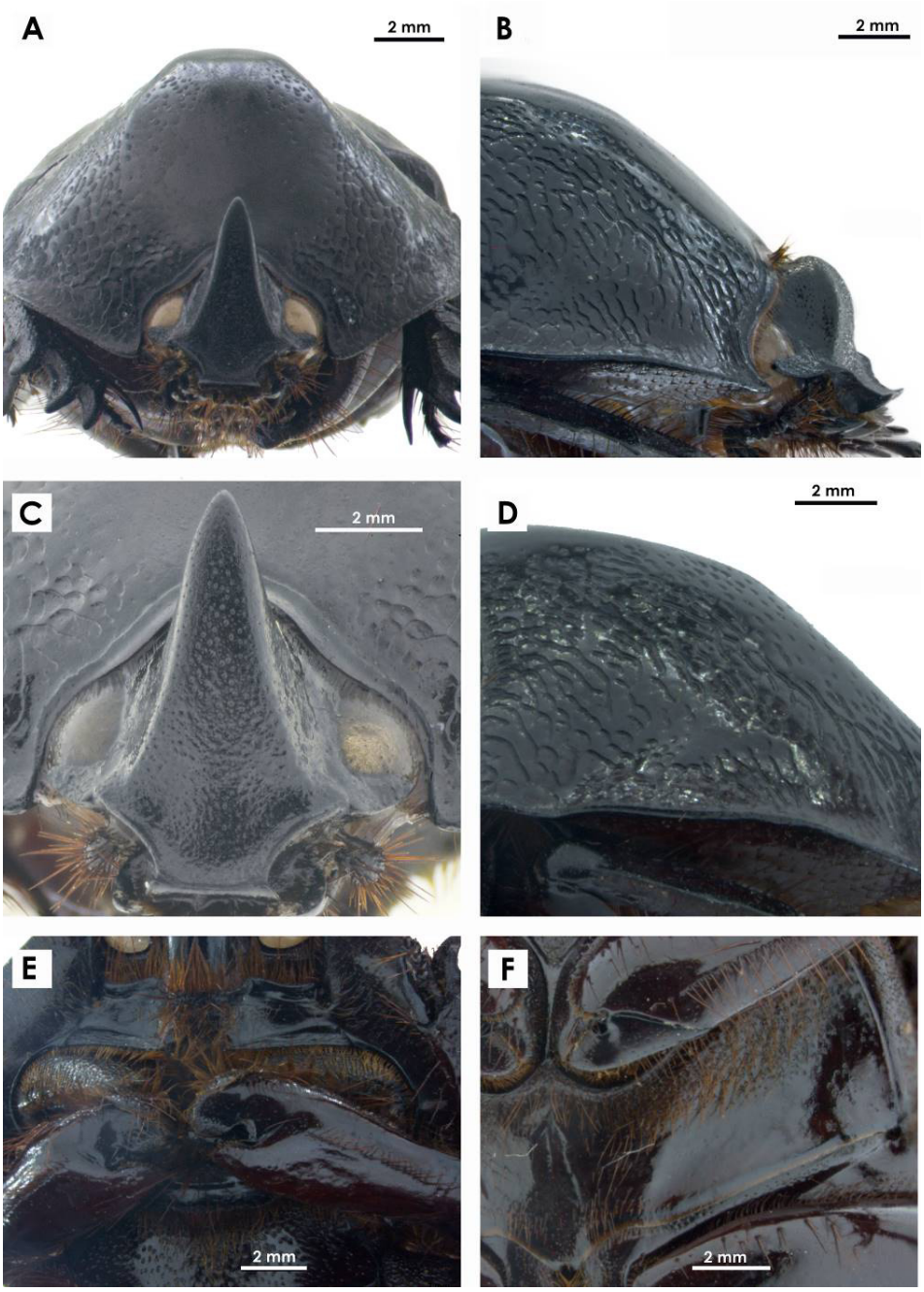

Figure 14. (A-F) Morphological structures of *Enema* sp.1 Mota, Grossi & Vaz-de-Mello, 2023, male: A. Front view of horn and pronotum; B. Lateral view of the horn; C. Front view of the horn; D. Punctures on the side of the pronotum; E. Prosternum and prosternal process laminated and shortened; F. Mesosternum punctures. Scale: A-F: 2mm;

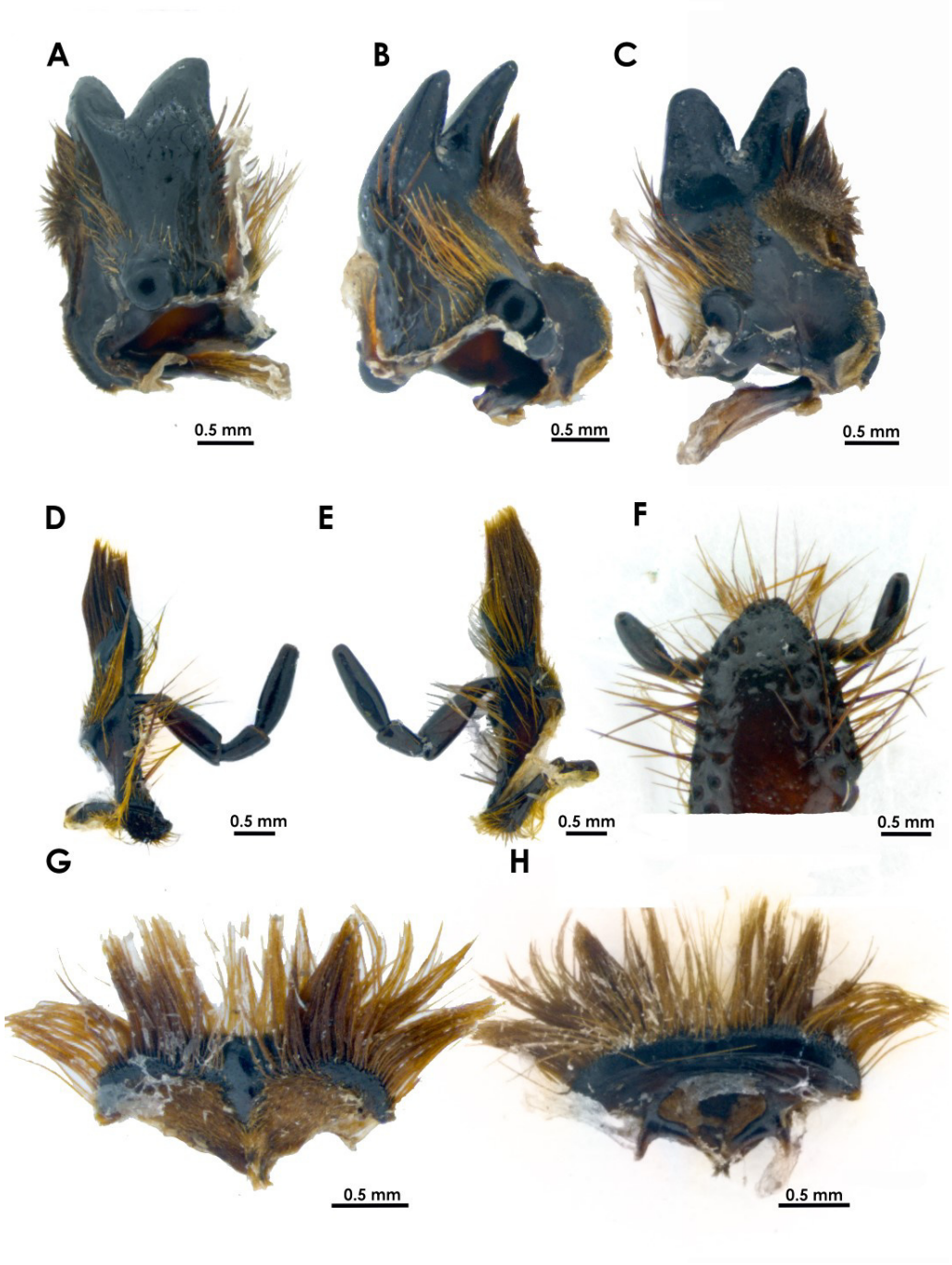

Figure 15. (A-H) Mouthpieces of Enema sp.1 Mota, Grossi & Vaz-de-Mello, 2023: A. Mandible dorsal view; B. Mandible, lateral view; C. Mandible ventral view; D. Maxilla dorsal view; E. Maxilla dorsal view and palpomere IV with oval sensory area; F. Mentum ventral view; G. Labrus dorsal view; H. Labro ventral view. Scale: A-H: 0.5 mm;

Figure 16. (A-D) Ventral structures of Enema sp.1 Mota, Grossi & Vaz-de-Mello, 2023: A. Hypomere surface; B. Sulcate and marginated epipleura; C. Male ventrites; D. Ventritos of the Female. Scale: A-D: 2mm;

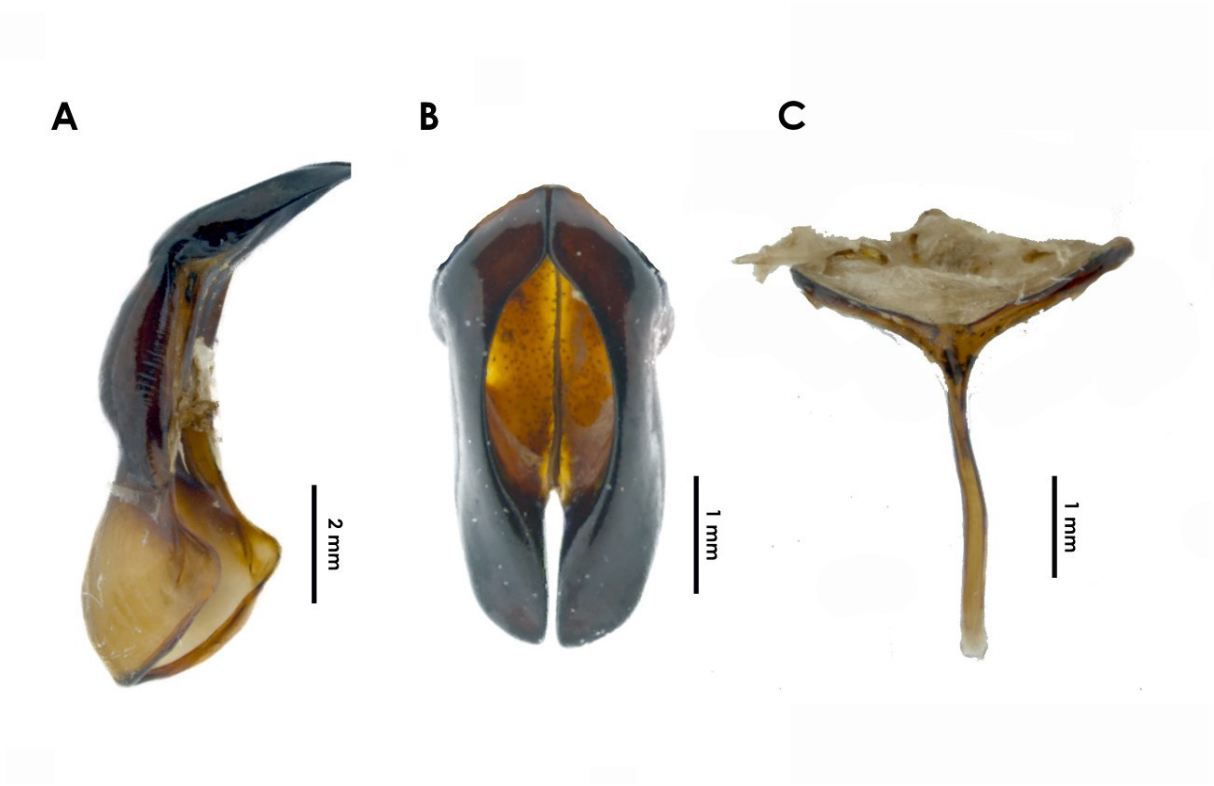

Figure 17. (A-C) Structures of terminalia, *Enema* sp.1 Mota, Grossi & Vaz-de-Mello, 2023: A. Edeago lateral view; B. Parameres dorsal view; C. Spiculum gastrale. Scale: A-C: 1mm;

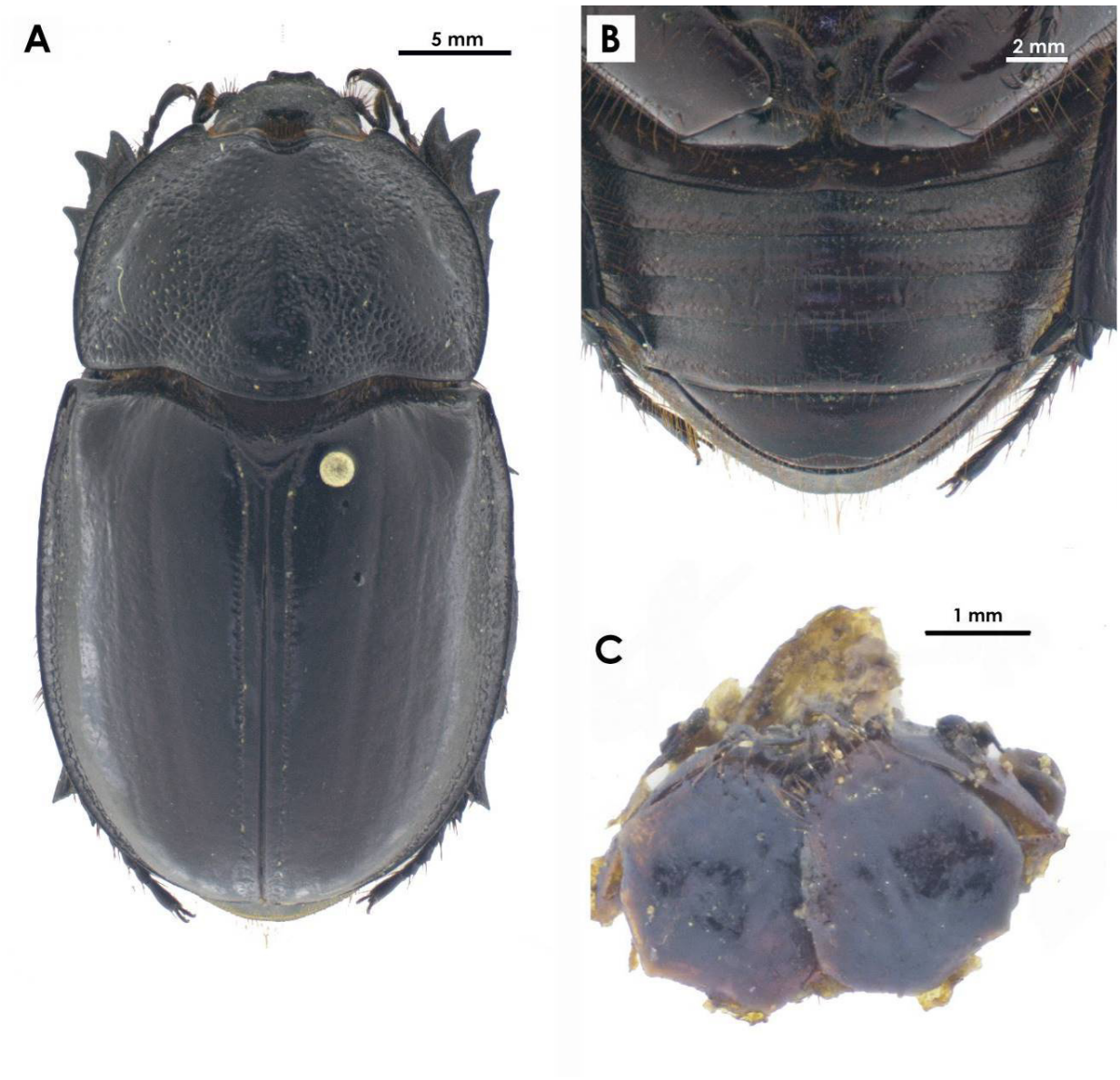

Figure 18. (A-C) Habitus Enema sp.1 Mota, Grossi & Vaz-de-Mello, 2023, female: A. Dorsal view; B. Ventrites; C. Gonocoxites. Scale: A: 5mm; B: 2mm; C: 1mm;

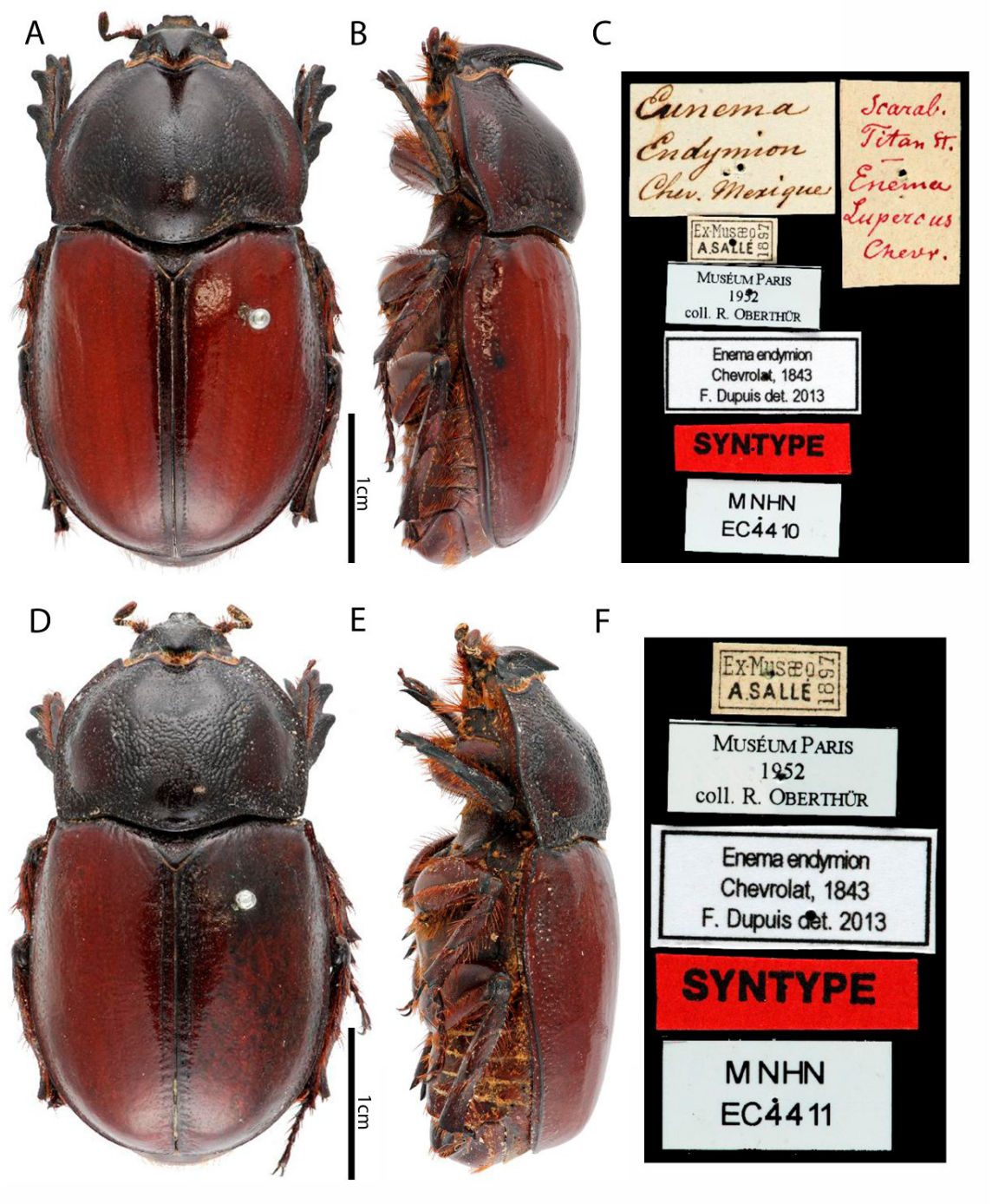

Figure 19. (A-F) Photos of the type material from *Enema endymion* Chevrolat, 1843: A. Habitus male, dorsal view; B. Male Habitus, side view; C. Labels of the male specimen; D. Habitus female, dorsal view; E. Habitus female, lateral view; F. Female specimen labels. Scale: A-B: 51 cm; D-L: 1cm;

Figure 20. (A-E) Photos of the type material from *Enema paniscus* Burmeister, 1847: A. Habitus male, dorsal view; B. Male Habitus, ventral view; C. Epipleura; D. Habitus male, side view; E. Labels of the copy;

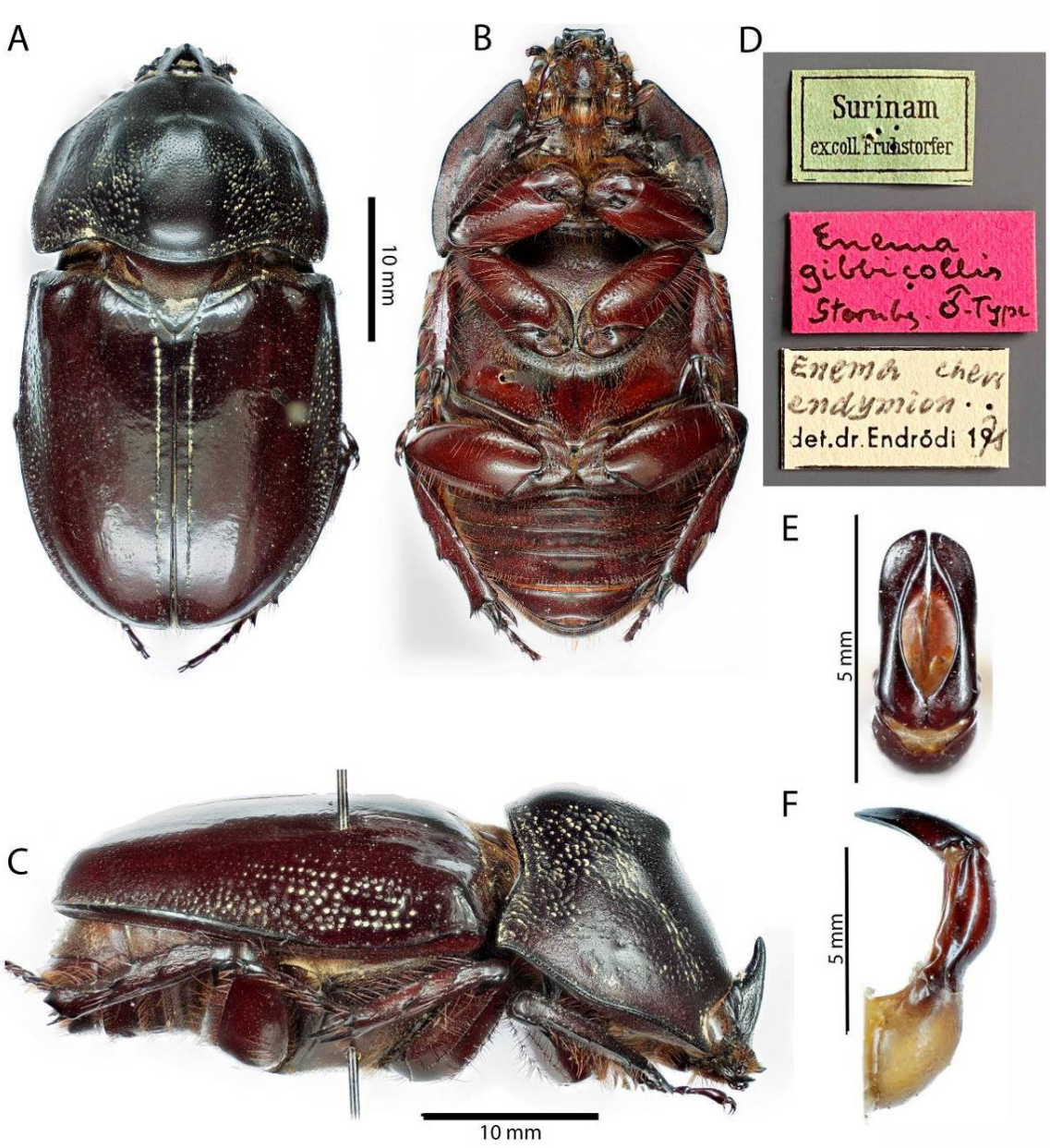

Figure 21. (A-F) Photos of the type material from *Enema gibbicollis* Sternberg, 1908: A. Habitus male, dorsal view; B. Male Habitus, ventral view; C. Habitus male, side view; D. Labels on the copy; E. Paramers; F. Edeago side view. Scale: A-C: 10mm; E-F: 5mm;

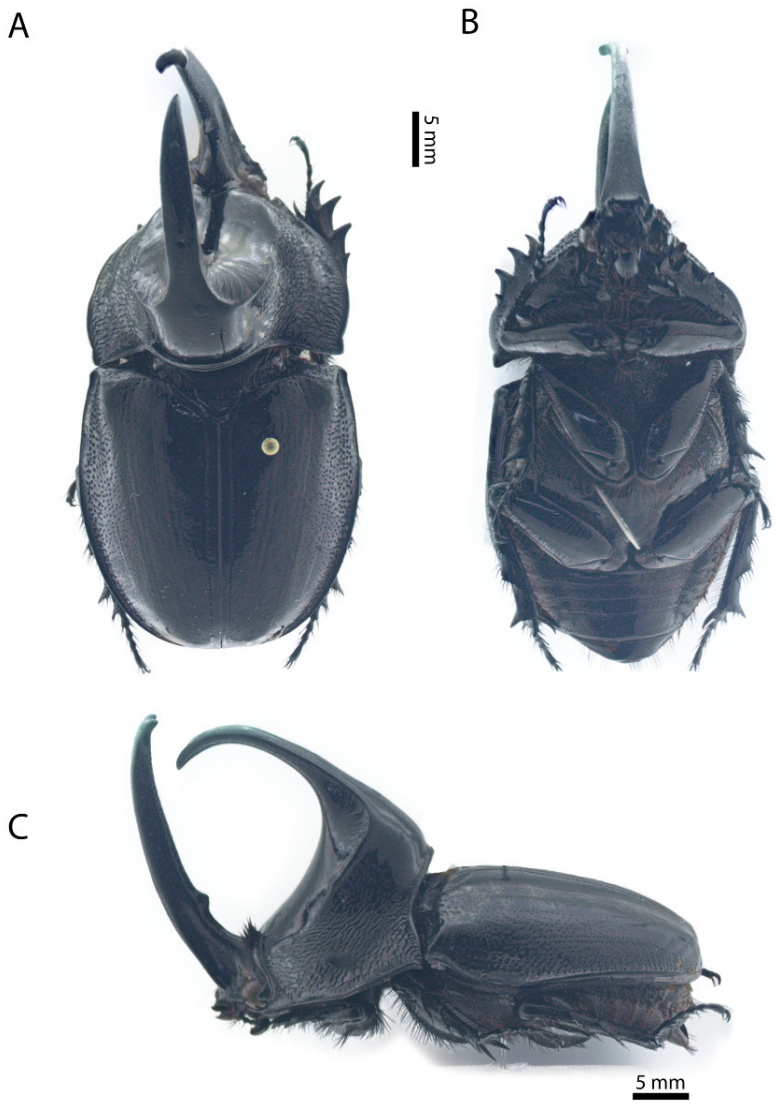

Figure 22. (A-C) Habitus de *Enema pan* Hope, 1837 male: A. Dorsal view; B. Ventral view; C. Side view. Scale: A-C: 5mm;

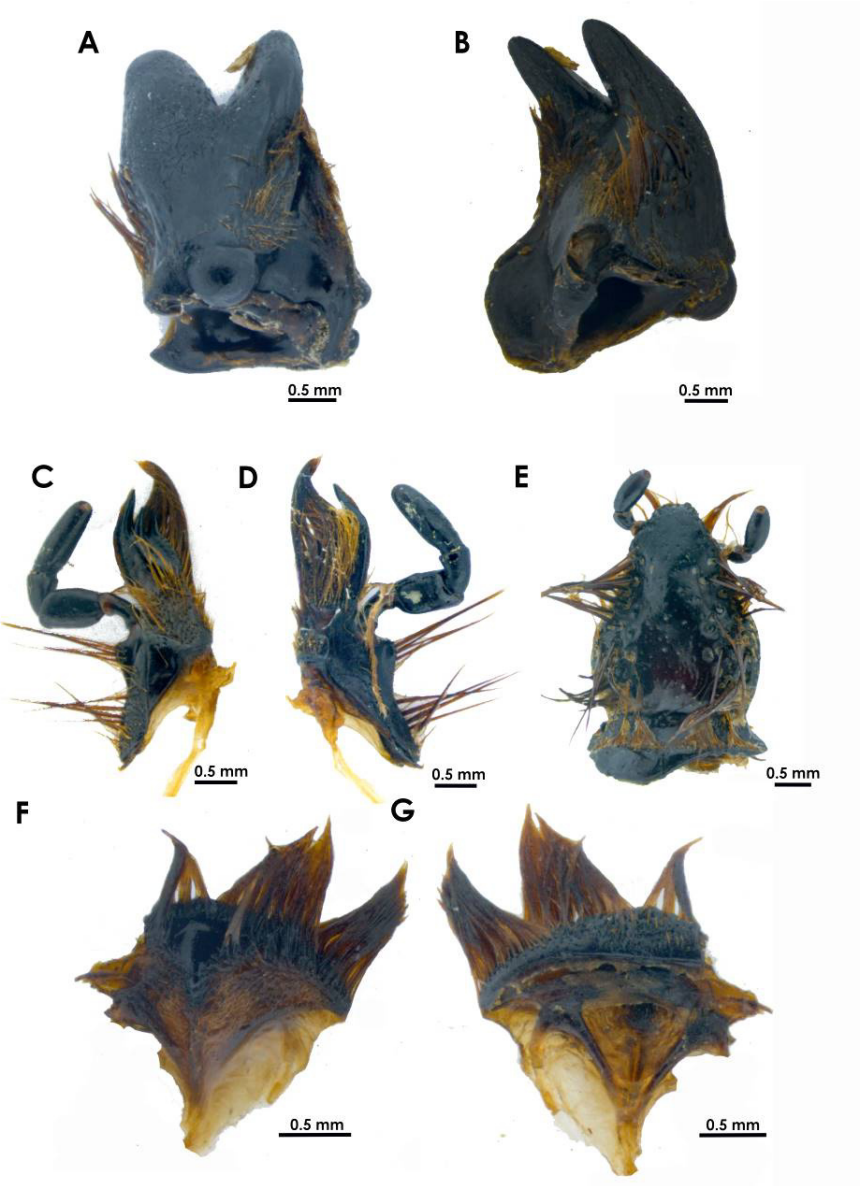

Figure 23. (A-G) Mouthparts of *Enema pan* (Fabricius, 1775): A. Mandible dorsal view; B. Mandible, lateral view; C. Maxilla dorsal view; D. Maxilla dorsal view and palpomere IV with sensory area; E. Mentum ventral view; F. Labrus dorsal view; G. Labrus ventral view. Scale: A-H: 0.5mm;

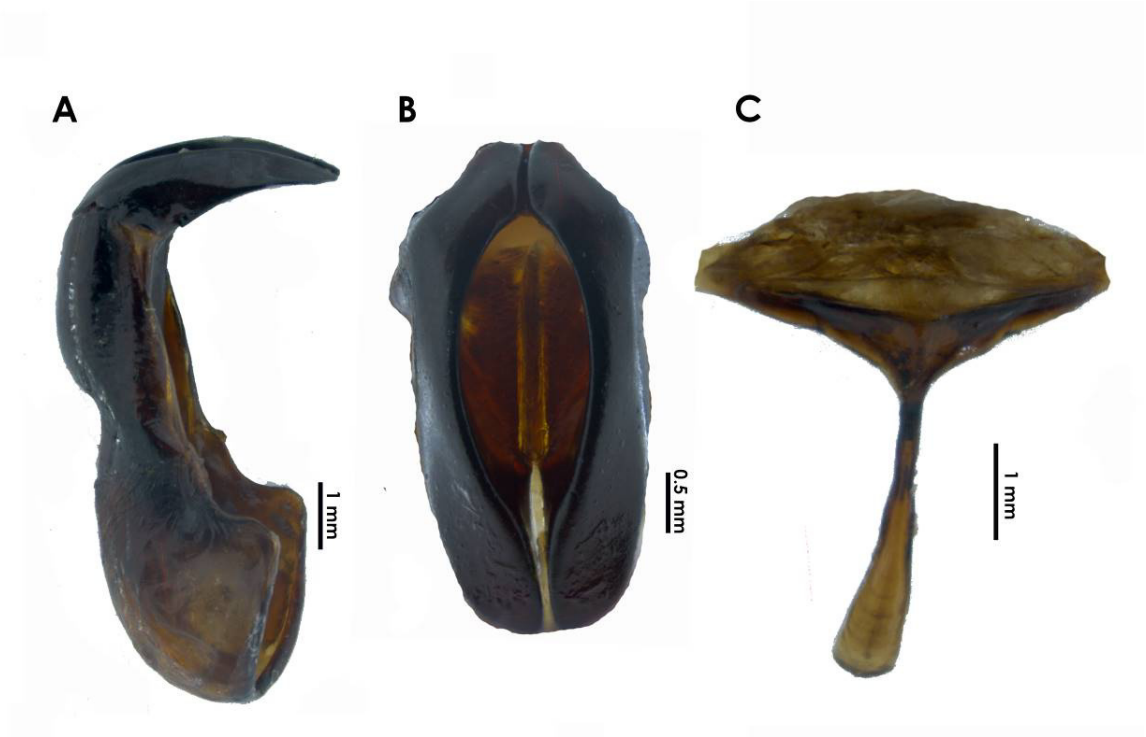

Figure 24. (A-C) Structures of terminalia, *Enema pan* (Fabricius, 1775): A. Aedeagus lateral view; B. Parameres dorsal view; C. Gastrointestinal spike. Scale: A-C: 1mm; B: 0.5mm;

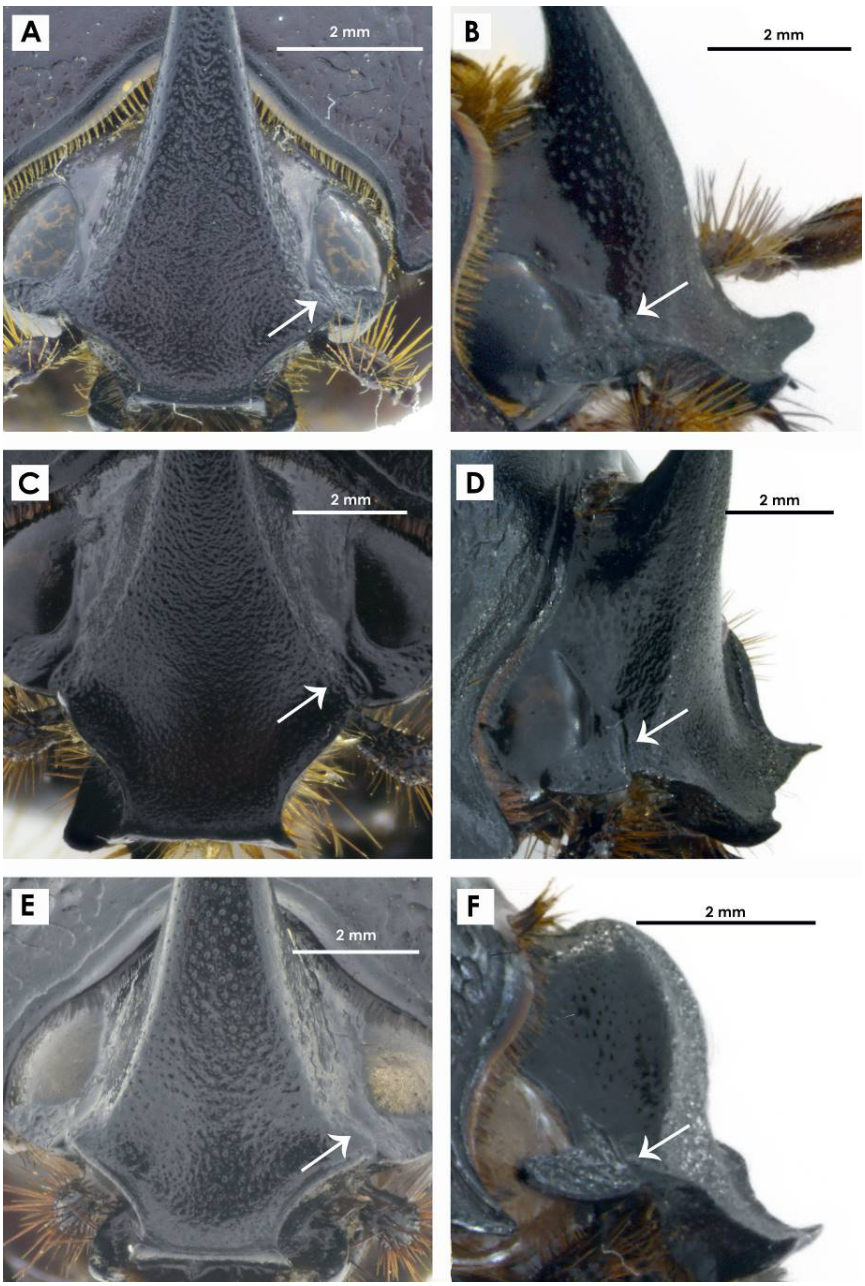

Figure 25. (A-F) Fronto Cliperal Suture: A-B. *Enema endymion*; CD. *Enema gibbicollis*; E-F. *Enema* sp.1;

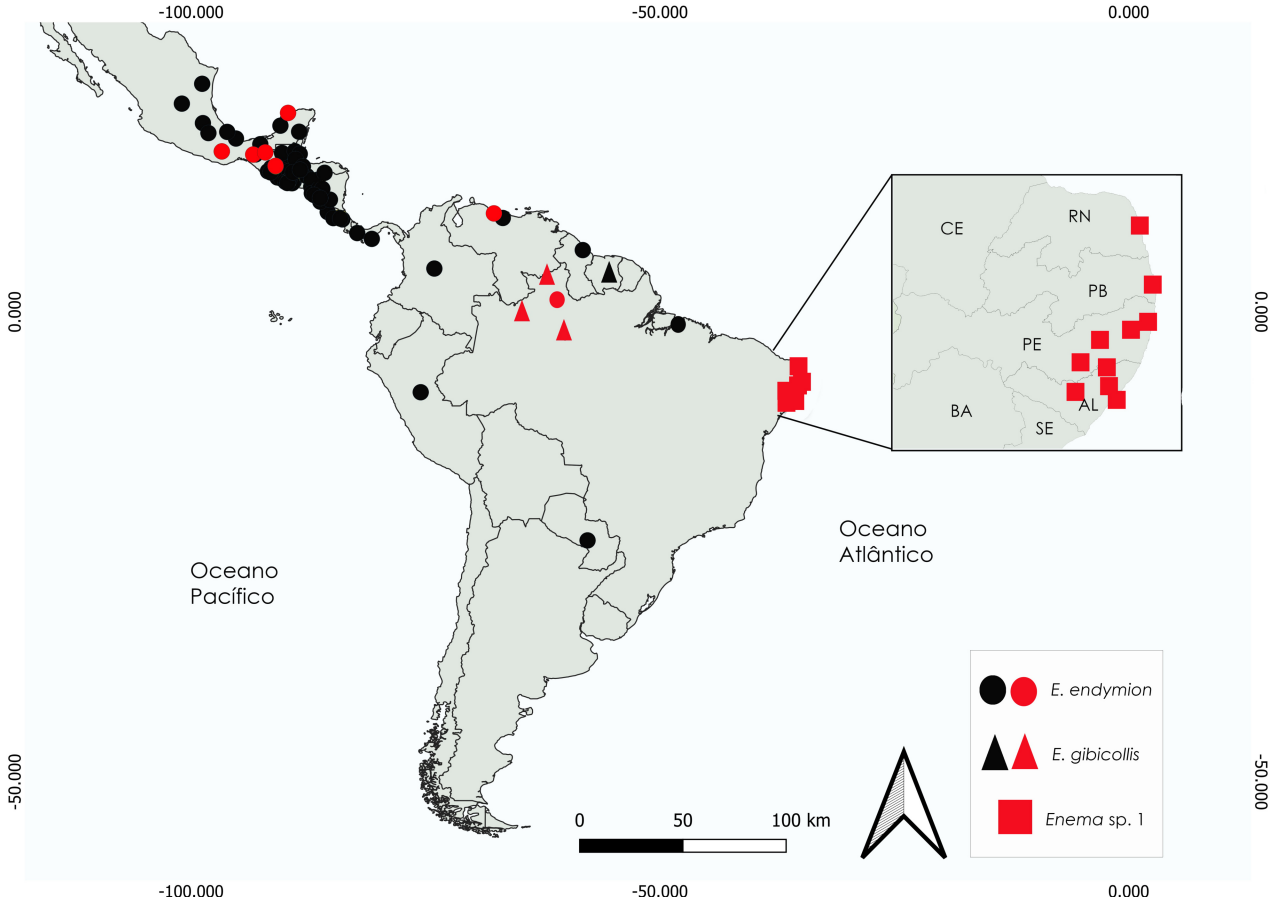

Figure 26. Species distribution map; Figures in Red to data from the examined material, figures in black are from the bibliography

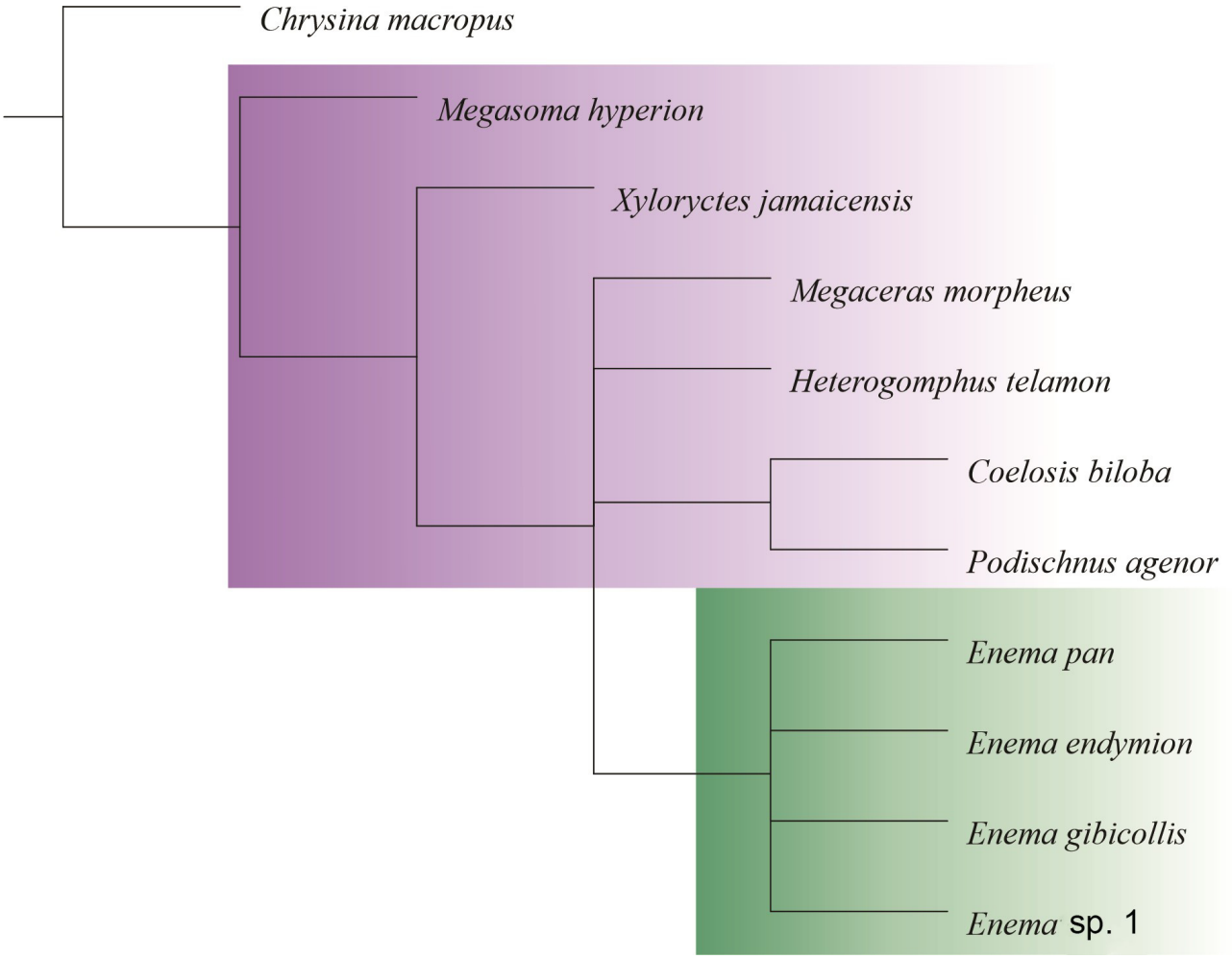

Figure 27. Equal Weight Consensus Tree (CI= 0.44; RI= 0.44);

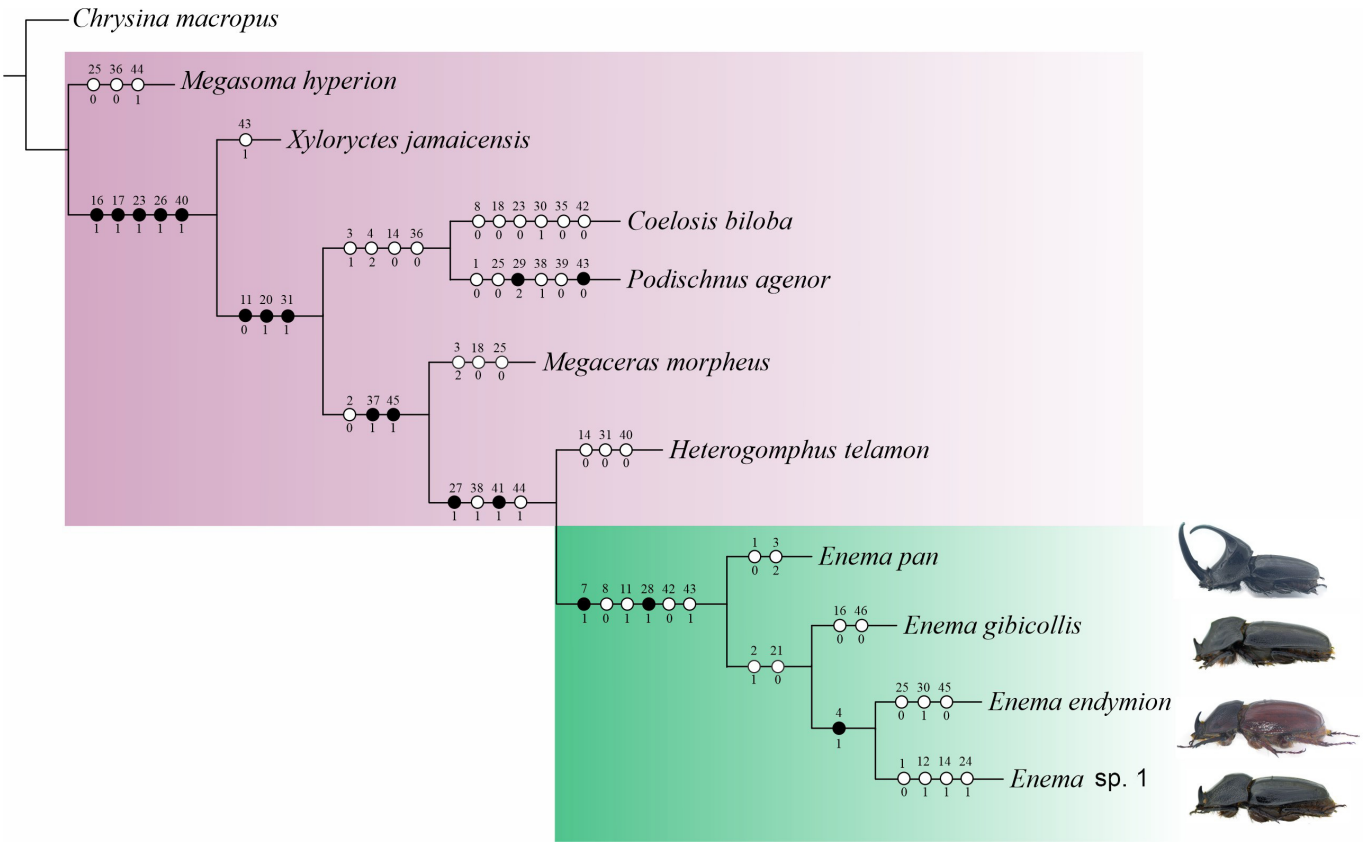

Figure 28. Tree with implicit weighting with a length of 109 steps (CI= 0.47 RI= 0.51) with k = 3000, black dots for synapomorphies and white dots for homoplasies;

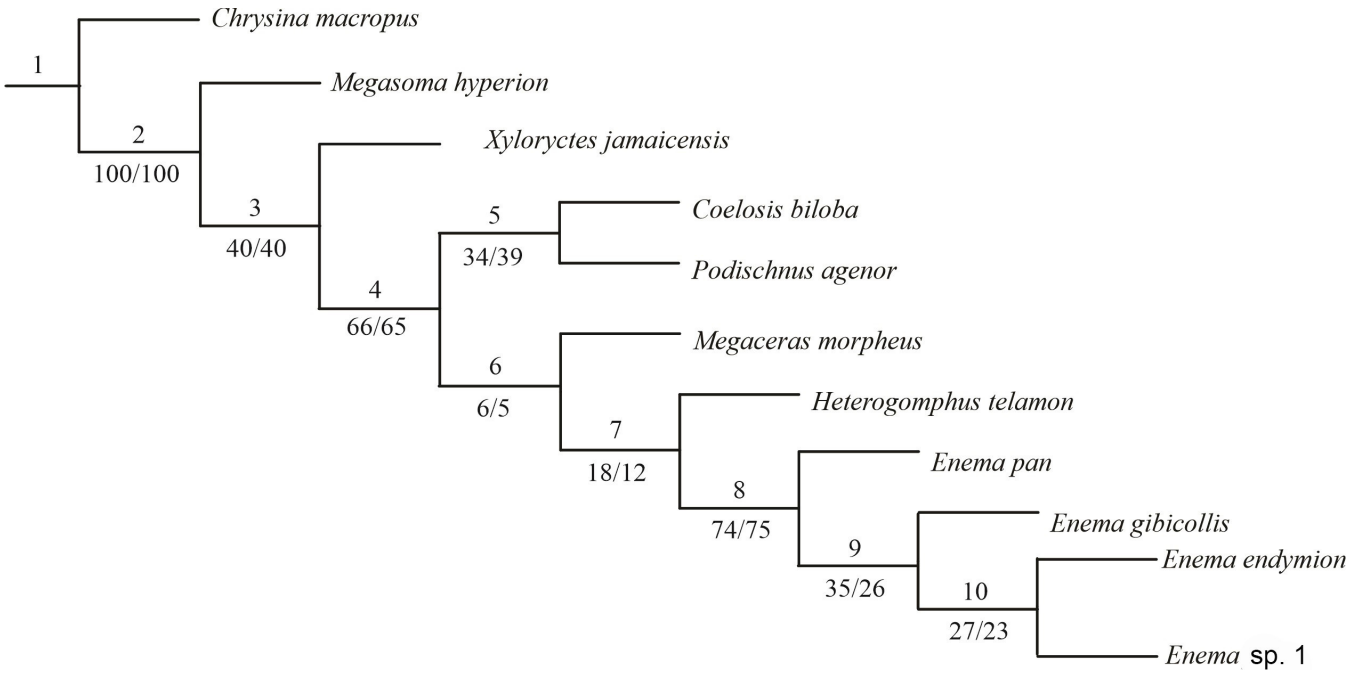

Figure 29. Implicit weight tree with length of 109 steps (CI= 0.47 RI= 0.51) with *k* = 3000 with values for symmetric resampling and bootstrap, indicating the number of nodes;

CAPÍTULO 3

FINAL CONSIDERATIONS

Enema consists of four species, namely; *E. pan, E. endymion, E. gibbicolis*, and *E.* sp.1. The species *E. pan*, need a taxonomic review, during the work I verified a morphological in species that occur in the Brazilian Pantanal, as well as in Colombia and Mexico, suggesting that they are complexes of different species. The hypothesis that the genus would be monophyletic was confirmed, with a high support, but for the internal relationship of the species it is necessary to include internal characters, such as endophallus, wing structures and, if possible, molecular analysis for all species.