

SISTEMÁTICA DO GÊNERO *BOTHYNUS* HOPE, 1837 (COLEOPTERA:

MELOLONTHIDAE: DYNASTINAE: PENTODONTINI)

por

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RESUMO

Entre os Pentodontini da Região Neotropical, *Bothynus* Hope, 1837 é terceiro maior gênero, com 31 espécies válidas, todas ocorrendo na América do Sul, somente duas estendem sua distribuição até o México. Diante da inexistência de trabalhos sistemáticos que abrangem o gênero com um todo, a presente tese teve os seguintes objetivos: 1) com bases em caracteres morfológico, testar filogeneticamente a hipótese de monofilia do gênero *Bothynus* e propor hipóteses de relacionamento para as espécies que compõe o gênero, tal como para os demais gêneros de Pentodontini do Novo Mundo (CHAPTER II); 2) apresentar uma revisão taxonômica detalhada para o gênero *Bothynus* (CHAPTER III). Para a análise filogenética foram encontrados 74 caracteres morfológicos obtidos pelo exame de 55 táxons, 38 do grupo interno e 17 do grupo externo. Os resultados da análise filogenética sugerem a parafilia do gênero *Bothynus*, com sua monofilia sendo dependente da exclusão de *B. herbivorus* (Arrow, 1937) e *B. complexus* Dechambre, 2006. Uma linhagem (excluso *B. herbivorus* e *B. complexus*) contendo 36 táxons de *Bothynus* foi recuperado com alto valor de bootstrap (87%). As relações internas mostram a linhagem *Bothynus* separadas em cinco clados aqui chamados de grupo *villiersi*, grupo *medon*, grupo *complanus*, grupo *entellus* e grupo *ascanius*. Com base na análise filogenética e na revisão taxonômica, *B. herbivorus* é movido para *Cephaloplanum* gen. nov. e *B. complexus* é movido para

Eremobothynus Ohaus, 1910. Na revisão taxonômica, *Bothynus* é redescrito juntamente com suas espécies, e são apresentados imagens, novos caracteres diagnósticos, uma chave de identificação e mapas de distribuição geográfica atualizados para as espécies de *Bothynus*. Adicionalmente, são apresentadas a descrição de oito novas espécies: *B. moroni* sp. nov. Duarte & Grossi, 2020, *B. andrezus* sp. nov. Duarte & Grossi, 2020, *B. tamare* sp. nov. Duarte & Grossi, 2020, *B. leidianae* sp. nov. Duarte & Grossi, 2020, *B. sebastiani* sp. nov. Duarte & Grossi, 2020, *B. aydanus* sp. nov. Duarte & Grossi, 2020, *B. simplex* sp. nov. Duarte & Grossi, 2020, and *B. belenensis* sp. nov. Duarte & Grossi, 2020. É proposto ainda a sinonimização de *B. striatellus* (Fairmaire, 1878) com *B. fabius* (Fairmaire, 1878), que passa a ter agora o nome válido.

PALAVRAS-CHAVE: América do Sul, diversidade, filogenia, novas espécies, Região Neotropical, Scarabaeoidea

SYSTEMATICS OF THE GENUS *BOTHYNUS* HOPE, 1837 (COLEOPTERA:
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ABSTRACT

Among the Neotropical Pentodontini, *Bothynus* Hope, 1837 is the most diverse, with 29 valid species, all occurring in South America, only two these extend its distribution to Mexico. Given the lack of systematic studies that cover the genus as a whole, the present thesis has the following objectives: 1) based on morphological characters, assess phylogenetically the monophyletic hypothesis of the genus *Bothynus* and propose relationship hypotheses for the species that compose the genus, as well as from other genera of Pentodontini of the New World (CHAPTER II); 2) expose a detailed taxonomic review for the genus *Bothynus* (CHAPTER III). For the phylogenetic analysis were found 74 morphological characters obtained by the examination of 55 taxa, 38 from the in-group, and 17 from the out-group. The cladistic analysis was based on 74 morphological characters obtained from the examination of 55 taxa, 38 of the in-group and 17 of the out-group. Results of the phylogenetic analysis suggest the paraphyly of the genus *Bothynus*, with its monophyly being conditioned to exclusion of *B. herbivorus* (Arrow, 1937) e *B. complexus* Dechambre, 2006. A lineage (excluded *B. herbivorus* and *B. complexus*) with 36 *Bothynus* was recovered with high bootstrap value (87%). Internal relationships showing the *Bothynus* lineage separated in five clades named here as *villiersi* group, *medon* group, *complanus* group, *entellus* group and *ascanius* group. Based on the phylogenetic analysis and

taxonomic revision, two new combinations are proposed: *B. herbivorus* is moved to *Cephaloplanum* gen. nov. and *B. complexus* is moved to *Eremobothynus* Ohaus, 1910. In the taxonomic revision, *Bothynus* is redescribed along with its species, where are presented images, new diagnostic characters, identification key, and geographic distribution maps for all *Bothynus* species. Additionally, the description of eight new species are presented: *B. moroni* sp. nov. Duarte & Grossi, 2020, *B. andrezus* sp. nov. Duarte & Grossi, 2020, *B. tamare* sp. nov. Duarte & Grossi, 2020, *B. leidianae* sp. nov. Duarte & Grossi, 2020, *B. sebastiani* sp. nov. Duarte & Grossi, 2020, *B. aydanus* sp. nov. Duarte & Grossi, 2020, *B. simplex* sp. nov. Duarte & Grossi, 2020, and *B. belenensis* sp. nov. Duarte & Grossi, 2020. The validation of the name *B. fabius* (Fairmaire, 1878) and the synonymization of *B. striatellus* (Fairmaire, 1878) with it are also proposed here.

KEY WORDS: diversity, Neotropical Region, new species, phylogeny, Scarabaeoidea, South America.

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RECIFE - PE

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DEDICATÓRIA

Aos meus pais Paulo Santana Duarte (*In memoriam*) e Maria Joana Marinho Duarte (*In memoriam*), que cuidaram, acreditaram e sempre fizeram o melhor por mim.

“There is a grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity from so simple a beginning endless forms most beautiful and most wonderful have been and are being evolved.” (**Charles Darwin**)

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RECOMMENDATIONS

New names proposed in this study should do not adopted to nomenclatural objective due the present thesis does not represent a valid publication in accord to the International Code of Zoological Nomenclature.

RECOMENDAÇÕES

Os novos nomes propostos neste estudo não devem ser adotados com objetivo nomenclatural, visto que a presente tese não representa uma publicação válida segundo o Código Internacional de Nomenclatura Zoológica.

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CAPÍTULO 1

INTRODUÇÃO

1.1 Scarabaeoidea: aspectos gerais

Scarabaeoidea está entre as maiores e mais diversificadas superfamílias de Coleoptera, com cerca de 39,529 espécies conhecidas Schoolmeesters (2020). Scarabaeoidea possui distribuição cosmopolita e táxons dessa superfamília diversificaram em vários ambientes, com diferentes hábitos alimentares, sendo fungívoros, necrófagos, saprófagos, coprófagos, herbívoros e carnívoros. Certos Scarabaeoidea apresentam cuidado parental, outros são termitófilos, mirmecófilos ou ectoparasitas (Jameson & Ratcliffe 2002). Alguns possuem importância agrícola, como *Diloboderus abderus* Sturm, 1826 e *Phyllophaga cuyabana* Moser, 1918, que são pragas de soja e algodão (Rodrigues & Pereira 2014). Há outros que exercem importante função ecológica, como os scarabaeíneos, que utilizam o solo para alocação de recurso, abrigo e nidificação (Davis *et al.* 2001). Assim, atuam como agentes na ciclagem de nutrientes, aeração do solo, dispersão secundária de sementes e redutores de parasitas presentes em fezes de mamíferos (Andresen 2002, Endres *et al.* 2005).

Os adultos de Scarabaeoidea são caracterizados pelo protórax adaptado à escavação, tal como as tíbias anteriores (geralmente providas de dentes), as coxas são largas (quase sempre com trocantinos escondidos e cavidades fechadas, as asas apresentam venação reduzida providas de um mecanismo de dobramento intrínseco, clava antenal lamelada, e ainda apresentam quatro túbulos de Malpighi. As larvas são do tipo scarabaeiforme, geralmente esbranquiçadas, em formato de “C”, a cabeça é distinta, quitinizada, pernas e antenas são bastante desenvolvidas (Lawrence & Britton 1991).

1.2 Classificação dos Scarabaeoidea

O sistema de classificação de Scarabaeoidea sofreu várias mudanças ao longo da história. Kohlmann & Morón (2003) e Kohlmann (2006) realizaram uma análise histórica detalhada acerca do processo de classificação dessa superfamília, baseados no número e tipo dos caracteres morfológicos, então dividiram em três períodos:

1. Pré-Darwinista (1736–1856): iniciado por Carl Von Linné e terminando em Lacordaire, aborda 14 autores diferentes, sendo a classificação dos táxons influenciada pelo pensamento essencialista que vigorou durante o período, não sofrendo nenhuma influência das ideias Darwinistas.

2. Pós Darwinista e Pré-Hennigiano (1859–1949): baseado em trabalhos taxonômicos e faunísticos de 17 autores, influenciados pela visão da ancestralidade comum proposta por Darwin. Novas abordagens surgiram, como a classificação pela caracterização larval feita por Mulsant & Rey (1871) e as relações evolutivas da através da comparação da genitália masculina entre os grupos de Scarabaeoidea (Sharp & Muir 1912). No entanto, apesar da abordagem evolucionista, não existia até então uma metodologia adequada a ser empregada na classificação.

3. Pós Hennigiano (1951–2006): com o advento de ferramentas computacionais, juntamente com o emprego de outras disciplinas, como a estatística, a matemática, a biologia celular e a genética, o processo de descrição da diversidade tornou-se mais analítico e informações sobre citologia, hábito alimentar, ecologia e distribuição geográfica foram utilizadas. Mas foi Hennig (1950) quem criou um novo paradigma metodológico para as classificações através da análise cladística.

Apesar da longa história de classificação, entretanto não existe um consenso quanto à posição das famílias e subfamílias dentro de Scarabaeoidea, havendo mudanças no número

relativo de táxons de acordo com o sistema adotado. Erichson (1848) separou os Scarabaeoidea em duas séries baseado na posição dos espiráculos abdominais e no hábito alimentar, reunindo dentro da série Pleurosticti aqueles táxons que apresentam os espiráculos situados no ápice dos esternitos e os hábitos fitófago ou fitosaprófago, e agrupou dentro da série Laparosticti, táxons com os espiráculos situados na membrana pleural e com hábito coprófago ou saprófago. Janssens (1949) divide a Superfamília em três famílias: Lucanidade, Passalidae e Scarabaeidae, mantendo as séries proposta por Erichson (1848) para esta última família. Posteriormente, Balthasar (1963) propôs um sistema de classificação, modificada por Paulian (1988), e elevou os táxons da série Pleurosticti à categoria de família (18) famílias, sendo este sistema adotado por autores Europeus. Mediante uso da taxonomia numérica, Endrödi (1966) analisou e dividiu Scarabaeoidea em cinco famílias: Lucanidade, Passalidae, Trogidae, Scarabaeidae e Melolonthidae, e propôs o abandono das séries Laparosticti e Pleurosticti pela inconsistência dos caracteres que dividem essas duas séries e reuniu dentro de Melolonthidae os táxons que apresentam hábitos fitófagos ou fitossaprófagos.

As propostas de classificação mais recentes são a de Browne & Scholtz (1995, 1999), que mediante análise cladística recuperaram 14 famílias, e Lawrence & Newton (1995) que consideram 13 famílias. As classificações destes últimos trabalhos são semelhantes, exceto o sistema de Lawrence & Newton (1995) que não consideram Bolborceratidae como família.

1.3 Scarabaeidae X Melolonthidae

Melolonthidae foi definida na classificação de Endrödi (1966) como um grupo cosmopolita, abrangendo táxons com hábitos fitófagos ou fitosaprófagos, compreendendo Melolonthinae, Euchirinae, Rutelinae, Phenomerinae, Dynastinae, Cetoniinae, Glaphyrinae e Systellopodinae. Na América Latina, essa classificação foi primeiramente seguida por Morón (1976), e adotada

também em trabalhos posteriores (Morón 1984, 1997), tendo grande influência na adesão dessa classificação por pesquisadores da escola Latino Americana, principalmente aqueles interessados no estudo de grupos associados à cultivos agrícolas (Ratcliffe *et al.* 2013, Cherman & Morón 2014). Entretanto, o sistema de Endrödi (1966) é contestado principalmente por autores da escola Norte Americana, que empregam os sistemas de Browne & Scholtz (1995, 1999) e Lawrence & Newton (1995), que consideram Melolonthidae como subfamília (Melolonthinae) de Scarabaeidae, sendo estes sistemas os mais utilizados mundialmente e adotados por autores como Jameson & Ratcliffe 2002, Löbl & Smetana (2006), Smith (2006) e Bouchard *et al.* (2011). Também autores como Ratcliffe & Jameson (2004) defendem que Melolonthidae não é um nome válido pelo princípio de prioridade do Código Internacional de Nomenclatura Zoológica (IZCN) (artigo 23.1), já que Cetoniinae foi estabelecido por Leach (1815) enquanto que Melolonthinae foi estabelecido por Samouelle (1819) e portanto Cetoniidae teria prioridade como nome da família por ser mais antigo.

Mediante profunda revisão de literatura, Cherman & Morón (2014) propõem a validação de Melolonthidae. Estes autores defendem que análises filogenéticas mais recentes, baseados em caracteres moleculares (ver Smith *et al.* 2006) e morfológicos de larvas e adultos (ver Lawrence *et al.* 2011) não apoiam a monofilia de Scarabeidae. Ainda Cherman & Morón (2014), apoiados na exceção contida no artigo 35.5 do IZCN, argumentam que o nome Melolonthidae foi mais utilizado que Cetoniidae, e, portanto, levaria o nome da família, além disso, propõem que Cetoniidae deveria ser considerado como uma família à parte de Melolonthidae. A filogenia molecular de Ahrens *et al.* (2014), recuperaram a polifilia de Scarabaeidae, separando o clado coprófago (Scarabaeinae + Aphodiinae) do clado fitófago (Melolonthinae + Rutelinae + Dynastinae + Cetoniinae (este último monofilético)), corroborando os estudos de Smith *et al.*

(2006) e Lawrence *et al.* (2011) e reforçando a separação de Cetoniidae e Melolonthidae como famílias distintas de Scarabaeidae.

1.4 Subfamília Dynastinae

Entre os Pleurosticti, Dynastinae é uma das subfamílias mais notáveis, ocorrendo na maioria das áreas biogeográficas do mundo (exceto nas áreas polares), principalmente nos trópicos (Ratcliffe & Cave 2006, Ratcliffe *et al.* 2013). A região Neotropical é detentora da maior diversidade de Dynastinae, com aproximadamente 2000 espécies (Endrödi 1985, Schoolmeesters 2018).

Os dinastíneos exercem função importante no ecossistema através da atividade decompositora. As larvas destes besouros degradam a madeira durante a alimentação, originando produtos através da excreção que facilitam a ação de outros organismos, o que torna estes coleópteros importantes para a ciclagem de nutrientes (Morón 1985). Algumas destas larvas também são benéficas em sistemas agroecológicos, pois constroem túneis através da movimentação, aumentando a areação do solo e facilitando a drenagem de água, além disso, incorporam matéria orgânica ao solo, aumentando a CTC deste (Oliveira *et al.* 2012). Os adultos geralmente são noturnos ou crepusculares sendo atraídos pela luz à noite. Alimentam-se de frutas maduras ou podres, raízes ou exsudados de plantas. Machos adultos geralmente possuem chifres extravagantes na cabeça, pronoto ou em ambas as partes, o que deu origem a nomes populares como besouro-rinoceronte, besouro-elefante, besouro-hércules, besouro-unicórnio (Ratcliffe *et al.* 2013). Também são chamados de besouro-escaravelho, besouro-de-chifre, cascudinho e em algumas regiões do Brasil são temidos pela aparência, pelo som do voo e pelas crenças de que estes besouros podem trazer malefícios (Lenko & Papavero 1996).

Dynastinae está dividida em oito tribos segundo Endrödi (1985): Dynastini, Phileurini, Oryctoderini, Hexodontini, Agaeocephalini, Cyclocephalini, Oryctini e Pentodontini. No entanto, a monofilia dessas tribos não é bem estabelecida. Membros de Dynastinae são reconhecido pelos seguintes caracteres: labro pequeno, delgado não ultrapassando a margem anterior do clipeo; mandíbulas expostas lateralmente ao clipeo; antenas com nove ou dez segmentos, base do escapo escondido pela expansão laterobasal do clipeo e pelo canto ocular; mesoepímeros escondidos pelos ângulos humerais do élitro; escutelo visível; pigídio exposto; garras meso- e metatarsais simples, não móveis, similar em forma; procoxas transversas (Ratcliffe & Morón 1997, Ratcliffe *et al.* 2013).

1.4.1 Dynastini MacLeay, 1819

Os Dynastini estão entre os maiores e mais conhecidos coleópteros (Casey 1915). Espécies do gênero *Dynastes* Kirby, 1825 podem alcançar os 170 mm (Lachaume 1985). Adultos dessa tribo são caracterizados como seguinte: corpo robusto e convexo; protarsômeros alongados (último protarsômero raramente alargado no macho); borda externa mandibular retas ou lobadas, fendidas no ápice; mento alargado, não cobrindo a base dos palpos labiais; propigídio com ou sem área estridulatória; apresentam dimorfismo sexual acentuado, os machos exibem ornamentos exuberantes na cabeça e no pronoto, além dos élitros lisos; nas fêmeas os ornamentos cefálico e pronotal estão ausentes, apresentando ainda os élitros esculpados (Endrödi 1976, 1985).

Os imaturos se caracterizam pelos seguintes aspectos: larvas com antenas apresentando de 4 a 28 pontos sensoriais no último artículo; denticulos estridulatórios das maxilas truncados; mandíbula esquerda com quatro dentes na área incisória; estigmas respiratórios com “bulla” proeminente em vista vertical; raster sem palidia nem septula; tarsúngulos com dois a cinco setas (Ritcher 1966, Morón 1977, 1987, 1995). As pupas apresentam de cinco a seis pares de órgãos

dioneiformes; primeiro estigma abdominal oculto; estigma II–IV desenvolvidos; VI–VIII pequenos, fechados, ocultos; laterais do tergo com tubérculos e urogomphi ausentes (Morón 1993).

Rowland & Miller (2012) verificaram as relações entre os gêneros de Dynastini mediante análise filogenética, baseada em dados morfológicos e moleculares. Estes autores dividiram a tribo em três subtribos: Dynastina, que compreende o clado Africano (*Augosoma*) mais o clado do Novo Mundo (*Dynastes*, *Megasoma*, *Golofa*) e grande clado Australasiano, composto pelas subtribos Xylotrupina (*Tryopoxylus*, *Xyloscapes*, *Allomyrina*, *Xylotrupes*) e Chalcosomina (*Haploscapanes*, *Chalcosoma*, *Beckius*, *Eupatorus*, *Pachoryctes*). Dutrillaux *et al* (2013) analisou o cariótipo de alguns membros de Dynastinae e testou filogeneticamente a relação destes baseados em dados moleculares, e mostrou que *Augosoma* (Dynastini) está mais relacionado com *Oryctes* (Oryctini) do que com membros de Dynastini. Tal resultado evidencia a fraca delimitação tribal em Dynastinae, carecendo de estudos que suportem a delimitação das tribos.

1.4.2 Agaocephalini Casey, 1915

Agaocephalini está restrita ao Novo Mundo e contém 11 gêneros e 48 espécies descritas (Gillett 2009, Neita-Moreno 2015, Sobral *et al.* 2018). Todos os gêneros e cerca de 42 espécies ocorrem na América do Sul, somente *Aegopsis* Burmeister e *Spodistes* Burmeister tem distribuição na América Central (Neita-Moreno 2015).

A delimitação de Agaocephalini é complicada devido à alta variabilidade dos caracteres apresentados pelos adultos entre os diversos gêneros, sendo em alguns casos muito similares à membros de Dynastini (Ratcliffe 2003). No entanto, os Agaocephalini podem ser caracterizados da seguinte forma: coloração de aspecto metálico, pontuações do élitro dispostas irregularmente; cabeça e pronoto dos machos geralmente providos de projeções, e tarsos anteriores algumas vezes

alargados; as fêmeas caracterizam-se pela ausência de projeções, somente com um ou dois tubérculos na frente, e tarsos simples, o propigídio apresenta área estridulatória fina ou ausente (Endrödi 1970, Endrödi 1985, Gillet 2009, Gasca-Álvares & Amat-García 2010). Quanto aos estágios imaturos, são conhecidas somente a larva e a pupa de três espécies: *Lycomedes hirtipes* Arrow, *Aegopsis bolboceridus* (Thomson) e *A. curvicornis* Burmeister (Pardo-Locarno & Morón 2006, Neita-Moreno *et al* 2014).

As larvas de Agaocephalini podem ser reconhecidas pela seguinte combinação de caracteres: labro ligeiramente assimétrico, epifaringe com margem lateral direita circular, sendo a margem lateral esquerda angular. Ápice do quarto dente incisor da mandíbula esquerda bífido ou inteiro. Último segmento antenal apresentando 6–10 pontos sensoriais. Ocelos presentes. Garras tarsais apresentando duas setas. Segmento abdominal 1 e 8 com espiráculos menores em tamanho comparado aos espiráculos 2–7 (Neita-Moreno *et al.* 2014).

A história natural da maioria dos Agaocephalini ainda é desconhecida. Os adultos são noturnos, sendo atraídos pela luz à noite (Neita-Moreno 2014). Oliveira *et al.* (2012) relataram larvas de *E. bolboceridus* alimentando-se de raízes de diversas plantas, em cultivos localizados na região central do Brasil. Até o presente momento não há estudos que definam a posição filogenética da tribo.

1.4.3 Oryctoderini Endrödi, 1966

Oryctoderini apresenta cerca de 11 gêneros e 48 espécies descritas até o momento (Krajcik 2005, Jameson & Ratcliffe 2009, Jákl & Zidek 2016). Endrödi (1966) definiu a tribo baseado em caracteres morfológicos e na distribuição geográfica, sendo que, anteriormente à essa publicação, gêneros dessa tribo pertenciam à Cyclocephalini. Táxons de Oryctoderini estão distribuídos nas

regiões Indo-malaio, Oriental e da Oceania, entretanto, membros de Cyclocephalini ocorrem no Novo Mundo (Endrödi 1966, 1971).

A diagnose de Oryctoderini é imprecisa e a sua posição filogenética necessita de avaliação, para busca de sinapormorfias que definam a tribo (Jameson & Ratcliffe 2009). Apesar disso, Endrödi (1966, 1971, 1985) distinguiu os adultos de Oryctoderini pelos seguintes aspectos: coloração geralmente de marrom a negro, algumas vezes com reflexos metálicos ou marcações brancas; ápice clipeal levantado e truncado, ou com 1–4 dentes; fronte uni- ou bituberculada; as mandíbulas podem estar cobertas pelo clipeo ou expostas lateralmente a este; antena com 9–10 segmentos, lamelas curtas em ambos os sexos; pronoto geralmente convexo, raramente apresentando tubérculo ou concavidade; élitros geralmente desprovido de pontuações; propigídio com ou sem área estridulatória; protíbia bi- ou tridentada; tíbias posteriores com ápice truncado ou apresentando 1–4 dentes oblíquos e triangulares; protarsos dilatados ou não nos machos, garra interna não incisas.

1.4.4 Cyclocephalini Laporte, 1840

Cyclocephalini figura como a segunda maior tribo de Dynastinae, com 16 gêneros e mais de 500 espécies, a maioria dessas, pertencentes ao gênero tipo *Cyclocephala* Dejean (Moore *et al.* 2018, Paucar-Cabrera & Moore 2018). A tribo possui distribuição Pantropical, com grande parte dos gêneros restritos ao Novo Mundo, somente *Ruteloricetes* Arrow, 1908 encontra-se na África ocidental e *Peltonotus* Burmeister, 1847 está na Ásia (Dechambre 2006, Jameson & Wada 2004).

Membros dessa tribo são importantes visitantes florais. Cerca de 97 espécies foram relatadas sobre flores de 58 gêneros de plantas, representadas por 17 famílias e 15 ordens, evidenciando relações mutualísticas de táxons de Cyclocephalini com as famílias Nymphaceae, Annonaceae, Magnoliaceae, Araceae, Cyclathaceae e Arecacea (Moore & Jameson 2013). Certos

Cyclocephalini são potenciais polinizadores de culturas agrícolas, como a da graviola *Annona muricata* L., sendo registradas seis espécies de *Cyclocephala* nesta cultura para o Brasil: *C. amazona* (L., 1767); *C. celata* Dechambre, 1980; *C. vestita* Höhne, 1923; *C. picipes* (Olivier, 1789); *C. brittoni* Endrödi, 1964; *C. stictica* Burmeister, 1847 (Parizotto & Grossi 2018). Entretanto, existem outras espécies que são consideradas pragas em cultivos agrícolas. Na Colômbia, *C. amazona* foi registrada causando injúrias em plantas de feijão (*Phaseolus vulgaris* L.) e dendê (*Elaeis guineensis* Jacq.), no Brasil, *Dyscinetus rugifrons* Burmeister, 1847, foi registrado atacando plantas de palmeira-real-da-austrália (*Archontophoenix* spp.) (Posada Ochoa 1989, Vitorino *et al.* 2008).

Historicamente, a diagnose dos adultos de Cyclocephalini baseou-se na ausência de características, como: cabeça sem tubérculos, chifres ou carenas; protórax sem concavidade, chifres ou tubérculos; propigídio sem área estridulatória; área molar mandibular com dentição ausente; articulação basal dos metatarsos simples, não apresentando a forma triangular; são pouco dimórficos sexualmente (Ratcliffe & Cave 2017). São conhecidos somente larvas e pupas de 4 dos 16 gêneros de Cyclocephalini, o que torna difícil a definição tribal baseada em características presentes nos imaturos (Moore *et al.* 2018).

Tal como as outras tribos pertencentes à Dynastinae, Cyclocephalini não é bem definida e sua monofilia deve ser testada (Ratcliffe & Cave 2006). Estudos realizados por Jameson (1998), Jameson *et al.* (2002), Jameson & Wada (2004), McKenna *et al.* (2014), para Rutelinae, mostram certa relação dessa subfamília com Dynastinae, principalmente com membros de Cyclocephalini. No entanto, como estes estudos estavam focados em Rutelinae, poucos táxons de Dynastinae foram utilizados na comparação, sendo necessários estudos filogenéticos que tenham como foco as relações entre os dinastíneos.

1.4.5 Hexodontini Lacordaire, 1856

Hexodontini é endêmica da ilha da Madagascar, representada apenas pelo gênero *Hexodon* Olivier, 1789 (Endrödi 1985). São conhecidas dez espécies, nove destas restritas ao sul da ilha, somente *Hexodon unicolor* (Olivier, 1789) ocorre em toda a ilha (Dechambre 1986). No entanto, Hexodontini parece não estar restrito à *Hexodon*, e a posição filogenética da tribo não é clara. No passado, os gêneros *Hemicyrthus* Reiche, 1860 e *Hexodon* foram inclusos na tribo Hemicyrtini por Paulian (1961). Endrödi 1976 transferiu *Hemicyrtus* para Oryctoderini baseado na distribuição geográfica. Dechambre (1986) discute a relação entre estes dois gêneros, fundamentado na morfologia das antenas e do canto ocular, que seriam sinapomorfias para Hexodontini, propondo a inclusão de *Hemicyrthus* nessa tribo. Krell & Theuerkauf (2015) explanam, biogeograficamente, a improvável relação entre esses dois gêneros, uma vez que *Hexodon* é restrito à Madagascar e *Hemicyrthus* é endêmico da Nova Caledônia, e que as sinapomorfias apresentadas por (Dechambre 1986) seriam características oriundas de convergência.

Hexodon são dinastíneos distinguidos por apresentarem braquipterismo, formato corporal largo e ovalar, ligeiramente achatado dorso-ventralmente, epipleura elitral disposta horizontalmente, as pernas são longas e delgadas (Endrödi 1985, Dechambre 1986, Le Tirant & Limoges 2016). Quanto aos estágios imaturos, somente é conhecida a larva de *H. unicolor*, na qual apresenta características similares a outros dinastíneos (Paulian 1961).

As espécies de *Hexodon* são diurnas, sendo capturadas com certa frequência sobre solo em áreas abertas ou estão ocasionalmente escondidos sob camadas de areia em praias. Alimentam-se de frutos maduros em decomposição, existindo relatos de espécies alimentando-se de plantas aquáticas secas na praia (Le Tirant & Limoges 2016).

1.4.6 Phileurini Burmeister, 1847

Os Phileurini são encontrados em quase todas as regiões do mundo, sendo conhecidos cerca de 31 gêneros e 231 espécies, com a maior diversidade da tribo concentrada no Novo Mundo, onde ocorrem 22 gêneros 138 espécies (Endrödi 1985, Grossi *et al.* 2008, Neita-Moreno & Ratcliffe 2010, Grossi & Grossi 2011, Ratcliffe 2011, Ratclife & Curoe 2011, Dupuis, 2012, Perger & Grossi 2013, Alberoni *et al.* 2014, Ratcliffe 2014, Neita-Moreno & Ratcliffe 2017).

Os adultos são caracterizados pelo dimorfismo sexual pouco aparente, corpo ligeiramente achatado dorso-ventralmente, clipeo geralmente acuminado, fronte geralmente com dois tubérculos ou chifres, mento amplo cobrindo a base dos palpos labiais, mandíbulas apresentando dentes agudos na borda interna ,pronoto geralmente com um sulco longitudinal, protórax visivelmente separado do pterotórax (Ratcliffe *et al* 1997, Ratcliffe *et al* 2013).

Quanto ao conhecimento dos imaturos da tribo, são conhecidos a larva de 13 espécies, pertencentes à 7 gêneros de Phileurini do Novo Mundo (Ibarra-Polesel *et al.* 2017, Arguez *et al.* 2017). Segundo Ritcher (1966) As larvas são caracterizadas pelo último segmento antenal com 2–5 pontos sensoriais dorsais, epifaringe apresentando chaetoparia com poucas ou nenhuma sensila, dentes estridulatórios maxilares truncados, dente mandibular esquerdo apresentando um dente pósincisivo (S4), raster sem palídia nem séptula. As pupas podem ser diagnosticadas pela presença de seis pares de órgãos dioneiformes (o primeiro mais evidente), estigma abdominal I escondido, II–IV grandes, V–VIII pequenos e fechados, tubérculos tergo-laterais ausentes e urogomphi ausentes (Morón 1993).

A história natural dos Phileurini ainda é pouco conhecida. Os adultos são noturnos, sendo atraídos pela luz à noite. Larvas e adultos de algumas espécies, como *Homophileurus interger* (Burmeister, 1847) e *H. luderwaldti* (Ohaus, 1910), são inquilinas de cupins (Costa *et al.* 1988, Ratcliffe & Skeller 2011). Outras espécies podem ser encontradas dentro de madeira em decomposição (Ratcliffe 2013). McCleve (2007) faz um apanhado com registros sobre

comportamento predatório de táxons adultos desta tribo sobre larvas de Coleoptera e Lepidoptera. Ibarra-Polese *et al.* (2017) observaram, em laboratório, adultos de *Phileurus valgus* (Olivier, 1789) predando larvas de *Leucothyreus costatus chaconus* Ohaus, 1931 e *Stenocrates holomelanus* (Germar, 1824).

Aparentemente, entre as tribos pertencentes à Dynastinae, Phileurini é a única que pode ser monofilética. Em sua tese, Ide (1998) (com resultados ainda não publicados) testou a posição tribal dos Phileurini da região Neotropical mediante análise cladística baseada em caracteres morfológicos. O autor recuperou a monofilia da tribo, sustentada por duas sinapomorfias: mento com área basal escavada e élitros estriados. O gênero *Platyphileurus* Ohaus, 1910, foi excluído da tribo por não compartilhar as sinapomorfias da mesma, sendo transferido para Pentodontini. Albertoni *et al.* (2014) estudou a história de vida e descreveu os estágios imaturos de *Platyphileurus felscheanus* Ohaus, 1910, e baseado nos caracteres da pupa, transferiu o gênero para Oryctini.

1.4.7 Oryctini Mulsant, 1842

Oryctinini é uma das tribos de Dynastinae com maior diversidade de espécies, a maioria destas, encontradas nas regiões Neártica e Neotropical, onde existe considerável endemismo (Mizunuma 1999). A tribo distribui-se mundialmente, exceto na Austrália, e partes do norte Europeu, Ásia e América do Norte (Ratcliffe 2003). São conhecidos aproximadamente 29 gêneros e 241 espécies, das quais, 46 estão na região Afrotropical, 31 na região Oriental e 141 estão no Novo Mundo (Endrödi 1985, Gasca-Álvarez & Ratcliffe 2011, Ratcliffe *et al.* 2013, Albertoni *et al.* 2014).

Os adultos da tribo podem ser distinguidos pelos seguintes aspectos: coloração negra ou marrom escura, raramente amarelada; corpo alongado e robusto; clipeo apicalmente emarginado,

acuminado ou bidentado; mento estreitado lateralmente; mandíbulas largas e visíveis dorsalmente; antenas com 9–10 antenômeros; margem externa das protíbias tri- ou quadridentadas; metatíbia geralmente modificada no ápice (dentes ou crenulações); cavidade coxal ampla; pigídio geralmente com área estridulatória. As larvas são diagnosticadas pela seguinte combinação de caracteres: crânio de coloração vermelho escuro, densamente pontuado; dentes estridulatórios maxilares truncados; antenômero 4 apresentando de 2–15 pontos sensoriais na superfície dorsal; garras tarsais com 2–4 cerdas alongadas; palídia ou séptula ausentes no raster (Morón & Ratcliffe 1990, Neita-Moreno & Orozco 2009).

Os adultos constroem abrigos onde ficam escondidos durante o dia, à noite são muito ativos, sendo frequentemente atraídos pela luz. Adultos de algumas espécies alimentam-se de frutas podres ou vegetação em decomposição, outros, no entanto, são conhecidos por formarem galerias em cana-de-açúcar ou plantas da família Arecaceae, onde são consideradas pragas de algumas culturas (Ratcliffe 2003, Lourenção *et al.* 1999). As larvas se desenvolvem no solo, alimentando-se de matéria orgânica, ou vivem dentro de troncos em decomposição, entretanto, há espécies cujas larvas estão associadas com ninhos de formigas do gênero (Ratcliffe *et al.* 1997, Pardo-Locarno *et al.* 2006).

1.4.8 Pentodontini Mulsant, 1842

Com aproximadamente 100 gêneros e mais de 550 espécies descritas, Pentodontini é a tribo mais diversa dentro de Dynastinae (Ratcliffe *et al.* 2013, López-García *et al.* 2016). A terceira maior diversidade da tribo está no Novo Mundo, logo após Oceania e Etiópia (Endrödi 1985). No Novo Mundo, as regiões Neártica e Neotropical apresentam 30 gêneros e 147 espécies válidas (López-García *et al.* 2016, Paucar-Cabrera & Moore 2018). O continente Sul-Americano abrange 94 dessas espécies, onde 81 são endêmicas; na América do Norte ocorrem 49 espécies, 39 são

endêmicas; na América Central há 27 espécies, sendo 8 endêmicas e nas Índias Ocidentais existem nove espécies, cinco são endêmicas (López-García *et al.* 2016).

Adultos de Pentodontini são reconhecidos pelas características a seguir: dimorfismo sexual geralmente pouco acentuado; machos com tarsos ocasionalmente dilatados; cabeça ou pronoto apresentando tubérculos, carenas ou concavidades; protíbia geralmente tridentada; metatíbias com ápice truncado (Ratcliffe *et al.* 2013). Algumas espécies da tribo apresentam características similares aquelas pertencentes à Oryctini, entretanto, podem ser distinguidas pelo ápice das metatíbias, truncada em Pentodontini, dentada ou crenulada em Oryctini (Endrödi 1985).

Quanto ao conhecimento dos estágios imaturos, somente dez gêneros, representados por 16 espécies, possuem suas larvas descritas (Ritcher 1966, Morón 1976, Lumaret 1991, Morón & Ratcliffe 1996, Morelli 1997, Ramírez-Salinas *et al.* 2004, 2010, Pereira *et al.* 2013, Morón 2017). As larvas são caracterizadas por apresentarem 1–3 pontos sensoriais dorsais no último antenômero; mandíbula esquerda com área molar dentada ou, na ausência de dentes, as maxilas possuem os dentes estriduladores agudos e projetados distalmente; o raster apresentando ou não palídia, quando a palídia está ausente, a epifaringe apresenta poucas setas na chaetoparia (Morón 1997).

A história natural e a biologia dos pentodontíneos ainda é pouco conhecida. Os adultos geralmente apresentam hábitos noturnos, sendo atraídos pela luz durante a noite. Alimentam-se de folhagens, matéria orgânica do solo e raízes de Plantas. As larvas se desenvolvem no solo, alimentando-se de raízes, humus, de folhas ou troncos em decomposição (Morón 1997, Ratcliffe 2013).

Larvas de certas espécies, como as pertencentes ao gênero *Tomarus* Erichson, 1847 possuem importância econômica, pois são pragas de algumas culturas agrícolas (Neita-Moreno & Ratcliffe 2017). Entretanto, há espécies cuja larvas são benéficas em sistemas agrícolas. Larvas de

Bothynus medon Germar, 1824 incorporam matéria orgânica ao solo, aumentando a capacidade de troca catiônica, tornando disponíveis certos nutrientes para as plantas, além disso, as larvas são responsáveis pela formação de túneis no solo, aumentando a drenagem e a aeração do solo (Gassen 1999).

1.5 Pentodontini ou Oryctini?

Por mais de 150 anos, não houve um consenso quanto à classificação de Pentodontini, sendo então tratado como família, subfamília e tribo por diferentes autores (López-García *et al.* 2015). Mulsant (1842) propôs Pentodonaire e Oryctesaire como grupos distintos. Burmeister (1847) classifica como família “Pentodontidae”. Bates (1888), reúne dentro da subfamília “Pentodontinae”, gêneros Americanos como *Tomarus (Ligyris)* Erichson, *Bothynus* Hope, 1837, e *Eutheola* Bates, 1888. Casey (1915) define pela primeira os pentodontíneos à nível tribal: “Pentodontini”. Entretanto, essas proposições não foram por muito tempo adotadas nas classificações. Autores como Arrow (1937), Blackwelder (1944), Saylor (1948) e Arnet (1969) incluem os pentodontíneos como membros de Oryctini. Endrodi (1969) reestabeleceu Pentodontini e Oryctini como tribos distintas. O autor baseia sua definição fundamentado nas características do ápice das metatíbias, truncada em Pentodontini e modificada em Oryctini (dentada ou crenulada), providenciando a primeira moderna classificação dessas tribos, vigorando até os dias atuais.

No entanto, as características observadas por Endrodi (1969) parecem ser insuficientes para a delimitação entre Pentodontini e Oryctini, pois tais características são variáveis entre os táxons presentes nas duas tribos, gerando controvérsias quanto a separação destas (Gasca-Álvarez *et al.* 2008). Ratcliffe (2003), Gasca-Álvares & Ratcliffe (2011), e López-García *et al.* (2015) especulam que Pentodontini seja parafilético e sugerem que análises filogenéticas devam ser efetuadas. Além

disso, um outro problema na diagnose da tribo é a relativa ausência de dimorfismo sexual, o que pode levar a certa confusão com outras tribos de Dynastinae, principalmente Cyclocephalini (López-García *et al.* 2015). Nos resultados filogenéticos apresentados na tese de Ide (1998), o autor classifica *Platyphileurus* Ohaus, 1910 (até então pertencente à Phileurini) como Pentodontini, sendo o gênero posteriormente transferido para Oryctini por Albertoni *et al.* (2014). A análise filogenética de Clark (2011), indica *Parapucaya* Prell, 1934 (até então Pentodontini) como membro de Cyclocephalini e *Stenocrates* Burmeister, 1847 (Cyclocephalini) como possível membro de Pentodontini. O estudo de Paucar-Cabrera & Moore (2018), baseado em dados morfológicos e moleculares, corroboram os indícios apresentados por Clark (2011) e então transferem *Parapucaya* Prell e *Pucaya* Ohaus, 1910 para Cyclocephalini.

Tal como a maioria dos gêneros de Pentodontini, não há estudos filogenéticos que ponham à prova a hipótese de monofiletismo de *Bothynus* Hope, 1837 nem a sua posição tribal, estando a sua delimitação genérica baseada somente na combinação de caracteres. Além disso, a última revisão taxonômica abrangente para o gênero são as monografias de Endrödi (1969, 1985), onde o autor apresenta diagnoses, ilustrações da genitália masculina, dados de distribuição e chaves de identificação.

Entretanto, apesar da incomensurável contribuição das monografias de Endrödi para os Dynastinae do mundo, alguns gêneros como *Bothynus*, o autor contempla somente imagens da genitália masculina, fundamentando a diagnose principalmente em caracteres masculinos. Estudos posteriores apresentam somente descrições de novas espécies (ver Dechambre 1981, Martínez 1983, Dechambre 2006, Ratcliffe 2010, Hardy 2017) ou tratam de poucas espécies de regiões particulares como Colômbia (Gasca-Álvarez *et al.* 2010, López-García *et al.* 2015), países da América Central (Ratcliffe 2003, Ratcliffe & Cave 2006), e México (Ratcliffe & Morón 1997, Ratcliffe *et al.* 2013). Ademais, não há diagnoses precisas para as fêmeas ou imagens da maioria

dos táxons pertencentes à *Bothynus*, nem dados de distribuição atualizados, havendo também a necessidade de uma nova chave de identificação que contemple todas as espécies do gênero.

Pela inexistência de estudos filogenéticos e revisões taxonômicas recentes, os capítulos 2 e 3 do presente trabalho tem os seguintes objetivos: Capítulo 2) prover a primeira filogenia para o gênero *Bothynus* testando a hipótese de monofilia do gênero mediante análise de caracteres morfológicos e descobrir possíveis sinapomorfias para o gênero; Capítulo 3) revisar taxonomicamente *Bothynus* e buscar características diagnósticas adicionais para melhor definir as espécies do gênero, além de prover dados de distribuição atualizados e uma chave de identificação para todas as espécies do gênero.

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CHAPTER 2

PHYLOGENETIC RELATIONSHIPS OF THE GENUS *BOTHYNUS* HOPE, 1837 (COLEOPTERA: MELOLONTHIDAE: DYNASTINAE: PENTODONTINI)¹

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¹Duarte, P.R.M., P.C. Grossi & D.R. Parizotto. Phylogenetic relationships of the genus *Bothynus* Hope, 1837 (Coleoptera: Melolonthidae: Dynastinae: Pentodontini). A ser submetido.

ABSTRACT – The New World assemblage the third largest generic Pentodontini richness with most of its species being found in South America. Despite this, phylogenetic relationships for most genera of New World Pentodontini still not addressed. *Bothynus* Hope, 1837 is the third largest genus of Neotropical Pentodontini and its phylogenetic relationships are assessed here. The phylogenetic results based on the examination of 74 morphological characters obtained from 55 taxa, evidenced the paraphyly of *Bothynus* and the monophyly of genus is conditioned to exclusion of *B. herbivorus* Arrow, 1837 and *B. complexus* Dechambre, 2006. The genus *Bothynus* (excluded *B. herbivorus* and *B. complexus*) was recovered in a lineage with high bootstrap value (87%) supported by three synapomorphic characters: metaventrite with a transversal groove, tergite VII with stridulatory apparatus, and tergite VII 1.5 times longer than tergite VIII. Three homoplasies also support the clade: clypeus convergent dorsoventrally in lateral view, mesoscutum with a longitudinal apodeme, and truncate mesotibial middle carina. Internal relations in the *Bothynus* lineage presented 36 taxa separated in five clades with the follow names: *villiersi* group, *medon* group, *complanus* group, *entellus* group, and *ascanius* group. Our analysis also recovered a clade formed by *B. herbivorus*, *Philoscaptus bonariensis* (Burmeister, 1847), *Saccharoscaptus laminifer* (Dechambre, 1979), *Eremobothynus cornutus* Ohaus, 1910, and *B. complexus* as the sister-group of *Bothynus*. The results also suggest that *B. complexus* is related to *E. cornutus* linked by one homoplasy (head with setose frons) and one synapomorphy (antennae with nine segments), and for this reason should moved to *Eremobothynus*. Moreover, the results also showed that *B. herbivorus* is not related to any genera adopted in the analysis, therefore, a new genus should be created to accommodate it.

KEY WORDS: Neotropical Region, New World, Phylogeny, Scarabaeoidea, South America

RELAÇÕES FILOGENÉTICAS DO GÊNERO *BOTHYNUS* HOPE, 1837 (COLEOPTERA:
MELOLONTHIDAE: DYNASTINAE: PENTODONTINI)

RESUMO – O Novo Mundo reúne a terceira maior riqueza genérica de Pentodontini com a maioria de suas espécies sendo encontrada na América do Sul. Apesar disso, as relações filogenéticas para a maioria dos gêneros ainda não foram abordadas. *Bothynus* Hope, 1827 é o terceiro maior gênero de Pentodontini Neotropical e suas relações filogenéticas são avaliadas aqui. Os resultados filogenéticos baseados no exame de 74 caracteres morfológicos obtidos a partir de 55 táxons evidenciaram a parafilia de *Bothynus*, com monofilia do gênero sujeita à exclusão de *B. herbivorus* Arrow, 1837 e *B. complexus* Dechambre, 2006. O gênero *Bothynus* (excluído *B. herbivorus* e *B. complexus*) foi recuperado em um clado com alto valor de bootstrap (87%) e suportado por três sinapomorfias: metaventrito com um sulco transversal, tergito VII com apresentando aparato estridulador, e tergito VII 1.5 vezes mais longo que o tergito VIII. Três homoplasias também suportam o clado: clipeo convergente dorsoventralmente, mesoescuto com um apódema longitudinal, e carena mesotibial truncada. As relações internas do gênero *Bothynus* apresentaram 36 táxons divididos em cinco linhagens chamadas aqui pelos seguintes nomes: grupo *villiersi*, grupo *medon*, grupo *complanus*, grupo *entellus* e grupo *ascanius*. Nossas análises também recuperaram como grupo irmão de *Bothynus*, um clado formado por *B. herbivorus*, *Philoscaptus bonariensis* (Burmeister, 1847), *Saccharoscaptus laminifer* (Dechambre, 1979), *Eremobothynus cornutus* Ohaus, 1910 e *B. complexus*. Os resultados mostram que *B. complexus* está relacionado com *E. cornutus* pela presença uma homoplasia (cabeça com fronte pilosa) e uma sinapomorfia (antena com nove artículos), e por esse motivo deve ser movido para *Eremobothynus*. Além disso, os resultados mostram que *B. herbivorus* não está relacionado a nenhum táxon adotado na análise e, portanto, um novo gênero deve ser criado para acomodar a espécie.

PALAVRAS-CHAVE: América do Sul, Filogenia, Novo Mundo, Região Neotropical,
Scarabaeoidea

Introduction

Dynastinae is one of the most remarkable, and one of the well-studied beetle groups of Coleoptera (Ratcliffe *et al.* 2013). Despite this, Dynastinae is poorly known from the phylogenetic point view, and the monophyly of its tribes remain uncertain. The lack of phylogenetic approaches has limited the ability to hypothesize sister relationships among tribes (Moore *et al.* 2018). Most of the accomplished phylogenies for the subfamily has focused on the Dynastini taxa, mainly on the giant rhinoceros beetles (Rowland & Miller 2012, Dutrillaux *et al.* 2013, Jin *et al.* 2016, Huang 2016a, Huang 2016b, Huang 2017). Cyclocephalini has also receiving initial phylogenetic attention, which contributed to clarifications of the genus *Mimeoma* Casey, 1915, and the new placement of the genus *Pucaya* Ohaus, 1910 and *Parapucaya* Prell, 1934 in the tribe (Moore *et al.* 2015, Paucar-Cabrera & Moore 2018). However, other closely related but weakly delimited tribes, such as Pentodontini and Oryctini, and have not been phylogenetically addressed (Gasca *et al.* 2008), and most of its taxa remain neglected.

Endrödi (1966) attempted to establish a first relationships hypotheses among Dynastinae tribes through a rudimentary cladistic analysis (Fig. 1). Oryctini and Pentodontini were considered as sister-groups by Endrödi (1966), who separated these two tribes based on characters of the metatibial apex (truncate or slightly crenulate in Pentodontini, strongly dentate in Oryctini), being this classification adopted until today. However, the characters used to diagnosis of Oryctini and Pentodontini are imprecise due to it be transitional among taxa of both tribes (Gasca-Alvares *et al.* 2011). Authors such as Sanabria-García (2012), Gasca-Álvares *et al.* (2011), López-García *et al.* (2015) and Ratcliffe & Cave (2015) speculate that these tribes are paraphyletic and suggest further taxonomic revisions and phylogenetic approaches.

Bothynus Hope, 1837 is a large genus of Pentodontini, with 31 valid species exclusive from New World (López-García *et al.* 2016, Hardy 2017, Duarte & Grossi 2020). All *Bothynus* species occur in South America, only two species extend its distribution toward Central America and Mexico (Morón 1997). Some species, such as *B. medon* (Germar 1824), are associated with agricultural areas and their larvae have been collected in soybeans (*Glycine max* (L.) Merrill) crops (Ávila & Santos 2009). However, the natural history, biology, and ecological traits from most *Bothynus* species are unknown. Riehs (2006) analyzed some phenological aspects of three *Bothynus* species collected with mercury steam lamp in Paraná state, Brazil. Pereira *et al* (2013) studied the biology of *B. medon* and described the third larval instar of this species, being the only known immature stage for the genus.

Historically, *Bothynus* has been related and confused with *Tomarus* Erichson, 1847, another diverse and widespread New World genus (López-García & Deloya 2019). Hope (1837) described the genus *Bothynus* based on two species: *Geotrupes cuniculus* Fabricius, 1801 (= *T. cuniculus*), designated as the type-species by him, and *Scarabaeus ascanius* Kirby, 1819 (= *B. ascanius*). However, the diagnosis of Hope from the genus *Bothynus* is congruent with *S. ascanius*, instead *G. cuniculus* (Prell 1936, Endrödi 1969). Based on Hope's designation, Cartwright (1959) mistakenly synonymized North American species of *Ligyris* Burmeister, 1847 with *Bothynus*. Arrow (1937) described a South America species and named it as *Ligyris herbivorus*, which posteriorly was transferred to *Bothynus* by Endrödi (1969), for considering it more related to this genus. Currently, *Ligyris* is considered a junior synonym of *Tomarus* (Ratcliffe 2002, Neita-Moreno & Ratcliffe 2017), but Morón & Grossi (2015) consider *Ligyris* and *Tomarus* as two separate taxa based on morphological characters used in keys and generic descriptions that lead to different taxa.

Bothynus differs from other genera of the New World Pentodontini by the contracted laterally clypeus, usually with two teeth (rarely with four teeth); mandibles with two or three teeth exposed laterally to clypeus; pronotum with apical tubercle and anterior concavity; tri- or quadridentate protibiae; metatibiae truncated at apex, covered with small spinules; tergite VII (=propygidium) with stridulatory apparatus; tergite VIII (=pygidium) short. Some species in the genus are sexually dimorphic with the male having remarkable pronotal horns, distinct concavity, enlarged protarsae, and incised inner claw (Hardy 2017, Duarte & Grossi 2020). Interspecific relations within the genus *Bothynus* were proposed by Dechambre (1981) and Martínez (1983), which assembled some morphologically related species in specie-groups. Dechambre (1981) grouped the species that featured horns and enlarge protarsae in males, while Martínez (1983) grouped the species with asymmetric parameres in males and mentum with coniform process. Arrow (1937) also assembled some species in a group but did not indicate which characters define it.

Due to absence of phylogenetic works that treating especially the generic relationships of the New World Pentodontini, the present chapter aims to assess the monophyletic hypothesis from the genus *Bothynus* through cladistic analysis based on the examination of morphological characters. Furthermore, to propose relationship hypotheses among the 31 *Bothynus* species and the possible relation of the genus as a sister-group of *Tomarus*.

Material and Methods

Taxon sampling

Due to a lack of previous phylogenetic studies, the choice of terminal taxa was based almost exclusively on personal observation. The out-group is mainly composed of South American genera of Pentodontini, except by the genus *Pentodon* Hope, 1837 (type-genus of Pentodontini),

represented here by the European species *Pentodon bidens* (Pallas, 1771). Two Cyclocephalini taxa also were added to the out-group. One of the characters that define Cyclocephalini, the poorly apparent sexual dimorphism, is shared with Pentodontini (Endrödi 1966, López-García *et al* 2015). The type species of each genera were analyzed, except to: *Pentodon* Hope, *Hylobothynus* Ohaus, 1910, and *Cyclocephala* Dejean, 1821. Other species, besides the type species, were added in the analysis for a more representative phylogenetic construction. The tree was rooted in *Rutela lineola* (L., 1767) (Rutelinae: Rutelini) based on the phylogeny of Browne & Scholtz (1999a, 199b), and on recent phylogenies of Bai *et al.* (2015), Gunter *et al.* (2015), and Mckkena *et al.* (2015) that recovered Rutelinae as sister-group of Dynastinae.

The in-group is represented by all 31 *Bothynus* valid species and further 8 unidentified species, but which are related to the genus. *Bothynus niger* (Blanchard, 1842) was not included in the analysis due to the species being known only for its illustration (see Blanchard 1842: plate 11). All terminal taxa used in the analysis are listed in Table I.

The examined specimens come from the following institutes and collections, with acronyms according to Evenhuis (2009), if available:

CECL = Coleção Entomológica Ângelo Moreira da Costa Lima, UFRRJ, Rio de Janeiro, Brasil (F. Racca-Filho);

CEMT = Sessão de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brasil (Fernando Z. Vaz-de-Mello);

CERPE = Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, Pernambuco (Paschoal C. Grossi);

CPATU = Coleção Entomológica da Embrapa Amazônia Oriental, Belém, Pará, Brasil (Márcia M. Maués);

CZMA = Coleção Zoológica do Maranhão, Universidade Estadual do Maranhão, CESC/UEMA, Caxias, Maranhão, Brasil (F. Limeira-de-Oliveira);

DZUP = Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brasil (Lúcia Massutti de Almeida);

EPGC = Coleção Entomológica Everardo & Paschoal Grossi, Nova Friburgo, Rio de Janeiro, Brasil (Everardo Grossi);

IBSP = Coleção Entomológica “Adolph Hempel, Instituto Biológico de São Paulo, São Paulo, Brasil (Sérgio Ide);

IRSNB = Royal Belgian Institute of Natural Sciences, Brussels, Belgium (Dekonink Wouter);

FIOC = Fundação Instituto Oswaldo Cruz, Rio de Janeiro, Rio de Janeiro, Brasil (Jane M. Costa);

NHM = Natural History Museum, London, England, (Max Barclay);

MACN = Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (Juan José Martínez);

MAHC = Martin Hardy Collection, Quebec City, Quebec, Canada (Martin Hardy);

MNHN = Muséum National d’Histoire Naturelle, Paris, France (Antoine Mantilleri);

MPEG = Museu Paraense Emílio Goeldi, Belém, Pará, Brasil (Orlando T. Silveira);

MZUSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (Sonia A. Casari);

UFRA = Coleção Entomológica da Universidade Federal Rural da Amazônia, Belém, Pará, Brasil (Paulo R. S. Farias).

Morphological study and terminology

The morphology was studied from dry (pinned) and humid specimens. Some specimens were soaked for ten minutes in hot water containing detergent to soften the musculature, allowing the posterior dissection and extraction of mouthparts, thorax, tergite VIII, and male genitalia. Extracted parts were washed with distilled water and stored along with its respective specimen in a falcon tube containing 80% alcohol. The characters were examined and photographed through stereomicroscope ZEISS STEMI 305 attached to a Nikon D90 digital camera assisted by the Helicon Remote software 3.8.1. Obtained images were combined with Combine ZP software 1.0. All plates were generated with GIMP software 2.1.0.

Lawrence *et al.* (2011) provided the most compressive morphological phylogenetic study in Coleoptera and the terminology is adopted here for the overall body aspect. However, there is not consensus about the terminology of some structures and others are not addressed in their study. For this reason, the terminology of Nel & Scholtz (1990) is employed here for the mouthparts, Matsuda (1970) for internal structures of thorax, and Hotman & Scholtz (1990) for the male genitalia. The classification system follows Chermán & Morón (2014).

Treatment of characters and analysis procedures

The characters were constructed based on external features of adult specimens accord to Sereno (2007). Most characters are applied to both sexes, being specified in the construction when applied to only one of the sexes. All characters are treated as binary, unordered, being the character contingency employed as alternative to the multistate character; autapomorphies were also considered in the analyses. Symbol (-) represents the inapplicable states, and (?) the missing data.

The data matrix was constructed using the software Mesquite 3.6 (Maddison & Maddison 2018) and the cladistic analyses were performed through the program TNT 1.5 (Goloboff *et al.*

2008b) in two procedures: 1) considering all characters with equal values (equal weight); 2) assigning a “*k*” value in each performed analysis (implicit weight) (Goloboff 1993), in this case, a “*script*” (setk.run) (Goloboff *et al.* 2008b) was employed to the obtention of an adequate *k* value. In both analyses, a traditional search utilizing the tree bisection and reconnection strategy (TBR) was performed with 1000 replications and 100 trees saved per replication. Branch support was evaluated using the bootstrap method with 10000 replications, being considered values above 70% as strong support for the clades according to Felsenstein (1985). The obtained trees were mapped and edited through the Winclada software (Nixon 1999-2002).

Results and Discussion

Character analysis

A total of the 74 characters were obtained. Character and character states used for the morphological cladistic assessment of *Bothynus* are listed below. Values of length (L), consistency index (ci) and retention index (ri) are presented after each character description. The data matrix is represented in Table II.

Head.

1. Head, sexual dimorphism:

(0) absent

(1) present

[L=1, ci=100, ri=100]

In the state (0), both sexes have a similar head; in the state (1), the male head has some ornament such as tubercles or horns, while the female head is devoid of ornament or it is more reduced.

2. Clypeal anterior margin, teeth:

(0) absent (Fig. 6C–D, I).

(1) present (Fig. 6A–B, E–H, J)

[L=3, ci=33, ri=60]

3. Clypeal anterior margin, teeth orientation [applicable only to taxa codified as state (1) for character 2]:

(0) transverse to clypeus (CHAP 3, Fig. 31B)

(1) parallel to clypeus (Fig. 6A)

[L=1, ci=100, ri=100]

4. Clypeus, anteroventral margin in dorsal view:

(0) hidden (Fig. 6A)

(1) visible (Fig. 6H)

[L=1, ci=100, ri=100]

5. Clypeus, lateral margins, reflexed middle-angle in dorsal view:

(0) absent (Fig. 6A–J)

(1) present (CHAP 3, Fig. 40C)

[L=1, ci=100, ri=100]

6. Clypeus, sides in dorsal view:

(0) inclined or attenuate toward anterior area (Fig. 1A)

(1) abruptly constricted anterolaterally (CHAP 3, Fig. 40C)

[L=1, ci=100, ri=100]

7. Clypeus, orientation in lateral view:

(0) parallel to frons (Fig. 7A–C, E–I)

(1) obliquely deflexed to frons (Fig. 7D)

[L=2, ci=50, ri=75]

8. Clypeus, dorsoventral area in lateral view:

(0) parallel (Fig. 7B–C, E–I)

(1) convergent (Fig. 7A, D)

[L=3, ci=33, ri=89]

9. Clypeus, posterolateral margin with a deflexed tooth in lateral view:

(0) absent

(1) present (Fig. 7C), autapomorphy of *Bothynus herbivorus*.

10. Clypeus, lateral edge, surface:

(0) glabrous

(1) setose

[L=5, ci=20, ri=82]

11. Cephalic capsule, epipharyngeal cavity:

(0) transverse, as wider than long

(1) longitudinal, as longer than wide

[L=1, ci=100, ri=100]

12. Frontoclypeal suture:

(0) absent or inconspicuous

(1) clearly visible

[L=1, ci=100, ri=100]

13. Frons, transversal furrow:

(0) absent (Fig. A–E, G–J)

(1) present (Fig. 6F)

[L=1, ci=100, ri=100]

14. Frons, surface:

(0) glabrous (Fig. B)

(1) setose (Fig. 6A)

[L=12, ci=8, ri=54]

15. Ocular canthus, ventral surface, setae:

(0) absent or confined to outer sides

(1) extended along of ocular canthus

[L=1, ci=100, ri=100]

Mouthparts.

16. Mandible, when closed:

(0) visible laterally to clypeus

(1) hidden under clypeus

[L=1, ci=100, ri=100]

17. Mandibles, teeth on the external edge:

(0) absent (Fig. 8B,D,F)

(1) present (Fig. 8A,C)

[L=4, ci=25, ri=57]

18. Mandibles, apical and medial teeth, orientation [applicable only to taxa codified as state (1)

for character 17]:

(0) longitudinal (Fig. 8E)

(1) transversal (Fig 8A)

[L=1, ci=100, ri=100]

19. Mandibles, molar area:

(0) excavated (Fig. 9A–B, D)

(1) flattened (Fig. 9C, E–F)

[L=1, ci=100, ri=100]

20. Mandibles, molar area, surface:

(0) striated (Fig. 9C–E, F)

(1) smooth (Fig. 9A–B, D)

[L=1, ci=100, ri=100]

21. Mandibles, molar area, size:

(0) small (Fig. 9A–B, D)

(1) large (Fig. 9C, E–F)

[L=1, ci=100, ri=100]

In state (0), the molar area is reduced and does not cover the basis of dorsal area in frontal view; in state (1), the molar area is broad, nearly or completely covered the basis of dorsal area in frontal view.

22. Mandibles, mesal brush, setae:

(0) homogeneous in shape

(1) heterogeneous in shape

[L=1, ci=100, ri=100]

State (0), the mesal brush is covered only by small and fine setae; State (1), the mesal brush is covered by two types of setae, one fine and small, other longer and stout.

23. Mandibles, ventral area, apical excavation in frontal view:

(0) absent (Fig. 9A, D)

(1) present (Fig. 9B–C, E–F)

[L=2, ci=50, ri=92]

State (1), the apical excavation is a local to recline the maxillae.

24. Maxillae, galea, teeth:

(0) absent (Fig. 10B)

(1) present (Fig. 10A, C–F)

[L=3, ci=33, ri=75]

25. Maxilla, shape of teeth [applicable only to taxa codified as state (1) for character 24]:

(0) strong and cuneiform (Fig. 10D–F)

(1) moderate and denticulate (Fig. 10A, C)

[L=1, ci=100, ri=100]

26. Maxillae, galea and lacinia:

(0) separated

(1) fused

[L=1, ci=100, ri=100]

State (0), the galea is separated from lacinia by a basal suture; State (1), galea and lacinia are completely fused.

27. Maxilla, palpomere I:

(0) visible (Fig. 10A)

(1) hidden under the lateral stipe (Fig. 10B)

[L=1, ci=100, ri=100]

28. Maxillar, palpomere IV, sensorial apical area:

(0) rounded and small (Fig. 10B)

(1) transverse and large (Fig. 10C), autapomorphy of *Hylobothynus pontis*.

29. Maxillary palpomere IV, latero-dorsal surface:

(0) rounded

(1) flattened.

[L=1, ci=100, ri=100]

State (0), the surface has a rounded aspect; state (1), the latero-dorsal surface provides a planar form in this region.

30. Hypopharynx, anterolateral carinae:

(0) divergent (Fig. 11B)

(1) subparallel (Fig. 11A)

[L=1, ci=100, ri=100]

31. Hypopharynx, anterolateral brush:

(0) absent (Fig. 11A, D)

(1) present (Fig. 11B–C, E–F)

[L=1, ci=100, ri=100]

32. Mentum:

(0) bilobed at apex (Fig. 12C–F)

(1) convergent at apex (Fig. 12A–B)

[L=1, ci=100, ri=100]

33. Labium, mentum and submentum:

(0) separated (Fig. 13A–B, D–F)

(1) fused (Fig. 13C)

[L=1, ci=100, ri=100]

Antennae.

34. Antennal segments, number:

(0) ten (Fig. 14A,C, E–F)

(1) nine (Fig. 14B, D)

[L=1, ci=100, ri=100]

35. Club, lamellae:

(0) overlapping at basis

(1) not overlapping at basis

[L=2, ci=50, ri=75]

36. Club, size:

(0) shorter or subequals to segments II–VII (Fig. B,D–F)

(1) as longer than segments II–VII (Fig. 14A,C)

[L=2, ci=50, ri=85]

37. Scape, size:

(0) long, length equals or more than twice the wide (Fig. 14C,F)

(1) short, less than 1,5 times longer than wide (Fig. 14A–B, D–E)

[L=1, ci=100, ri=100]

Thorax.

38. Pronotum, sexual dimorphism:

(0) absent

(1) present

[L=6, ci=16, ri=73]

State (0), the pronotum is similar in both sexes; state (1), males have modifications or ornaments, usually horns or concavities more pronounced than females.

39. Proepisternum, surface:

(0) completely setose

(1) partially setose

[L=1, ci=100, ri=100]

State (0), the proespisternal surface is covered with setae along of its extension; in state (1), the proepisternal surface is covered with setae only on the lateroanterior region.

40. Mesoscutum, longitudinal apodeme:

(0) absent

(1) present

[L=6, ci=16, ri=70]

41. Scutellar plate, surface:

(0) smooth or covered with fine punctures

(1) covered with large and deep punctures

[L=1, ci=100, ri=100]

42. Prosternal process, middle spine:

(0) absent

(1) present, autapomorphy of *Aceratus davus*.

43. Metaventricle, transversal groove:

(0) absent (Fig. 15B–F)

(1) present (Fig. 15A)

[L=1, ci=100, ri=100]

44. Metaventricle, surface:

(0) densely setose

(1) glabrous or weakly setose

[L=3, ci=33, ri=77]

State (0), the metaventral surface is barely visible due to high density of setae that cover the entire surface; State (1), the metaventral surface is clearly visible.

45. Metaventricle, sculpturation:

(0) punctate (Fig. 15F)

(1) rugopunctate (Fig. 15A)

[L=2, ci=50, ri=90]

46. Phragma, internal limit:

(0) emarginated

(1) truncate

[L=1, ci=100, ri=100]

47. Phragma, lateral branches:

(0) long

(1) short

[L=1, ci=100, ri=100]

State (0), the lateral branches are not extended beyond the phragma boundary; State (1), the lateral branches are extended beyond of the phragma boundary.

48. Elytra, discal punctures:

(0) inconspicuous

(1) conspicuous

[L=3, ci=33, ri=77]

State (0), the discal punctures are observed above 50X magnification; State (1), the punctures are observed under 10X magnification.

49. Elytral epipleurum, dorsal view:

(0) contiguous to elytral border (CHAP 3, Fig. 20A)

(1) separated from elytral border (CHAP 3, Fig. 40B)

[L=2, ci=50, ri=92]

Legs.

50. Male, inner protarsal claw:

(0) simple (CHAP 3, Fig. 44C)

(1) modified (CHAP 3, Fig. 20C)

[L=8, ci=12, ri=69]

State (0), the inner protarsal claw does not present modification and is similar in shape to outer claw; State (1), the inner protarsal claw features some modifications such as: ventral tooth, incision, or is broader than outer claw.

51. Male, protarsomere V, ventral process:

(0) absent (CHAP 3, Fig. 45C)

(1) present (CHAP 3, Fig. 20C)

[L=4, ci=25, ri=80]

52. Male, protarsomere V, position of ventral process [applicable only to taxa codified as state (1) for character 51]:

(0) at basis

(1) at apex

[L=1, ci=100, ri=100]

53. Protibiae, sexual dimorphism:

(0) absent (CHAP 3, Fig. 20A–B)

(1) present (CHAP 3, Fig. 45A–B)

[L=4, ci=25, ri=57]

In state (0), the outer teeth are similar in shape in both sexes; in state (1), the female tibiae are broader and rounded compared to males.

54. Protibiae, outer margin, basal tooth separated from the subsequent tooth by a small notch:

(0) absent (CHAP 3, Fig. 20A)

(1) present (CHAP 3. Fig. 45A)

[L=2, ci=50, ri=50]

State (0), the character is absent in taxa with tridentate protibiae; State (1), the character is present in taxa with quadridentate protibia.

55. Protibiae, inner margin:

(0) with a right angle at apex

(1) with two right angles at apex (one subapical, one apical)

[L=2, ci=50, ri=0]

56. Mesotibiae, middle carina:

(0) truncate

(1) dentate or crenulate

[L=5, ci=20, ri=50]

57. Mesotibiae, middle carinae, inner teeth:

(0) absent

(1) present

[L=2, ci=50, ri=0]

58. Mesotibiae, middle-carinae, ornamentation:

(0) like-spinules

(1) like-tooth

[L=2, ci=50, ri=83]

59. Mesotibial apex, discal surface:

(0) smooth (Fig. 16A–B, D–F)

(1) covered with spinules (Fig. 16C)

[L=1, ci=100, ri=100]

60. Mesotibial apical margins, spinules:

(0) absent (Fig. 16B), autapomorphy of *Bothynus herbivorus*

(1) present

[L=1, ci=100, ri=100]

61. Metatibial inner spur, apex:

(0) pointed (Fig. 17A–B, D–E)

(1) spatulate (Fig. 17C)

[L=1, ci=100, ri=100]

62. Metatibiae, spurs:

(0) similar to mesotibial spurs

(1) at least one distinct from the mesotibial spurs

[L=1, ci=100, ri=100]

63. Metatibial apex, margins:

(0) dentate

(1) truncated or weakly crenulate

[L=2, ci=50, ri=66]

64. Metatibiae, sexual dimorphism:

(0) absent

(1) present

[L=1, ci=100, ri=100]

In state (0), the metatibial shape is similar in both sexes; in state (1) the female has the metatibia broader at apex compared to males.

Abdomen.

65. Tergite VII, stridulatory apparatus:

(0) absent (Fig. 18 B–F)

(1) present (Fig. 18A)

[L=1, ci=100, ri=100]

66. Tergite VII, length:

(0) Equal or shorter than tergite VIII

(1) 1.5 times longer than tergite VIII

[L=1, ci=100, ri=100]

67. Tergite VII, spiracle position:

(0) above the pleural suture (Fig. 19A, F)

(1) under the pleural suture (Fig. B–F)

[L=1, ci=100, ri=100]

68. Tergite VII, anterior margin:

(0) straight (Fig. 18B)

(1) posteriorly projected (Fig. 18A)

[2=1, ci=50, ri=94]

69. Female, tergite VIII, pit:

(0) absent

(1) present, autapomorphy of *Bothynus herbivorus* (see Lopéz-García *et al.* 2015, Fig. 15)

Genitalia.

70. Parameres, apical half, lateroventral margins in shape of longitudinal “lateral-flaps”:

(0) absent

(1) present

[L=1, ci=100, ri=100]

State (0), the lateroventral margins do not expand longitudinally; in state (1), the lateroventral margins is flattened and expanded laterally in a longitudinal “flap”.

71. Parameres, inner margins, tooth:

(0) absent (CHAP 3, Fig. 20E)

(1) present (CHAP 3. Fig. 46A)

[L=1, ci=100, ri=100]

72. Parameres, ventral area in lateral view:

(0) flattened or slightly sinuous (CHAP 3, Fig. 20F)

(1) strongly projected downward (CHAP 3. Fig. 37I)

[L=2, ci=50, ri=75]

73. Parameres, middle area in lateral view:

(0) broad dorsoventrally

(1) narrow dorsoventrally

[L=2, ci=50, ri=75]

74. Parameres, ventral carinae:

(0) present

(1) absent

[L=142, ci=52, ri=87]

Cladistic analysis

Parsimony analysis with equal value resulted in twelve equally parsimonious trees with L=142, ci=51, and ri=87. The analysis with implicit weigh resulted in a single tree with L=144, k=4.76, fit=60.53, ci=51, and ir=87 (Fig. 3). Due to many homoplastic characters, the analysis with implicit weigh is presented as a better alternative to interpreting the phylogenetic hypotheses between the studied taxa and therefore it will be discussed here. The obtained tree with bootstrap support values is represented in Fig. 1. The tree with the transformations series is shown in Fig 4 for the out-group and Fig. 5 for the in-group respectively.

Our analysis recovered Cyclocephalini (*C. cearae* and *C. ohausiana*) as a monophyletic lineage (bootstrap 98%) supported by one synapomorphy (character 12, state 1) and two homoplasies (character 17, state 0; character 36, state 1). However, Pentodontini arose as a paraphyletic clade formed by an external and unresolved lineage composed by taxa of the genus *Tomarus* (in part), *Euetheola*, and *Oxyligyrus* as sister-group of an internal and large lineage, in which belong taxa of the genus *Pentodon*, *Tomarus*, *Hylobothynus*, *Aceratus*, *Philoscaptus*, *Saccharoscaptus*, *Eremobothynus*, and *Bothynus*.

Among the genera that form the Pentodontini external lineage, only *Tomarus* is unresolved, *Euetheola* (*E. humilis* and *E. bidentata*), and *Oxyligyrus* (*O. zoilus* and *O. rostratus*) were recovered as monophyletic but poorly supported. In the performed analysis, *T. ebenus* and *T. gyas* appeared in the external lineage, while *T. nasutus* and *T. gibbosus* appeared in the internal lineage, however, without support in both cases. Perhaps, *T. nasutus* and *T. gibbosus* belong to the genus *Ligyris* Burmeister, 1847, which was synonymized with *Tomarus* by Ratcliffe (2002), however, authors as Escalona & Joly (2006) and Morón & Grossi (2015) disagree with the synonym of *Ligyris* under *Tomarus*. A phylogenetic approach with greater specific representativeness or a taxonomic revision is required to better delimit the genus *Tomarus*.

Regarding genera that integrate the Pentodontini internal lineages, the genus *Bothynus* was recovered as paraphyletic, and their monophyly is conditioned to exclusion of *B. herbivorus* and *B. complexus*, which arose as *Bothynus* sister-clade along with *P. bonariensis*, *S. laminifer*, and *E. cornutus*. Our analysis suggests that *B. herbivorus* is not related to *Bothynus* or any other genus adopted here by the presence of three characters that are unique among the examined taxa: each side of clypeus with a deflexed tooth on the posterolateral margin (character 9, state 1) (Fig. 7C), mesotibial apex without spinules (character 60, state 0) (Fig. 16B), female with a pit on tergite VIII (character 69, state 1). At first, *B. herbivorus* was described in the genus *Ligyris* (= *Tomarus*) by Arrow (1937a) and transferred to *Bothynus* by Endrodi (1969), that considered the species more related to this genus based on the anterior emargination of tergite VIII, furthermore, he also described the presence of a stridulatory apparatus on tergite VII formed by innumerable transverse ridges. Despite the presence of an emargination on tergite VIII in *B. herbivorus*, however, we noticed which this taxon does not have a stridulatory apparatus as described by Endrödi (1969), instead of this, the tergite VII is covered only by several punctures that are transversal and narrow in form (Fig. 18C). Moreover, our analysis evidenced three synapomorphic characters for the *Bothynus* lineage (discussed below) not shared with *B. herbivorus*, reinforcing that this taxon can be removed from the current genus.

Bothynus complexus was recovered out from *Bothynus* lineage, appearing in a poorly supported clade (bootstrap 62%) along with *E. cornutus*, grouped by one homoplasy: head with setose frons (character 14, state 1); and one synapomorphy: antennae with nine segments (character 34, state 1) (Fig. 14 B,D). Antennae with nine segments are also present in other four genera of the New World Pentodontini which not were included in the analysis: *Anoplognatho* Rivers, 1889, *Neoryctes* Arrow, 1908, *Pentondina* Endrödi, 1968, and *Adeleus* Ratcliffe, 2014. The reason why *B. complexus* is more related to the genus *Eremobothynus*, can be explained by

morphological and biogeographical aspects. Apparently, on the biogeographic point of view, *B. complexus* is not related to *Neoryctes* or *Adeleus*, two exclusive genera from Galápagos Islands (Ratcliffe 2014), neither with the North American genus *Anoplognatho* (Ratcliffe 2002). Regarding *Pentodina*, a monotypic genus from Peru and Bolivia (Endrödi 1968), however, the set of characters that define the genus is incompatible with *B. complexus*. Dechambre (2006) described *B. complexus* with characteristics that are congruent with *Eremobothynus*, as presented in the description of the genus by Ohaus (1910), and in redescriptions of Endrödi (1969, 1985): Head with a frontal horn in male; clypeal anterior margin rounded, reflexed and without teeth; antenna with nine segments; pronotum strongly convex, without tubercle, and with an anterior declivity in male. *Eremobothynus* species are endemic from Argentina (Abadie & Grossi 2008), and *B. complexus* is known from a specific dry area in the Brazilian southeast, knowing as “Mata Seca” (see Chapter 3). There is evidence of Dynastinae taxa associated with this Brazilian dry area and which are related to Dynastinae from Argentina dry areas, as related by Sobral *et al.* (2019). The authors sustain that the wide geographic separation of the Brazilian species *Colacus rubrofemoratus* (Sobral, Morais & Grossi, 2019) from the other *Colacus* species, was occasioned by contraction events within the dry biomes throughout the Pleistocene, resulted in populations dispersal and isolation, which probably occurred with *B. complexus* concerning the *Eremobothynus* species.

***Bothynus* lineage and internal relationships**

A lineage comprising 36 *Bothynus* taxa (excluded *B. herbivorus* and *B. complexus*) was recovered with high bootstrap value (87%), supported by three synapomorphic characters: metaventrite with a transversal groove (character 43, state 1) (Fig. 15A), tergite VII with stridulatory apparatus (character 65, state 1) (Fig. 18A), and tergite VII 1.5 times longer than

tergite VIII (character 66, state 1); and three homoplastic characters: clypeus convergent dorsoventrally in lateral view (character 8, state 1) (Fig. 7A,D), mesoscutum with longitudinal apodeme (character 40, state 1), and truncate mesotibial middle carina (character 56, state 0). The phylogenetic analysis also revealed that the *Bothynus* lineage is separated in five distinct clades named here as: *villiersi* group, *medon* group, *complanus* group, *entellus* group and *ascanius* group.

Among the synapomorphies for *Bothynus*, the presence of a metaventral transverse groove (character 43, state 1) is a new character state obtained in our analysis, that not was mentioned either in the original description or in subsequent redescriptions of the genus (Hope 1837, Burmeister 1847, Endrödi 1969, 1985). This newly discovered character is unique to *Bothynus* lineage and probably was not noted anteriorly because it is obscured by the dense “pilosity” that covers the metaventral surface, making it difficult to observe, moreover, has still interspecific variations from well-marked to barely marked, observed under high magnifications only.

The stridulatory apparatus of tergite VII (character 65, state 1) is a character state used by (Endrödi 1969, 1985) to distinguish *Bothynus* from other Pentodontini of the New World and also has been frequently used in identification keys (e.g Endrödi 1969, 1985, Gasca-Álvarez *et al.* 2010, Ratcliffe & Mendoza 2014, Ratcliffe 2014, Morón & Grossi 2015). This character appears in the form of one or two paired bands of numerous transverse carinae, longitudinally arranged along of the discal area of tergite VII or restricted anteriorly. Despite the character appears in our analysis as a synapomorphy, however, it is not exclusive to *Bothynus* lineage, and also is present in other Pentodontini genera of the New World such as *Neoryctes* and, in the introduced African species *Heteronichus arator* (Fabricius, 1775). Differently, the length of tergite VII (about 1.5 times longer than tergite VIII) (character 66, state 1) is a synapomorphic character exclusive to *Bothynus* lineage and was used by Ratcliffe (2010) in the diagnosis of the genus.

The *villiersi* group

The phylogenetic analysis recovered four species within the lineage named *villiersi* group: *B. villiersi*, *B. horridus*, *B. alvarengai* and *B. sp.8*. This lineage is supported by high bootstrap values (93%), and three synapomorphic characters were found: maxillary palpomere I hidden under the lateral stipe (character 27, state 1) (Fig. 10B), discal surface of mesotibial apex covered with spinules (character 59, state 1) (Fig. 16C), and presence of process on the inner margins of parameres (character 71, state 1) (CHAP. 3, Fig. 20E). The same clade also present three homoplastic characters: clypeus obliquely deflexed (character 7, state 1) (Fig. 7D), maxillary galea without teeth (character 24, state 0) (Fig. 10B), and lamellae not overlapping at basis (character 35, state 1).

Our analysis was congruent with the proposition of Martinez (1983), where the author considers that *B. villiersi*, *B. horridus*, and *B. alvarengai* are part of a natural group based on the characters of mentum and by the asymmetry of parameres. The asymmetric parameres is not a character exclusive to *villiersi* group, but it is also observed in *B. complexus*. However, in the *villiersi* group, the presence of a triangular process on the inner margins of parameres confers a “symmetry” to it, while in *B. complexus* the asymmetry is marked by an expansion of the right parameres only. Probably, the synapomorphic character related to parameres (character 71, state 1) be the most remarkable of the *villiersi* group, however, other two synapomorphies found here are exclusive to this group: maxillary palpomere I hidden under the lateral stipe (character 27, state 1) and discal surface of mesotibial apex covered with spinules (character 59, state 1). These three synapomorphies confers precise diagnostic characters that immediately separates the *villiersi* group from other groups within the *Bothynus* lineage.

The *medon* group

To this group belongs: *B. medon*, *B. dasypleurus*, *B. herteli*, *B. cunctator*, *B. exaratus*, *B. validus*, and *B. sp.7*. The *medon* group was recovered with a unique synapomorphy: ventral area of parameres strongly projected downward (character 72, state 1). This reflected in a clade with low bootstrap value, which collapsed after the analysis, evidenced a poorly delimitation of the group, and for this reason, is required the search of new characters for better delimited the group.

The *complanus* group

The *complanus* group is composed of two closely related species: *B. complanus* and *B. quadridens*. This clade was recovered with high bootstrap value (94%), supported by four homoplasies: absent pronotal sexual dimorphism (character 38, state 0), mesoscutum without longitudinal (character 40, state 0), protibial basal tooth separated from the subsequent tooth by a small notch (character 54, state 1), and crenulate mesotibial middle carina (character 56, state 1). Despite the characters that support the clade be homoplastic and poorly informative, however, they were important to assemblage *B. complanus* and *B. quadridens* as species-group and can be used in combination to distinguish it.

Bothynus complanus and *B. quadridens* are unique among the *Bothynus* species with four protibial teeth (character 54, state 1), and mesotibia with crenulate middle carina (character 56, state 1). The protibiae with four teeth is a feature used in the identification keys for separation of those two from the other *Bothynus* species (Endrödi 1969, 1985, López-García *et al.* 2015). Besides the morphological link, distributional factors also suggest the separation of *B. complanus* group from other *Bothynus*. The *complanus* group occur in tropical forests from north of South America to Mexico (Morón 1997, Ratcliffe 2003, Ratcliffe & Cave 2006, Ratcliffe 2015), while other *Bothynus* species occur nearly exclusively in central and southern areas of South American

(Endrödi 1985, Abadie *et al* 2008). Our analysis showing a possible relationship among the *complanus* group with *entellus* group, whose most species occur in Brazilian Atlantic forest areas (Duarte & Grossi 2020). Probably, the *complanus* group was separate from the *entellus* group along the Eocene/Miocene, when drastic climate changes and the Andean uplift resulted in the formation of a drier area separating the Amazon forest to Atlantic forest, which were connected in the Paleogene (Sobral-Souza 2015).

The *entellus* group

Our analysis recovered six species within the *entellus* group: *B. entellus*, *B. stenelus*, *B. tricornis*, *B. lancifer*, *B. araya*, and *B. condacki*. The clade presented high bootstrap value (93%), supported by four exclusive synapomorphies: labium with submentum fused to mentum (character 33, state 1), mesotibial inner spur spatulate in shape (character 61, state 1), metatibiae with inner spurs distinct from those of mesotibiae (character 62, state 1), apical half of parameres expanded lateroventrally (character 70, state 1). A unique homoplasy also supported the group: tarsomere V with ventral in process in males (character 51, state 1).

The *entellus* group recovered here is congruent with the species group proposed by Dechambre (1981), followed by Duarte & Grossi (2020). Dechambre (1981) grouped *B. entellus*, *B. stenelus*, *B. tricornis* and *B. lancifer* based on characteristics of clypeus strongly bidentate, smooth elytra, tridentate protibiae and thickened protarsomeres in males. However, most characters used by him are present in other groups within the *Bothynus*, except by the thickened protarsomeres in males, exclusive from the *entellus* group. Three characters used by Duarte & Grossi (2020) to define the *entellus* group and assessed in our analysis arose as synapomorphies: labium with submentum fused to mentum (character 33, state 1), mesotibial inner spur spatulate in shape (character 61, state 1), and apical half of parameres expanded lateroventrally (in shape of

lateral “flaps”) (character 70, state 1). Besides this, the synapomorphic character: metatibiae with inner spurs distinct from those of mesotibiae (character 62, state 1), had not yet been reported and represent a new character, and together with the other characters, reinforce the group’s relationship.

The *ascanius* group

This group was recovered as the most diverse among the groups within the *Bothynus* lineage, comprising 17 species: *B. ascanius*, *B. deiphobus*, *B. striatellus*, *B. laticifex*, *B. minor*, *B. cribrarius*, *B. cyclops*, *B. cylindricus*, *B. laevipennis*, *B. nyx*, *B. trix*, *B. sp. 1*, *B. sp. 2*, *B. sp. 3*, *B. sp. 4*, *B. sp. 5*, and *B. sp. 6*. Despite of the low bootstrap support, the phylogenetic analysis found two synapomorphies exclusive for the *ascanius* group: ocular canthus with arranged setae along the ventral surface (character 15, state 1), maxilla with galea fused to lacinia (character 26, state 1). One homoplastic character is also present in the clade: clypeus with setose lateral edge (Character 10, state 1).

In the analysis, the *ascanius* group arose in two separated and not supported clades, one formed by *B. trix*, *B. minor*, *B. deiphobus* and *B. striatellus*; and other composed by *B. ascanius*, *B. laticifex*, *B. cribrarius*, *B. cyclops*, *B. cylindricus*, *B. laevipennis*, *B. nyx*, *B. sp. 1*, *B. sp. 2*, *B. sp. 3*, *B. sp. 4*, *B. sp. 5*, and *B. sp. 6*., and for this reason, both clades are considered as a unique lineage. The two synapomorphies found here (ocular canthus with arranged setae along the ventral surface (character 15, state 1), and maxilla with galea fused to lacinia (character 26, state 1)), are exclusive to *ascanius* group and clearly separate it in a distinct clade within the *Bothynus* lineage. However, further phylogenetic approaches are required to clarify the relationship regarding the *ascanius* clade to test if the two clades which formed the group here, are distinct.

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Table I. Taxa employed in the phylogenetic analysis.

| SUBFAMILY | TRIBE | SPECIES |
|-----------------------|--|---|
| Rutelinae | Rutelini | <i>Rutela lineola</i> (L., 1767) |
| Dynastinae | Cyclocephalini | <i>Cyclocephala cearae</i> Höhne, 1923 |
| | | <i>Cyclocephala ohausiana</i> Höhne, 1923 |
| | Cyclocephalini | <i>Aceratus davus</i> (Burmeister, 1847) |
| | <i>Bothynus alvarengai</i> Martínez, 1983 | |
| | <i>Bothynus ascanius</i> (Kirby, 1819) | |
| | <i>Bothynus araya</i> (Duarte & Grossi) | |
| | <i>Bothynus condacki</i> (Duarte & Grossi) | |
| | <i>Bothynus complexus</i> Dechambre, 2006 | |
| | <i>Bothynus complanus</i> (Burmeister, 1847) | |
| | <i>Bothynus cribrarius</i> (Fairmaire, 1878) | |
| | <i>Bothynus cunctator</i> (Mannerheim, 1829) | |
| | <i>Bothynus cyclops</i> (Burmeister, 1847) | |
| | <i>Bothynus cylindricus</i> Arrow, 1937 | |
| | <i>Bothynus dasypleurus</i> (Germar, 1824) | |
| | <i>Bothynus deiphobus</i> (Burmeister, 1847) | |
| | <i>Bothynus entellus</i> (Serville, 1828) | |
| | <i>Bothynus exaratus</i> (Burmeister, 1847) | |
| | <i>Bothynus herbivorus</i> (Arrow, 1937) | |
| | <i>Bothynus herteli</i> Endrödi, 1968 | |
| | <i>Bothynus horridus</i> Endrödi, 1968 | |
| | <i>Bothynus laevipennis</i> Arrow, 1937 | |
| | <i>Bothynus lancifer</i> Dechambre, 1981 | |
| | <i>Bothynus laticifex</i> Burmeister, 1847 | |
| | <i>Bothynus medon</i> (Germar, 1824) | |
| | <i>Bothynus minor</i> Steinheil, 1872 | |
| | <i>Bothynus nyx</i> Ratcliffe, 2010 | |
| | <i>Bothynus quadridens</i> (Taschenberg, 1870) | |
| | <i>Bothynus stenelus</i> (Burmeister, 1847) | |
| | <i>Bothynus</i> sp. 1 | |
| | <i>Bothynus</i> sp. 2 | |
| <i>Bothynus</i> sp. 3 | | |

| | | |
|--|--|--|
| | | |
| | | <i>Bothynus</i> sp. 4 |
| | | <i>Bothynus</i> sp. 5 |
| | | <i>Bothynus</i> sp. 6 |
| | | <i>Bothynus</i> sp. 7 |
| | | <i>Bothynus</i> sp. 8 |
| | | <i>Bothynus stenelus</i> (Burmeister, 1847) |
| | | <i>Bothynus striatellus</i> (Fairmaire, 1878) |
| | | <i>Bothynus tricornis</i> Arrow, 1937 |
| | | <i>Bothynus thrix</i> Hardy, 2017 |
| | | <i>Bothynus validus</i> (Burmeister, 1847) |
| | | <i>Bothynus villiersi</i> Endrödi, 1968 |
| | | <i>Eueteola bidentata</i> (Burmeister, 1847) |
| | | <i>Eueteola humilis</i> (Burmeister, 1847) |
| | | <i>Hylobothynus pontis</i> Ratcliffe, 1982 |
| | | <i>Oxyligyrus rostratus</i> (Burmeister, 1847) |
| | | <i>Oxyligyrus zoilus</i> (Oliver, 1789) |
| | | <i>Pentodon bidens</i> (Pallas, 1771) |
| | | <i>Philoscaptus bonariensis</i> (Burmeister, 1847) |
| | | <i>Saccharoscaptus laminifer</i> (Dechambre, 1979) |
| | | <i>Tomarus cuniculus</i> (Fabricius, 1801) |
| | | <i>Tomarus ebenus</i> (De Geer, 1774) |
| | | <i>Tomarus gyas</i> Erichson, 1848 |
| | | <i>Tomarus similis</i> (Endrödi, 1968) |

Table II. Data matrix including 55 taxa and 74 morphological characters.

| SPECIES | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 74 |
|---------------------------------|------------|------------|-------------|------------|------------|------------|------------|-----------|
| <i>Rutela lineola</i> | 00-0000001 | 0000001-10 | 1111000000 | 1000001001 | 0000000101 | 0-00100101 | 0010000000 | 0010 |
| <i>Pentodon bidens</i> | 0100000100 | ?000001000 | 1111000000 | 0000001001 | 000110010? | ??01000001 | 001000000? | ???? |
| <i>Cyclocephala cearae</i> | 00-0000000 | 0101000-10 | 1111000000 | 1000011000 | 0001000101 | 0-10000001 | 0010000000 | 0010 |
| <i>Cyclocephala ohausiana</i> | 00-0000000 | 0100000-10 | 1111000000 | 1000011000 | 0001000101 | 0-00000001 | 0010000000 | 0010 |
| <i>Eremobothynus cornutus</i> | 10-0000000 | 0001000-01 | 0000-00001 | 010100010? | 0000111100 | 0-00000001 | 0010001000 | 0000 |
| <i>Sccharoscaptus laminifer</i> | 10-0000000 | 0000001001 | 0000-00001 | 010000010? | 1000111100 | 0-00010001 | 0000001000 | 0010 |
| <i>Philoscaptus bonariensis</i> | 1101000000 | 0000001001 | 0000-00001 | 010000000? | 1000111100 | 0-00010001 | 0000001000 | 0010 |
| <i>Aceratus davus</i> | 0100001000 | 0000001001 | 0011100001 | 0100100000 | 0100111000 | 0-00111001 | 0010000000 | 0000 |
| <i>Hylobothynus pontis</i> | 0100000000 | 0000001001 | 0011100101 | 0100000000 | 0001011100 | 0-00010001 | 0010000000 | 0001 |
| <i>Oxyligyrus rostratus</i> | 0100000000 | 1010000-10 | 11110000001 | 1000001010 | 0001000101 | 0-00000101 | 0010000000 | 0000 |
| <i>Oxyligyrus zoilus</i> | 0100000000 | 1010000-10 | 1111000000 | 1000001010 | 0001000100 | 0-00000101 | 0010000000 | 0000 |
| <i>Euetheola bidentata</i> | 0100000000 | 0000010-10 | 1111000000 | 1000001010 | 0001000101 | 0-00000101 | 0010000000 | 0000 |
| <i>Euetheola humilis</i> | 0100000000 | 0000010-10 | 1111000000 | 1000001010 | 0001000100 | 0-00000101 | 0010000000 | 0000 |
| <i>Tomarus ebenus</i> | 0100000000 | 0000001010 | 1111000000 | 1000001010 | 0001000101 | 0-00000101 | 0010000000 | 0000 |
| <i>Tomarus gyas</i> | 0100000000 | 0000001010 | 1111000000 | 1000001010 | 0001000101 | 0-00000101 | 0010000000 | 0000 |
| <i>Tomarus gibbosus</i> | 0100000000 | 0000001001 | 0011100001 | 0000000000 | 0000000100 | 0-00000001 | 0010000000 | 0000 |
| <i>Tomarus nasutus</i> | 0100000000 | 0000001001 | 0011100001 | 0000000000 | 0000000100 | 0-00000001 | 0010000000 | 0000 |
| <i>Bothynus herbivorus</i> | 0100000010 | ?000001001 | 0011100001 | 010000010? | 0000111100 | 0-00010000 | 0000001110 | 0000 |
| <i>Bothynus complexus</i> | 10-0000000 | 0001001-01 | 0000-00001 | 0101000100 | 0000111101 | 0-00011001 | 0000001000 | 0000 |
| <i>Bothynus horridus</i> | 0100001101 | 0000001001 | 0000-01001 | 0100100101 | 0010111100 | 0-00000011 | 0010110100 | 1000 |
| <i>Bothynus alvarengai</i> | 0100001101 | 0000001001 | 0000-01001 | 0100100101 | 0010111100 | 0-00000011 | 0010110100 | 1000 |
| <i>Bothynus villiersi</i> | 0100001101 | 0000001001 | 0000-01001 | 0100100101 | 0010111100 | 0-00000011 | 0010110100 | 1000 |
| <i>Bothynus quadridens</i> | 0100010100 | 0001001001 | 0001100001 | 0100000000 | 0010111011 | 0-11010001 | 0010110100 | 0000 |
| <i>Bothynus complanus</i> | 0100010100 | 0001001001 | 0001100001 | 0100000000 | 0010111011 | 0-11010001 | 0010110100 | 0000 |
| <i>Bothynus herteli</i> | 0100110101 | 0000001001 | 0001100001 | 0100000100 | 0010111100 | 0-00010001 | 0010110100 | 0100 |
| <i>Bothynus dasypleurus</i> | 0100010100 | 0001001001 | 0001100001 | 0100000101 | 0010111110 | 0-10000001 | 0010110100 | 0100 |
| <i>Bothynus cunctator</i> | 0100110100 | 0001001001 | 0001100001 | 0100000001 | 0010111110 | 0-10000001 | 0010110100 | 0100 |
| <i>Bothynus validus</i> | 0100110000 | ?0000010?? | ??0??000? | ?10000010? | 00101??111 | 0-?0000001 | 001?110100 | 0?0? |
| <i>Bothynus medon</i> | 0100110000 | 0001001001 | 0000-00001 | 0100000101 | 0010111111 | 1-10000001 | 0011110100 | 0100 |

| SPECIES | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 74 |
|-----------------------------|------------|------------|------------|------------|-------------|------------|------------|-----------|
| <i>Bothynus exaratus</i> | 0100110100 | 0000001001 | 0001100001 | 0100000101 | 0010111110 | 0-10000001 | 0011110100 | 0000 |
| <i>Bothynus entellus</i> | 0100010100 | 0001001001 | 0001100001 | 0110000101 | 0010111011 | 1000000001 | 1110110101 | 0000 |
| <i>Bothynus araya</i> | 0100010100 | 0001001001 | 00011?0001 | 0110000101 | 0010111011 | 1000000001 | 1110110101 | 0000 |
| <i>Bothynus tricornis</i> | 0100010100 | 0001001001 | 0001100001 | 0110000101 | 0010111011 | 1000000001 | 1110110101 | 0000 |
| <i>Bothynus lancifer</i> | 0100010101 | ?0010010?? | ??011?000? | ?110000?0? | 00101??011 | 10?0000001 | 111?1101?1 | 0000 |
| <i>Bothynus stenelus</i> | 0100010100 | 0001001001 | 0001100001 | 0110000101 | 0010111011 | 1000000001 | 1110110101 | 0000 |
| <i>Bothynus condacki</i> | 0100010101 | 00000010?? | ??0110000? | ?110000?0? | 00101??011 | 1000000001 | 111?1101?1 | 0000 |
| <i>Bothynus ascanius</i> | 0100000101 | 0001101101 | 0001110011 | 0010111101 | 0010111101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus cylindricus</i> | 0100000101 | 0001101101 | 0001110011 | 0010111101 | 0010111101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus laevipennis</i> | 0100000101 | 0001101101 | 0001110011 | 0010111101 | 0010111101 | 0-00000001 | 0010110100 | 0000 |
| <i>Bothynus nyx</i> | 0100000101 | ?001101101 | 0001110011 | ?10001010? | 00101???101 | 0-00000001 | 0010110100 | 0000 |
| <i>Bothynus laticifex</i> | 0100000101 | 0001101101 | 0001110011 | 0100000101 | 0010111101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus cribrarius</i> | 0100000101 | ??01101001 | 000111000? | ?10000010? | 0010111101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus cyclops</i> | 0100000101 | 0000101001 | 0001110001 | 0100000101 | 0010111101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus deiphobus</i> | 0100000101 | 0000101001 | 0001110001 | 0100000100 | 0010111100 | 0-00000001 | 0010110100 | 0001 |
| <i>Bothynus striatellus</i> | 0100000101 | 0000101001 | 0001110001 | 0100000000 | 0010111100 | 0-00000001 | 0010110100 | 0001 |
| <i>Bothynus thrix</i> | 0100000101 | ??011010?? | ??011?000? | 010000010? | 00101???100 | 0-00000001 | 0010110100 | 0000 |
| <i>Bothynus minor</i> | 0100000101 | ??011010?? | ??0???000? | 010000010? | 00101???100 | 0-?0000001 | 001?1101?0 | 0001 |
| <i>Bothynus sp.1</i> | ?110000101 | ??001011?? | ??011?001? | 0100010?0? | 00101???10? | 1100000001 | 0010110100 | ?0?? |
| <i>Bothynus sp.2</i> | 0100000101 | 0000101001 | 0001110001 | 0100000?0? | 00101???101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus sp.3</i> | 0100000101 | 0000101101 | 0001110011 | 010000010? | 00101???101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus sp.4</i> | 0110000101 | 0001101101 | 0001110011 | 010001010? | 00101???101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus sp.5</i> | 0100000101 | 0001101101 | 0001110001 | 010000010? | 00101???101 | 1100000001 | 0010110100 | 0000 |
| <i>Bothynus sp.6</i> | ?100000101 | ??0010110? | 000111001? | 0100010?0? | 00101???101 | 01?0000001 | 001?1101?0 | 0000 |
| <i>Bothynus sp.7</i> | 0100110100 | 0001001001 | 0001100001 | 0100000101 | 0010111010 | 0-10000001 | 0011110100 | 0100 |
| <i>Bothynus sp.8</i> | 0100001100 | 0000000001 | 0000-01001 | 0100100001 | 0010111100 | 0-00000011 | 0010110100 | 1000 |

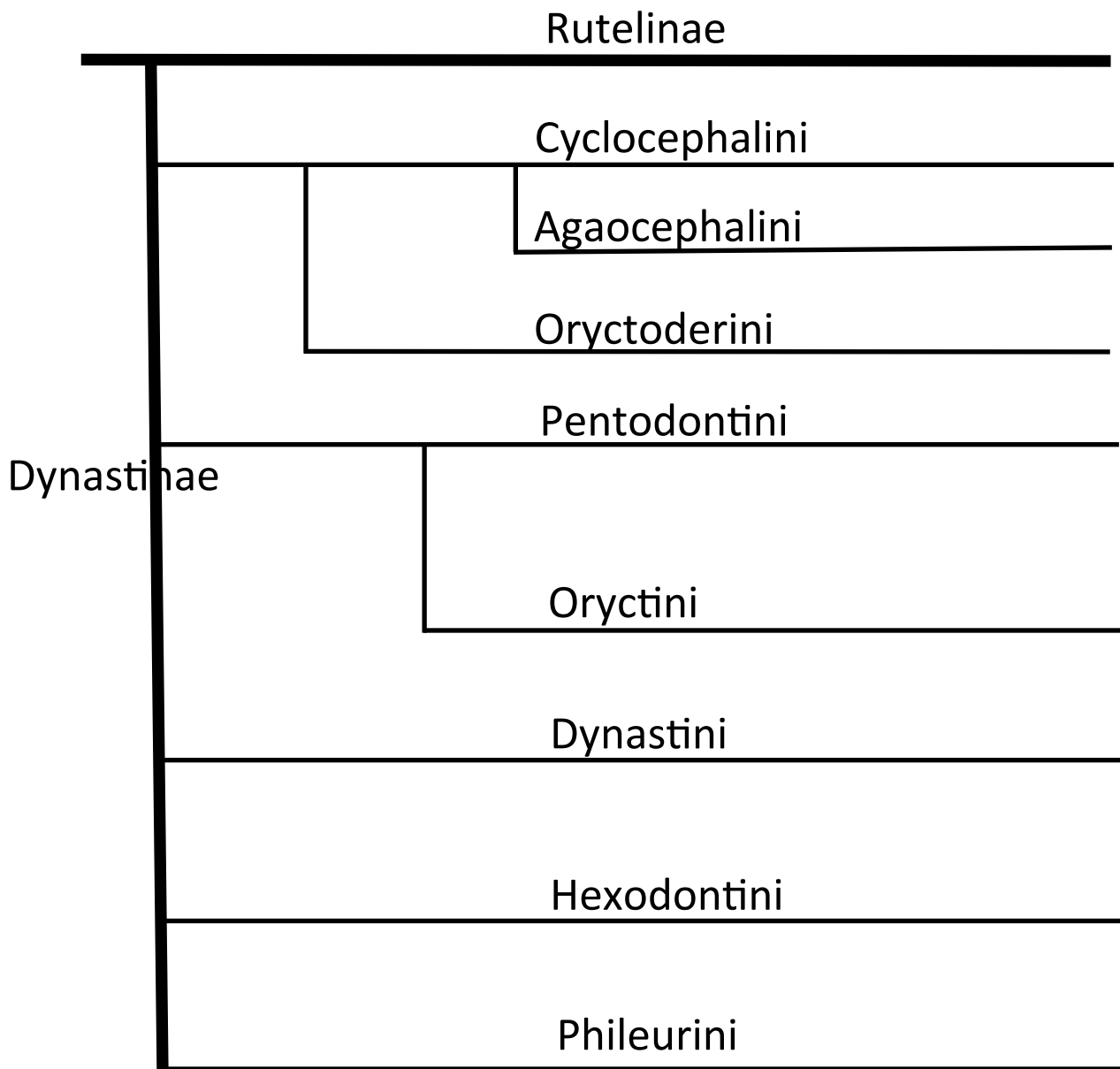


Figure 1. Relationship hypothesis among the Dynastinae tribes, adapted from Endrodi (1966).

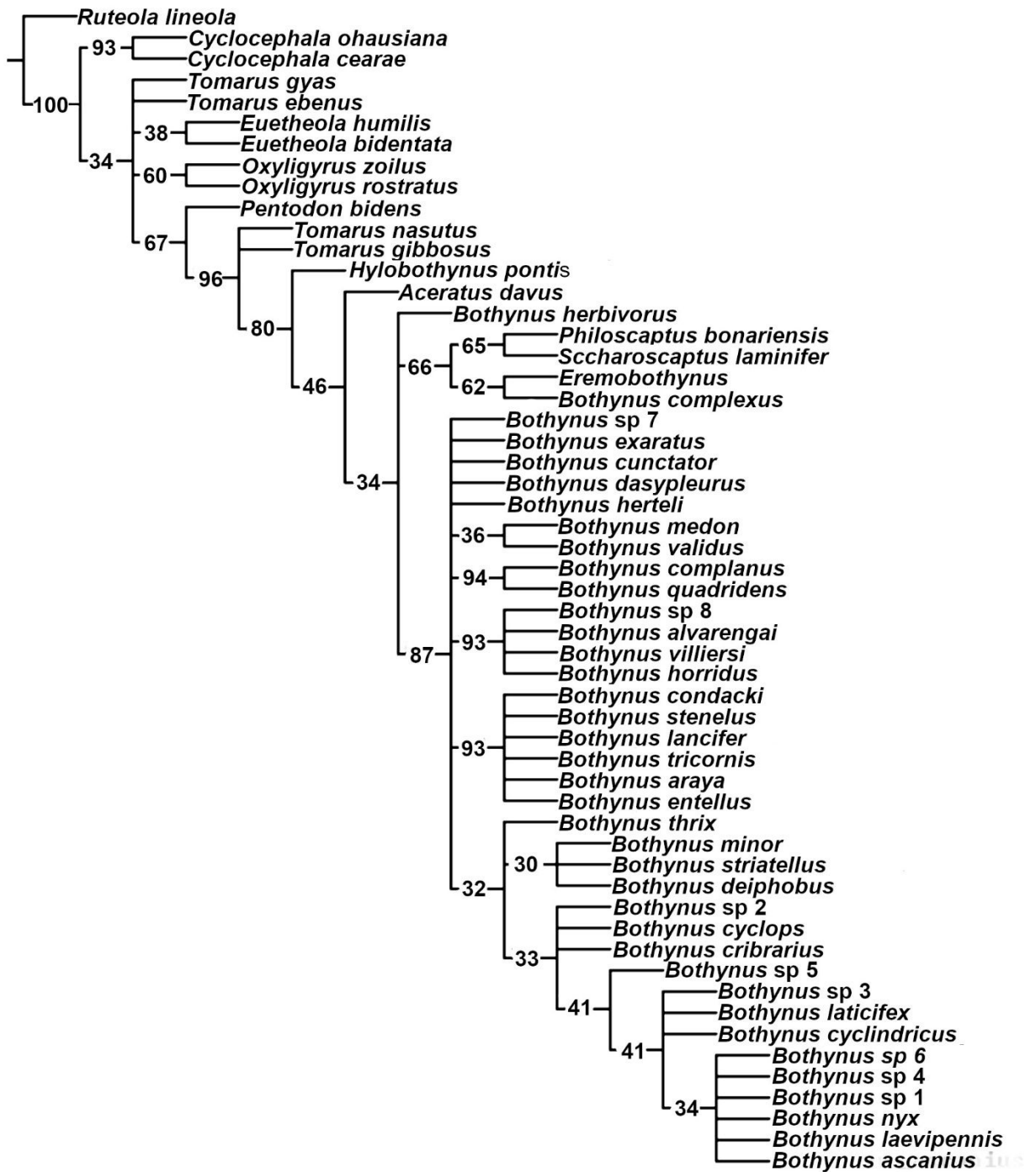


Figure 2. Strict consensus tree with bootstrap values (≥ 30) indicated between nodes.



Figure 3. Topology of the only tree obtained in the analysis with implicit weighting (L=144, $k=4.76$, fit=60.53, ci=51, ri=87) showing the phylogenetic relationships among the taxa.

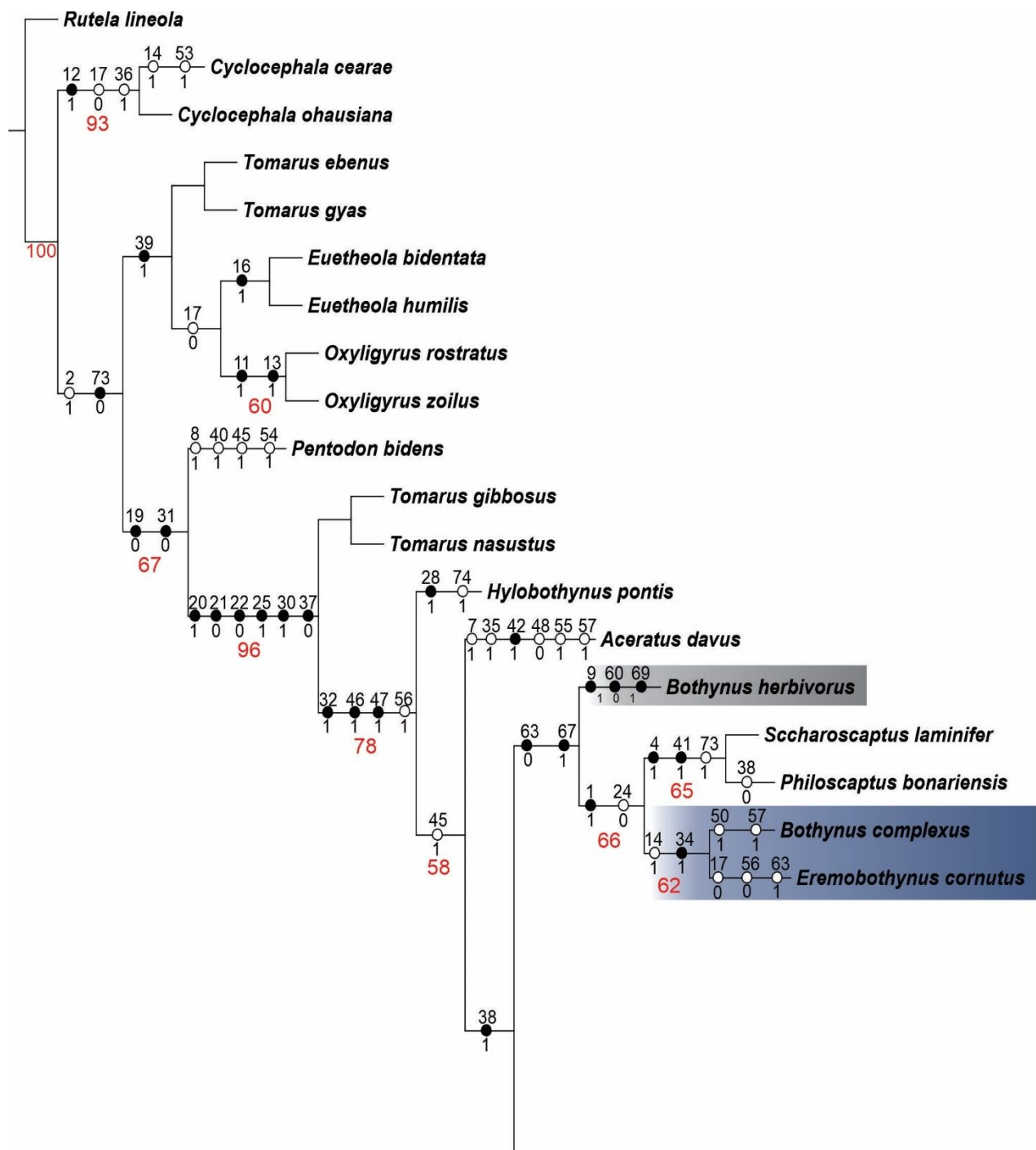


Figure 4. The out-group and its commons transformations in black dots (synapomorphies) and white dots (homoplasies). Bootstrap support values (>50) are indicated in red just below the nodes.

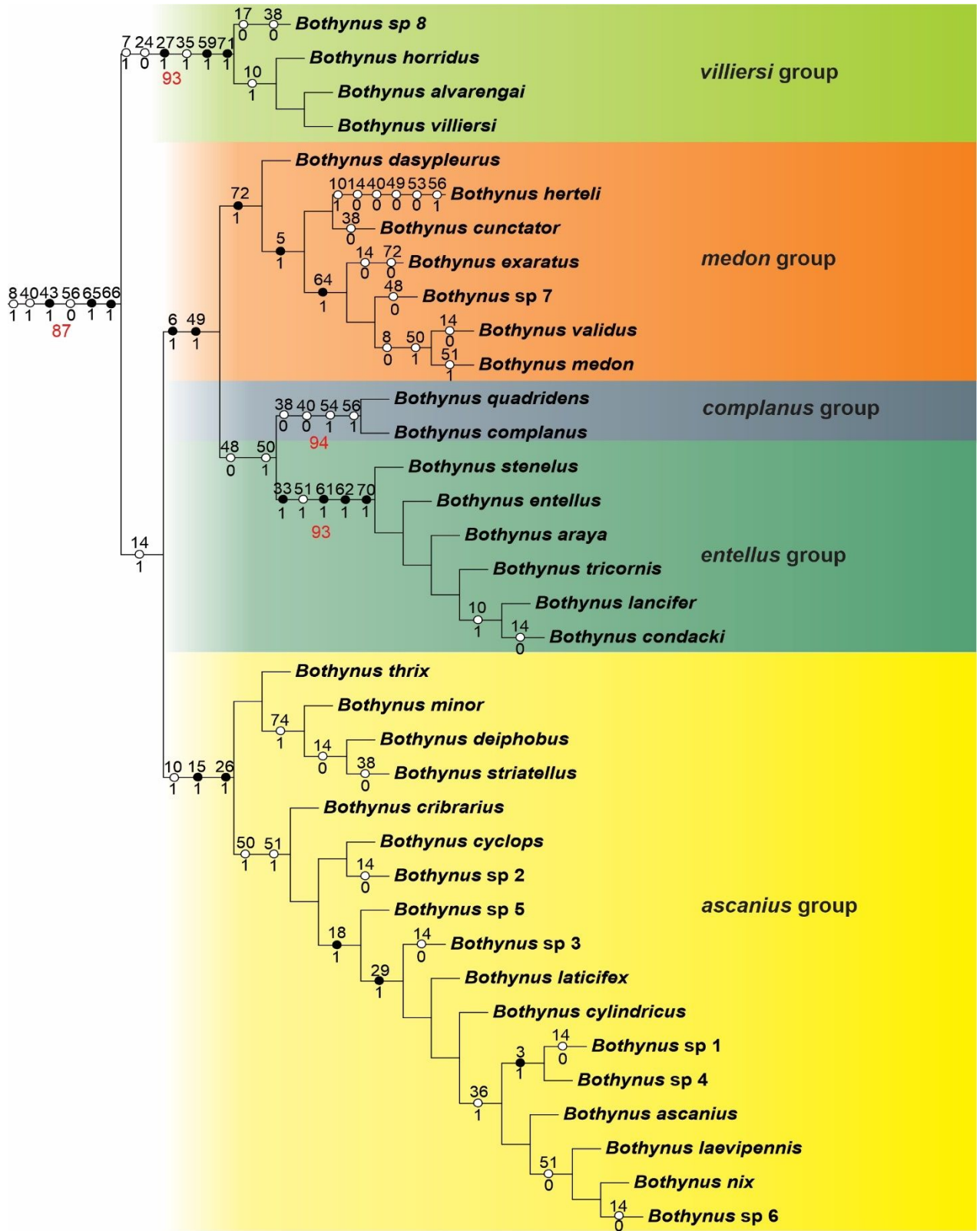


Figure 5. Relations among the species within the *Bothynus* lineage with its commons transformations in black dots (synapomorphies) and white dots (homoplasies). Bootstrap support values (>50) are indicated in red just below the nodes.

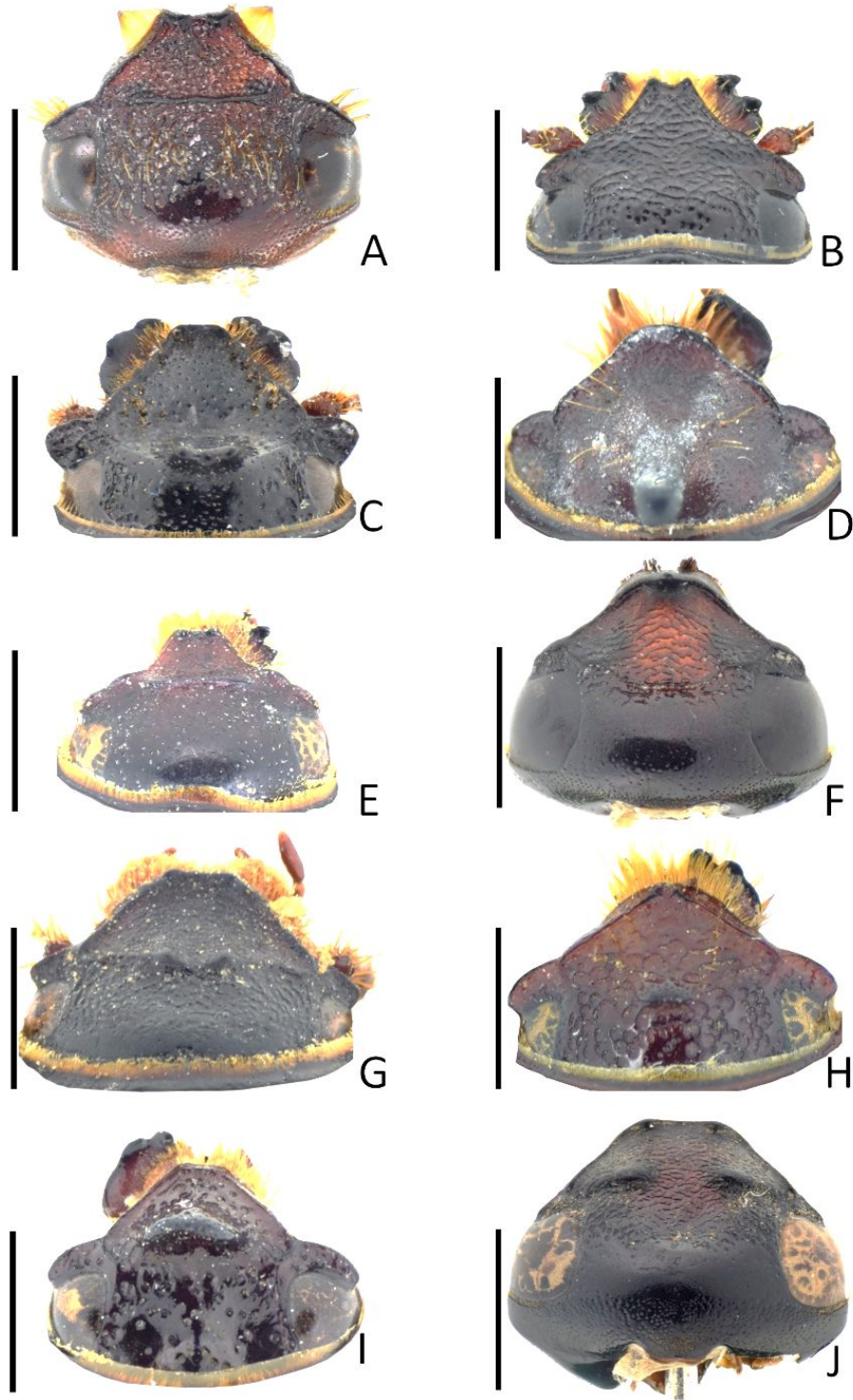


Figure 6. Head in dorsal view: A) *Bothynus ascanius*; B) *Bothynus herbivorus*; C) *Bothynus complexus*; D) *Eremobothynus cornutus*; E) *Tomarus gibbosus*; F) *Oxyligyrus zoilus*; G)

Pentodon bidens; H) *Philoscaptus bonariensis*; I) *Saccharoscaptus laminifer*; J) *Tomarus ebenus*.
 Scale bars = 2 mm.

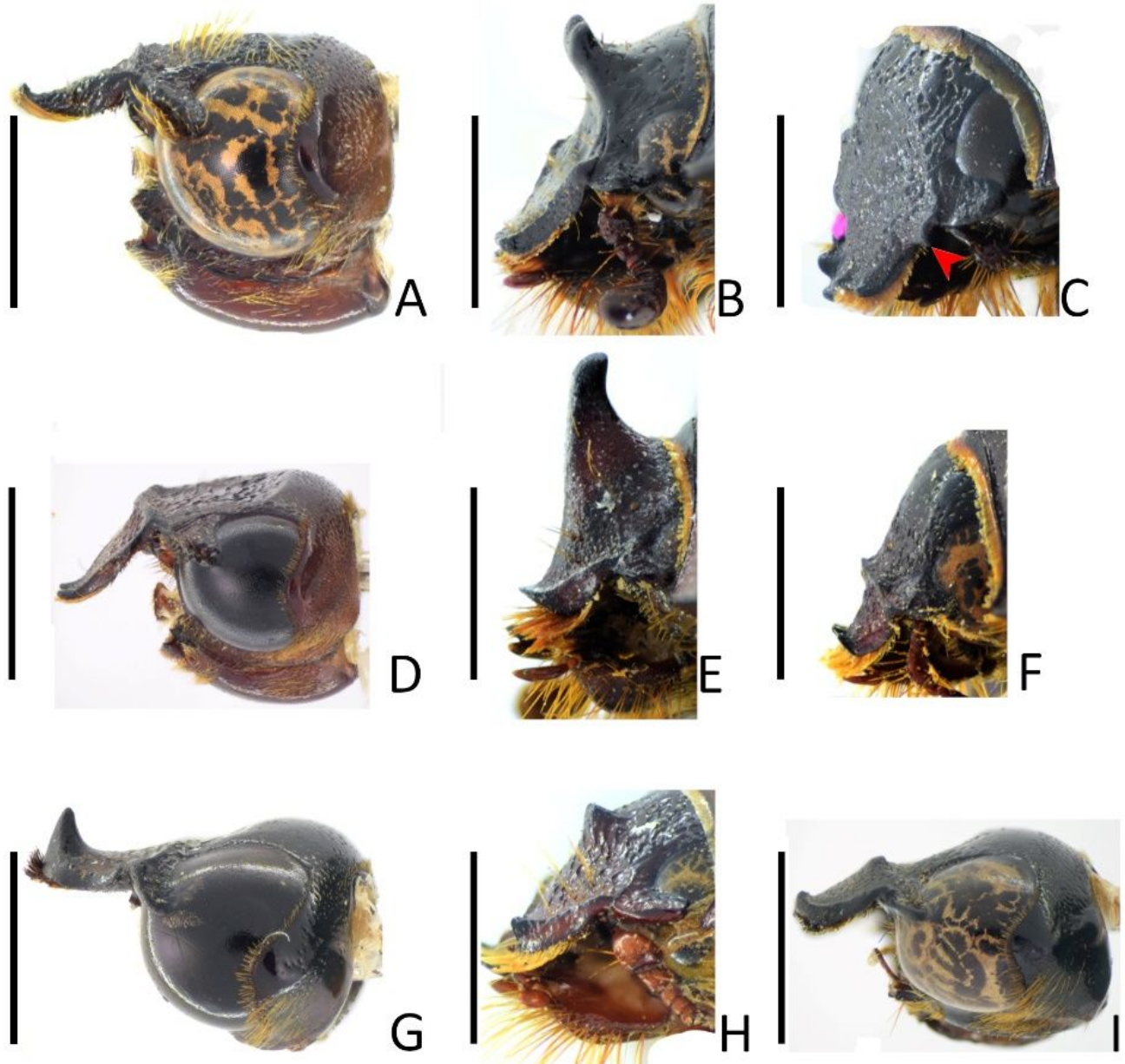


Figure 7. Head in lateral view: A) *Bothynus ascanius*; B) *Bothynus complexus*; C) *Bothynus herbivorus*; D) *Bothynus horidus*; E) *Eremobothynus cornutus*; F) *Tomarus gibbosus*; G) *Oxyligyus zoilus*; H) *Philoscaptus bonariensis*; I) *Tomarus ebenus*. Red arrow: deflexed basal tooth in C. Scale bars = 2 mm.

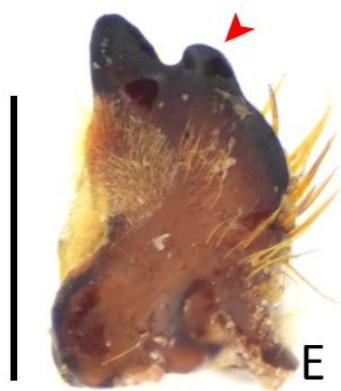
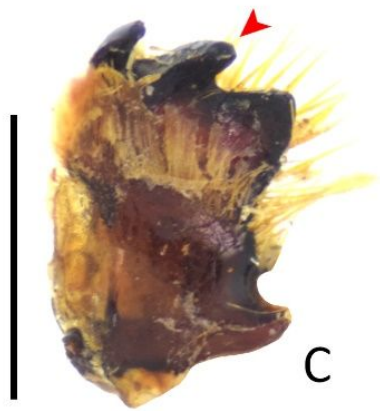


Figure 8. Right mandible in dorsal view: A) *Bothynus ascanius*; B) *Euetheola humilis*; C) *Tomarus gibbosus*; D) *Oxylygyrus zoilus*; E) *Philoscaptus bonariensis*; F) *Tomarus ebenus*. Red arrow: outer teeth. Scale bars = 2 mm.

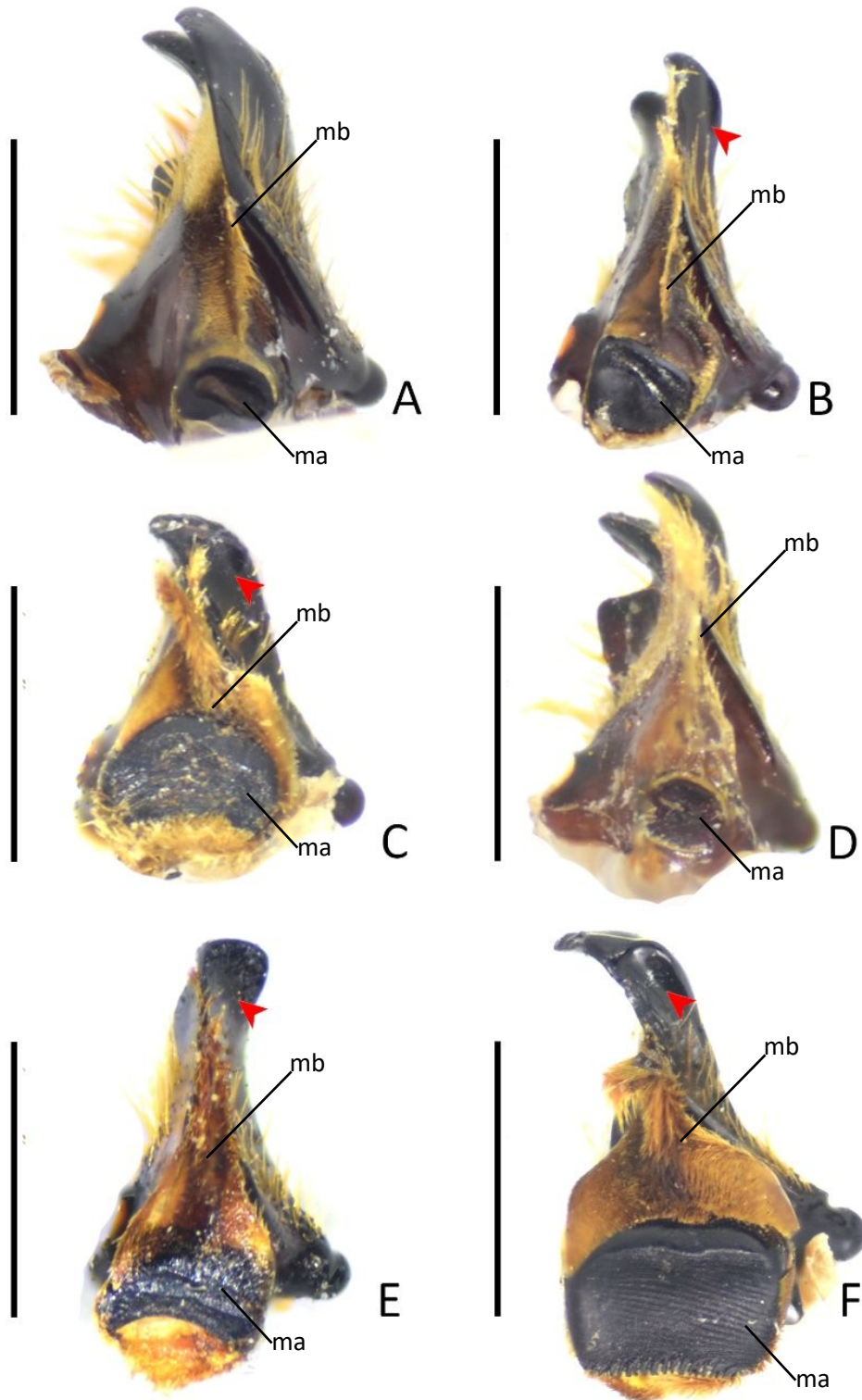


Figure 9. Inner view of the right mandible: A) *Bothynus ascanius*; B) *Bothynus herbivorus*; C) *Euetheola humilis*; D) *Philoscaptus bonariensis*; E) *Oxyligyrus zoilus*; F) *Tomarus ebenus*. ma–molar area, mb–mesal brush. Red arrow: apical excavation. Scale bars = 2 mm.

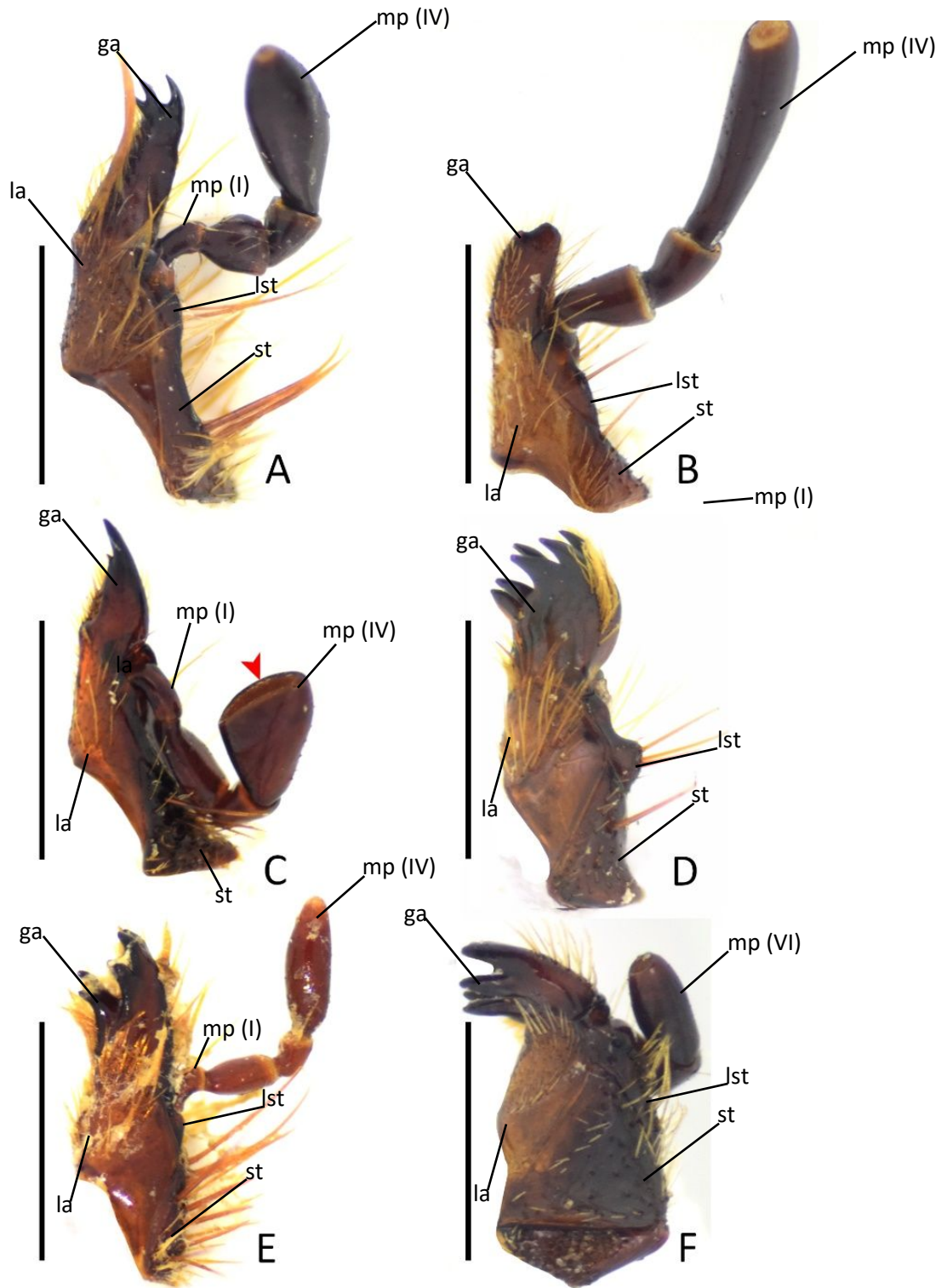


Figure 10. Left maxilla in ventral view: A) *Bothynus ascanius*; B) *Bothynus horridus*; C) *Hylobothynus pontis*; D) *Oxylogyrus zoilus*; E) *Pentodon bidens*; F) *Tomarus ebenus*. mp (I)–maxillary palpomere I, ga–galea, la–lacinia, mp (IV)–maxillary palpomere IV, lst– lateral stipe, st–stipe. Red arrow: sensorial apical area. Scale bars = 2 mm.

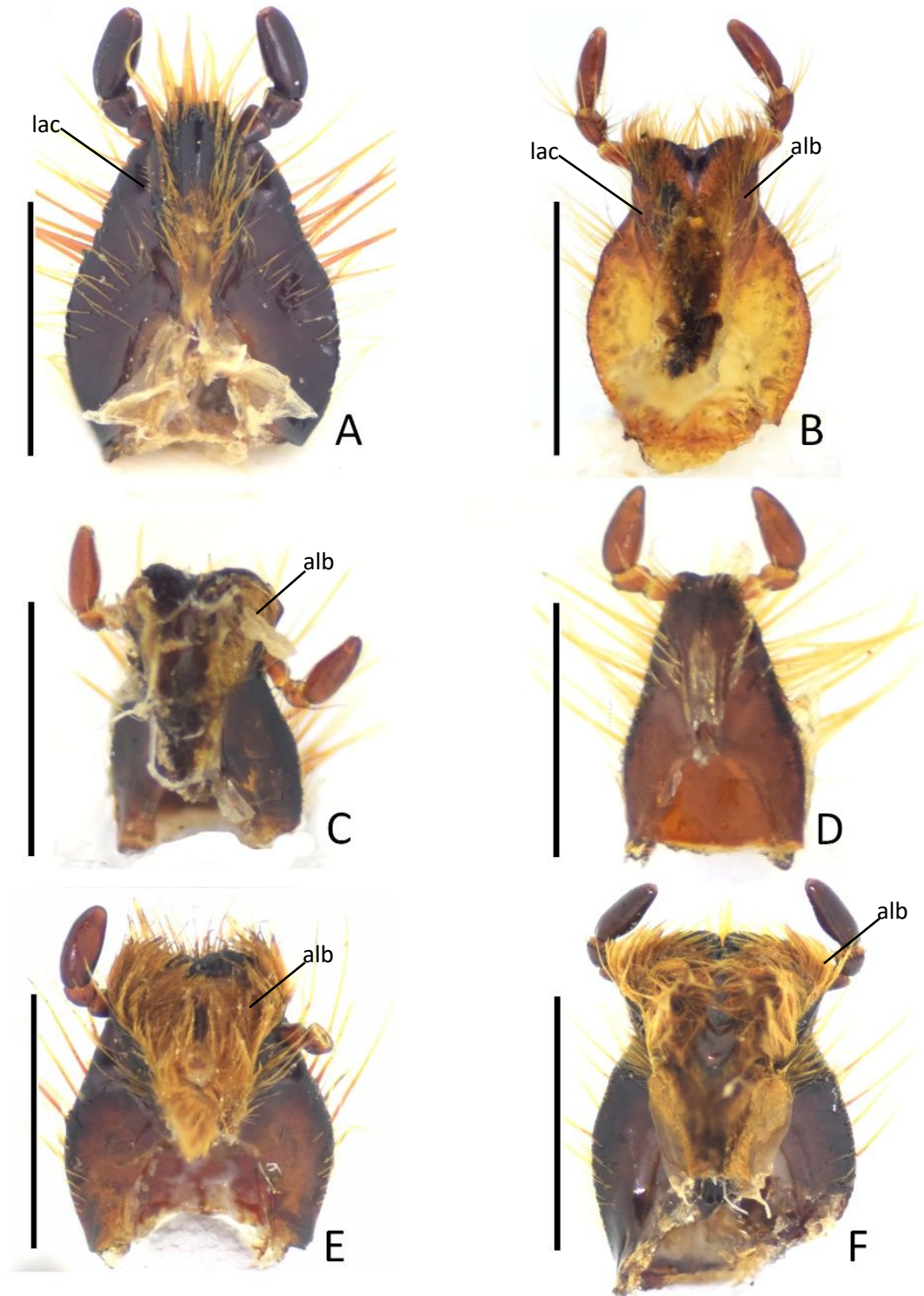


Figure 11. Hypopharynx: A) *Bothynus ascanius*; B) *Cyclocephala cearae*; C) *Euetheola humilis*; D) *Tomarus gibbosus*; E) *Oxylygyrus zoilus*; F) *Tomarus ebenus*. alb—anterolateral brush, lac—anterolateral carina. Scale bars = 2 mm.

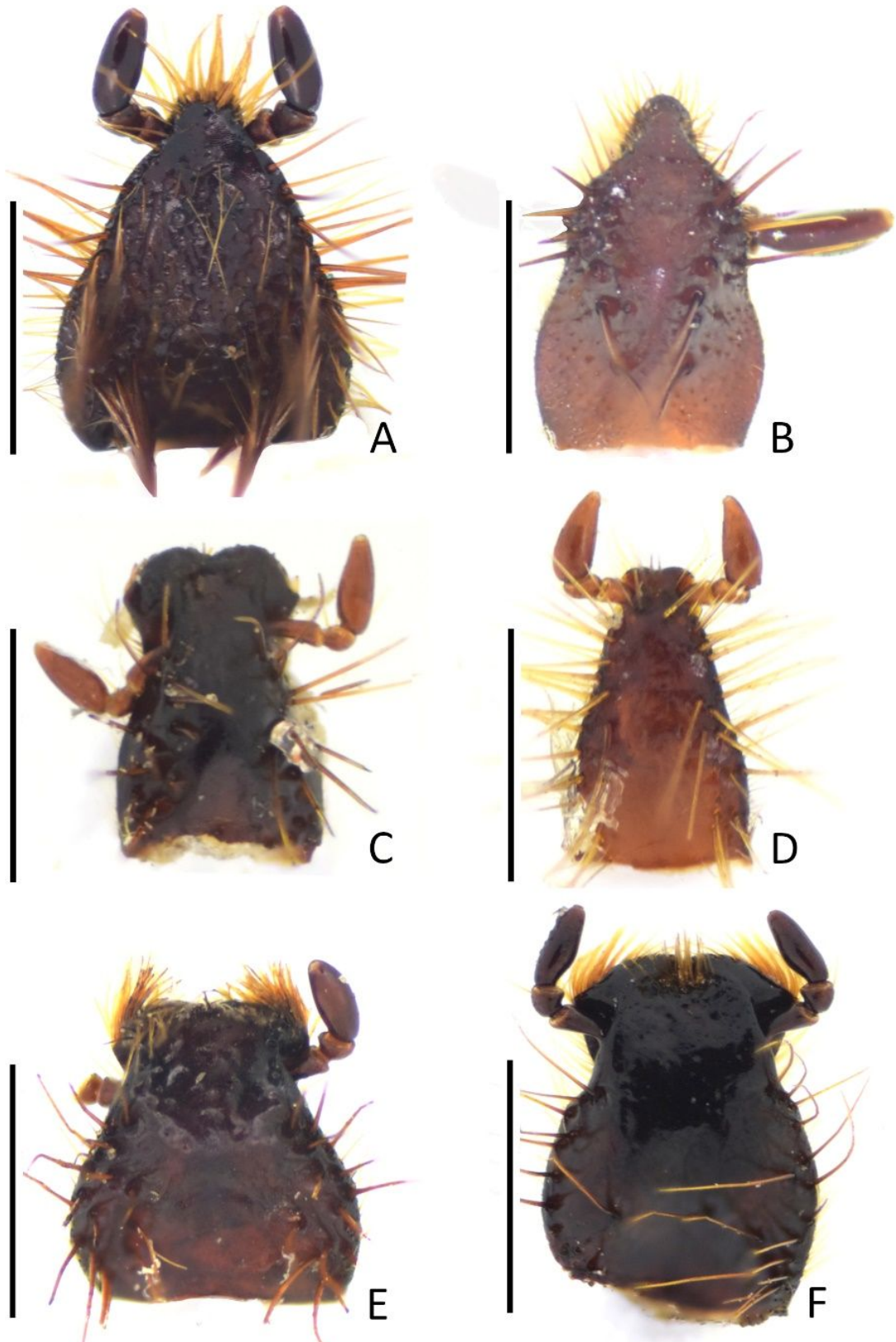


Figure 12. Mentum: A) *Bothynus ascanius*; B) *Bothynus horridus*; C) *Euetheola humilis*; D) *Tomarus gibbosus*; E) *Oxyligyus zoilus*; *Tomarus ebenus*. Scale bars = 2 mm.

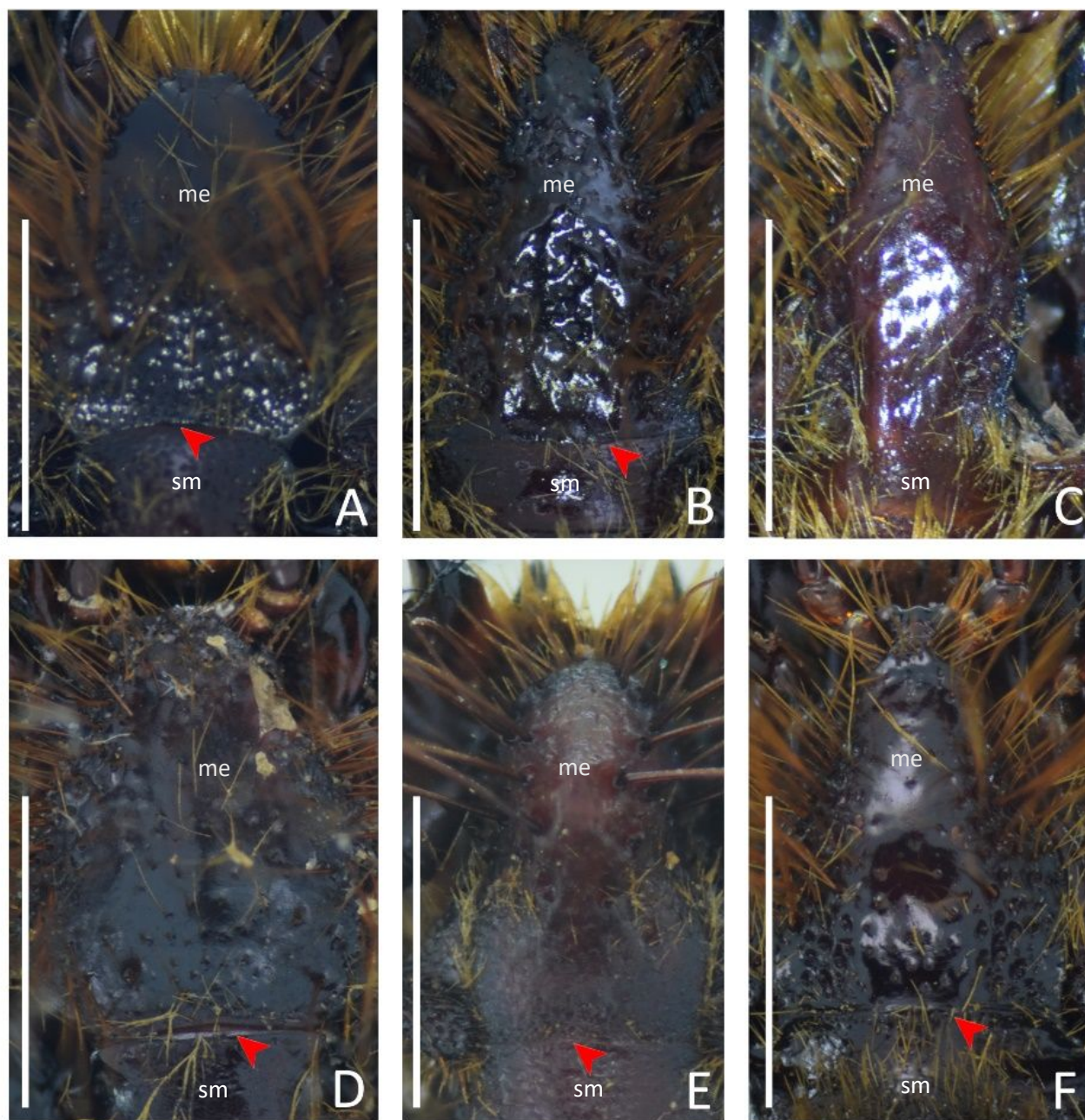


Figure 13. Labium: A) *Bothynus ascanius*; B) *Bothynus complanus*; C) *Bothynus entellus*; D) *Bothynus herteli*; E) *Bothynus horridus*; F) *Bothynus medon*. me–mentum, sm–submentum. Red arrow: transversal suture. Scale bars = 2 mm.

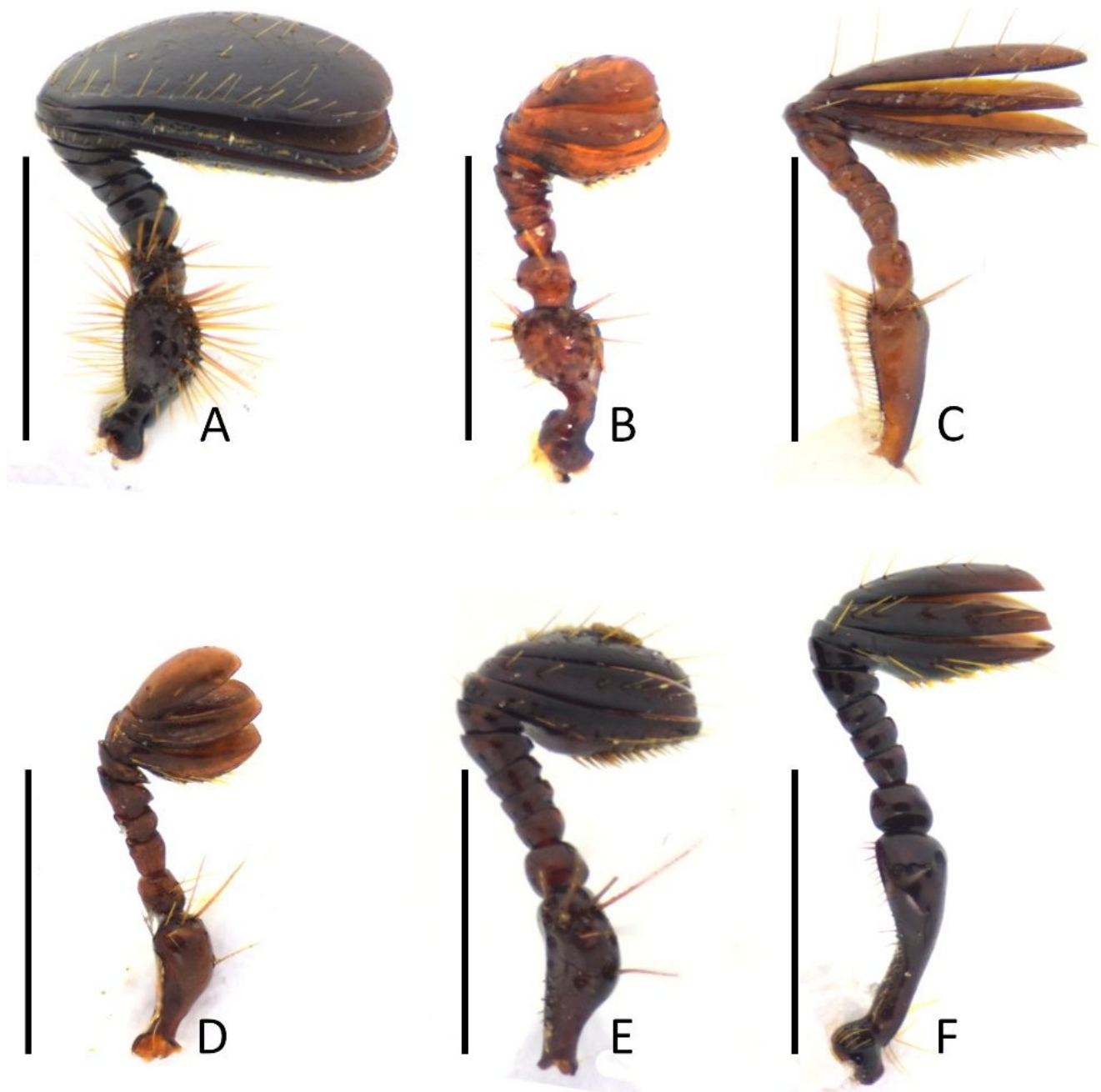


Figure 14. Antennae: A) *Bothynus ascanius*; B) *Bothynus complexus*; C) *Cyclocephala cearae*; D) *Eremobothynus cornutus*; E) *Oxyligyris zoilus*; F) *Tomarus ebenus*. Scale bars = 2 mm.

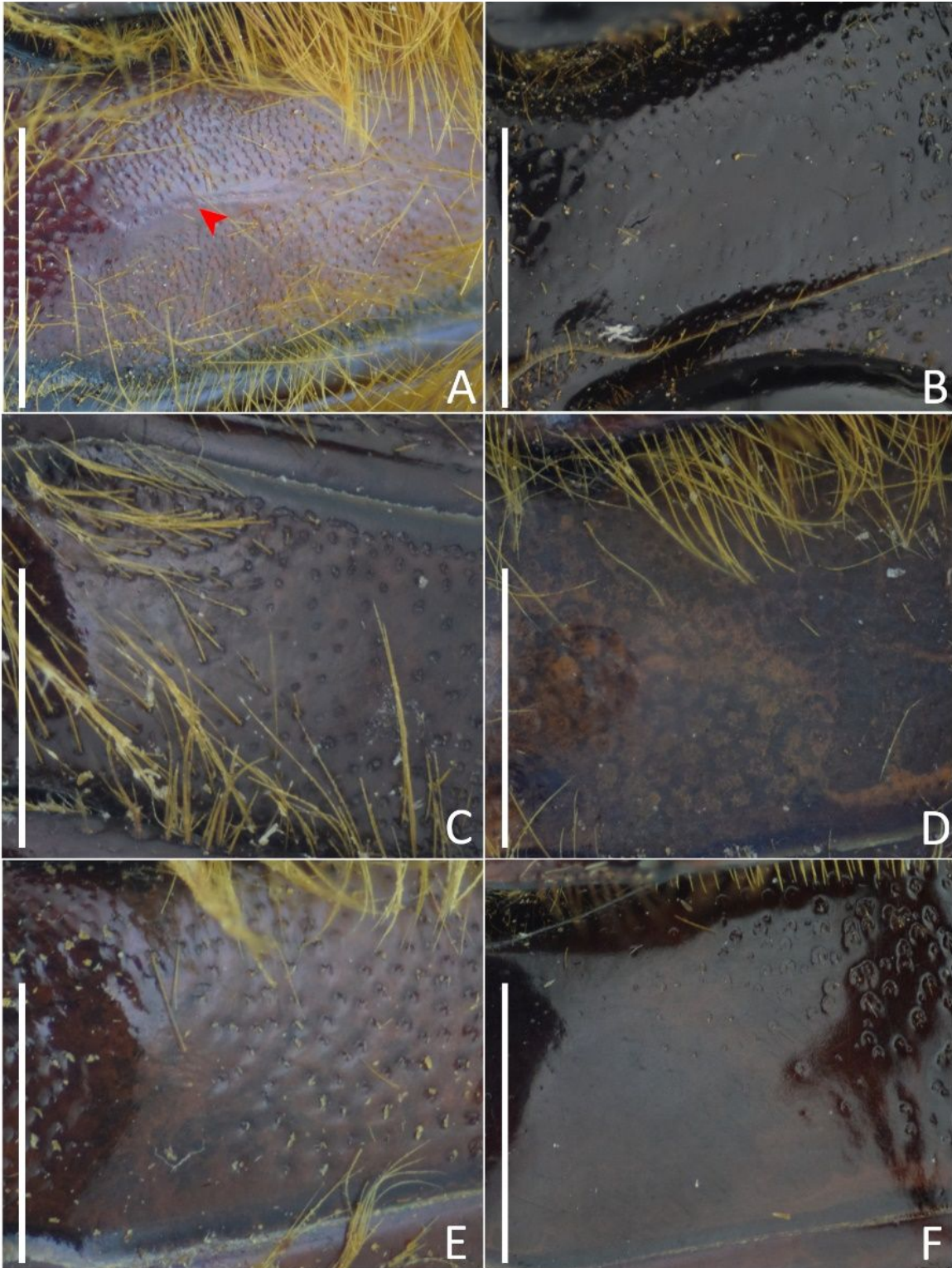


Figure 15. Left side of metaventricle: A) *Bothynus ascanius*; B) *Bothynus complexus*; C) *Bothynus herbivorus*; D) *Eremobothynus cornutus*; E) *Tomarus gibbosus*; F) *Tomarus cuniculus*. Red arrow: transversal groove. Scale bars = 2 mm.

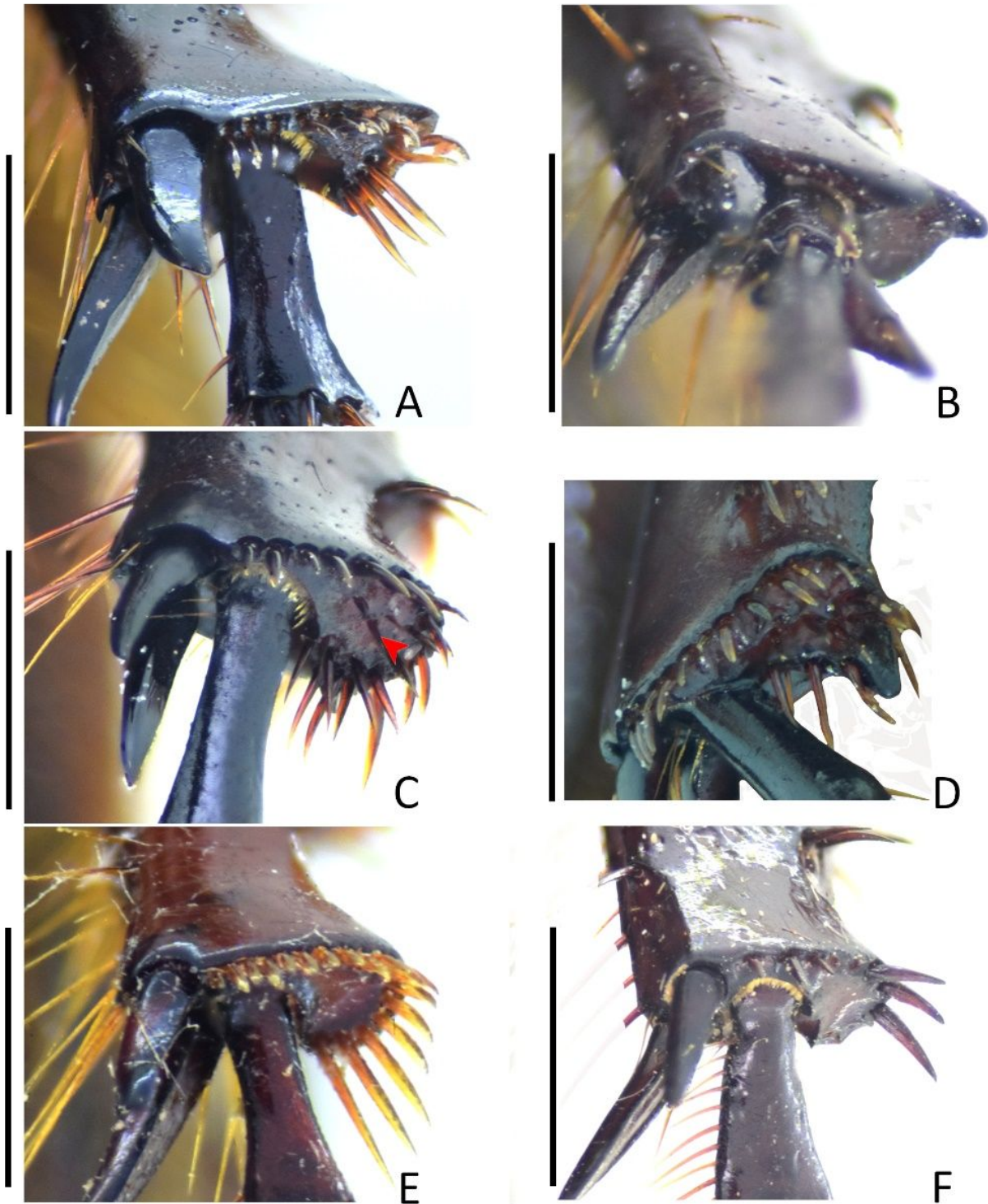


Figure 16. Mesotibial apex: A) *Bothynus Ascanius*; B) *Bothynus herbivorus*; C) *Bothynus horridus*; D) *Eremobothynus cornutus*; E) *Tomarus gibbosus*; F) *Tomarus ebenus*. Red arrow: setae on discal area. Scale bars: 2 mm.

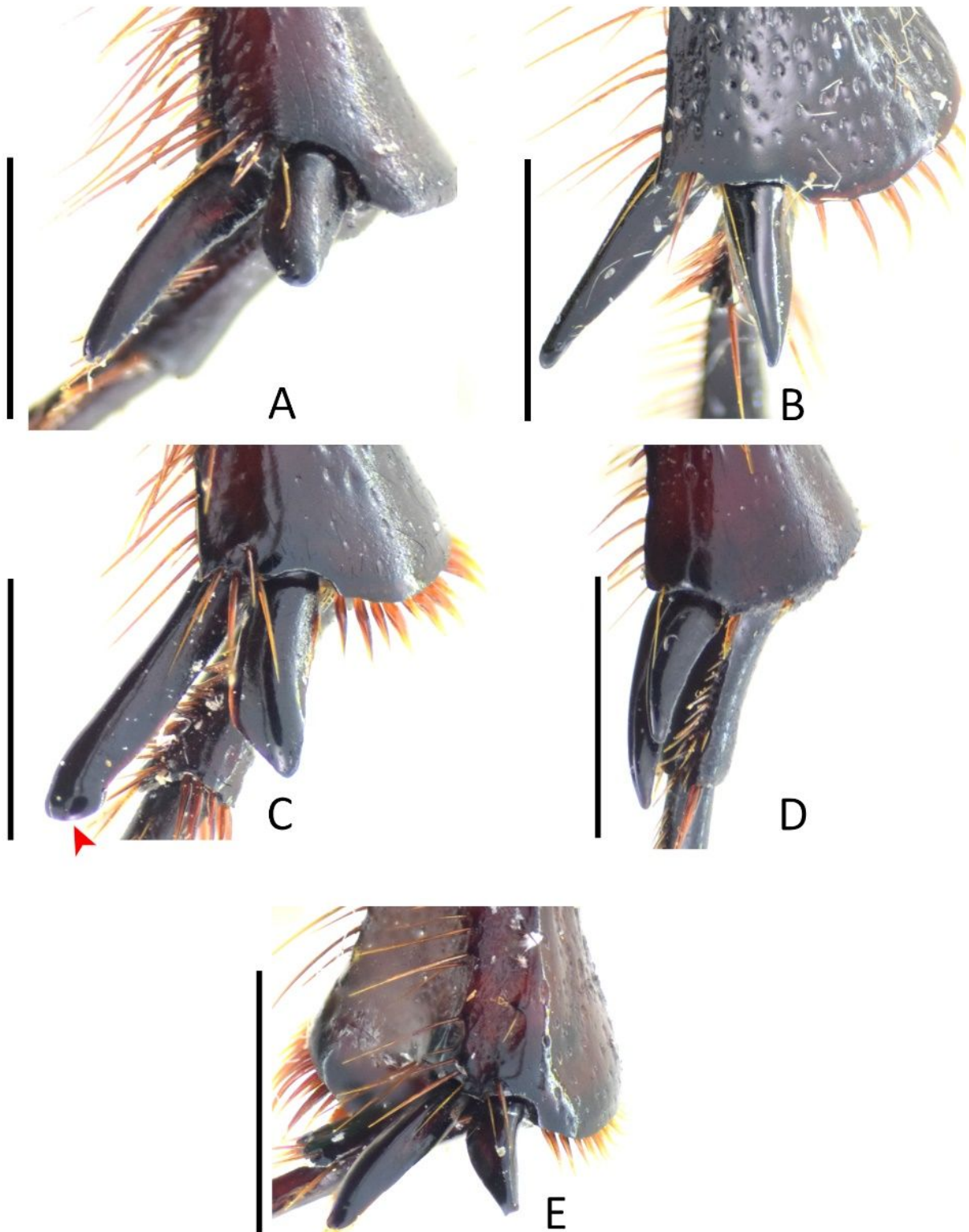


Figure 17. Metatibial spurs: A) *Bothynus ascanius*; B) *Bothynus complanus*; C) *Bothynus entellus*; D) *Bothynus horridus*; E) *Bothynus medom*. Red arrow: apex of inner spur. Scale bars = 2 mm.

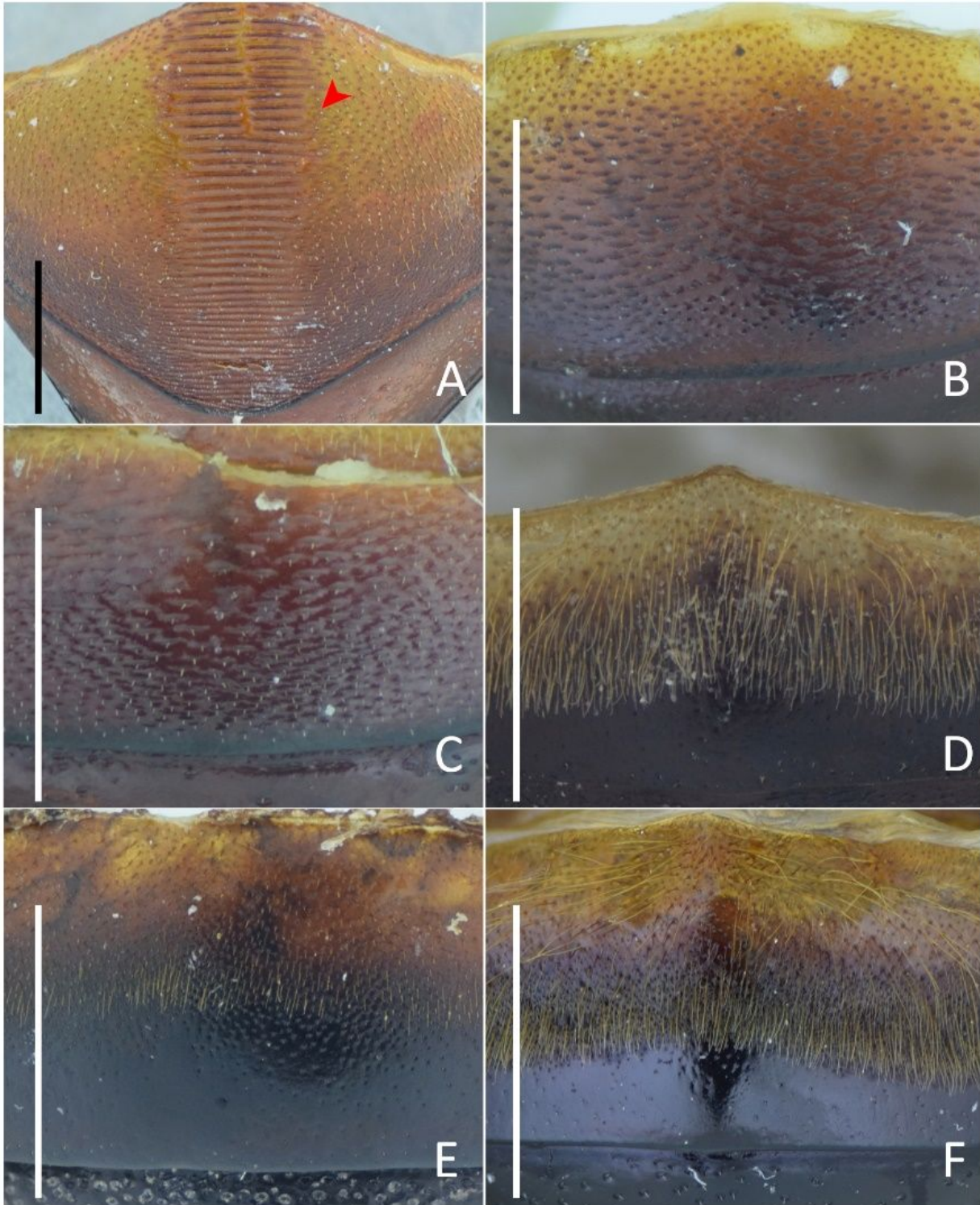


Figure 18. Discal area of tergite VII: A) *Bothynus medon*; B) *Bothynus complexus*; C) *Bothynus herbivorus*; D) *Euetheola humilis*; E) *Oxyligyrus zoilus*; F) *Tomarus ebenus*. Red Arrow: stridulatory apparatus. Scale bars = 2 mm.

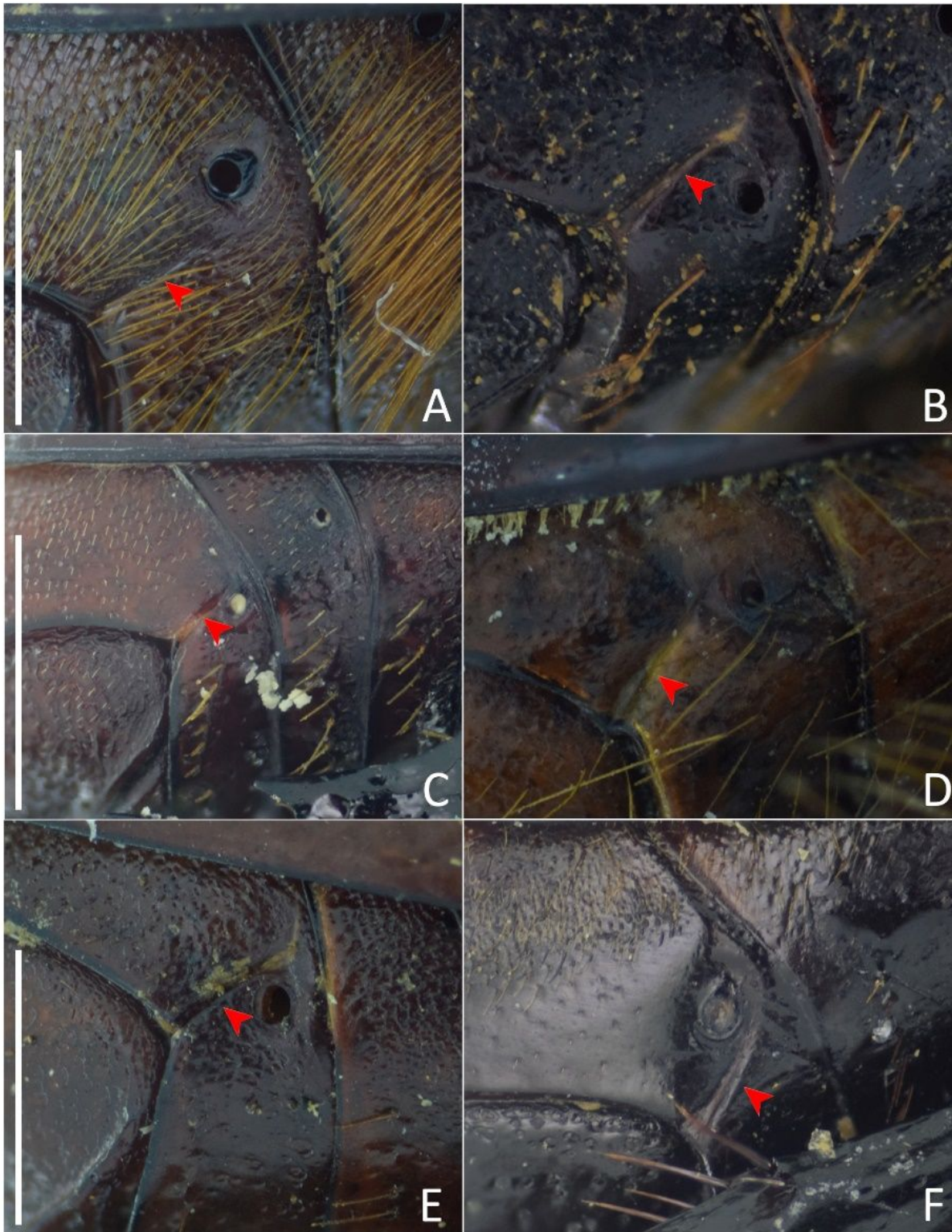


Figure 19. Spiracle of Tergite VII: A) *Bothynus Ascanius*; B) *Bothynus complexus*; C) *Bothynus herbivorus*; D) *Eremobothynus cornutus*; E) *Philoscaptus bonariensis*; F) *Tomarus ebenus*. Red arrow: pleural suture. Scale bars = 2 mm.

CHAPTER 3

TAXONOMIC REVIEW OF THE GENUS *BOTHYNUS* HOPE, 1837 (COLEOPTERA:
MELOLONTHIDAE: DYNASTINAE: PENTODONTINI)

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¹Duarte, P.R.M., P.C. Grossi & D.R. Parizotto. Taxonomic review of the genus *Bothynus* Hope, 1837 (Coleoptera: Melolonthidae: Dynastinae: Pentodontini). A ser submetido.

ABSTRACT – *Bothynus* Hope, 1837 is a large genus of Pentodontini exclusively distributed in the Neotropics. The genus occurs from Mexico to Argentina, with all species occurring in South America. The last comprehensive taxonomic study on the genus was published 51 years ago by Endrödi in his work “Monographie der Dynastinae”. Posterior studies made by other authors deal only with new species or some species from specific regions. Most species in the genus have not been addressed since the Endrödi’s work, being necessary a review that compasses all *Bothynus* species. For this reason, a completed taxonomic revision for *Bothynus* is presented here and the following points are addressed: redescrptions, diagnoses with its respective illustrations, locality data with new records, updated distribution maps, updated identification key, description of new species. The genus *Bothynus* is redefined here and two new combinations are proposed: *B. complexus* Dechambre was moved to *Eremobothynus* Ohaus and *B. herbivorus* (Arrow) moved to *Cephaloplanum* gen. nov. Also, *B. fabius* (Fairmaire) is revalidated and *B. striatellus* (Fairmaire) synonymized with it. Females of *B. ascanius* (Kirby), *B. cylindricus* Arrow, and *E. complexus* (Dechambre)comb. nov. are described. The stridulatory apparatus and female genitalia are described and illustrated for the first time for *Bothynus* species. In addition, eight new species are described: *B. moroni* sp. nov., *B. andreus* sp. nov., *B. tamarae* sp. nov., *B. leidiana* sp. nov., *B. sebastiani* sp. nov., *B. aydanus* sp. nov., *B. simplex*., *B. belenensis* sp. nov.

KEY WORDS: Diversity, Neotropical region, new species, new world, Scarabaeoidea, South America

REVISÃO TAXONÔMICA DO GÊNERO *BOTHYNUS* HOPE, 1837 (COLEOPTERA:

SCARABAEIDAE: DYNASTINAE: PENTODONTINI)

RESUMO – *Bothynus* Hope, 1837 é um grande gênero de Pentodontini com distribuição exclusiva para a região Neotropical. O gênero ocorre do México à Argentina, com todas as espécies sendo encontradas na América do Sul. O último estudo taxonômico abrangente sobre o gênero foi publicado há 51 anos atrás por Endrödi em seu trabalho “Monographie der Dynastinae”. Trabalhos posterior realizados por diferentes autores tratam apenas de novas espécies ou somente de algumas espécies de regiões específicas. A maioria das espécies do gênero não tem sido abordadas desde o trabalho de Endrödi, sendo necessário uma revisão que contemple todas as espécies de *Bothynus*. Por isso, revisão completa para o gênero é apresentada aqui sendo abordados os seguintes pontos: redescrições, descrição de novas espécies, caracteres diagnósticos com suas respectivas imagens, dados de localidades com novas ocorrências, mapas de distribuição atualizados, chave de identificação atualizada. *Bothynus* é redefinido aqui e duas novas combinações são propostas: *B. complexus* Dechambre é movido para *Eremobothynus* Ohaus e *B. herbivorus* (Arrow) é movido para *Cephaloplanum* gen. nov. *Bothynus fabius* (Fairmaire) é revalidado e *B. striatellus* é sinonimizado com este. São descritas as fêmeas de *B. ascanius* (Kirby), *B. cylindricus* Arrow e *E. complexus* (Dechambre) comb. nov. O aparato estridulador e a genitália feminina são descritos e ilustrados pela primeira vez para as espécies de *Bothynus*. Adicionalmente são descritas oito novas espécies: *B. moroni* sp. nov., *B. andreus* sp. nov., *B. tamarae* sp. nov., *B. leidiana* sp. nov., *B. sebastiani* sp. nov., *B. aydanus* sp. nov., *B. simplex*., *B. belenensis* sp. nov

PALAVRAS-CHAVE: América do Sul, diversidade, novas espécies, novo mundo, Região Neotropical, Scarabaeoidea

Introduction

Bothynus Hope, 1837 is a genus of Pentodontini with exclusive distribution in the New World, occurring in the Neotropical realm more precisely (Endrödi 1985). All 31 valid species in the genus have South American occurrence (López-García *et al.* 2016, Hardy 2017, Duarte & Grossi 2020). Only *B. quadridens* (Taschenberg, 1879) and *B. complanus* (Burmeister, 1847) reaching Central América and Mexico (Morón *et al.* 1997, Ratcliffe *et al.* 2013). The majority of South American *Bothynus* are found in Brazil with 22 species (López-García *et al.* 2016, Grossi and Vaz-de-Mello 2020).

Bothynus species are nocturnal and feature positive phototropism, being easily attracted by light traps at night, making the genus usually well represented in collections. Despite this, the natural history and biology of the genus remain poorly understood. The taxonomic knowledge of immature stages is incipient and only the third larval instar of *B. medon* (Germar, 1824) was described (Pereira *et al.* 2013).

Regarding the adult taxonomy, monographies published by Endrödi (1969, 1985) were the last comprehensive works about the genus, where are addressed 23 of the 24 *Bothynus* species, only *B. niger* (Blanchard, 1846) not was included. In his works are presented identification keys, diagnoses, male genital scheme, distribution data, lectotypes and neotypes designations, and imagens for some species. However, despite the immeasurable Endrödi's contribution, most of his diagnoses revolve around the male genitalia, diagnoses based on female characters are nonexistent or imprecise.

Subsequently, complete studies were carried out for some *Bothynus* species from specific regions. In Morón *et al.* (1997), Ratcliffe (2003), Ratcliffe & Cave 2006, and Ratcliffe *et al.*

(2013) only two *Bothynus* species from Central and North America region were included. Gasca-Álvarez & Amat-García (2010) and López-García (2015) addresses only *Bothynus* species from Colombia. The field guide provided by Abadie *et al.* (2008) addresses the species distributed to the south of South America. Furthermore, seven new *Bothynus* species were described, increasing the number of species in the genus to 31 (Dechambre 1981, 2006, Martínez 1983, Ratcliffe 2010, Hardy 2017, Duarte & Grossi 2020). However, some these new species do not were included in any know identification key for the genus an up to date is need.

The present chapter aims to provide a complete review for the genus *Bothynus*, and the following points are addressed here: 1) redescribe the genus and its species; 2) describe possible new species; 3) provide new diagnoses for the species along with its respective images; 4) provide an up to date identification key for species in the genus; 5) provide geographical maps with new distribution data; 6) provide the pertinent taxonomic changes based on results of Chapter 2.

Material and Methods

This study was based on the examination of 661 specimens loaned from institutions and collections with the same acronyms of Chapter 2. The species identification was based on their original description and the study of Endrödi (1969), when the type-specimens were not available. Photography and dissection procedures follow Chapter 2. Geographic distribution maps were based on label data and generated with the SimpleMappr online tool (Shorthouse 2010). Characteristics of type labels are described between brackets after the label's information, in the following format: "label information [shape of label (when rounded), color of label, information format (e.g. handwritten)]". Different labels are separate by a slash "/". Labels of non-type material are described according to the following example: "ARGENTINA: CÓRDOVA: La Cumbre, Km 6, 12.xi.2005, P. Smith leg. – 1♂ 1♀ (CERPE)". Measurements were delineated

from largest to smallest specimens as follow: body length from clypeal anterior margin to elytral posterior margin, and body width as the distance between humeri. In some situations, where it was not possible to examine one of the sexes, the description was based on relevant literature, as specified in the species description. The terminology used follows Lawrence *et al.* (2011) for overall morphology, Nel & Scholtz (1990) for mouthparts, Hotman & Scholtz (1990) for male genitalia, and Dupuis (2005) for female genitalia. The classification system is based in Chermán & Morón (2014).

Results and Discussion

***Bothynus* Hope, 1837**

Bothynus Hope 1837, p. 95. (Type species: *Bothynus ascanius* Kirby, 1819, by posterior designation)

Cratocnemis Blanchard 1842 plate II, fig. 1 (Synonym). (Type species: *Cratocnemis niger* Blanchard, 1842 by monotypy)

Scaptophilus Burmeister 1847, p. 122 (Synonym). (Type species not specified)

Corynoscelis Burmeister 1847, p. 126 (Synonym). (Type species not specified)

Diagnosis. *Bothynus* differs from other Neotropical genera of Pentodontini by the following combination of characters: Clypeus with two anterior teeth separated by a emargination; clypeus dorsoventrally subtriangular in lateral view (rarely flattened); protibiae usually tridentate, rarely quadridentate; metaventrite with a transverse sulcus on each side (sometimes only observed through dissection); tergite VII with stridulatory apparatus; tergite VIII with emarginate anterior margin.

Remarks. Hope (1837) described the genus *Bothynus* based on two species: *Geotrupes cuniculus* Fabricius, 1801, and *Scarabaeus ascanius* Kirby, 1819. In his description of the genus are addressed characteristics of body aspect, head, mouthparts, thorax, and legs, however, characteristics related to the abdomen are not mentioned. Hope (1837) probably not observed two important features that define the genus, located on the latest abdominal segments: presence of the stridulatory apparatus at tergite VII, and tergite VIII with emarginate anterior margin. This fact possibly led the author to a mislabeled identification of *G. cuniculus* and its designation as the type species of *Bothynus*. These two characters were first observed and described by Lacordaire (1856), where he also arguments which the characters that define *Bothynus* is concise with *S. ascanius* and propose it as type species of genus instead *G. cuniculus*. Subsequent authors as Bates 1888, Prell 1936, Arrow 1937b, Blackwelder 1944, Endrödi 1969, Dechambre 1981, Martínez 1983, Lachaume 1992, Morón *et al.* 1997, and Ratcliffe 2003 as also agree with the Lacordaire's designation. The exception was Cartwright (1959) that maintained the name *Bothynus* based on the Hope's designation.

We found here a new and exclusive diagnostic character for the genus *Bothynus*: the presence of a transverse sulcus on the metaventrite. This feature is externally visible in most *Bothynus* species, while in some cases is inconspicuous and only visible internally under high magnifications, being a dissection required. Therefore, *Bothynus* is redefined according to combination of characters mentioned in the diagnosis.

Generic redescription. **Length:** 30.5–15.0 mm. **Width:** 18.2–8.5 mm. **Color:** From reddish-brown to dark reddish-brown, or completely dark. **Head:** Clypeus from subtriangular to subpentagonal in shape; surface from rugopunctate to rugose, glabrous or covered with setae; anterior area with two teeth separated by an middle emargination; sides slightly attenuated toward

anterior area or abruptly constricted at apical half; clypeus usually triangular dorsoventrally in view lateral view, rarely flattened. Frontoclypeal suture formed by a transverse ridge (sometimes reaching the sides), or by tubercles (1–2). Frons from coarsely rugose to densely punctate, sometimes smooth posteriorly between eyes; surface glabrous or with setae confined at sides. Ocular cantus usually transverse, triangular, setose. **Mouthparts:** Mandibles bi- or tridentate at outer edge, visible to clypeus laterally, with lobed or pointed teeth. Maxillae usually with dentate galea, teeth rarely absent; galea separated from lacinia, sometimes fused to it. Mentum usually flattened, rarely with a medial process; surface surrounded with long setae, disc from densely punctate to weakly punctate. **Antennae:** Ten-segmented; club with lamellae subequal in length to antennomeres II–VII or with lamellae nearly two times longer than antennomeres II–VII combined. **Thorax:** In males, pronotum horned or only with an apical tubercle, followed by a deep concavity, surface from finely to moderately punctate, usually rugopunctate at concavity, posterior area usually strongly convex in lateral view; in females, pronotum with horn absent, only with an apical tubercle, usually smaller compared to male, concavity usually shallow, surface more punctate compared to males, posterior area usually weakly convex in lateral view. Scutellar plate from parabolic to triangular, usually smooth. Elytral surface rarely smooth, rarely setose, usually glabrous and with 9 well marked striae (1 sutural, 4 discal, 4 lateral), punctures usually deep and ocellated. Mesoventrite nearly completely rugopunctate, weakly setose. Metaventricle densely setose and rugopunctate on sides, discal area usually smooth, each side with a transversal sulcus. **Legs:** Protibiae tri- or quadridentate. In males, inner protarsal claw simple, incised, or with a ventromedial tooth; in female, protarsal claw simple, similar to outer claw. In both sexes, protarsomeres usually elongate, sometimes thickened in male. Meso- and metatibia usually with two carinae on outer surface (1 proximal, 1 medial); apex usually truncate, bordered with small spinules. **Abdomen:** Tergite VII with stridulatory apparatus confined at discal area; stridulatory

apparatus formed by two (rarely one) paired rows of innumerable, transverse striae. Tergite VIII with anterior middle-margin from slightly to widely emarginated; surface convex in lateral view in males, usually flattened in females; in females, posterior margin sometimes with an invaginate plate. Ventrite VI emarginate posteriorly at middle in males, complete in females. **Parameres:** Usually symmetric, with apical half broad laterodorsally, longitudinally excavated lateroventrally; rarely asymmetric, with triangular process at inner edges.

***Bothynus ascanius* species-group (Kirby, 1819)**

The *B. ascanius* species group comprises 17 species immediately distinguished from other species groups in *Bothynus* by the following characters: Frontoclypeal suture with an incomplete transverse ridge (not reaching the lateral margins); ocular canthus with setae confined on ventral surface; maxillary galea fused to lacinia. Species of the *ascanius* group occurs in Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

***Bothynus ascanius* (Kirby, 1819) (Fig. 20A–G; Fig. 53)**

Scarabaeus ascanius Kirby 1819, p. 399 (original description)

Bothynus ascanius, Hope 1837, p. 116

Diagnosis. *Bothynus ascanius* resembles *B. laevipennis* but differs from this species in the following aspects: In male, protarsal claw incising (Fig. 20C), tarsomere V with a ventrolateral process located at apex (Fig. 20C), spiculum gastrale with a triangular basal sclerite (Fig. 20D); In female, pronotal concavity shallow (Fig. 20B), metafemoral ventral surface covered with large punctures (Fig. 20G).

Remarks. Among the material examined was found one aberrant male specimen of *B. ascanius* with the inner protarsal claw with no incised. In a first view, this feature can lead to confusion with *B. laevipennis*, however, other diagnostic characters for the *B. ascanius* distinction remained stable. *Bothynus ascanius* has its distribution expanded here with new occurrences in Brazil and the first record from Argentina. In Brazil, the species occurs associated with the Cerrado areas from Midwest region, and with coastal Atlantic Forest areas from Southeast to South regions. In Argentina, *B. ascanius* is found in Chaco areas.

Type material. Not examined

Additional material examined. ARGENTINA: CÓRDOVA: La Cumbre, Km 6, 12.xi.2005, P. Smith leg. – 1♂ 1♀ (CERPE). BRASIL: DISTRITO FEDERAL: Brasília, Embrapa Hortaliças, 3-8.xi.2016, N. G. Souza leg. – 1♂ (CERPE). GOIÁS: Cristalina, Fazenda Larga Grande, 30.i.2017/3-8.xi.2017, luz, N. G. Souza leg – 2♂ (CERPE). MINAS GERAIS: Vila Monte Verde, 21.xi.1966 – 1♂ (DZUP). PARANÁ: Guarapuava, 05.x.1986 – 1♂ (DZUP); Pinhais, 16.xi.2008, F. Dias leg. – 1♂ (CERPE); Piraquara, Mananciais da Serra, 17.x.2007, 1000 m, luz, Grossi & Caron legs. – 1♂ (CERPE); Tibagi, Fazenda São Damásio, 04.ii.2008, P. Grossi & Parizotto legs. – 1♂ 1♀ (CERPE). SANTA CATARINA: Urubici, Parque Nacional São Joaquim, 16-19.iii.2012, Grossi, Parizotto & Leivas legs. – 1♂ 1♀ (CERPE); no data – 1♀ (DZUP). SÃO PAULO: São João do Barreiro, Serra da Bocaina, 9-10.ii.2016, 1540 m, luz, C. G. Mielke leg. – 26♂ 18♀ (CERPE).

Male redescription (Fig. 20A). **Length:** 30.8–20.5mm. **Width:** 21.1–10.9 mm. **Color:** Dark reddish to dark reddish-brown. **Head:** Clypeus subtrapezoidal; surface transversely rugose,

glabrous; anterior margin bidentate; teeth raised, triangular, transverse, separated by a slightly emargination; lateral edge convergent dorsoventrally. Frontoclypeal suture with a raised, transverse, incomplete ridge (not reaching the lateral margins). Frontal surface coarsely rugopunctate, scarcely setose. Ocular canthus transverse, subtriangular, with a row of setae ventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth triangular, transverse; basal tooth lobed, smaller than previous ones. Maxillae with galea tridentate at apex; lacinia fused to galea. Maxillary palpomere IV with broad, diagonally truncated sensorial area. Labium subtriangular, flattened, rugose, densely setose. **Antennae:** Ten-segmented; club with lamellae nearly two times as longer as antennomeres II–VII combined. **Thorax:** Pronotal apical area with a tubercle moderate in size, followed by a rounded concavity; anterior corners densely covered with coalescent punctures, concavity transversely rugose, sides moderately punctate, becoming weak toward disc. Scutellar plate from triangular to parabolic in shape, smooth. Elytra with 9 well-marked longitudinal striae (1 sutural, 4 discal, 4 lateral); each stria covered with a row of moderated punctures (observed under 10X magnification), spaced about one diameter of punctures, interstriae irregularly punctate. Proventrite narrow, weakly setose. Meso- and meta ventrites densely covered with yellowish setae. **Legs:** Protibiae tridentate; inner proclaws incised; tarsomere V ventrally with a small process at apex. Mesotibiae with two carinae on external surface, one basal transverse, one medial diagonally projected; carinae and apex ornamented with setae. Metatibiae similar to mesotibiae. Meso- and metaclaws simple. **Abdomen:** Tergite VII with stridulatory apparatus formed by one band of innumerable, transverse, barely marked rows of carinae. Tergite VIII slightly emarginate at anterior margin, convex in lateral view, densely rugopunctate on sides, punctate on disc, surface near to posterior margin covered with small, scarce setae. Ventrite I completely setose; ventrites II–V setose and rugopunctate on sides, glabrous and punctate on disc; ventrite VI densely punctate, covered with setae at posterior

margin, disc glabrous. **Spiculum gastrale (Fig. 20D)**: Y-shaped; medial branch as short as the lateral branches, broad at basis, rounded at apex; basal sclerite triangular, with a basal row of setae. **Aedeagus (Fig. 20E–F)**: Parameres in caudal view (Fig. 20E), symmetric; basal half rounded laterally, surface covered with deep punctures; apical half excavated lateroventrally, oval-shaped dilated laterodorsally. Parameres in lateral view (Fig. 20F), arched dorsally, ventral area with a basal small process.

Female description (Fig. 20B). **Length**: 29.6– 22.7 mm. **Width**: 16.5– 13.0 mm. **Color**: Dark reddish to dark reddish-brown. **Head**: Clypeus subtrapezoidal, bidentate anteriorly, coarsely rugopunctate, glabrous. Frontoclypeal suture with an incomplete, transverse ridge. Frons strongly rugopunctate, with scarce setae scattered on sides. **Thorax**: Pronotum weakly convex in lateral view, apical tubercle small, concavity shallow, surface densely punctate on concavity and on sides, rugopunctate finely punctate on disc. **Legs**: Inner protarsal claw usually simple, rarely with a small, middle-ventral lobe. Protarsomere V with apical lateroventral process absent. Metafemoral ventral surface covered with large, oval-shaped punctures. **Abdomen**: Tergite VIII nearly flattened in lateral view. Ventrite VI triangular, setose on disc. **Genitalia**: Coxite parabolic in shape, moderately covered with long setae. Subcoxite transverse, rectangular shaped, covered with scarce and irregularly scattered setae.

Geographic distribution. Argentina (Córdoba), Brazil (Distrito Federal, Goiás, Minas Gerais, Paraná, Santa Catarina, São Paulo) (Fig. 53).

***Bothynus laticifex* Burmeister, 1847 (Fig. 21A–F; Fig. 53)**

Bothynus laticifex Burmeister 1847, p. 115 (original description)

Diagnosis and comments. *Bothynus laticifex* resembles *B. cylindricus*, but differ from this species in the following characters: In male, pronotal posterior corners rugose (Fig. 21C), basal half of parameres constricted laterally in frontal view (Fig 21E); in female, pronotum with shallow concavity (Fig. 21B).

Remarks. *Bothynus laticifex* can be confused with *B. cylindricus* due to high morphological similarity featured by these two species. Nevertheless, in male, sculptural differences on the pronotal posterior corners (rugose) along with configuration of parameres in frontal view (constricted laterally at basal half), are concise diagnostic characters to distinguished *B. laticifex* and separate it from *B. cylindricus*. However, females of both species are distinguished only by the pronotal concavity: shallow in *B. laticifex*, deep in *B. cylindricus*. In Argentina, *B. laticifex* occurs in Chaco and Pampean areas, while in Brazil, the species occurs in Cerrado areas of Midwest and Atlantic Forest of Southeast. The occurrence for Misiones is the first record from Argentina since the species description made by Burmeister (1847) from Buenos Aires. In Brazil, the species was recorded for the first time by Endrödi (1969) from Minas Gerais state, and now, *B. laticifex* has its distribution expanded from Distrito Federal and São Paulo states.

Type material. Not examined.

Additional material examined. ARGENTINA: MISIONES: 22.i.1995, R. Foester leg. – 1♂ (CERPE). BRASIL: DISTRITO FEDERAL: Planaltina, Embrapa Cerrado, 26.vii.2005, C. Oliveira leg. – 1♂ (CEMT). MINAS GERAIS: Lavras, 05.viii.1999, M. Sampaio leg. – 1♂

(CERPE); Lavras, 19.viii.2006, luz, G.A. Souza leg – 1♀ (CERPE). SÃO PAULO: Lins, Fazenda Santa Clara, 19.ix.1981, luz, L. Evandro leg. – 1♂ (CEMT).

Male redescription (Fig. 21A). **Length:** 20.0–19.0 mm. **Width:** 11.0–10.6 mm. **Color:** Nearly completely reddish brown; pronotal surface, meso- and metatibiae sometimes dark reddish brown. **Head:** Clypeus triangular, coarsely rugose, glabrous, bidentate anteriorly. Frontoclypeal suture with a transverse, incomplete ridge. Frons coarsely rugose, scarcely setose laterally, disc glabrous. ocular canthus transverse, usually subrectangular, with setae scattered ventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth flattened, apical tooth triangular, medial tooth slightly lobed apically, basal tooth lobed. Maxillae with tridentate galea. Labium subtriangular, slightly rounded at sides, surrounded with long setae, weakly rugose at disc. **Thorax:** Weakly convex posteriorly in lateral view; anterior area with small apical tubercle; concavity deep, rounded, with a posterior constriction at middle area; surface surrounded with dense, large, punctures; punctures coalescent near margins, disc finely punctate, concavity transversely rugose, with large, C-shape punctures on the edge of posterior corners (Fig. 21C). Scutellar plate nearly parabolic, smooth. Elytra with 9 well-marked striae (one sutural, 4 discal, 4 lateral); each stria covered with moderate, ocellate punctures, spaced about one diameter of punctures. **Legs:** Inner protarsal claw slightly broad, curved about 90 degrees, with acute tooth at inner side. Meso- and metatibiae only with a middle carina. **Abdomen:** Tergite VII with stridulatory apparatus formed by one band of transverse, finely marked carinae. Tergite VIII glabrous, rugose on sides and on an area near to posterior margin, disc moderately punctate. Ventrite I completely setose; Ventrites II–V with sides moderately punctate, weakly setose, discal area smooth; Ventrite VI rugose on sides, smooth on disc. **Aedeagus (Fig. 21D–F):** Parameres in caudal view (Fig. 21D), symmetric; basal half rounded at sides, surface rugopunctate; apical half excavated lateroventrally, dorsolaterally

broad, oval shaped. Parameres in lateral view (Fig. 21F), ventral area with a small tooth at basis. Parameres in frontal view (Fig. 21E), basal half constricted laterally.

Female redescription (Fig. 21B). Similar to male in overall aspect, except in the following characters: **Length:** 19.2 mm. **Width:** 10.9 mm. **Thorax:** Pronotal surface completely, densely punctate; apical tubercle small; concavity shallow. **Legs:** Inner protarsal claw simple, similar to outer claw. Tarsomere V with lateroventral process absent. **Abdomen:** Ventrite VI triangular, densely rugopunctate, moderately setose.

Geographic distribution. Argentina (Misiones), Brazil (Distrito Federal, Minas Gerais, São Paulo) (Fig. 53).

***Bothynus deiphobus* (Burmeister, 1847) (Fig. 22A–G; Fig. 53)**

Podalgus deiphobus Burmeister 1847, p. 123 (original description)

Scaptophilus deiphobus, Lacordaire 1856, p. 412

Bothynus deiphobus, Arrow 1937b, p. 40

Bothynus deiphobus, Endrödi 1969, p. 136 (lectotype designation)

Diagnosis. *Bothynus deiphobus* resembles *B. fabius*, but differs from this species in the following aspects: In both sexes, pronotal posterior area strongly convex in lateral view (Fig. 22B), elytral striae shallow (Fig. 22D); male, pronotal anterior tubercle moderate in size (Fig. 22B), spiculum gastrale with a broad and rounded basal sclerite (Fig. 22E).

Remarks. In *Bothynus*, the shape of male parameres has been used as the main character in species distinction. However, this character showed to be highly similar, with subtle differences among parameres of *B. deiphobus* and *B. fabius*. Nevertheless, *B. deiphobus* can be distinguished by features of pronotum (anterior tubercle moderated in size, posterior area convex), elytra (striae shallow), and spiculum gastrale (basal sclerite broad and rounded). *Bothynus deiphobus* occurs from Northeast to Southern of Brazil, in Atlantic Forest, Cerrado and Pampa areas. There is a record from Amazonia forest in Endrödi (1968), however this may be mislabeled locality data.

Type material. Not examined.

Additional material examined. BRASIL: BAHIA: Piatã, xii.1976 – 1♂ (J. Becker ver sigla). PARANÁ: Curitiba, i.1935 – 1♀ (IBSP); Jaguaraiá, Parque Estadual do Cerrado, 800 m, 1-4.ii.2011, Parizotto, Leivas, Herzog & Manfio legs. – 1♀ (EPGC); Palmas, 1.iv.2013, V.R.I. Rosário leg. – 1♀ (CERPE); Palmas, 21.v.2011, R. Teixeira leg. – 1♂ (CERPE). MATO GROSSO DO SUL: CASSILÂNDIA: 5.xi.2014, luz, C.A.F. Barbosa leg. – 1♂ (CERPE). PERNAMBUCO: Recife, 16.i.2014, P.M.M. Evaristo leg. – 1♂ (CERPE). RIO GRANDE DO SUL: Arroio do Meio, 2.i.1949 – 1♀ (J. Becker ver coleção); Porto Alegre, ii.1942 – 1♂ 1♀ (MZUSP), 17.xii.1943 – 1♂ (J. Becker ver coleção). SANTA CATARINA: Praia Grande, Pousada Aracema, luz, D. Santa leg. – 2♀ (CERPE); no data – 1♂ (DZUP).

Male redescription (Fig. 22A–B). **Length:** 25.9–20.9 mm. **Width:** 14.0–11.0 mm. **Color:** Nearly completely reddish brown. **Head:** Clypeus subtriangular, with two anterior acute teeth, dorsal surface strongly rugopunctate, glabrous, lateral edge scarcely setose. Frontoclypeal suture with an incomplete transverse ridge, sometimes weakly constricted at middle. Frons coarsely

rugopunctate. Ocular canthus transverse, slightly arched, transversely setose ventrally.

Mouthparts: Mandibles tridentate; apical and medial teeth triangular, acute; basal tooth lobed, smaller than previous ones. Maxillae with three subequal, apically teeth on galea. Labrum transverse, apical margin slightly emarginated at middle. Labium subtriangular, completely setose. **Antennae:** Club with lamellae subequal in length to antennomeres II–VII combined.

Thorax: Pronotal posterior area strongly convex in lateral view (Fig. 22B); anterior area with a middle conic tubercle, moderate in size, slightly recurved, followed by a broad, deep concavity, sometimes interrupted behind; surface densely rugopunctate on anterior corners, moderately punctate on sides and on area near to posterior margin, disc smooth, concavity transversely rugose. Scutellar plate usually triangular. Elytral longitudinal striae shallow (1 sutural, 4 discal, 4 lateral), each stria covered with moderate, ocellate punctures; sutural punctures contiguous, other striae with punctures spaced about two diameters of punctures; interstriae irregularly punctate.

Legs: Inner protarsal claw simple, similar to outer claw. Mesotibial outer surface with two carinae, one basal short and transverse, one medial long and oblique; apex broad, emarginate; carinae and apex covered with long setae. Metatibiae truncate at apex. **Abdomen:** Tergite VII as long as tergite VIII, stridulatory apparatus with carinae barely marked. Tergite VIII glabrous, rugose on sides, punctate on disc; punctures moderate, oval shaped. Ventrite I completely setose; ventrites II–V with an incomplete row of setose punctures confined on sides, disc smooth; ventrite VI with rugopunctures confined on corners, disc weakly punctate. **Spiculum gastrale (Fig. 22E):**

Y-shaped; branches subequal in length; medial branch truncated at apex, lateral branches rounded at apex; basal sclerite broad, parabolic in shape, apical margin transversely covered with setae.

Aedeagus (Fig. 22F): Parameres in caudal view (Fig. 22G), symmetric, smooth, lateroventrally excavated at apical half, apex laterodorsally with a short and oval shaped dilatation. In lateral

view, ventral margin nearly parallel, with no basal process, apex rounded, dorsal surface slightly arched.

Female redescription (Fig 22C). Extremely similar to male, except in the following aspects:

Length: 23.0–21.0 mm. **Width:** 13.0–11.2 mm. **Thorax:** Pronotal apical tubercle small, concavity shallow, rugopunctate. **Abdomen:** Tergite VIII flattened in lateral view. Ventrite V triangular. **Genitalia:** Coxite parabolic shaped, moderately covered with long setae. Subcoxite rhomboid in shaped.

Geographic distribution. Brazil (Bahia, Mato Grosso do Sul, Pernambuco, Paraná, Rio Grande do Sul, Santa Catarina) (Fig. 53).

***Bothynus cyclops* (Burmeister, 1847) (Fig. 23A–F; Fig. 53A)**

Corynoscelis cyclops Burmeister 1847, p. 127 (original description)

Bothynus cyclops, Arrow 1937b, p. 40

Bothynus cyclops, Endrödi 1969, p. 136 (lectotype designation)

Diagnosis. *Bothynus cyclops* resembles *B. andreus* sp. nov, but differs from this species in the following characters: In both sexes, maxillae with quadridentate galea (teeth gradually increasing in size toward apex of galea), elytral punctures deep (Fig. 23A-B); in female, tergite VIII rugose at discal area and covered with scarce setae scattered over entire surface (Fig. 23D).

Remarks. *Bothynus cyclops* occur in Atlantic Forest areas from Northeast toward Brazilian Southern. In literature, there are records from Paraguay (Endrödi 1985) and Guyana (Burmeister

1847). Burmeister (1847) based the description of *B. cyclops* on material from “Guyana” and Endrödi 1969 designated the lectotype from this local. However, this is a dubious record because there is not a defined record from this local or in adjacent areas as the French Guiana (Ponchel 2011, Dupuis 2016) and the original specimen of Burmeister was likely mislabeled.

Materia type. Not examined.

Additional material examined. BRASIL: BAHIA: Encruzilhada, 11.xii.2007, 800 m, Grossi, Rafael & Parizotto legs. – 1♂ (CERPE); Erico Cardoso, Pico do Barbado, Capão, 1.ii.2007, 1300 m, Mielke & Casagrande legs. – 1♂ (EPGC). ESPÍRITO SANTO: Conceição do Castelo, Ribeirão do Meio, xi/xii.2010, R. Falqueto leg. – 1♀ (CEMT). MINAS GERAIS: Águas Vermelhas, xi.1994, E. Grossi leg. – 1♂ (CERPE); Águas Vermelhas, 16.xii.2012, E. & P. Grossi legs. – 1♀ 2♂ (CERPE); Buritis, Fazenda Querência, 03.xii.2012, luz, C. M. Oliveira leg. – 1♀ (CEMT); Lavras, 30.ii.2008, B.P. Oliveira leg. – 1♂ (CERPE); Lavras, 18.ix.2015, B. Gazolla leg. – 1♂ (CERPE); Lima Duarte, Parque Nacional do Ibitipoca, 21.xi.2010, C.A.O Antunes leg. – 1♂ (CERPE); Passa Quatro, 22.xi.2014, M.G. Hermes leg. – 1♂ (CERPE). PARANÁ: Curitiba, 25.ii.2003, Pereira. H. R. leg. – 1♂ (CERPE); Ibitiporã, Fazenda Doralice, 27.v.2007, A.A. Santos leg. – 1♂ (EPGC); São José dos Pinhais, xi.2016, 896 m, A.C. Domahovski leg. – 1♀ 2♂ (CERPE); Tibagi, Parque Estadual do Guartelá, 02.xi.2009, 900 m, P.C. Grossi leg. – 1♂ (CERPE). PERNAMBUCO: Caruaru, Brejo dos Cavalos, 02.v.2008, luz, Cavalcanti et al. legs. – 1♀ (CEMT); Caruaru, Brejo dos Cavalos, 06-07.viii.2015, 900 m, Grossi, Rafael & Duarte legs. – 1♀ (CERPE); Recife, 25.xi.2018, D. Ximenes leg. – 1♂ (CERPE). RIO DE JANEIRO: Arcádia, Miguel Pereira, 09.xi.2002, F. Racca leg. – 1♂ (CECL); Copacabana, ii.2004, A. Bello leg. – 1♂ (CEMT); Nova Friburgo, Sans Souci, xii.2009/ii.2010, E. & P. Grossi legs. – 1♀ (CERPE); Nova

Friburgo, Sítio Caturama, 31.xii.2007, 1100 m, E. & P. Grossi legs. – 1♀ (CERPE); Nova Friburgo, xi.2014, luz, P.C. Grossi leg. – 2♀ 2♂ (CERPE); Seropédica, 3.x.2016, L. Oliveira leg. – 1♂ (CERPE). SANTA CATARINA: G. Pross leg. – 1♀ 2♂ (CERPE).

Male redescription (Fig. 23A). **Length:** 26.0–18.9 mm. **Width:** 15.0–10.1. **Color:** Nearly completely dark reddish brown. **Head:** Clypeus subtriangular, strongly constricted laterally toward apex, anteriorly with two conic and acute teeth, strongly rugopunctate, glabrous. Frontoclypeal suture with a weak, incomplete, transverse ridge. Frons strongly rugopunctate, usually glabrous, sometimes with scarce setae, basal area smooth. Ocular canthus subrectangular, slightly arched. **Mouthparts:** Mandibles tridentate, all teeth triangular shaped; apical and medial teeth strong, apically acute, medial tooth as longer in size as apical tooth; basal tooth smaller than previous ones. Maxillae with 4 teeth increasing in size toward apex of galea. Labium subtriangular, densely surrounded with long setae, disc rugopunctate, scarcely covered with small setae. **Antennae:** Club subequal in length to antennomeres II–VII combined. **Thorax:** Pronotal posterior area strongly convex in lateral view; anterior area with a conic apical tubercle, moderate in size, slightly curved, followed by a deep, broad, rounded concavity; anterior corners rugopunctate, sides weakly punctate, disc finely punctate. Scutella plate parabolic shaped. Elytral surface with 9 well-marked striae (1 sutural, 4 discal, 4 lateral), striae densely punctate; punctures large, ocellated, contiguous; second and third interstriae smooth. **Legs:** Protarsal inner claw strongly recurved, incise at apex; protarsomere V with a small ventro-apical process. Mesofemoral disc densely setose ventrally. Mesofemora with two carinae on external surface, basal carinae short, medial carinae long and diagonally projected, apex truncate; carinae and apex bordered with setae. Metafemoral ventral disc smooth. Metatibial apex broad, truncate. **Abdomen:** Middle area of tergite VII twice longer than tergite VIII; stridulatory apparatus formed

by two bands of paired rows of carinae, separated by a narrow mid-line, well-marked near to anterior area, merged near the posterior area. Tergite VIII with anterior margin emarginated at middle, surface glabrous, completely rugopunctate (Fig. 23C). Ventrite I completely setose; ventrite II with densely punctate and setose sides, disk weakly punctate; ventrites III–VI with sides moderately setose, densely punctate, discal area finely punctate, glabrous. **Spiculum gastrale**: Y- shaped; medial branch shorter than lateral branches; basal sclerite formed by two plates, oval shaped, with setae confined on the anterior inner corners. **Aedeagus**: Parameres in caudal view (Fig. 23E), symmetric, smooth, apical half constricted laterally, slightly elongated, convergent at apex. Parameres in lateral view (Fig. 23F), apex dorsoventrally acute at apex.

Female redescription (Fig. 23B). Similar to male, except in the following aspects: **Length**: 24.2–16.0 mm. **Width**: 14.0–8.9 mm. **Head**: Frons scarcely setose. **Thorax**: Pronotal concavity slightly shallow, rugopunctate; posterior area weakly convex in lateral view. **Abdomen**: Tergite VIII weakly setose (Fig. 23D). Ventrite VI weakly setose. **Genitalia**: Coxite oval shaped, inward inclined, inner margin slightly narrow, surface moderately punctate on discal area, covered with long setae. Subcoxite oval shaped, scarcely setose.

Geographic distribution. Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro) (Fig. 53).

***Bothynus minor* Steinheil, 1872 (Fig. 24A–D; Fig. 52A; Fig. 53A)**

Bothynus minor Steinheil 1872, p. 561 (original description)

Bothynus minor, Endrödi 1969, p. 133 (lectotype designation)

Diagnosis. *Bothynus minor* differs from the other species of group by the following characters: Small specie (15 mm), frontoclypeal ridge raised in lateral view (Fig. 24B), clypeus short (two times wider than long), pronotal concavity broad and deep with a small tubercle on each side, apical half of parameres with lateroventral surface not visible, hidden under the laterodorsal surface in caudal view (Fig. 24C).

Remarks. The parameres are unknown in previous literature, however, aedeagus and parameres images are presented for the first time here and provide additional character in the species diagnosis. *Bothynus minor* is known only from Buenos Aires, Argentina.

Type material.

Lectotype (Fig. 52A). *Bothynus minor*, male, at MNHN, with the following labels: Patagones [beige, handwritten]/minor Steinh. [beige, handwritten]/ExMusaeo E. Steinheil [beige with black margins, printed in black]/ Muséum Paris 1952 coll. R. OBERTHÜR [white, printed in black]/Lectotypus *Bothynus minor* Steinh. [beige with red margins, Lectotypus printed in red, handwritten]/MNHN EC7109 [white, printed in black].

Additional material examined. ARGENTINA: BUENOS AIRES: Cañuelas, 15.xi.2010, P. Wagner leg. – 1♂ (EPGC).

Male redescription (Fig. 24A). **Length:** 15.0 mm. **Width:** 8.5 mm. **Color:** Reddish brown. **Head:** Vertex moderately raised in lateral view. Clypeus subtriangular, two times wider than long, bidentate anteriorly, surface slightly rugose in a longitudinal area at middle, sides weakly punctate, glabrous. Frontoclypeal suture with a weak, transverse ridge, raised at middle in lateral

view. Frontal surface scarcely setose, coarsely punctate at basal area; punctures large, deep. Ocular canthus with setae scattered ventrally. **Mouthparts:** Mandibles tridentate; teeth slightly lobed. Maxillae lacking teeth on galea, rounded apically. Labium slightly short, as longer as wide, concave at disc, surrounded with long setae, discal setae shorter than lateral setae. **Antennae:** Club 1.3 times longer than segments II–VII combined. **Thorax:** Anterior area with a conic tubercle, moderate in size, followed by a broad and deep concavity, with a weak tubercle on each side; surface densely rugopunctate at anterior corners, becoming moderately punctate on sides, finely punctate on disc, concavity with large, C-shaped punctures, lateral margins with few setae scattered near to posterior corners. Scutellar plate parabolic shaped, smooth. Elytral surface with 8 longitudinal well-marked striae; striae covered with ocellate, small punctures (observed under 90X magnification). **Legs:** Inner potarsal claw simple, similar to outer claw. Meso- and metatibial outer surface only with a diagonal middle carinae, apex broad. Meso- and metatarsomeres I–IV decreasing gradually in size. **Abdomen:** Tergite VII with stridulatory apparatus formed by a one band of finely marked, transverse carinae. Tergite VIII densely rugopunctate and scarcely setose on sides, moderately punctate and glabrous on disc. Ventrites I–VI moderately setose on sides, becoming weakly setose toward discal area. **Aedeagus (Fig. 24C–D):** Parameres in caudal view (Fig. 24C), basal half with rounded sides, laterodorsal surface expanded in an oval shaped dilatation, lateroventral area strongly excavated, hidden under the laterodorsal surface. Parameres in lateral view (Fig. 24D), rounded at apex.

Female. Not examined.

Geographic distribution. Argentina (Buenos Aires) (Fig. 53).

***Bothynus fabius* (Fairmaire, 1878) (Fig. 25 A–G; Fig. 52B; Fig. 53)**

Scaptophilus fabius Fairmaire 1878, p. 264 (original description)

Scaptophilus striatellus Fairmaire 1878, p. 264 (original description) new synonym

Scaptophilus quadratus Fairmaire 1878, p. 265 (original description)

Bothynus fabius, Arrow 1937b, p. 40

Bothynus fabius, Endrödi 1969, p. 131 (lectotype designation)

Bothynus striatellus, Arrow 1937b, p.41

Bothynus striatellus, Endrödi 1969, p. 131 (lectotype designation)

Bothynus quadratus, Arrow 1937b, p. 41

Bothynus quadratus, Endrödi 1969, p. 108

Diagnosis. *Bothynus fabius* resembles *B. deiphobus*, but differ from this species in the following characters: In both sexes, pronotal posterior area weakly convex in lateral view (Fig. 25B); in male, pronotal tubercle small (Fig. 25B), spiculum gastrale with basal sclerite separated in two by a mid-line (Fig. 25E).

Remarks. *Bothynus fabius*, *B. striatellus*, and *B. quadratus* were originally described in the same work, within the genus *Scaptophilus* by Fairmaire (1878). Posteriorly, Endrödi (1969) examined the types and synonymized *B. fabius* and *B. quadratus* with *B. striatellus*, prevailing this latter name over the other two. However, in the Fairmaire's descriptions, *S. fabius* appears as the first of three species described by him. According to the International Code of Zoological Nomenclature (ICZN), when then more of one available name for the same taxa, the oldest name has priority over the others, therefore, the name *B. fabius* is proposed here as a valid named, with preference

under *B. striatellus*. The species has a widespread distribution, occurring from northern Brazil to Uruguay.

Type material

Lectotype. *Bothynus fabius*, male, at MNHN, with the following labels: *Scaptohilus fabius* Farm. amer. mer. [beige, handwritten]/MUSEUM PARIS Collection Léon Fairmaire 1906 [green, printed in black]/TYPE [red, printed in black]/Lectotypus *Bothynus (Scapt.) fabius* Fairm. [beige with red margins, Lectotypus printed in red, handwritten]/penis default!! [beige]/MNHN EC7112 [white, printed in black].

Lectotype. *Bothynus striatellus*, female, at MNHN, with the following labels: *Bothynus striatellus* Entrerios Fairm. [beige, handwritten]/Museum Paris ex. Coll. R. Oberthur [green, printed in black]/Lectotypus *Both. (Scaptoph.) striatellus* Fairm. [beige with red margins, Lectotypus printed in red, handwritten]/MNHN EC7110 [white, printed in black].

Paralectotype (Fig. 52 B). *Bothynus striatellus*, male, at MNHN, with the following labels: Entrerios Deprn [beige, handwritten]/*Scaptoph. striatellus* Fairm [beige, handwritten]/MUSEUM PARIS Collection Léon Fairmaire 1906 [green with sides and top margin black, printed in black]/Paratypus *Both. (Scaptoph) striatellus* Fairm. [beige with red margins, Paratypus printed in red, handwritten]/PARALECTOTYPE [red, printed in black]/MNHN EC7111 [white].

Type. *Bothynus quadratus*, not examined.

Additional material examined. BRASIL: GOIÁS: Mineiros, Parque Nacional das Emas, 27.i.1989, B.B. Santos leg. – 1♂ (CERPE), x.1989, B.B. Santos leg. – 1♂ (CERPE); São João D'Aliança, Chapada dos Veadeiros, Fazenda Sendai, 14.xi.2007, R.M. Koike leg. – 2♂ (EPGC). MATO GROSSO: Cuiabá, 18.v.1994, A.B. Kênia leg. – 1♂ (CEMT); Diamantino, Alto Rio

Arinos, 05.xi.1998, E. Furtado leg. – 1♂ (CERPE); iii.2011, E. Furtado leg. – 1♂ (CERPE); Fazenda Vale da Solidão, 21.x.2014, G. Furtado leg. – 1♀ (CERPE); Nossa Senhora do Livramento, 25.iii.2017, D.E.M Reis leg. – 1♀ (CERPE). MATO GROSSO DO SUL: CASSILÂNDIA: 1.x.2014, C.A.F. Barbosa leg. – 1♂ (CERPE), 30.x.2014, C.A.F. Barbosa leg. – 1♂ (CERPE). MINAS GERAIS: Lavras, 18.ix.2005, L. Durães leg. – 1♂ (CERPE); 05.x.2008, J.V.C Leitão leg. – 1♂ (CERPE). PARÁ: Belém, Parque Estadual Utinga, xi.2012, F. Silva leg. – 2♀ (CERPE). PARANÁ: Diamante do Norte, 27.xi.2011, Pitfall, M. A. Chermán leg. – 1♂ (CERPE); Foz do Iguaçu, 17.xii.2014, luz, R. Barros leg. – 1♂ 1♀ (CERPE); Jaguaraiá, Parque Estadual do Cerrado, 18-19.xi.2009, 800 m, P.C. Grossi leg. – 2♂ (CERPE); Palmas, 18.xi.2013, S. Castilho leg. – 1♂ (CERPE); Palmas, 1.xii.2013, S. Boese leg. – 1♂ (CERPE); Palmas, 21.v.2011, R. Teixeira leg. – 1♂ (CERPE). PERNAMBUCO: Recife, 15.Viii.2013, E.M.F Morais leg. – 1♂ (CERPE). SANTA CATARINA: 25.v.2012, A. Mozer leg. – 1♂ (CERPE). RIO GRANDE DO SUL: Cerro Azul, 1932 – 1♀ (CECL); Porto Alegre, xii.1949 – 1♂ (J. Becker ver sigla); Santa Rosa, xii.1931, E. Viana leg. – 1♀ (CECL). SÃO PAULO: Serra da Bocaina, Pousada Lageado, 9-10.ii.2016, 1540 m, C.G. Mielke leg. – 1♂ (CERPE); Pederneiras, 14.x.2016, luz, M. Bento leg. – 1♂ (CERPE). PARAGUAY: CONCEPCIÓN: Estancia Cororo, 10-20.iii.2001, luz, C. Aguilar leg. – 7♂ (CERPE); PARAGUARI, La Colmena: Salto Cristal, 28.xi.2004, 317 m, B. Garcete leg. – 1♂ 1♀ (CERPE). URUGUAY: MALDONADO: 1924, Barattini leg. – 1♀ (CECL).

Male redescription (Fig. 25A). **Length:** 25.0–17.1 mm. **Width:** 13.1–10.0 mm. **Color:** Nearly completely dark reddish brown. **Head:** Clypeus subtriangular, bidentate anteriorly, slightly constricted laterally, surface glabrous, strongly rugopunctate. Fontoclypeal area with incomplete, transverse, slightly marked ridge. Frons coarsely rugopunctate, posterior area between eyes

smooth. Ocular canthus rectangular. **Mouthparts:** Mandibles tridentate; apical and medial teeth triangular, subequal in size; basal tooth lobed, smaller than previous ones. Maxillae usually with three subequal teeth at apex of galea, rarely with two teeth. Labrum with apex truncate at middle. Labium subtriangular, laterally covered with long setae, disc scarcely setose. **Antennae:** Club subequal in length to antennomeres II–VII combined. **Thorax:** Pronotal anterior tubercle small (Fig. 25B), concavity from moderate to shallow in deep, posterior area weakly convex in lateral view; anterior surface with corners densely covered with large, sometimes coalescent punctures, sides moderately punctate, disc finely punctate, concavity from densely punctate to transversely rugose. Scutellar plate subtriangular or subparabolic in shape. Elytral striae well marked (Fig. 25D), ocellate punctures; sutural punctures spaced less than one diameter of punctures, other striae spaced about two diameters of punctures. **Legs:** Protarsus with inner claw simple, similar to outer claw. Mesotibiae usually featuring only a middle, long, oblique, projected carinae; carinae and apex covered with long spinules. Metatibia similar to mesotibiae. **Abdomen:** Stridulatory apparatus of tergite VII formed by two bands of paired, well-marked carinae. Tergite VIII glabrous, rugopunctate on sides and an area near to anterior margin, disc smooth. Ventricle I moderately setose; ventrites II–V scarcely setose and rugopunctate sides, disc smooth; ventrite VI rugose on sides, weakly punctate on disc. **Spiculum gastrale (Fig. 25E):** Y-shaped; medial branch rounded at apex, basal area emarginate between the lateral branches; basal sclerite separated in two plates by a narrow, longitudinal mid-line, each plate oval in shaped, with scattered setae at apical margin. **Aedeagus (Fig. 25F–G):** Parameres in caudal view (Fig. 25F), symmetric, smooth, basal half rounded laterally, apical half strongly excavated lateroventrally, laterodorsally expanded in a short and oval shaped dilatation. Parameres in lateral view (Fig. 25G), arched dorsally, ventral surface abruptly constricted at apical half, apex rounded.

Female redescription (Fig. 25C). Similar to male, distinguished only in the following aspects: **Length:** 22.2–20.0 mm. **Width:** 12.9–11.9 mm. **Abdomen:** Tergite VIII flattened in lateral view. Ventrite VI triangular. **Genitalia:** Coxite oval shaped, moderately covered with long setae, finely punctate. Subcoxite rhomboid shaped, glabrous.

Geographic distribution. Brazil (Goiás, Mato Grosso, Minas Gerais, Pará, Paraná, Pernambuco, Santa Catarina, São Paulo, Rio Grande do Sul), Paraguay (Concepción, Paraguari), Uruguay (Maldonado) (Fig. 53).

***Bothynus cribrarius* (Fairmaire, 1878) (Fig. 26A–F; Fig. 52C; Fig. 53)**

Scaptophilus cribrarius Fairmaire 1878, p. 266 (original description)

Bothynus cribrarius, Arrow 1937b, p. 40

Bothynus cribrarius, Endrödi 1969, p. 125 (lectotype designation)

Diagnosis. *Bothynus cribrarius* is related to *B. cyclops*, but differs from this species in the following aspects: Dorsal surface with opaque aspect in both sexes (Fig. 26A–B); in male, tergite VIII completely rugose (Fig. 26C), parameres with a basal ventrolateral tooth and apex rounded in lateral view (Fig. 26E); in female, pronotal concavity shallow, tergite VIII and ventrite VI densely setose (Fig 26D).

Remarks. This is a rare species, where are known only five specimens in literature. *Bothynus cribrarius* is endemic of high areas from southeast Brazilian Atlantic Forest (Duarte & Grossi 2016).

Type material

Lectotype (Fig. 52C). *Bothynus cribrarius*, female, at MNHN, with the following labels: *Scaptophilus cribrarius* Brasil [beige, handwritten]/MUSEUM PARIS Collection Léon Fairmaire 1906 [green, printed in black]/TYPE [red, printed in black]/Lectotypus *Bothynus cribrarius* Fairm. [beige with red margin, Lectotypus printed in red]/HOLOTYPE [red, printed in black]/MNHN EC7107 [white, printed in black]

Additional material examined. BRASIL: RIO DE JANEIRO: Itatiaia, 20.iv.1933, Col. F. Zikán – 1♂ (FIOC); Itatiaia, Parque Nacional do Itatiaia, Casa do Pesquisador, 27.ii-01.iii.2012, 750 m, M. Cupelo leg. – 1♀ (MNRJ); Resende, Serrinha do Alambari, ii.2010, U. Caramaschi & H. de Niemeyer legs. – 1♂ (MNRJ).

Female redescription (Fig. 26B). **Length:** 22.5 mm. **Width:** 12.5 mm. **Color:** Nearly completely reddish brown, dorsal surface with opaque bright. **Head:** Clypeus subtriangular, with two conic anterior teeth, surface coarsely rugose, glabrous. Frontoclypeal suture with a transverse, incomplete, weakly marked ridge. Frons coarsely rugopunctate, scarcely setose on sides, glabrous on disc. **Mouthparts:** Mandibles tridentate; apical and medial teeth conic, acute apically; basal tooth lobed, smaller than previous ones. Labium subtriangular, densely setose on sides, scarcely setose on disc, basal area with a middle longitudinal pit. **Antennae:** Club 1.5 times longer than segments II–VII combined. **Thorax:** Pronotum weakly convex in lateral view; apical tubercle small, concavity shallow; surface nearly completely, densely punctate, disc finely punctate. Scutellar plate subparabolic in shape, smooth. Elytral surface densely covered with large, ocellate punctures, lateral area with irregularly scattered punctures. **Legs:** Inner protarsal claw simple, similar to outer claw. Mesotibiae with a truncate middle carina at outer surface. Metatibiae with

one basal and one medial carina. **Abdomen:** Tergite VII with stridulatory apparatus formed by two bands of innumerable, barely marked carinae interrupted by a narrow mid-line. Tergite VIII coarsely rugose, completely, densely setose (Fig. 26D). Ventrites I–II completely, densely setose; ventrites III–V with surface densely setose and rugopunctate on sides, glabrous and punctate on disc; ventrite VI triangular, completely, densely setose, strongly rugose. **Venter:** Nearly completely covered with dense, yellowish, long setae.

Male redescription (Fig. 26A). Nearly similar to female, except in the following aspects: **Length:** 21.1–19.9 mm. **Width:** 11.5–10.8. **Color:** Varying from completely reddish-brown specimens to specimens with head, pronotum, legs and venter dark reddish brown. **Thorax:** Pronotum strongly convex posteriorly in lateral view; anterior tubercle moderate in size; concavity moderately deep, oval shaped; surface densely surrounded with large punctures, discal area finely punctate, concavity transversely rugose. **Legs:** Inner protarsal claw incised at apex; last protarsomere with a ventro-apical process. Meso- and metatibiae with two carinae at outer surface (one basal, one medial). **Abdomen:** Tergite VIII weakly setose (Fig. 26C). Ventrite VI weakly emarginate apically. **Aedeagus (Fig. 26E–F):** Parameres in caudal view (Fig. 26E), smooth, apical half constricted excavated lateroventrally, laterodorsally expanded in an elongated dilatation, oval in shaped. Parameres in lateral view (Fig. 26F), dorsal area arched, lateroventral area with a small tooth at basis, apex rounded.

Geographic distribution. Brazil (Rio de Janeiro) (Fig. 53).

***Bothynus cylindricus* Arrow, 1937 (Fig. 27 A–F; Fig. 52D; Fig. 53 A–B)**

Bothynus cylindricus Arrow 1937a, p. 45

Diagnosis. *Bothynus cylindricus* is related to *B. laticifex* and *B. cribrarius*, but differ from these two species by the following combination of characters: In both sexes, dorsal surface shiny (never opaque), tergite VIII glabrous; in male, pronotal posterior corners covered with punctures only (Fig. 27C), basal half of parameres subparallel in frontal view (not constricted laterally), apex of parameres slightly acute in lateral view (Fig. 27E); in female, concavity shallow and rounded, not interrupted posteriorly at middle (Fig. 27B).

Remarks. *Bothynus cylindricus* occurs from Southeast to South Brazil, in Atlantic Rainforest and Pampa areas. In Endrödi (1969, 1985), there are an imprecise record from Cordoba, Argentina.

Type material

Syntype (Fig. 52D). *Bothynus cylindricus*, male, at NHM, with the following labels: Minas Brasil [beige, handwritten]/3745 [beige, handwritten]/686. [blue, handwritten]/Columbus Brasilia [beige, handwritten]/*Bothynus cylindricus* type Arrow [beige, handwritten]/SYNTYPE [circular label, central areal beige with blue marginal, printed in black]/Type [circular label, central areal beige with red marginal, printed in black].

Additional material examined. BRASIL: MINAS GERAIS, Lavras, 24.iii.2002, A.F. Noronha leg. – 1♂ (CERPE); Lavras, 10.xi.2002, A. Melo leg. – 1♀ (CERPE); Lavras, 20.iii.2004, F.V. Nunciato leg. – 1♀ (CERPE); Lavras, 05.iii.2006 – 1♀ (CERPE); Itamonte, Parque Nacional do Itatiaia, Brejo da Lapa, 11.x.2013, 2000 m, luz, W.R.M Souza leg. – 1♂ (CERPE); São Miguel do Anta, Fazenda Monte Sinai, 16.x.2014, 642 m, A. Pucker leg. – 1♂ (CERPE); Três Rios, 18.vii.1984, F.Z. Vaz-de-Mello leg. – 1♂ (CERPE). RIO DE JANEIRO: xi.1995, Patricia leg. –

1♂ (CERPE). RIO GRANDE DO SUL: Eldorado do Sul, 11.x.1996, luz, Carvalho & Silva legs – 1♂ (CERPE). SÃO PAULO, Barueri, 22.i.1967, K. Lenko leg. – 1♂ (IBSP); Santo Amaro, xi.1933 – 11♂ (IBSP). No data – 1♂ (CERPE).

Male redescription (Fig. 27A). **Length:** 20.8–18.8 mm. **Width:** 10.9–9.5 mm. **Color:** Nearly completely reddish-brown; meso- and metatibiae dark reddish brown. **Head:** Clypeus subtriangular, bidentate anteriorly, rugose, glabrous. Frontoclypeal suture with a transverse, moderately marked, incomplete ridge. Frons rugose at middle area, densely punctate on des, with scarce setae scattered laterally near eyes. Ocular canthus triangular, transverse, with setae scattered ventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth flattened, triangular; basal tooth lobed, smaller than previous ones. Maxillae with tridentate galea. Labium subtriangular, slightly convex, surrounded with long setae, disc weakly punctate. **Thorax:** Pronotum weakly convex posteriorly in lateral view; area near to anterior middle margin with a small tubercle, followed by a shallow concavity; surface densely rugopunctate at anterior corners, becoming densely punctate at sides, with sparse punctures at posterior corners (Fig. 27C), concavity covered with large, C-shaped punctures. Scutellar plate triangular shaped, irregularly covered with large, deep punctures. Elytral surface usually with 10 well-marked striae (1 sutural, 4 discal, 5 lateral), each stria moderately covered with ocellate punctures, space about one diameter of punctures. **Legs:** Inner protarsal slightly thickened, obliquely curved, with a small inner tooth. Tarsomere V with a ventrolateral process at apex. Meso- and metatibiae only with a medial carinae. **Abdomen:** Tergite VII with stridulatory apparatus formed by one band of transverse, finely marked carinae. Tergite VIII densely rugose on sides, weakly on disc, glabrous. Ventrite I completely setose; ventrites II–V with a row of setose punctures confined to sides, disc weakly punctate; ventrite VI bordered with setae at posterior margin. **Spiculum gastrale:** Y-

shaped; branches subequal in length; basal sclerite transverse, subrectangular, with six setae at apex. **Aedeagus (Fig. 27D–F)**: Parameres in caudal view (Fig. 27D), weakly punctate, basal half rounded laterally, apical half constricted lateroventrally, dorsolaterally expanded in an elongated oval shape. Parameres in lateral view (Fig. 27F), dorsal area arched, ventral area with a transverse carina at basis, apex slightly acute. Parameres in frontal view (Fig. 27E), basal half with parallel sides.

Female description (Fig. 27B). **Length**: 21.2–18.2 mm. **Width**: 11.0–9.2 mm. **Color**: Nearly completely reddish brown; meso- and metatibiae dark reddish brown. **Head**: Clypeus subtriangular, rugose, glabrous. Frontoclypeal suture with a transverse, incomplete ridge. Frons coarsely rugopunctate, with scarce setae confined laterally, disc glabrous. Ocular canthus triangular, transverse, setose ventrally. **Mouthparts**: Mandibles tridentate. Maxillae tridentate apically at galea. Labium subtriangular, densely punctate, surrounded with long setae, discal setae as short as lateral setae. **Thorax**: Pronotum weakly convex in lateral view, anterior tubercle small, concavity shallow, rounded, surface densely punctate; punctures large, from contiguous to coalescent, disc weakly punctate. Scutellar plate triangular, irregularly punctate, punctures large. Elytral punctures large, spaced about one diameter of punctures. **Legs**: Inner protarsal claw simple, similar to outer claw. **Abdomen**: Tergite VIII transversely rugose, glabrous. Ventrite VI triangular, completely rugose, completely setose.

Geographic distribution. Brazil (Minas Gerais, Rio de Janeiro, São Paulo) (Fig. 53A).

***Bothynus laevipennis* Arrow, 1937 (Fig. 28 A–G; 53)**

Bothynus laevipennis Arrow 1937a, p. 46

Diagnosis. *Bothynus laevipennis* resembles *B. nyx*, but differs from this specie in the following characters: in both sexes, pronotal concavity clearly rounded shaped and elytra covered with fine punctures (observed under 90X magnification). (Fig. 28A–B); In male, apical half of parameres with strong excavation lateroventral in caudal view (Fig. 28D) and broad apex in lateral view (Fig. 28E); in female, metafemora with smooth discal area (Fig. 27F) and tergite VIII flattened in lateral view. (Fig. 28G).

Remarks. Distributional information obtained from label data suggests that *B. laevipennis* occurs associated with open field landscapes, in the rupestrian fields and Cerrado areas from Brazilian Southeast. In Endrödi (1969, 1985), there are records from Rio de Janeiro and Espírito Santo states, where Atlantic Forest is predominant. Is the same work, there also record from Argentina (Cordoba) and Bolivia (Songo).

Type material. Not examined.

Additional material examined. BRASIL: MINAS GERAIS: Barbacena, 26.xii.2006, A. Assis leg. – 1♀ (CEMT); Belo Horizonte, x.1945, A. Penna leg. – 1♂ (CERPE); Lambari, ix.1935 – 1♂ (CECL); Lavras, 10.x.2003, F.C. Santos leg. – 1♂ (CERPE), 19.iv.2006, A. Costa leg. – 1♂ (CERPE), 14.x.2007, C.C. Moreira leg. – 1♂ (CEMT), 04.iii.2008, R. Stockmann leg. – 1♂ (CEMT), 23.iii.2008, S. M. Borba leg. – 1♀ (CERPE); Resende Costa, viii.2002, L. Fernandes leg. – 1♀ (CEMT); São João del Rei, iv. 2007, F. Fernandes leg. – 1♂ (CEMT). SÃO PAULO: Holambra, 20.iii.2008, T. Reijers leg. – 1♂ (CEMT); Sorocaba, 03.xi.2000, Izaura leg. – 1♂ (CERPE).

Male redescription (Fig. 28A). **Length:** 30.5–24.0 mm. **Width:** 17.1–13.0 mm. **Color:** Nearly completely reddish brown, pronotum dark reddish brown. **Head:** Clypeus triangular, bidentate anteriorly, surface glabrous, coarsely rugose. Frontoclypeal suture with transverse, raised, incomplete ridge. Frontal surface scarcely setose, coarsely rugopunctate. Ocular canthus transverse, slightly arched, with setae confined at ventral area. **Mouthparts:** Mandibles tridentate; apical and medial teeth transverse, from slightly lobed to triangular; basal tooth triangular, smaller than previous ones. Maxillae with galea tridentate on apex. Labium subtriangular; discal area usually flattened, sometimes slightly concave, rugopunctate, scarcely setose; sides densely covered with long setae. **Antennae:** Club two times longer than antennomeres II–VII combined. **Thorax:** Pronotum strongly convex in lateral view; marginal anterior area with a tubercle moderate in size, followed by a rounded, deep concavity, with two posterior small tubercles; anterior corners densely covered with coalescent punctures, concavity transversely rugose, sides moderately punctate, disc smooth. Scutellar plate from subtriangular to parabolic in shape. Elytral surface with barely marked longitudinal striae; each stria with a row of fine punctures (observed under 90X magnification); interstriae smooth. **Legs:** Inner protarsal claw with a small ventromedial lobe. Mesotibiae with two transverse carinae on external surface; basal carina short, transverse; medial carina long, strongly projected diagonally; carinae and apex covered with spinules. Metafemora smooth at disc. Metatibiae apically wider compared to mesotibiae. **Abdomen:** Tergite with stridulatory apparatus barely marked. Tergite VIII completely rugose, densely covered with long yellowish setae. Ventrites I–II completely setose; ventrites III–V densely rugopunctate on sides, and with a row of incomplete, setose punctures, disc glabrous, weakly punctate; ventrite VI densely rugopunctate on sides, weakly punctate on disc, posterior margin transversely covered with setae. **Spiculum gastrale (Fig. 28C):** Y-shaped; medial branch

shorter compared to lateral branches, apex rounded; basal sclerite formed by two oval shaped plates, covered with setae at apical margin. **Aedeagus (Fig. 28 D–E)**: Parameres in caudal view (Fig. 28D), symmetric, usually with longitudinal punctures oval in shape, apical half strongly excavated lateroventrally, laterodorsally dilated in oval shaped. Parameres in lateral view (Fig. 28E), ventral margin with a basal process, apex broad dorsoventrally.

Female redescription (Fig. 28B). Very similar to male in overall aspect, except in the following aspects: **Length**: 29.2–27.0 mm. **Width**: 17.0–15.0 mm. **Thorax**: Pronotal anterior area with a small marginal tubercle, concavity shallow. **Legs**: Metafemora smooth at discal area (Fig. 28F). **Abdomen**: Tergite VIII weakly convex in lateral view (Fig. 28G). Ventrite VI triangular shaped, completely setose.

Geographic distribution. Brazil (Minas Gerais, São Paulo) (Fig. 53).

***Bothynus nyx* Ratcliffe, 2010 (Fig. 29A–E; Fig. 53)**

Bothynus nyx Ratcliffe 2010, p. 105

Diagnosis. *Bothynus nyx* resembles *B. laevipennis*, but differs from this species in the following characters: In both sexes, pronotal concavity transverse and oval in shape (Fig. 29A–B), punctures well-marked; apical half of parameres with lateroventral area weakly excavated (nearly with parallel sides) in caudal view (Fig. 29C) and flattened apex in lateral view (Fig. 29D); in female, posterior area of concavity with a tubercle and tergite VIII strongly convex in lateral view (Fig. 29E).

Remarks. The male specimen examined here do not presented the ventral tooth at inner protarsal claw. Ratcliffe (2010) used the presence of a ventral tooth at protarsal claw in male to differ *B. nyx*. from *B. laevipennis*. However, this character appears to be variable in *B. nyx* and should not be singly used for diagnosis but should be combined with other characters, as presented in the diagnosis above. *Bothynus nyx* is known only from the south-central slope of the Bolivian Andes.

Type material. Not examined.

Additional material examined. BOLIVIA: Coroico, 22.i.2009, B. Juvisy leg. – 1♂ 1♀ (EPGC).

Male redescription (Fig. 29A). **Length:** 32.5 mm. **Width:** 18.0 mm. **Color:** Nearly completely reddish-brown. **Head:** Clypeus subtrapezoidal, strongly rugopunctate, glabrous, with two triangular and raise teeth anteriorly, lateral with long setae scarcely scattered. Frontoclypeal suture with a weakly transverse ridge, nearly reaching the lateral margins. Frontal surface strongly rugose, scarcely setose at sides, glabrous at middle area. Ocular canthus subrectangular, transverse, slightly arched, setose ventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth flattened, triangular, transverse; basal tooth lobed, smaller than previous ones. Maxillae with tridentate galea. Labium suboval shaped, densely surrounded with long setae, disc flattened, rugose, scarcely covered with small setae at middle area. **Antennae:** Club 1.8 times larger than segments II–VII combined. **Thorax:** Pronotum strongly convex posteriorly in lateral view; anterior marginal area with a conic tubercle, moderate in size, raised above a transverse edge, followed by an oval shaped, transverse concavity, with two weak posterior tubercles; pronotal surface surrounded with dense rugopunctures, becoming finely marked toward disc, concavity transversely rugose. Scutellar plate triangular, finely punctate, glabrous. Elytral surface with

seven well-marked striae (one sutural, 4 discal, two lateral); overall punctures well-marked, ocellate; striae with punctures spaced about three diameters of punctures, area between discal and lateral stria with irregularly scattered punctures. **Legs:** Inner protarsal claw with a middle-ventral tooth, lobed in shape. Mesofemora nearly completely setose ventrally. Mesotibial outer surface transversely bicarinate; basal carina short, medial carinae long, strongly projected; apex broad. Metafemoral surface finely punctate ventrally, carina slightly crenulate. **Abdomen:** Tergite VII with stridulatory apparatus formed by one band of barely marked carinae. Tergite VIII strongly concave in lateral view, emarginate anteriorly in dorsal view, surface completely rugose, weakly setose. Ventrites I–II completely setose; ventrites III–V densely setose on sides, smooth on disc; ventrites I–III completely, densely punctate; ventrites IV–VI densely punctate on sides, weakly punctate on disc. **Aedeagus (Fig. 29C–D):** Parameres in caudal view (Fig. 29C), elongated (three times longer than wide), smooth, apical half with lateroventral area weakly excavated, nearly parallel, apex broad dorsolaterally. Parameres in lateral view (Fig. 29D), apex flattened dorsoventrally.

Female description (Fig. 29B). **Length:** 33.0 mm. **Width:** 18.4 mm. **Color:** Reddish brown.

Head: Clypeus trapezoidal, bidentate at apex, coarsely rugose, glabrous. Frontoclypeal suture with a transverse carina. Frons coarsely rugose, scarcely setose on sides, glabrous on disc. Ocular canthus transverse, slightly arched, setose ventrally. **Mouthparts:** Mandibles tridentate. Labium oval shaped, apex slightly constricted laterally. **Thorax:** Pronotum strongly convex posteriorly in lateral view; anterior area with a marginal tubercle, followed by a transverse, oval shaped concavity, with a weak and transverse tubercle posteriorly; pronotal surface surrounded with dense, coalescent punctures, concavity transversely rugose. Scutellar plate subtriangular, with 9 small, irregularly scattered punctures. Elytra with 9 well-marked striae (1 sutural, 4 discal, 4

lateral); punctures spaced about two diameters of punctures. **Legs:** Inner protarsal claw simple, without ventromedial tooth. Mesotibiae with a middle carina at outer surface. Metatibiae similar to mesotibiae. **Abdomen:** Tergite VIII transversely rugose, completely setose, convex in lateral view (Fig. 29E). Ventricle VI triangular, densely rugopunctate, moderately covered with short setae.

Geographic distribution. Bolivia (Coroico) (Fig. 53).

***Bothynus thrix* Hardy, 2017 (Fig. 30A–D; Fig. 53)**

Bothynus thrix Hardy 2017, p. 141

Diagnosis. *B. thrix* is related to *B. deiphobus* and *B. fabius*, but is easily distinguished from these two species by the following characters: In both sexes, dorsal surface of elytra covered with yellowish setae Fig. (30A–B); in male, anterior middle area declivous.

Remarks. *Bothynus thrix* is a remarkable species by the presence of innumerable setae that cover the elytral surface, until now unique in the genus. The species is known from northern Argentina, and from central Bolivia, in Andean and sub Andean regions.

Type material.

Paratype male (CERPE), examined, labeled: “Bolivia, Santa Cruz 5K ESSE Warnes, Hotel Rio Selva, 20-21.x.00, Morris & Wappes”. Paratype female (CERPE), examined, labeled: “Bolivia, Santa Cruz, 4-6K SSE Buena Vista F&F Hotel, 14-16.x.2000, Wappes & Morris”.

Male redescription (Fig. 30A). **Length:** 19.2 mm. **Width:** 11.1 mm. **Color:** Nearly completely reddish brown. **Head:** Clypeus subtriangular, sides straight, with two small teeth anteriorly, coarsely rugopunctate, glabrous. Frontoclypeal suture with an incomplete, transverse ridge. Frons coarsely rugopunctate, with scarce setae confined on sides. Ocular canthus subtriangular, slightly arched. **Mouthparts:** Mandibles tridentate; apical tooth truncate at apex, medial tooth subtriangular, basal tooth lobed. Maxillae with quadridentate galea; teeth subequals in size. Labium subtriangular in shape. **Antennae:** Club subequal in length to segments II–VII combined. **Thorax:** Pronotal anterior margin with a small tubercle at middle, anterior middle area declivous; surface setose, covered with large rounded punctures, smaller on disc. Scutellar plate parabolic shaped, smooth. Elytra completely setose, striae barely marked, with disc with 5 rows of punctures (1 sutural, 4 discal), sides with punctures irregularly punctate. **Legs:** Protarsal claws simple, without modification. Mesotibiae only with a middle, produced carina on outer surface, apex emarginate. Metatibiae with two carinae on outer surface (1 basal, 1 medial), apex truncate. **Abdomen:** Tergite VII with stridulatory apparatus formed by two bands of finely marked carinae, separated by a narrow mid-line. Tergite VIII coarsely rugose and weakly setose on sides, glabrous and punctate on disc, punctures large, oval in shape. Ventrite I completely setose; ventrite II nearly completely setose, middle area glabrous; ventrites III–V with a row of setose punctures confined on sides; ventrite VI covered with setae at apex; ventrites II–VI rugopunctate on sides, smooth on disc. **Aedeagus (Fig. 30A–B):** Parameres in caudal view (Fig. 30C), apical half excavated lateroventrally, dorsoventrally broad in oval shaped. Parameres in lateral view (Fig. 30D), ventral area with a basal tooth.

Female redescription (Fig. 30B). Similar to male, except in the follow aspects: **Length:** 19.0 mm. **Width:** 10.9 mm. **Thorax:** Pronotum weakly convex posteriorly in lateral view; anterior area

with small apical tubercle, surface densely punctate. **Abdomen:** Tergite VIII completely covered with scarce setae. Ventricle VI triangular.

Geographic distribution. Bolivia (Santa Cruz) (Fig. 53).

***Bothynus moroni* Duarte, Grossi & Parizotto sp. nov. (Fig. 31A–B; Fig. 54)**

Diagnosis. *Bothynus moroni* sp. nov. differs from other species of the group by the following combination of characters: Body elongated, clypeal teeth projected longitudinally, anterior clypeal margin deeply emarginated between teeth; (Fig. 31B), pronotal anterior tubercle small and raised on a conic edge, pronotal concavity wide and deep, featuring strongly rugose surface (Fig. 31A).

Remarks. Compared to males, *Bothynus* females are more similar interspecifically, becoming its diagnosis is more difficult. *Bothynus moroni* sp. nov. was described based on two female specimens that appear morphologically related to females of *B. nyx* and *B. leidianae* sp. nov. Aspects of the clypeal teeth, longitudinally projected in *B. moroni* and transverse in *B. nyx*, are concise characters that distinguish these species. Regarding *B. leidianae* sp. nov., *B. moroni* sp. nov. differ by pronotal features, as the small tubercle raised under a conic edge, besides the wide and deep concavity, completely covered with strong rugosity. *Bothynus moroni* sp. nov. was collected at a peculiar area marked by the transition between Cerrado of the Brazilian central plateau and Amazonia plain.

Etymology. The specific epithet “*moroni*” is a homage to the late Dr. Miguel Ángel Morón Rios (*In Memoriam*), who contributed magnificently with the knowledge of Neotropical Scarabaeoidea fauna.

Type material. Holotype female, not dissected, labeled: “BRASIL: MATO GROSSO: Chapada dos Guimarães, Parque Nacional da Chapada dos Guimarães, vale do eco, 17.i.2013, luz, M. Savaris & S. Lampert legs” – 1♀ (CERPE). Paratype: one female, same data as holotype – 1♀ (CEMT).

Holotype description (Fig. 31A). **Length:** 30.0 mm. **Width:** 16.1. **Color:** Nearly completely reddish brown; head, pronotum, pro-, meso and metatibiae dark reddish brown. **Head:** Clypeus subtrapezoidal (1.8 times wider than long), coarsely rugopunctate, glabrous, slightly raised at middle area, anterior margin with two longitudinal teeth separated by a deep emargination (Fig. 31B). Frontoclypeal suture with a transverse, incomplete ridge. Frontal surface strongly, transversely rugose, glabrous. Ocular canthus subrectangular, transverse, slightly crenulated at anterior margin, covered with scattered setae ventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth flattened; apical tooth subquadrate, emarginate apically; medial tooth subparabolic; basal tooth lobed, smaller than previous ones. Labium subtriangular, coarsely rugopunctate, surrounded with long setae, glabrous at disc. **Antennae:** Ten-segmented; club 1.8 times longer than antennomeres II–VII combined. **Thorax:** Pronotum strongly convex in lateral view; concavity broad, with a deep pit on each side, separated by a longitudinal, slightly raised edge; anterior marginal tubercle small, raised under a conic edge; surface surrounded with dense rugopunctures, disc finely punctate, concavity completely, transversely rugose. Scutellar plate subparabolic, smooth. Elytral surface with 9 well-marked striae (1 sutural, 4 discal, 4 lateral);

each stria covered with ocellate, deep punctures; punctures contiguous on sutural striae, other striae with punctures spaced about one diameter of punctures; interstriae irregularly punctate. **Legs:** Proclaws similar in shape. Protibiae tridentate, teeth acute apically, basal tooth smaller than previous ones. Mesofemoral ventral area covered with C-shaped punctures. Mesotibiae only with a medial carinae; apex broad, truncate. Metafemoral ventral area covered with large, C-shaped punctures. Metatibiae bicarinate at outer surface (1 basal, 1 medial). **Abdomen:** Tergite VII with stridulatory apparatus formed by one band of transverse, well-marked carinae. Tergite VIII completely rugose, moderately setose. Ventrite I completely, densely setose; ventrites II–V with a row of setose punctures confined on sides; ventrites II–IV densely rugopunctate on sides, moderately punctate on disc; ventrite V nearly completely covered with dense rugopunctures, disc with a punctate transverse area; ventrite VI triangular, completely rugose, weakly setose.

Variation. The paratype do not varies significantly from holotype, except in size: **Length:** 28.9 mm. **Width:** 15.8.

Geographic distribution. Brazil (Mato Grosso) (Fig. 54)

***Bothynus andrezus* Duarte, Grossi & Parizotto sp. nov. (Fig. 32A–F; Fig. 54)**

Diagnosis. *Bothynus andrezus* sp. nov. resembles *B. cyclops*, but differs from this species in the following aspects: In both sexes, maxillary teeth with 6 teeth irregularly in shape and size (Fig. 32C), elytral punctures shallow (Fig. 32A–B); male, apical half of parameres with broad dorsolateral area (Fig. 32D); female, discal area of tergite VIII punctate (Fig. 32F).

Remarks. The occurrence of *B. andrezus* sp. nov. are inserted in open field landscapes of the South America dry diagonal. The species is associated with Cerrado areas and Rupestrian Fields from Brazil and with Chaco areas from Paraguay.

Etymology. The specific epithet “*andrezus*” is a homage to laboratory colleague Dr Andrezo Santos, who is the currently vice curator at Coleção Entomológica da Universidade Federal Rural de Pernambuco (CERPE).

Type material. Holotype male, dissected, labeled: “ARGENTINA: MISIONES: Eldorado, 22.i.1995 – 1♂ (CERPE). Paratypes, three males and two females with the following labels: “BRASIL: DISTRITO FEDERAL: Brasília, x.1992, E. & P. Grossi legs.” – 1♀ (CERPE); “BRASIL: DISTRITO FEDERAL: Planaltina, Embrapa Cerrados, área agrícola, -15.3554 S / -47.4251 W, 17.xii.2005, luz, C. Oliveira leg.” – 1♂ (CEMT); “BRASIL: GOIÁS: São João D’Aliança, Chapada dos Veadeiros, Faz. Sendai, 900 m, 14.xi.2007, R. M. Koike leg.” – 1♂ (CERPE); “BRASIL: MINAS GERAIS: Lavras, 12.iv.2008, L. G. Paranhos leg”. – 1♂ (CERPE); “PARAGUAY: CAAZAPÁ: Estero Cristal, 20.x.1999” – 1♀ (CERPE).

Holotype description (Fig. 32A). **Length:** 25.9 mm. **Width:** 14.1 mm. **Color:** Completely reddish brown. **Head:** Clypeus subtriangular, constricted laterally, rugose, glabrous, anteriorly with two acute teeth. Frontoclypeal suture with a transverse, incomplete ridge. Frons coarsely rugose, glabrous. Ocular canthus subrectangular, setose ventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth acute at apex, slightly bent backward; basal tooth lobed, smaller than previous ones. Labium subtriangular, flattened, surrounded with long setae, rugopunctate at disc. **Antennae:** Club 1.3 times longer than antennomeres II–VII combined.

Thorax: Pronotum strongly convex posteriorly in lateral view; anterior area with a marginal, conic tubercle, moderate in size; concavity broad, rounded, moderately deep, transversely rugose; anterior and lateral areas densely rugopunctate; punctures large, C-shaped, coalescent; basal area weakly punctate; disc smooth. Scutellar plate parabolic, smooth. Elytral surface with 9 well-marked striae (1 sutural, 4 discal, 4 lateral); each stria covered with ocellate punctures, moderate in size; sutural stria with contiguous punctures, other striae with punctures spaced about one diameter of punctures. **Legs:** Inner protarsal claw curved, incise at apex. Protarsomere V with a ventrolateral process at apex. Mesotibial outer surface only with a middle carinae. Metatibial outer surface with two carinae (one basal, one medial), apex broad. **Abdomen:** Tergite VII with stridulatory apparatus formed by one band of innumerable, transverse, finely marked carinae. Tergite VIII glabrous, nearly completely rugopunctate, discal area moderately punctate. Ventricle I completely setose; ventrite II moderately setose, with scattered setae on sides, disc smooth; ventrites III–V with a row of setose punctures confined to sides, disc smooth; ventrite VI smooth, bordered with on posterior margin. **Aedeagus (Fig. 32D–E):** Parameres in caudal view (Fig. 32D), smooth, basal half with subparallel sides, apical half abruptly excavated lateroventrally, broadly exploded laterodorsally, apex rounded. In lateral view (Fig. 32E), dorsal area arched, with a small, basal process at basis.

Paratypes variation. Males vary from the holotype in the following aspects: **Length:** 26.0–25.0 mm. **Width:** 14.1–14.0 mm. **Mouthparts:** Maxillae with 6 teeth at galea (Fig. 32C); 2 teeth at apex (1 strong, 1 weak), 1 medial (strong), 3 basal (weak). **Thorax:** Elytral punctures slightly larger compared with the holotype punctures. Female (Fig. 32B) paratypes differ from the holotype male in the following aspects: **Length:** 25.5–24.5 mm. **Width:** 14.5–13.0 mm **Thorax:** Pronotal tubercle small, concavity shallow and rugopunctate. **Legs:** Inner protarsal claw simple,

similar to outer claw. **Abdomen:** Tergite VIII weakly setose (Fig. 32F). Ventricle VI densely rugose, moderately setose.

Geographic distribution. Argentina (Misiones), Brazil (Distrito Federal, Goiás, Minas Gerais), Paraguay (Caazapá) (Fig. 54).

***Bothynus tamarae* Duarte, Grossi & Parizotto sp. nov. (Fig. 33 A–F; Fig. 54)**

Diagnosis. *Bothynus tamarae* sp. nov. resembles *Bothynus sebastiani* sp. nov., but differ from this species in the following aspects: In both sexes, tergite VIII completely rugose (Fig. 33D); males, inner protarsal with wide incision, outer tooth broader than inner tooth (Fig. 33C), apical half of parameres with laterodorsal areal abruptly expanded toward apex. (Fig. 33E).

Remarks. *Bothynus tamarae* sp. nov. is closely related to some small species of the *ascanius* group that have the inner protarsal claw splitted, such as *B. cribrarius*, *B. cylindricus* and *B. sebastiani* sp. nov. However, this last species is more related to *B. tamarae* by the last protarsomere shorter compared to other species.

Etymology. The specific epithet “*tamarae*” is a homage to laboratory colleague Tamara Carvalho, who currently working with Rutelinae immature stages in her doctoral degree.

Type material. Holotype male, dissected, labeled: “PARAGUAY: PARAGUARÍ: Sapucaí, 19.viii.1994, Drechsel leg.” – 1♂ (CERPE). Paratypes: Three males, same data as holotype – 3♂ (CERPE); two females, same data as holotype, except by “28.vii.1997” – 2♀ (CERPE).

Holotype description (Fig. 33A). **Length:** 18.0 mm. **Width:** 9.5 mm. **Color:** Completely reddish brown. **Head:** Clypeus triangular, subparallel laterally, bidentate anteriorly, coarsely rugose, glabrous. Frontoclypeal suture with a transverse, incomplete ridge. Frons coarsely rugose, with scarce setae laterally scattered near eyes. Ocular canthus subrectangular, transverse, slightly crenulated at outer margins, setose ventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth flattened, subtriangular in shape, transverse; basal tooth lobed, smaller than previous ones. Maxillae with tridentate galea. Labium subtriangular, slightly rounded laterally, surrounded with long setae, strongly rugopunctate at disc. **Antennae:** Club subequal in length to antennomeres II–VII combined. **Thorax:** Pronotum strongly convex posteriorly in lateral view; anterior area with marginal tubercle small in size; concavity oval shaped, shallow, transversely rugose; anterior corners strongly rugopunctate, sides densely punctate, disc weakly punctate. Scutellar plate subparabolic, finely punctate, punctures irregularly scattered. Elytra with 9 well-marked striae (1 sutural, 4 discal, 4 lateral); discal and lateral striae covered with ocellate punctures, moderate in size; sutural stria with punctures smaller than discal and lateral striae. **Legs:** Inner proclaw broadly incised at apex; outer tooth broader than inner tooth (Fig. 33C). Protarsomere V as twice long as the apical width, ventral area with lateral process at apex. Meso- and metatibial outer surface only with a middle carina, apex broad. **Abdomen:** Tergite VII with stridulatory apparatus formed by two bands of innumerable, finely marked carinae. Tergite VIII convex in lateral view, strongly rugose, glabrous (Fig. 33D). Ventrite I completely setose; ventrite II nearly completely setose, with setae irregularly scattered, surface nearly completely rugopunctate; ventrites III–V with a row of incomplete, setose punctures confined to sides, surface rugopunctate on sides, smooth on disc; ventrite VI transversely bordered with setae posteriorly, densely rugopunctate at sides, smooth at disc. **Aedeagus:** Parameres in caudal view (Fig. 33E), symmetric, surface finely

punctate, basal half rounded laterally, lateroventrally excavated at apical half, laterodorsally expanded in oval shaped at apex, with basal sides projected outward. Parameres in lateral view (Fig. 33F), ventrolateral margin with a small process at basis, not visible in caudal view.

Paratypes variation. Males vary from the holotype in the following aspects: **Length:** 17.0–16.8 mm. **Width:** 10.1–9.1 mm. **Parameres:** Ventrolateral tooth sometimes visible in caudal view. Female (Fig. 33B) paratypes differs in the following aspects: **Length:** 19.9–18.5 mm. **Width:** 10.8–9.9 mm. **Thorax:** Pronotum weakly convex posteriorly in lateral view; surface nearly completely covered with dense, large, deep punctures; apical tubercle small; concavity shallow, rugopunctate. **Legs:** Inner protarsal claw simple, similar to outer claw. Tarsomere V apically without lateroventral process. **Abdomen:** Ventrite VI triangular, completely rugopunctate, scarcely covered with short setae.

Geographic distribution. Paraguay (Paraguari) (Fig. 54).

***Bothynus leidiana* Duarte, Grossi & Parizotto sp. nov. (Fig. 34A–G; Fig 54)**

Diagnosis. *Bothynus leidiana* sp. nov. resembles *B. laevipennis* and *B. nyx*, but differs from these two species by the following combination of characters: In both sexes, clypeal teeth projected longitudinally (Fig. 34C), scutellar plate punctate, elytral striae visibly well-marked and with deep punctures; in male, inner protarsal claw deeply incised (outer tooth broader compared to inner tooth) (Fig. 34D), protarsomere V with a apical lateroventral process, discal area of tergite VIII punctate only (Fig. 34E).

Remarks. Female of *B. leidiana* sp. nov. can be also confused with *B. moroni* sp. nov. due to clypeal teeth similarly arranged in both species, however, *B. leidiana* sp. nov. features a shallow pronotal concavity and the marginal tubercle does is not raised under a conic edge, while in *B. moroni* sp. nov. the pronotal concavity is deep and the marginal tubercle is raised under a conic edge. *Bothynus leidiana* sp. nov. occur associated with Cerrado areas from central Brazil.

Etymology. The specific epithet “*leidiana*” is a homage to laboratory colleague, Leidiani Costa, who studied the genus *Gibboryctes* (Dynastinae) in her master’s degree.

Type material. Holotype male, dissected, labeled: “BRASIL: DISTRITO FEDERAL: Brasília, UnB, 16.x.1970, Kunz leg.” – 1♂ (CERPE). Paratypes: three males and three females, same data as holotype, except by “coleção didática UnB, no date” – 1♂ (CEMT), “ii.1985, L. Matos leg.” – 1♀ (CERPE), “17.x.1971, B. Dias leg. – 1♂ (CERPE), “5.x.1973” – 1♀ (CERPE), “Fazenda Ivone, 25.xii.1985” – 1♀ (CERPE), “Fazenda Ivone, 18.ix.1986 – 1♂ (CERPE); two males, labeled: “BRASIL: MATO GROSSO, Cuiabá, 14.xii.1987, Diana de Lima leg. – 2♂ (CEMT).

Holotype description (Fig. 34A). **Length:** 30.1 mm. **Width:** 17.0 mm. **Color:** Nearly completely reddish brown. **Head:** Clypeus subtrapezoidal (two times wider than long), anteriorly with two longitudinal, marginal teeth (Fig. 34A), surface coarsely rugopunctate, glabrous. Frontoclypeal suture with an incomplete, transverse, weakly marked ridge. Frons coarsely rugopunctate, glabrous. Ocular canthus subtriangular, transverse, with slightly crenulate external margin, ventral area setose. **Mouthparts:** Mandibles tridentate; teeth lobed. Labium subtriangular, flattened, surrounded with long setae, disc moderately punctate, with short setae at basis. **Antennae:** Club 1.9 times longer than antennomeres II–VII combined. **Thorax:** Pronotum strongly convex

posteriorly in lateral view; anterior area with an apical, conic, curved apical tubercle, moderated in size; concavity broad, rounded, moderately deep, transversely rugose; surface densely punctate at anterior corners, sides weakly punctate, posterior area near basal margin densely rugopunctate, disc smooth. Scutellar plate with two moderately punctate areas at sides, separate by a longitudinal, smooth middle area. Elytra with 9 well marked striae (1 sutural, 4 discal, 4 lateral); each stria covered with ocellate, deep punctures, spaced about one diameter of punctures; interstriae irregularly punctate. **Legs:** Inner protarsal claw deeply incised apically, with outer tooth broader than inner tooth (Fig. 34D). Tarsomere V with lateroventral process at apex. Meso- and metatibia with two carinae at outer surface (one basal, one medial), apex broad. **Abdomen:** Tergite VII with stridulatory apparatus formed by two bands of well-marked carinae near to anterior margin, merged in one band of finely marked carinae near to posterior margin. Tergite VIII scarcely covered with short setae scattered near to anterior margin, sides strongly rugopunctate, disc weakly punctate (Fig. 34E). Ventricle completely, densely setose; ventrite II completely, moderately setose; ventrites III–V with lateral surface moderately rugopunctate, weakly setose, disc weakly punctate, glabrous; ventrite VI weakly punctate on sides, smooth on disc. **Aedeagus (Fig. 34F–G):** Parameres in caudal view (Fig. 34F), surface rugopunctate, basal half with parallel sides, apical half strongly excavated lateroventrally, laterodorsally expanded in oval shaped. Parameres in lateral view (Fig. 34G), dorsal area arched, ventral area only with a basal carina.

Paratypes variation. Male paratypes vary concerning holotype in the following aspects: **Length:** 31.7–28.0 mm. **Width:** 17.5–15.5 mm. **Head:** Frontal surface sometimes covered with scarce setae. **Thorax:** Scutellar plate with punctures irregularly scattered. Last lateral striae sometimes indistinct. **Abdomen:** Tergite VIII moderately setose basally. Ventricle VI densely punctate at

sides, finely punctate on disc. Female (Fig. 34B) paratypes differs in the following aspects: **Length:** 28.0–27.5 mm. **Width:** 15.8–15.5 mm. **Head:** Frons scarcely setose. **Thorax:** Pronotal surface nearly completely, densely punctate; apical tubercle small; concavity moderately shallow. **Legs:** Inner protarsal claw simple, similar to outer claw. Tarsomere V with lateroventral process absent. **Abdomen:** Tergite VIII completely, densely rugose, densely setose. Ventricle VI densely rugopunctate, moderately setose.

Geographic distribution. Brazil (Distrito Federal, Mato Grosso) (Fig. 54).

***Bothynus sebastiani* Duarte, Grossi & Parizotto sp. nov. (Fig. 35A–G; Fig. 54)**

Diagnosis. *Bothynus sebastiani* sp. nov. resembles to *B. tamarae* sp. nov., but differs from this species in following aspects: In both sexes, maxillae with teeth variable in size (Fig. 35C), tergite VIII with discal area punctate only (Fig. 35 E); in males, inner protarsal claw incised, with teeth subequal in size (Fig. 35D), apical half of parameres with laterodorsal area gradually expanded toward apex (Fig. 35 E).

Remarks. *Bothynus sebastiani* sp. nov. occurs in the Andean region from northern Argentina and in Paraguayan Chaco.

Etymology. The specific epithet “*sebastiani*” is a homage to laboratory colleague Sebastian Caceres, who currently works with the systematic of Neotropical Lucanidae in his doctoral degree.

Type material. Holotype male, dissected, labeled: “PARAGUAY: PRESIDENTE HAYES: Laguna Escalante, 07.x.1995, Drechsei leg.” – 1♂ (CERPE). Paratypes: Two females, same data as holotype – 2♀ (CERPE); one male, same data as holotype, except by “-23.783S/-60.783W, 27-28.xi.2003, 151 m, B. Garcete leg. – 1♂ (CERPE); two females and one male, labeled: “ARGENTINA: SALTA: Parque Nacional, El. Req, Km 26, 1010 m, 28.i.2006, P. Smith leg. – 2♀ (CERPE); “Jujuy, xii.1942” – 1♂ (DZUP).

Holotype description (Fig. 35A). **Length:** 15.0 mm. **Width:** 8.2 mm. **Color:** Dorsal surface dark reddish brown, ventral surface reddish brown. **Head:** Clypeus subtriangular, short (1.7 times wider than long), with two conic teeth anteriorly, surface coarsely rugose, glabrous. Frontoclypeal suture with an incomplete, moderately marked, transverse ridge. Frontal surface transversely rugose, merged with small punctures among it, setae scarcely scattered laterally. Ocular canthus subrectangular, slightly arched at outer margin, setose ventrally. **Mouthparts:** Mandibles tridentate; apical tooth truncate at apex, medial tooth rounded apically, basal tooth lobed (smaller than previous ones). Maxillae with five teeth at galea; two teeth on apex (weak), one medial tooth (strong), two basal teeth (one small, one strong). Labium triangular shaped, surrounded with long setae, discal area densely punctate, with short setae (shorter than lateral setae). **Antennae:** Club subequal in length than antennomeres II–VII combined. **Thorax:** Pronotum strongly convex posteriorly in lateral view; anterior area with a marginal, conic tubercle, moderate in size, followed by a rounded and shallow concavity; surface densely covered with large, deep punctures, coalescent at anterior corners, weakly punctate on disc, rugose on tubercle basis, concavity with large and C-shaped punctures. Scutellar plate finely punctate. Elytra with 9 well marked striae (1 sutural, 4 discal, 4 lateral); striae covered with large, ocellate, deep punctures; punctures contiguous, spaced less than one diameter of punctures. **Legs:** Inner protarsal claw incise at apex,

with teeth subequal in size (Fig. 35D). Protarsomere V with a lateroventral process at apex. Mesotibial outer surface only with a medial carina; apex angular. Metatibial apex truncate. **Abdomen:** Tergite VII with two bands of innumerable, finely marked, transverse carinae. Tergite VIII with surface strongly rugose on sides, becoming densely punctate toward disc (Fig. 35E). Ventricle I nearly completely, densely setose; ventrite II rugopunctate on sides, weakly punctate on disc, moderately setose; ventrites III–V with an incomplete row of setose punctures, sides densely rugopunctate, disc weakly punctate; ventrite V with a row of setose punctures nearly reaching the discal area; ventrite VI moderately punctate on sides, disc smooth. **Aedeagus (Fig. 35F–G):** Parameres in caudal view (Fig. 35F), basal half with rounded sides, lateroventrally with a visible process on each side, apical half lateroventrally excavated, laterodorsal area gradually expanding toward apex in oval shape. Parameres in lateral view (Fig. 35G), dorsal surface arched, ventral surface with basal process.

Paratypes variation. Male paratypes vary concerning holotype in the following aspects: **Length:** 17.2–16.9 mm. **Width:** 10.1–9.9 mm. **Thorax:** Concavity broad, moderately deep, nearly completely rugose. **Legs:** Mesotibial apex rounded. **Parameres:** In lateral view, apex downward curved. Female (Fig. 35B) paratypes differs in the following aspects: **Length:** 17.1–13.5 mm. **Width:** 10.0–8.0 mm. **Thorax:** Pronotal surface densely punctate, marginal tubercle small, concavity shallow. Scutellar plate sometimes with large punctures. **Legs:** Inner protarsal claw simple, similar to outer claw. **Abdomen:** Ventricle V with a transverse, complete row of setose punctures; ventrite VI triangular, completely setose, coarsely rugose.

Geographic distribution. Argentina (Jujuy, Salta), Paraguay (Presidente Hayes) (Fig. 54)

***Bothynus aydanus* Duarte, Grossi & Parizotto sp. nov. (Fig. 36 A–E; Fig. 54)**

Diagnosis. *Bothynus aydanus* sp. nov. resembles *B. nyx*, but differs from this species in the following aspects: Pronotal concavity with two tubercles at posterior area, protarsomere with lateroventral process at apex (Fig. 36B), metatrochanter smooth (Fig. 36C), parameres smooth and with apical half excavated lateroventrally in caudal view (Fig. 36D).

Remarks. The species was described based on a male specimen that presented wear signals in some structures. *Bothynus aydanus* sp. nov. is known from Central Brazil, associated with Cerrado areas.

Etymology. The specific epithet “*aydanus*” is a homage to laboratory colleague Carlos Aydanus, who studied Brazilian species of the genus *Phyllophaga* (Melolonthinae) in his doctoral degree.

Type material. Holotype male, dissected, labeled: “BRASIL: MATO GROSSO: Barra do Bugres, Vão Grande, 31.xii.2011, J. Esteves leg.” – 1♂ (CERPE).

Holotype description (Fig. 36A). **Length:** 30.5 mm. **Width:** 18.2. **Color:** Nearly completely reddish brown; pronotum and protibiae dark reddish brown. **Head:** Clypeus subtrapezoidal (1.8 times wider than long), coarsely rugopunctate, glabrous. Frontoclypeal suture with an incomplete, transverse ridge, slightly notched at middle. Frons coarsely rugose, glabrous. Ocular canthus subrectangular, slightly arched, setose ventrally. **Mouthparts:** Mandibles tridentate. Labium triangular in shape, surrounded with long setae, disc area with short setae. **Antennae:** Club 1.8 times longer than antennomeres II–VII combined. **Thorax:** Pronotum strongly convex posteriorly

in lateral view; anterior area with a marginal tubercle small in size, raised under a transverse edge; concavity broad, oval in shape, moderately deep, transversely rugose, with two rounded tubercles posteriorly; anterior corners densely rugopunctate, sides moderately punctate, posterior middle area densely punctate near to margin. Scutellar plate densely punctate basally, discal area with eight irregularly scattered punctures. Elytra with 9 well-marked striae (one sutural, 4 discal, 4 lateral); striae moderately punctate; punctures ocellated, spaced about two diameters of punctures; interstriae irregularly punctate. **Legs:** Inner protarsal claw incised at apex (Fig. 36B). Protarsomere V with a ventrolateral process at apex. Mesofemora densely setose latero-externally. Metatrochanter smooth (Fig. 36C). Meso- and metatibiae with two carinae on external surface (one basal, one medial); apex broad. **Abdomen:** Tergite VII formed by one band of innumerable, finely marked carinae. Tergite VIII completely rugose, weakly covered with short setae. Ventrite I densely, completely setose; ventrite II moderately, completely setose; ventrites III–V laterally with an incomplete row of setose punctures, surface densely rugopunctate laterally, becoming weakly punctate toward disc; ventrite VI glabrous, nearly completely rugopunctate, middle area near apex weakly punctate. **Aedeagus (Fig. 36D–E)** Parameres in caudal view (Fig. 36D), elongated (4 times longer than wide), finely punctate, basal half with subparallel sides, apical half strongly excavated lateroventrally, laterodorsally expanded in oval shaped (as broader as basal half). In lateral view (Fig. 36E), dorsal surface convex, ventral surface with weakly marked basal carina.

Geographic distribution. Brazil (Mato Grosso) (Fig. 54).

***Bothynus medon* (Germar, 1824) species-group**

Members of the *B. medon* species group are recognized by the presence of the following combination of characters: Dark or dark reddish brown color; clypeus usually with raised, obtuse lateral margins (except in *B. dasypleurus*); pronotum usually convex, only with small anterior marginal tubercle, and small or absent pronotal concavity (except in *B. herteli*); proclaws and last protarsomere usually simple, without modifications in both sexes (except in *B. medon*); elytral surface usually with well impressed striae (except in *B. simplex* sp. nov.). To this group belong six species: *Bothynus medon* (Germar, 1824), *B. dasypleurus* (Germar, 1824), *B. cunctator* (Mannerheim, 1829), *B. exaratus* (Burmeister, 1847), and *B. validus* (Burmeister, 1847) *B. herteli* Endrödi, 1968 and *B. simplex* sp. nov. Duarte, Grossi & Parizotto.

***Bothynus medon* (Germar, 1824) (Fig. 37A–J; Fig. 55)**

Geotrupes medon Germar 1824, p. 115 (original description)

Bothynus medon, Burmeister 1847, p. (synonymized with *B. ascanius*)

Bothynus medon, Arrow 1911, p. 156 (revalidated species)

Diagnosis. *Bothynus medon* differs from other species of the group by the following combine characters: In both sexes, clypeal teeth small, contiguous and located at middle of the anterior margin (Fig. 37C), maxillary galea triangular and with no teeth (Fig. 37D), stridulatory apparatus with well-marked carinae separated by a mid-line on an area near to anterior margin (Fig. 37F); in male, inner protarsal claw incised (Fig. 37), medial branch of the spiculum gastrale with broad apex (Fig. 37G); apical half of parameres elongated in caudal view (Fig. 37H), in lateral view with a strong process ventrobasally (Fig. 37I); in female, tergite VIII with a rounded apical invaginated plate (Fig. 37J).

Remarks. This species was originally described in the genus *Geotrupes* by Germar (1824), being posteriorly transferred to *Bothynus* by Burmeister (1847), that considered *B. medon* as synonym of *B. ascanius* (1847), where both remaining accepted as equal taxa until Arrow (1911) reestablish again *B. medon* as a valid species. Arrow (1911) analyzed the type species of *B. ascanius* and concluded that it is distinct by the strong pronotal tubercle and large and deep excavation in the male, besides of the distinctly striated elytral, while *B. medon* is a species with almost smooth elytra. *Bothynus medon* is a species with widespread South America distribution, occurring from Colombia to Argentina. The species has adapted to the most diverse landscapes and has been collected from dense rainforests areas (Amazonia and Atlantic forests), open areas from dry diagonal (Cerrado and Chaco), and associated with no-till agricultural crops.

Type material. Not examined.

Additional material examined. BRASIL: BAHIA: Caetit , Mania u, 08-11.xii.2005, 850 m, Mielke & Casagrande legs. – 1♂ (CERPE); Valen a,  rea de floresta, 2013, pitfall, C.M.P.L. Leite leg. – 2♂ (CERPE). GOI AS: Cristalina, Fazenda Larga Grande, 03-07.xi.2016, luz, Nayara leg. – 6♂ 8♀ (CERPE); Santa Rita do Araguaia, xi.1936 – 1♀ (IBSP). MINAS GERAIS: Lambari, 8.xi.1967, J. Balik leg. – 1♂ (MZUSP); Lavras, UFLA, 16-21.x.2016, manual, Grossi, Vaz-de-Mello, Duarte & Carvalho legs. – 7♂ 7♀ (CERPE); x.2016, F.Z. Vaz-de-Mello leg. – 7♂ 7♀ (CERPE). MATO GROSSO: Campo Verde, Centro de treinamento IMAMIT, ix.2017, G. Rolim leg. – 8♂ 7♀ (CERPE). PARAN : Diamante do Norte, Est a o Ecol gica Caiua, 10.x.2011, O. Mauro leg. – 5♂ 1♀ (CERPE); Diamante do Norte, 27.xi.2011, F.W. Leivas leg. – 1♂ (CERPE); Diamante do Norte, 27.xi.2011, pitfall, M.A. Cherman leg. – 2♀ (CERPE); Jaguaria va, Parque Estadual do Cerrado, 18-19.xi.2009, 850 m, luz, P.C. Grossi leg. – 1♂

(CERPE). SÃO PAULO: Assis, xii.1942, B. Pohl leg. – 1♂ (MZUSP); Ipiranga, i.1928, R. Spitz leg. – 1♂ (IBSP); Pederneiras, 13.x.2015, M. Bento leg. 1♂ (CERPE); Piedade, xii.1933 – 1♂ (IBSP); Pindorama, 03.xii.1938 – 1♂ (IBSP). No data – 2♂ (UFRA).

Male redescription (Fig. 37A). **Length:** 29.0–21.0 mm. **Width:** 16.0–12.7 mm. **Color:** Reddish brown and shiny in overall aspect. **Head (Fig. 37C):** Clypeus subpentagonal, surface strongly rugopunctate, with scattered setae on sides; anterior middle margin with two small, contiguous teeth; apical half strongly constricted laterally, basal half with parallel margins; lateral middle-margins raised, angularly obtuse. Frontoclypeal suture inconspicuous or with two weak tubercles only. Frons strongly rugopunctate, setose. Ocular canthus transverse, with setae scattered dorsoventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth triangular, basal tooth lobed. Maxillae with triangular galea; galea smooth, teeth absent (Fig. 37D). Labium subtriangular, weakly convex, densely setose on sides, from weakly setose to glabrous on disc. **Antennae:** Ten-segmented; club subequal in length to antennomeres II–VII combined. **Thorax:** Pronotum weakly convex in lateral view, with rounded sides in dorsal view; anterior area with a marginal, small, conic tubercle, followed by a shallow concavity; surface densely punctate laterally and anteriorly, finely punctate on discal area, concavity rugopunctate or punctated only. Elytra sometimes nearly smooth or covered with 9 (1 sutural, 4 discal, 4 lateral), usually well marked striae; surface covered by finely punctures only observed under 50X magnification; posterior area rugose. Scutellar plate parabolic in shape, smooth. Meso- and metaventrites densely covered with yellowish setae; metaventrite rugopunctate. **Legs:** Protibiae tridentate; teeth triangular, apically acute; proximal tooth smaller than previous ones. Inner protarsal claw with incised apex (Fig. 37E); protarsomere V with a small ventrolateral process at apex. Mesofemora completely setose ventrally. Mesotibial outer surface usually with one medial, diagonally

projected carina; apical margin diagonally truncate, bordered with short spinules. Metafemora ventrally smooth at disc. Metatibiae similar to mesotibiae. **Abdomen:** Tergite VII with stridulatory apparatus formed by innumerable well-marked carinae (Fig. 37F), separated by a mid-line confined anteriorly, merged toward apex. Tergite VIII with basal margin narrow at middle; surface glabrous, rugopunctate on sides, finely punctate or smooth on disc. Ventricle I completely setose; II–V rugopunctate and setose on sides, smooth on disc; VI nearly smooth, with setae confined on posterior margin. **Spiculum gastrale (Fig. 37G):** Y-shaped; medial branch spatulate in shape, wide at apex; basal area between lateral branches with transverse. **Aedeagus:** Parameres in caudal view (Fig. 37H), symmetric, basal half rounded on sides, narrowed to a parallel and elongate apical half. Parameres in lateral view (Fig. 37I), ventrobasally area with a strong, downward projected process, apex truncated, wider than middle area.

Female redescription (Fig. 37B). Similar to male, but distinct in the following aspects: **Length:** 28.6–21.0, **width:** 15.8–11.9. **Thorax:** Pronotum weakly convex in lateral view, surface nearly completely punctate, tubercle and concavity absent or vestigial only. **Legs:** Inner protarsal claw simple, similar to outer claw. Protibial teeth rounded apically, wider compared to male. Metatibia widening toward apex. **Abdomen:** Tergite VIII with invaginate apical plate; apical plate wide, rounded (Fig. 37J). Ventricle VI triangular shaped. **Genitalia:** Coxite subequal in size compared to subcoxite. Coxite oval shaped, moderately covered with long setae, disc slightly convex. Subcoxite rhomboid in shape, glabrous.

Geographic distribution. Brazil (Bahia, Goiás, Mato Grosso, Minas Gerais, Paraná, São Paulo) (Fig. 55).

***Bothynus dasypleurus* (Germar, 1824) (Fig. 38A–I; Fig. 52E; Fig. 55)**

Geotrupes dasypleurus Germar 1824, p. 116. (original description)

Podalgus dasypleurus, Burmeister 1847, p. 124

Bothynus dasypleurus, Arrow 1937b, p. 40

Diagnosis. *Bothynus dasypleurus* is distinguished from other species of the group by the following combination of characters: In both sexes, clypeus with sinuous lateral margins (Fig. 38C); in male, parameres are similar those *B. dasypleurus* but differ from this specie by the parameres with outer sides weakly constricted at middle in caudal view (Fig. 38E), ventral carinae sinuous (Fig. 38F), spiculum gastrale with slender medial branch (Fig. 38D); in female, tergite VIII with transverse (four times wider than long) invaginated plate (Fig. 38H), coxite subrectangular, two times wider than long (Fig. 38I).

Remarks. This species occurs in Atlantic rainforest areas from Northeast to Brazilian South, with scattered records in Argentina and Paraguay (Endrödi 1969, 1985, Abadie *et al.* 208), and an apparently mislabeled record from French Guiana (Dupuis 2016).

Type material. Not examined

Additional material examined. BRASIL: RIO DE JANEIRO: Nova Friburgo, Sítio Caturama (S 22°13', W 42°52'), 1100 m, 1-31 xi.2007, E. Grossi & P.C. Grossi legs. – 1♂ (EPGC); Nova Friburgo, Macaé de Cima (S 22°40', W 42°51'), xii.2008/i-ii.2009, P.C. Grossi leg. – 3♂ 16♀ (CERPE); Nova Friburgo (S 22°28'30, 42° 53' W), xi.2014, P.C. Grossi leg. – 6♂ 5♀ (CERPE); Nova Friburgo, Sans Souci (S 22°28', W 42°51'), 1050 m, 28.xii2013/07.I.2014, P.C. Grossi leg. –

2♂ 1♀ (CERPE); Nova Friburgo (S 22°28'30, 42° 53' W), 25.xii.2015/i.2016, P.C. Grossi leg. – 1♂ (CERPE); Rezende, Maromba (S 22°32', W 44°59'), 28.ii.2018, P.R.M. Duarte – 1♂ (CERPE).

Male redescription (Fig. 38A). **Length:** 24.0–22.0 mm. **Width:** 13.5–11.5 mm. **Color:** Variable, with completely dark specimens, or specimens displaying two colors, being dark on elytra and reddish brown on pronotum, legs and venter. **Head (Fig. 38C):** Clypeus subpentagonal, surface glabrous, from coarsely rugose to rugopunctate; anterior corners with two conic teeth conic; lateral margins sinuous. Frontoclypeal suture with two weak, transverse tubercles. Frons with scarce setae scattered on sides; surface strongly crenulate; interocular width equals 1.4 transverse eye diameters. Ocular canthus transverse, slightly arched, with scattered setae dorsoventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth conic, basal tooth lobed (smaller than previous ones). Maxilla with four teeth on galea (two apical, one medial, one basal); basal tooth centrally situated in frontal view. Labium with rounded sides on basal half, convergent on apical half; sides densely covered with setose punctures, disc convex, finely punctate, sometimes with scarce, short setae. **Thorax:** Pronotum weakly convex in lateral view; anterior margin with a middle, small, conic tubercle; anterior middle area with a shallow, rounded concavity; margins rounded lateroanteriorly, lateroposteriorly parallel, posterior corners truncate; anterior area and sides densely covered with large punctures, becoming fine toward disc. Elytra longitudinally covered with 9 well-marked striae (1 sutural, 4 discal, 4 lateral); sutural and discal striae with barely impressed punctures; lateral striae with incomplete rows of large, ocellate punctures; interstriae finely, irregularly punctate. Scutellar plate subtriangular. Mesoventrite finely punctate. Metaventrite rugopunctate on sides, punctate on disc. **Legs:** Protibia tridentate; proclaws simple, without modifications. Mesotibia usually with 2 carinae on outer surface (1 basal short, 1 medial

long); apex strongly emarginate; apical inner spur with outward curved apex, outer spur conic; carinae and apex ornamented with spinules. Metatibial outer spur with an obliquely truncate apex. **Abdomen:** Tergite VII with stridulatory apparatus formed by innumerable transverse carinae; anterior area with two-banded and well-marked carinae, posterior area with a band of finely marked carinae. Tergite VIII convex in lateral view; sides rugopunctate, scarcely setose, disc finely punctate, glabrous. Ventrites I–VI from punctate to weakly rugopunctate on sides, finely punctate on disc; II–V with setae confined to sides; VI setose on posterior margin. **Spiculum gastrale (Fig. 38D):** Y-shaped; medial branch spatulate, slender compared to lateral branches; basal sclerite small, poorly sclerotized. **Aedeagus (Fig. 38E–G):** Parameres in caudal view (Fig. 38E), symmetric, apical half with rounded sides, outer margins weakly constricted at middle, apical half excavated laterodorsally, lateroventrally expanded, apex elongated. In ventral view (Fig. 38F), each paramere with transverse, sinuous carinae. In lateral view (Fig. 38G), ventral middle area slightly projected downward, apex curved down.

Female redescription (Fig. 38B). Similar to male, except in the following aspects: **Length:** 23.8–22.5 mm. **Width:** 14.0–13.0 mm. **Thorax:** Pronotal concavity smaller compared to male. **Abdomen:** Tergite VIII with a posterior, invaginated plate (Fig. 38H); invaginated plate transverse, slightly emarginate, weakly convex; surface weakly convex in lateral view. Ventricle VI subtriangular. **Genitalia (Fig. 38I):** Coxite transverse subrectangular, two times wider than long, arched, covered with long setae on apex; discal surface slightly concave, covered with small tubercles. Subcoxite transverse, two times wider than long; inner margins straight; discal area covered with small, scarce setae.

Geographic distribution. Brazil (Espírito Santo, Rio de Janeiro) (Fig. 55).

***Bothynus cunctator* (Mannerheim, 1829) (Fig. 39A–I; Fig. 55)**

Scarabaeus cunctator Mannerheim 1829, p. 48 (original description)

Bothynus cunctator, Burmeister 1847, p. 116

Diagnosis. *Bothynus cunctator* resembles *B. dasypleurus* and *B. exaratus*, but differ from these two species by the following combination of characters: In both sexes, clypeus angular laterally (Fig. 39C), mandibles tridentate, pronotum with rounded lateral margins (Fig. 39A–B); in male, outer sides of parameres strongly constricted at middle, parameres with rounded ventral carinae (Fig. 39F), spiculum gastrale with medial branch wider than other species of group (Fig. 39D), basal sclerite transverse and well sclerotized; in female, tergite VIII with strongly emarginate invaginated plate (Fig. 39H), coxite arched (Fig. 39I).

Remarks. A first view of the dorsal aspect of *B. cunctator* can lead to an association with *B. exaratus*. However, the tridentate mandibles and labium with convergent apex in both sexes, besides the shape of male parameres, are characteristics that lead *B. cunctator* to have a greater affinity with *B. dasypleurus*. *Bothynus cunctator* occurs in coastal Atlantic Forest areas from Northeast toward Southern of Brazil, with an imprecise record from Pará state in Endrödi (1969). There are also record from Paraguayan Chaco Bolivia (Endrödi 1969, 1985).

Type material. Not examined.

Additional material examined. BRASIL: PARANÁ: Londrina, i.1935 – 1 ♂ (IBSP). RIO DE JANEIRO: Nova Friburgo, Caledônia (S 22°27', W 42°54'), 2220 m, 1-30.xi.2004, E & P. Grossi

legs. – 1♀ (EPGC); Nova Friburgo, Conquista (S 22°28'26, W 42°68'31), xi.2008, P.C. Grossi leg. – 4♂ (CERPE); Nova Friburgo, Macaé de Cima (S 22°40'08, W 42°51'13), xi.2008/i-ii.2009, P.C. Grossi leg. – 2♂ 1♀ (CERPE); Nova Friburgo, Sans Souci (S 22°28', W 42°51'), 1000 m, xi.2003, E & P. Grossi legs. – 1♂ (CERPE); Nova Friburgo (S 22°28'57, W 42°54'40), 18-22.i.2000, S. Ide leg. – 2♂ 1♀ (IBSP); Nova Friburgo (S 22°30'47, W 42°27'28), xii.2009/i-ii.2010, P.C. Grossi leg. – 3♂ 14♀ (CERPE); Nova Friburgo (S 22°28'30, W 42°53'99), xi.2014, P.C. Grossi leg. – 2♂ 1♀ (CERPE). SÃO PAULO: Bananal, Estrada do Bananal (S 22°46'15, W 44°19'), 13.xii.2003, J.A. Giorgi leg. – 1♂ 4♀ (CEMT); Ilha Cardoso (S 25°12'81, W 47°96'26), i.2000, Machado leg. – 2♂ (CERPE); Salesópolis, Estação Ecológica de Boracéia (S 23°58'59, W 45°85'67), 850 m, 23-29.xi.2006, P. Grossi & D. Parizoto legs. – 1♀ (EPGC); São Bernardo (S 23°68'31, W 46°56'23), ix.1933 – 1♀ (IBSP); São José do Barreiro, Parque Nacional Serra da Bocaina (S 22°27'21, W 44°62'50), 1560 m, 23.x.2011, Cavichioli & Melo legs. – 1♂ 2♀ (CERPE).

Male redescription (Fig. 39A). Length: 22.0–18.0 mm. Width: 12.2–10.5 mm. Color: Usual coloration completely dark, rarely dark reddish-brown. **Head (Fig. 39C):** Clypeus subpentagonal, surface rugopunctate, with scarce setae on sides; anterior teeth conic, located near corners; lateral middle-margins with raised, obtuse angles. Frontoclypeal suture with two weak, transverse tubercles. Frons coarsely rugopunctate; interocular width equals 1.5 transverse eye diameters. **Mouthparts:** Labium with rounded sides on basal half, convergent on apical half. Mandibles tridentate; basal tooth slightly lobed, smaller than previous ones. Maxilla with 3 teeth on galea (1 apical, 1 medial, 1 basal); apical and medial teeth situated at middle area in frontal view, basal tooth situated laterally in frontal view. **Thorax:** Pronotum weakly convex in lateral view; lateral margins rounded; anterior marginal tubercle small, concavity from small or vestigial, confined near to anterior middle margin; surface densely punctate near to lateral margins, becoming from

moderately to finely punctate toward disc. Elytral surface with 9 well-marked striae, covered with well impressed, ocellate punctures; punctures anteriorly large, posteriorly becoming fine toward apex; first interstria with punctures confined to anterior area, other interstriae completely, finely punctate. Scutellar plate triangular. Mesoventrite finely punctate. **Legs:** Protibiae tridentate. Mesotibiae with two transversals (1 basal, 1 medial) carinae on outer surface; apical margin slightly sinuous; apical inner spur with apex curved to inside, outer spur conic. Metatibial basal carina interrupted at middle or sometimes absent. **Abdomen:** Tergite VII with stridulatory area formed by two bands of transverse, well-marked carinae confined to anterior area, becoming in a band of finely marked carina toward posterior area. Tergite VIII rugopunctate and weakly setose on sides; disc with few oval-shaped punctures. Ventrites I–VI rugopunctate on sides, finely punctate on disc; II completely setose; III–V with setae confined to sides. **Spiculum gastrale (Fig. 39D):** Y-shaped; medial branch slightly wide on apex, slight narrow on basis; area between lateral branches with two basal sclerites; basal sclerite well-sclerotized, covered with short setae. **Aedeagus (Fig. 39E–G):** Parameres in caudal view (Fig. 39E), symmetric, outer sides strongly constricted at middle, apical half laterodorsally excavated, lateroventrally expanded, apex elongated. In ventral view (Fig. 39F), each paramere with a rounded, transverse carina. In lateral view (Fig. 39G), parameres with apex curved down.

Female redescription (Fig. 39B). Similar to male, except in the following aspects: **Length:** 23.2–22.5 mm. **Width:** 14.7–12.5 mm. **Head:** Frontoclypeal suture with barely marked tubercles. **Legs:** Protibiae distinctly wider compared to male, with distal tooth rounded apically. **Abdomen:** Tergite VIII weakly convex compared to male; apical invagination weakly emarginate (Fig. 39H). Ventrite VI subtriangular. **Genitalia (Fig. 39I):** Coxite subparabolic in shape, inner margins

diagonally projected; inner and outer margins covered with long setae, discal surface scarcely covered with small setae. Subcoxite rhomboid in shape.

Geographic distribution. Brazil (Paraná, Rio de Janeiro, São Paulo) (Fig. 55).

***Bothynus exaratus* (Burmeister, 1847) (Fig. 40A–J; Fig. 55)**

Podalgus exaratus Burmeister 1847, p.124 (original description)

Scaptophilus exaratus argentinus Ohaus 1910, p. 183 (original description)

Bothynus exaratus Arrow 1937b, p. 40

Bothynus exaratus argentinus, Endrödi 1969, p. 127–128 (revised status)

Bothynus exaratus var. *burmeisteri*, Endrödi 1969, p. 128 (original description) revised status

Diagnosis. *Bothynus exaratus* differs from other species of the group by the following combination of characters: In both sexes, clypeal lateral margins angular (Fig. 40C), bidentate mandibles expose laterally to clypeus (Fig. 40C), maxilla with teeth increasing distally in size (Fig. 40D), labium notched at apex (Fig. 40E); in male, parameres elongated and subparallel (Fig. 40G), spiculum gastrale with wide basal sclerite (Fig. 40F); in female, invaginated plate transverse, strongly emarginate and strongly concave (Fig. 40I), subcoxite subquadrangle in shape (Fig. 40J).

Remarks. Some specimens examined here exhibited a remarkable variation in the shape of male parameres, that have the apical half narrow and more separated from each other in caudal view, besides the bent down apex in lateral view. The characteristic of parameres presented by these specimens are congruent with the description and draws of Endrödi (1969) for a variety named by

him as *burmeisteri*. Nevertheless, parameres from other specimens featured progressive variations toward the *burmeisteri* configuration, with transitory aspects in the parameres format. For this reason, *B. exaratus* var. *burmeisteri* must be abandoned. *Bothynus exaratus* occurs associated with Atlantic Forest areas from Brazil and Paraguay, also being found in Cerrado areas from central Brazil. There are still record from Argentina (Endrodi 1969, 1985) and a possible mislabeled record from “Guyanes” in Arrow (1937b).

Type material. Not examined.

Additional material examined. BRASIL: ALAGOAS: Maceió, BR 104 Posto Reforço 6 (S 9°43', W 35°83'), 145 m, 22.i.2018, P. C. Grossi leg. – 3♀ (CERPE). BAHIA: Encruzilhada (S 15°53', W 40°90'), 16.xii.2012, P.C. Grossi, E. Grossi, F. Melo & Rafael legs. – 2♂ 1♀ (CERPE). MINAS GERAIS: Águas Vermelhas (S 15°69'19, W 41°48'38), xii.1997, Vaz-de-Mello & Bello legs. – 1♀ (CEMT); Berizal, Fazenda Veredão (S 15°66', W 41°65'), 850 m, 15.xii.2007, Grossi, Rafael & Parizoto legs – 1♂ (EPGC); Bocaiúva, Fazenda Corredor (S 17°10', W 43°81'), 5.XI.1998, A.A. Azevedo leg. – 1♂ (EPGC); Ipatinga (S 19°47', W 42°54'), xi.1985 – 2♂ (CERPE); Lavras (S 21°26'55, W 44°99'31), 16.x.2003, H.P.A. Azevedo leg. – 1♀ (CERPE); Lavras (S 21°24'90, W 44°99'78), 10.xii.2003, Silvane Barbosa leg. – 1♂ (CERPE); Lavras, UFLA (S 21°22'70, W 44°97'95), 16.x.2016, C. Tamara leg. – 1♂ (CERPE). MATO GROSSO: Chapada dos Guimarães, (S 15°46'75, W 55°74'58), 12-30.xi.2011, M. Mayara leg. – 2♂ (CEMT). RIO DE JANEIRO: Nova Friburgo, Macaé de Cima (S 22°40'08, W 42°51'13), xi.2008/ii.2009, P.C. Grossi leg. – 1♂ (CERPE); Nova Friburgo (S 22°28'30, W 42°53'99), xii.2009/ii.2010, P.C. Grossi leg. – 1♂ 1♀ (CERPE); Nova Friburgo (S 22°28'30, W 42°53'99), xi.2014, P.C. Grossi leg. – 2♀ (CERPE). SÃO PAULO: Botucatu (S 22°88'87, W 48°44'38), 24.x.1970 – 1♂ (IBSP);

Campinas (S 22°92'37, W 47°06'28), i.1938 – 2♀ (IBSP). RIO GRANDE DO SUL: Feliz, Rodovia RS 452 (S 29°44'41, W 51°29'67), 320 m, 19.i.2010, E.J. Grossi leg. – 1♂ (EPGC). PARAGUAY: CONCEPCIÓN: Estancia Cororo (S 23.43'94, W 56°50'13), 10-20.iii.2001, C. Aguilar J. leg. – 2♂ 3♀ (CERPE). GUAIRÁ, Vilarejo (S 25°85'27, W 56°20'14), 10.x.1994, U. Drechsel leg. – 1♂ 1♀ (CERPE).

Male redescription (Fig. 40A). Length: 26.0–22.0 mm. Width: 14.9–12.9 mm. Color: Completely dark. **Head (Fig. 40C):** Clypeus subpentagonal; surface from transversely rugose to rugopunctate, glabrous; anterior corners with two conic, raised teeth; lateral middle-margins with obtuse, raised angles. Frontoclypeal suture without tubercles. Frons from transversely rugose rugopunctate; interocular width equals 1.6 transverse eye diameters. Ocular canthus subquadrate. **Mouthparts:** Labium subpentagonal, completely punctate, notched at apex (Fig. 40E). Mandibles bidentate; teeth conic in shape. Maxilla quadridentate galea (1 apical, 2 medial, 1 basal), with teeth increasing gradually in size toward apex (Fig. 40D); first medial tooth incised in frontal view. **Thorax:** Pronotum weakly convex in latera view, with rounded lateral margins in dorsal view; surface completely, densely punctate; anterior marginal tubercle small, usually followed by a small, rounded, transversely rugose concavity. Elytral surface with 9 well-marked striae; striae covered with ocellate punctures; punctures from large to moderate anteriorly, posteriorly decreasing gradually in size to fine punctures; sutural stria with punctures extending laterally to scutellar plate, nearly reaching the anterior margin; interstriae finely punctate. Scutellar plate subtriangular. **Legs:** Protarsomeres slightly enlarged; proclaws usually simple, inner claw rarely with a small, ventral tooth. Mesotibiae usually with two transverse (1 basal, 1 medial) carinae; carinae from truncate to slightly crenulate; apical margin truncate. **Abdomen:** Tergite VII with stridulatory area formed by two bands of well-marked, transverse carinae. Tergite VIII with

surface nearly completely rugose, with a weakly punctate area near to anterior margin, scarce setae confined on sides, disc glabrous. Ventrites I–VI rugopunctate and setose on sides, finely punctate and glabrous on disc; discal punctures from rounded to oval-shaped. **Spiculum gastrale (Fig. 40F)**: Y-shaped; basal sclerite in shape of an inverted triangle. **Aedeagus (Fig. 40G–H)**: Parameres in caudal view (Fig. 40G), elongate, usually with subparallel sides, apical half from separated to contiguous parameres, sometimes curved to inside on apex. Parameres in lateral view (Fig. 40H), with apex short or strongly curved down.

Female redescription (Fig. 40B). Similar to male, except in the following aspects: Usually larger than male in size: **Length**: 30.0–29.0 mm. **Width**: 19.0–17.5 mm. **Head**: Frontoclypeal suture with two transverse tubercles. **Legs**: Protibial teeth distinctly wider compared to male, with rounded apex. **Abdomen**: Tergite VIII completely setose, weakly convex in lateral view; invaginated plate transverse, strongly concave, strongly emarginate at middle (Fig. 40I). **Genitalia (Fig. 40J)**: Coxite subparabolic shaped, with marginal and ventral surface covered with long setae. Subcoxite rhomboid in shape, inner margins clearly divergent.

Geographic distribution. Brazil (Alagoas, Bahia, Mato Grosso, Minas Gerais, Rio de Janeiro, São Paulo), Paraguay (Concepción, Guairá) (Fig. 55).

***Bothynus validus* (Burmeister, 1847) (Fig. 41A–B; Fig. 55)**

Podalgus validus Burmeister 1847, p. 125 (original description)

Bothynus validus, Arrow 1937b, p. 40

Bothynus validus, Endrödi 1969, p. 125–126 (lectotype designation)

Diagnosis. Based on Endrödi (1969), the male of *B. validus* differs from other males of the group by the inner protarsal claw incised and parameres as in **Figs. 1106–1107** (see **Endrödi 1985: 270**); the female differs by the pronotal surface without tubercle or concavity, covered with large, dense and deep punctures (Fig. 41A); the ventrite VI has two small contractions on the posterior margin (Fig. 41B).

Remarks. A detailed examination of the species was limited by the lack of available material and has only possible to assess a single female specimen. *Bothynus validus* is an uncommon species that has not been found in Brazilian collections and neither has been recently collected. Latest collection data were made by Riehs (2006), that collected four specimens (one male and three females) in Araucaria, Paraná state. We attempt to access the Riehs's material, but unsuccessfully. *Bothynus validus* occurs in Brazilian Atlantic Forest areas from Southeast and South regions, there are also a scattered record from Argentina (Endrödi 1969).

Type material. Not examined

Additional material examined. BRASIL: SÃO PAULO, Serra azul – 1♀ (EPGC)

Male redescription based on Endrödi (1969). **Length:** 32.0–26.0 mm. **Color:** Reddish-brown.

Head: Completely rugose, carina or tubercles absents, anterior margin with two pointed and broadly separated teeth; sides angularly raised. **Thorax:** Pronotum nearly two times wider than long; anterior corners acute, posterior rounded; anterior marginal tubercle strong, transverse; concavity broad; surface densely punctate on anterior area, finely punctate on posterior area, rugose on concavity. Elytra with striae barely marked, evenly punctate. **Legs:** Inner protarsal claw

incised. Protibiae tridentate. Metatibia enlarged toward apex, covered with about 50 spinules.

Abdomen: Stridulatory apparatus large, finely marked at basis. **Aedeagus:** Parameres as in **Figs. 1106–1107 (see Endrödi 1985: 270).**

Female redescription (Fig. 41). **Length:** 31.1 mm. **Width:** 19.0. **Color:** Completely reddish brown. **Head:** Clypeus subpentagonal, coarsely rugose, glabrous, bidentate anteriorly; teeth pointed, raised, slightly arched, separated by a wide emargination. Frons coarsely rugose, glabrous. Ocular canthus transverse, slightly arched, with scattered setae dorsoventrally. **Mouthparts:** Mandibles tridentate; apical and medial teeth triangular, pointed; basal tooth lobed. Labium surrounded with long, dense, yellowish setae; disc weakly punctate, glabrous. **Thorax:** Pronotum simple convex, apical tubercle absent, surface nearly completely densely rugopunctate, discal area densely punctate; punctures contiguous, large, deep. Scutellar plate subtriangular, finely punctate. Elytra disc with barely marked striae, sutural and lateral striae well-marked; surface covered with large, dense, deep punctures mixed with fine punctures. **Legs:** Protarsal claw simple. Protibiae tridentate. Metatibia triangular, apex as broad as middle area. **Abdomen:** Tergito VIII widely emarginate at basal margin, surface densely punctate, moderately setose. Ventricle VI with a small contraction on each side of apical margin (Fig. 41B).

Geographic distribution. Brasil (São Paulo) (Fig. 55).

***Bothynus herteli* Endrödi, 1968 (Fig. 42A–F; Fig. 55)**

Bothynus herteli Endrödi 1968, p. 173 (original description)

Diagnosis. *Bothynus herteli* differs from other species of the group by the following characters: In both sexes, clypeus with 4 teeth (two on the anterior margin, one in each side of clypeus) (Fig. 42C), apical maxillary galea with an acute and elongated teeth at (Fig. 42D), pronotal posterior border complete (Fig. 42A–B), elytral punctures large and deep; in male, parameres with two inner crossed teeth at basal half in dorsal view (Fig. 42E).

Remarks. *Bothynus herteli* is as remarkable species by exhibit two exclusive characters that are unique within the genus: presence of a quadridentate clypeus and pronotum with complete posterior border. Furthermore, figures as one of the larger *Bothynus* species, where the male can be reaching 33.7 mm in length. *Bothynus herteli* is endemic to Amazonia coastal areas with records from Guyana and French Guyana (Endrödi 1968, Dupuis 2016).

Material type. Not examined.

Additional material examined. FRENCH GUYANA: Kourou, RN1-PK 76, ix.2007, Y. Ponchel leg. – 1♂ 1♀ (EPGC); Saint Laurent du Maroni, no date, Soula leg. – 1♀ (EPGC); Sinnamary, RN1-PK102, ix.2000, Y. Ponchel – 1♂ (EPGC); Sinnamary, RN1-PK80, viii.2001, – 1♀ (EPGC).

Male redescription (Fig. 42A). **Length:** 31.8–33.7 mm. **Width:** 17.3–17.6 mm. **Color:** Head and pronotum dark reddish-brown, other surfaces reddish-brown. **Head (Fig. 42C):** Clypeus subpentagonal, transverse (two times wider than long), strongly rugose, glabrous; anterior corners with two strong, conic, raised teeth, separated by a wide emargination; lateral middle-margins with a pointed, raised tooth on each side. Frontoclypeal suture with two weak, transverse tubercles. Frons strongly rugose, glabrous. Ocular canthus subquadrate, with small setae confined

to outer sides. **Mouthparts:** Mandibles bidentate; teeth conic, pointed, slightly curved backward; apical tooth smaller than medial tooth. Maxillary galea with a long, pointed apical teeth (Fig. 42D). Labium subtriangular, slightly rounded laterally, slightly excavated at basis; sides densely surrounded with long setae, disc scarcely covered with short setose. **Antennae:** Club subequal in length to antennomeres II–VII combined. **Thorax:** Pronotal posterior margin complete; anterior area with a middle, strong, conic tubercle near to anterior margin; 1/3 of pronotal area occupied by a deep, rounded, wide concavity; lateral limit of concavity with a triangular tubercle on each side; surface near margins densely covered with strongly, coalescent punctures, disc finely punctate, concavity transversely rugose. Scutellar plate with scarce punctures, irregularly scattered. Elytra with 9 barely marked striae (1 sutural, 4 discal, 4 lateral); striae covered with denser, large, coalescent, ocellate punctures. Prosternal process subtrapezoidal, short, confined below the coxae. Mesoventrite strongly rugopunctate, moderately setose. Metaventrite with sides moderately setose, strongly rugopunctate; disc smooth. **Legs:** Protibiae tridentate. Mesotibiae with 2 crenulate carinae on outer surface (1 basal, 1 medial), bordered with spinules; apical margin angularly projected, featuring only one spinule. Metatibiae with sinuous apical margin, with one spinule. **Abdomen:** Tergite VII with stridulatory apparatus formed by two bands of finely marked carinae, separated by a mid-line. Tergite VIII glabrous, densely punctate on sides, disc smooth, area near to posterior margin with a transverse tubercle. Ventrite I completely rugopunctate, setose; II–V rugopunctate on sides, with an incomplete row of setose punctures, disc smooth; VI nearly completely smooth, with setae confined to posterior margin. **Aedeagus (Fig. 42E–F):** Parameres in caudal view (Fig. 42E), narrow and rounded at basal half, with inner margins featuring two pointed and crossed process, apical half convergent, wider than basal half. In lateral view (Fig. 42F), dorsal area constricted, ventral middle area downward projected, apex strongly curved downward.

Female redescription (Fig. 42B). Female differs from male in the following aspects: **Length:** 31.2–32.2 mm. **Width:** 17.4–17.7 mm. **Thorax:** Pronotum weakly convex in lateral view, with two weakly concavity areas in dorsal view, anterior middle area with dense, large, deep, coalescent punctures. Scutellar plate smooth. **Abdomen:** Tergite VIII slightly concave in lateral view. Ventricle VI triangular.

Geographic distribution. French Guyana (Fig. 55).

***Bothynus simplex* Duarte, Grossi & Parizotto sp. nov. (Fig. 43A–G; Fig. 55)**

Diagnosis. *Bothynus simplex* sp. nov. differs from other species of the group by the following combination of characters: In both sexes, elytral punctures finely impressed and striae barely marked, stridulatory apparatus of tergite VII with one band of well-marked carinae (Fig. 43C); in male, spiculum gastrale with absent basal sclerite, parameres broad in ventral view (Fig. 43F).

Remarks. In the first moment, this new species can be confused with *B. medon* due to characters present in both species: body aspect oval in shape and almost smooth elytra. However, a detailed analysis suggests that *B. simplex* sp. nov. is more related with *B. cunctator* and *B. dasypleurus*, than *B. medon*, by the clypeal teeth located on the anterior corners, inner protarsal claw not incised in male, besides the parameres very similar in shape. In *B. medon*, the clypeal teeth are located at middle of the anterior margin, male have incised inner protarsal claw and the parameres are very distinct from other species in the *medon* group.

Etymology. The specific epithet “*simplex*” refers to body overall aspect, without remarkable ornamentations in male.

Type material. Holotype male, not dissected, labeled: “BRASIL: PARANÁ, Ivaí (S 25°03'92, W 50°86'00), XII.2010, luz, S. Ribeiro leg.” – 1♂ (CERPE). Paratypes, thirty one males and thirty females, same data as holotype – 31♂ 30♀ (CERPE). 1♂, Brasil: Minas Gerais, Itajubá (S 22°42', W 45°45'), 15.VI.1967, O. H. Mielke (DZUP); 2♀, Vila Monte Verde (S 22°88', W 46°03'), 10.XII.1966, Halik (MZUSP); same anterior data but 2♀, 08.IX.1967; same data anterior data but 1♂, 01.XII.1971. 1♀, Paraná, Palmas (S 26°48', W 51°99'), 12.X.2013, Ramos, M. (CERPE); same data but 02.X.2013, Eliert, J. B; same data but 1♂, 07.IX.2013, Brustolin, C.; same data but, 02.XII.2013, Lourenço, L.; 2♀, Ponta Grossa (S 25°15', W 49°93'), 03.II.1965, Moses (MZUSP). 3♀, Rio de Janeiro, Itatiaia (S 22°40', W 44°69'), I.1969, Mielke (DZUP). 1♀, Rio Grande do Sul, Pelotas (S 31°76', W 52°32'), 11.II.1970, Mielke (DZUP). 1♂, Santa Catarina, New Bremen, XII.1937, B. Pohl (DZUP); 1♂, Três Barras (S 26°12', W 50°31'), 13.IX.1966, Pe. Moure & Mielke (DZUP).

Holotype description (Fig. 43A). **Length:** 25.0 mm. **Width:** 14.5 mm. **Color:** Nearly completely dark reddish-brown. **Head:** Clypeus subpentagonal, surface transversely rugose, glabrous; anterior corners with two conic teeth; lateral margins with obtuse, raised angles. Frontoclypeal suture without ornamentations. Frons strongly crenulated; interocular width equals 1.5 transverse eye diameters. Ocular canthus transverse, slightly arched, dorsoventrally setose. Labium triangular; basal half with subparallel sides, convergent on apical half; setae and punctures confined to sides, disc convex, smooth. Mandibles tridentate; apical and medial teeth triangular, basal tooth lobed. **Thorax:** Pronotal surface densely covered with large and deep punctures near

margins, becoming finely punctate toward disk; anterior marginal area with a small, conic tubercle; concavity shallow, rounded, confined to anterior area; concavity covered with large, C-shaped punctures, coalescent on tubercle basis. Elytral surface nearly smooth, with barely marked striae; discal area finely, irregularly punctate; lateral area below humerus with 4 incomplete rows of large punctures. Mesoventrite finely punctate, densely setose. Metaventricle rugopunctate on sides, punctate on disc, completely setose. Scutellar plate triangular. **Legs:** Protibiae tridentate; teeth acute on apex. Mesotibiae with two carinae on outer surface (1 basal, 1 medial); basal carina transversely short, medial carinae diagonally long; apical margin sinuous. Metatibiae with basal carina interrupted at middle, apex truncate. **Abdomen:** Tergite VII with stridulatory apparatus formed by one central band of continuous, transversal carinae, well-marked near to anterior margin, finely marked toward posterior margin (Fig. 43C). Tergite VIII convex in lateral view; surface with rugopunctate, setose sides; disc punctate, punctures oval shaped. Ventriles I–VI with setose, rugopunctate sides; disc glabrous, finely punctate.

Paratypes variation. Length: 25.0–21.0 mm. **Width:** 14.0–12.0 mm. **Color:** Nearly completely dark reddish. **Head:** Frontoclypeal suture sometimes with two weak tubercles. Maxilla with 5 (2 apical, 2 medial, 1 basal) or 6 teeth on galea (2 apical, 2 medial, 2 basal). **Legs:** Meso- and metatibiae with basal carina sometimes absent. **Spiculum Gastrale (Fig. 43D):** Y-shaped, slender, with basal sclerite transverse, barely evident, with few short setae. **Aedeagus (Fig. 43 E–G):** Parameres in caudal view (Fig. 43E), oval shaped, with sinuous outer sides, basal half slightly excavated on sides. Parameres in ventral view (Fig. 43F), apical half broad. Parameres in lateral view (Fig. 43G), apex curved downward. Female paratypes differs in the following aspects: **Length:** 26.0–24.2 mm. **Width:** 15.8–14.0 mm. **Thorax:** Pronotal surface completely, densely punctate. **Legs:** Protibial teeth wider compared to male. **Abdomen:** Ventricle VI triangular. Tergite

VIII weakly convex in lateral view; invaginated plate deeply emarginate. **Genitalia:** Coxite parabolic in shape, bordered with long setae; disc slightly concave, with scarcely scattered setae; inner margins slightly constricted. Subcoxite rhomboid shaped, scarcely covered with setae.

Geographic distribution. Brazil (Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina) (Fig. 55A).

***Bothynus complanus* species-group (Burmeister, 1847)**

The *Bothynus complanus* species group (Burmeister, 1847) distinguishes from other species groups by the following characters: Frontoclypeal area with a central, conic shaped tubercle; tridentate mandibles, with all teeth triangular shaped and pointed at apex; quadridentate protibiae. Belong to *B. complanus* species group only two species: *B. complanus* and *B. quadridens*. These species are unique in the genus with widespread Neotropical distribution, occurring from north of South America to Mexico.

***Bothynus complanus* (Burmeister, 1847) (Fig. 44A–G; Fig. 52F; Fig. 56)**

Podalgus complanus Burmeister 1847, p. 123 (original description)

Bothynus complanus, Arrow 1937, p. 40

Bothynus simplicitarsis Bates 1888, p. 319 (original description)

Bothynus simplicitarsis ab. *lineatus*, Endrödi 1959, p. 122 (description)

Bothynus monstrosus Bates 1888, p. 320 (original description)

Bothynus monstrosus, Arrow 1911, p. 156 (synonymized with *B. simplicitarsis*)

Diagnosis. *Bothynus complanus* differs from *B. quadridens* in the following characters: In male, inner protarsal claw lacking ventromedial tooth (Fig. 44C), medial branch of spiculum gastrale with broad apex and with wide and oval shaped basal sclerite (Fig. 44E), parameres elongated (Fig. 44F); in both sexes, stridulatory apparatus with well-marked carinae near to anterior margin of tergite VII (Fig. 44D).

Remarks. The high similarity between females of *B. complanus* and *B. quadridens* difficult its diagnosis. While the males of both species can be distinguished by characters of the anterior inner claw, spiculum gastrale and parameres, females do not have own diagnostic characters and its distinction is conditioned to association with the males. However, observations of tergite VII evidenced a distinct stridulatory apparatus for both species, allowed the female distinction without a comparison with the male. Both sexes of *B. complanus* exhibit a well impressed stridulatory apparatus on the anterior area of tergite VII, while both sexes of *B. quadridens* have the barely impressed carinae.

Type material.

Lectotype. *Podalgus complanus* (not examined).

Syntype (Fig. 52F). *Bothynus simplicitarsis*, male, at MNHN, with the following labels: Coban Vera Paz Conradt. [beige, printed in black]/*Bothynus simplicitarsis* Bates ♂ [beige, handwritten]/♂ [beige, handwritten]/H.W.Bates Biol.Cent.Amer. [beige with dark margins, printed in black] SYNTYPE [red, printed in black]/ SYNTYPE *Bothynus simplicitarsis* Bates, 1888 [white, printed in black]/ *Bothynus complanus* (Burmeister, 1847) det F. Dupuis 2013 [white com black margins, printed in black]/ MNHN EC7104 [white, printed in black].

Type. *Bothynus monstrosus* (not examined)

Holotype. *Bothynus complanus* ab. *lineatus* (not examined)

Additional material examined. MEXICO: Guerrero, Zoyatepec, 20.Vii.1963 – 1♂ (CERPE). Oaxaca, Ejutla (16°33'16'' N, 96°43'45''W), 1450 m, 06.xi.2005 – 1♂ 1♀ (CEMT); Oaxaca, Pluma Hidalgo (15°52'45''N, 96°23'58''W), 02.xi.2005, Abundis, Carrillo & Vaz-de-Mello – 17♂ 21♀ (CEMT). Vera Cruz, Est. Bio. Tropical Los Tuxhas, vii.2006, S. Arreguita, A. Diaz & R. Sorges – 3♂ (CEMT). PANAMA: no data – 1♂ (CERPE). VENEZUELA: Táchira, Gallardin, 01–15.v.1994, Jofre Blanco – 1♀ (CERPE).

Male redescription (Fig. 44A). **Length:** 27.49–30.58 mm. **Width:** 14.82–17.7 mm. **Color:** Dorsal surface completely dark; ventral surface dark reddish brown. **Head:** Clypeal surface coarsely rugopunctate, glabrous, sometimes with scarce, short setae; anterior margins with two conic, raised pointed teeth. Frontoclypeal suture with a central, conic tubercle; tubercle from pointed to rounded on apex. Frons from flattened to slightly concave; surface coarsely rugopunctate, moderately setose. Ocular canthus subquadrate with short setae confined at outer side. **Mouthparts:** Mandibles tridentate; teeth triangular shaped; medial tooth longer than apical and basal teeth; basal tooth smaller than previous ones. Mentum subtriangular, flattened, densely setose at sides, glabrous or scarcely setose on disc. **Thorax:** Pronotal area near margin with a small tubercle raised under a transverse edge; anterior middle area with a rounded concavity, sometimes with an inconspicuous on the limit of posterior area; concavity rugopunctate or with large, coalescent punctures; anterior and posterior areas densely covered with large, deep, coalescent punctures, becoming from moderately to finely punctate on disc. Scutellar plate parabolic in shape, usually transverse (about two times wider than long). Elytral surface with barely marked striae; discal area finely punctate; anterolateral area weakly punctate, posterolateral

area densely punctate. **Legs:** Protibiae quadridentate, teeth pointed apically. Inner protarsal claws simple, similar to outer claw. Meso- and metabiae with two carinae diagonally projected on external surface; apex strongly emarginate on outer surface. **Abdomen:** Ventrites I–VI rugopunctate on sides, becoming from weakly punctate to smooth on disc. Ventrites I–II nearly entirely setose; III–IV setose on sides, glabrous on disc; V transversely covered with a row of setae; VI covered with a row of setae transversely scattered on posterior margin. Tergite VII with stridulatory apparatus confined on disc (Fig. 44C); stridulatory apparatus formed by numerous transverse rows of well-marked carinae; anterior carinae more prominent and sparser than posterior carinae. Tergite VIII strongly rugopunctate on sides, discal area covered with oval shaped punctures only; surface moderately setose on sides and in transverse rows near to anterior area. **Spiculum gastrale (Fig. 44E):** Y-shaped, with medial branch oval shaped at apex; basal plate with two broad, oval shaped plates, covered with setae on apical margin. **Aedeagus (Fig. 44F–G):** Parameres in caudal view (Fig 44F), elongated, symmetric, with parallel sides on basal half, abruptly constricted on apical half; apex with wide, transverse sides. Parameres in lateral view (Fig. 44G), lateroventral margins usually with a small basal tooth.

Female redescription (Fig. 44B). Similar to male, except by the following aspects. **Length:** 27.63 –31.21 mm. **Width:** 14.32 –17.75. **Legs:** Protibial teeth with rounded apex. **Abdomen:** Ventricle VI triangular shaped, densely setose. Tergite VIII flattened in lateral view, densely setose compared to males.

Geographic distribution. México (Guerrero, Oaxaca, Vera Cruz), Panama, Venezuela (Táchira) (Fig. 56).

***Bothynus quadridens* (Taschenberg, 1870) (Fig. 45A–G; Fig. 56)**

Corynoscelis quadridens Taschenberg 1870, p. 185 (original description)

Bothynus quadridens, Bates 1888, p. 319

Type material. Not examined.

Additional material examined. BRASIL: ACRE, Rio Branco, 02.vii.1995, S.F. Silva & A.W.F. Melo – 1♂ (CERPE); Rio Branco, 09.vii.1995, T.G. Vogel – 1♂ 1♀ (CERPE); Rio Branco, 25.iii.1996, R.C.B. Lima – 1♂ (CERPE). MATO GROSSO: Cotriguaçu, Fazenda São Nicolau, III.2008, O. Perez Filho 2♂ 2♀ (CEMT). PARÁ: Belém, Embrapa, v.2007, Mauro – 1♀ (CERPE); Dom Eliseu, 8.ii.2007, Reginaldo – 1♂ 2♀ (CPATU); Pau D’arco, 06.ii.2007, Reginaldo – 2♂ 2♀ (CPATU); Serra Norte, Rio Salobo, 19.iii.1984 – 1♂ (MPEG); Serra Norte, 19.iii.1986 – 1♂ (MPEG); Serra Norte, N1, 25.ii.1984, L.B. Albuquerque 1♂ (MPEG). VENEZUELA: Aragua, Cuyagua, vii.2005, Daniel G. Fagre – 1♀ (CERPE); Táchira, Gallardin, iv.1992, J. Blanco – ♂ (CERPE).

Diagnosis. *Bothynus quadridens* differs from *B. complanus* by the following characters: In male, inner protarsal claw with a ventromedial tooth (Fig. 45A), medial branch of spiculum gastrale weakly oval at apex and with triangular shaped basal sclerite (Fig. 45E), parameres wide (Fig. 45F); in both sexes, stridulatory apparatus with barely marked carinae VII (Fig. 45D).

Remarks. *Bothynus quadridens* is recorded for the first time in Brazil, expanded their distribution area in South America.

Male redescription (Fig. 45A). **Length:** 24.92–29.21 mm. **Width:** 14.39–15.92 mm. **Color:** Dorsal surface dark; ventral surface reddish brown. **Head:** Clypeal surface coarsely rugopunctate, from scarcely to moderately setose; sides narrowed to a bidentate anterior margin; teeth raised, conic. Frontoclypeal suture with strong, pointed, conical shaped tubercle. Frons usually concave, sometimes weakly flattened; surface strongly rugopunctate, weakly setose. **Mouthparts:** Mandibles tridentate, teeth triangular. Maxilla with five teeth at apex; basal tooth smaller than previous ones. Mentum subtriangular; ventral surface flattened, densely covered with long setae on sides. **Thorax:** Pronotal concavity oval shaped, with a small tubercle at middle of posterior area. Surface strongly rugopunctate on anterior area and on concavity; posterior area rugopunctate near to lateral margins, becoming from moderately to finely punctate toward disc. Scutellar plate transverse, from subtriangular to parabolic in shape. Elytral surface with barely marked striae; disc finely punctate; anterolateral area with moderate punctures, becoming fine toward the posterolateral area; posterolateral area densely punctate near margins. **Legs:** Inner protarsal claw with a pointed ventromedial tooth. **Abdomen:** Tergite VII with stridulatory apparatus formed by innumerable transverse rows of barely marked carinae (Fig. 45D). Tergite VIII strongly rugose on sides and on an area near to anterior margin, disc weakly punctate; surface densely setose at sides, weakly setose on disc. Ventrites I–V strongly rugopunctate on sides, becoming from moderate to finely punctate on disc; VI moderately punctate; ventrites I–II completely setose; III–V setose on sides, glabrous on disc; VI covered with setae on posterior margin. **Spiculum gastrale (Fig. 45E):** Y-shaped, medial branch slightly oval at apex; basal sclerite separated in two subtriangular, diagonally directed sclerites; each sclerite with a row of long setae at apex. **Aedeagus (Fig. 45F–G):** Parameres in caudal view (Fig. 45F), symmetric, basal half with rounded sides, gradually constricted toward to apical half, apex wide. Parameres in lateral view (Fig. 45G), lateroventral margins usually with a small, basal tooth.

Female redescription (Fig. 45B). Similar to male, except in following aspects. **Length:** 27.62–32.41 mm. **Width:** 15.04–18.53 mm. **Legs:** Protibial teeth rounded at apex; inner protarsal claw with no ventromedial tooth, rarely with a weakly lobed tooth. **Abdomen:** Ventrite VI triangular shaped. Tergite VIII flattened in lateral view.

Geographic distribution. Brazil (Acre, Mato Grosso, Pará), Venezuela (Aragua, Táchira) (Fig. 56).

***Bothynus villiersi* Endrödi, 1968 species-group**

Four species are known in the *B. villiersi* group: *B. villiersi*, *B. alvarengai*, *B. horridus*, and *B. belenensis* sp. nov. This group differ from other species group in *Bothynus* by the following aspects: Clypeus obliquely deflexed in lateral view; frontoclypeal suture with a complete transverse ridge (reaching the lateral margins); mentum with a conic process; mesotibial discal apex completely covered with spinules; parameres asymmetric.

***Bothynus villiersi* Endrödi, 1968 (Fig. 46A–D; Fig. 57)**

Bothynus villiersi Endrödi 1968, p. 170 (original description)

Diagnosis. *Bothynus villiersi* differ from other species of the group by the characteristics of male genitalia only: parameres elongated and oval shaped, where each paramere has a middle process on the inner edge (Fig. 46C–D).

Remarks. Due to lack of available material, it was not possible to evaluate female specimens, these must be recognized only in association with males. Information from the label data examined here along with literature data suggest that *B. villiersi* has been collected almost exclusively in open field areas. In faunistic survey of Grossi *et al.* (2011), the species was collected in an area named “Campos Gerais”, Paraná state, Brazil, characterized by an open field landscape, phytophysiognomically marked by herbaceous and subarbustive vegetation. Instituto Florestal (2015) also recorded the occurrence of *B. villiersi* in a confluence area between Cerrado and Atlantic Forest in Mogi Guaçu, São Paulo state, Brazil. Endrödi (1968) designated two paratypes with locality data from two states: one from Goiás, other from Mato Grosso. Both states are inserted in central Brazil, where Cerrado biome is predominant. Endrödi (1968) also designated one paratype with locality data from Pará state, northern Brazil. However, it may be a mislabeled record, as it is inserted in Amazon Biome, known to be a dense forest.

Type material. Not examined.

Additional material examined. BRASIL: MATO GROSSO DO SUL: Dourados, 15.ii.2006, K.V. Filho leg. – 1♂ (CERPE); xi. 2002, E. Gelain leg. – 1♂ (CERPE). PARANÁ: Jaguariaíva, Parque Estadual do Cerrado, v.2011, 870 m, C.S. Costa & Equipe legs. – 2♂ (CERPE). SÃO PAULO: Bauru, Instituto APA, vargem limpa, 10.x.2008, luz, L. Santos leg. – 1♂ (CERPE).

Male redescription (Fig. 46A). **Length:** 25.1–16.62 mm. **Width:** 12.69–7.56. **Color:** Nearly completely reddish brown. **Head:** Clypeus subtriangular, obliquely deflexed in lateral view, surface transversely rugose, with setae confined to lateral borders; anterior margin bidentate. Frontoclypeal suture with a transverse, strongly raised ridge, reaching the lateral margins. Frontal

surface transversely rugose, glabrous, slightly concave; interocular width equals 3.48 times transverse eye diameters. Ocular canthus subtriangular, covered with erect setae on outer sides. **Antennae:** Ten-segmented. **Mouthparts:** Mandibles tridentate, teeth exposed laterally to clypeus; apical and medial teeth triangular, basal lobed. Maxillary galea with a small apical tooth. Maxillary palpomere I two times shorter than II, hidden under the lateral stipe; palpomere IV clavated. Labium subtriangular, sinuous laterally; discal area with a conic process; surface covered by long setae on sides. **Thorax:** Pronotum with a small, conic tubercle near to middle of anterior margin; anterior area concave in dorsal view, posterior area convex in lateral view; pronotal surface densely punctate on sides, transversely rugopunctate on concavity, smooth on disc. Elytral surface with 9 longitudinal striae (1 sutural, 4 discal, 4 lateral); last lateral stria barely marked, other striae well-marked; striae covered by a row of ocellated punctures, nearly reaching to posterior margin; sutural punctures spaced less than one diameters of punctures; other striae with punctures spaced about one diameter of punctures; interstriae irregularly punctate. Scutellar plate triangular, smooth. Meso- and metaventrite moderately covered by yellowish setae. **Legs:** Protibiae tridentate; basal outer margins sinuous; inner protarsal claw shorter than outer claw, abruptly curve at apex (Fig. 46.B). Mesotibial external surface usually with two carinae (one basal, one medial) diagonally projected, ornamented with spinules; apical discal surface nearly completely covered with spinules. Metatibiae triangular, with two external carinae (one basal, one medial); distal surface with spinules confined to margin. **Abdomen:** Tergite VII with discal stridulatory apparatus formed by two paired rows of carinae barely impressed. Tergite VIII strongly convex in lateral view; surface glabrous, striated on sides and on area near to anterior margin, disc weakly punctate. Ventrites I–II covered by irregularly scattered setae, reaching to discal area; III–V with strong punctures and a row of setae confined to sides, disc finely punctate; VI covered with setae on posterior margin, sides weakly punctate, disc smooth. **Aedeagus (Fig.**

46C–D): Parameres, in caudal view (Fig. 46C), asymmetric, oval shaped in overall aspect (1.51 times longer than wide); apex elongated, outer edge with a lateroventral process on each paramere; inner edge with a middle process on each paramere; right paramere with process two times longer in size as those of left paramere. Parameres in lateral view (Fig. 46D), with apex bent downward.

Female redescription. Not examined.

Geographic distribution. Brazil (Mato Grosso do Sul, Paraná, São Paulo) (Fig. 57).

***Bothynus horridus* Endrödi, 1968 (Fig. 47A–G; Fig. 57)**

Bothynus horridus Endrödi 1968, p. 171

Diagnosis. *Bothynus horridus* differ from other species of the group by the following combination of characters: in male, right paramere with a long basal process on the inner edge, left paramere with no process (Fig. 47D), spiculum gastrale with nearly straight lateral branches (nearly as longer as the medial branch) (Fig. 47C); in female, subcoxite oval shaped, invaginate plate of tergite VIII large and deeply emarginate (Fig. 47F).

Remarks. *Bothynus horridus* has the most widespread distribution among species of the group, with records from Argentina, Brazil, and Paraguay (Endrödi 1969, 1985). The locality data of material examined by us suggest that *B. horridus* occurs associated with Brazilian areas of Cerrado and Atlantic Forest. There are also two scattered records from northern Brazil (Ratcliffe & Dechambre 1983): one from Vilhena (Rondônia state), one from Belém (Pará State). These

records make sense only in the first case, because “Vilhena” is located adjacent to a large occurrence area of *B. horridus* from central Brazil, however, in the second case, it may be a mislabeled record because “Belém” is located in northern Brazilian Amazon, widely separated from the occurrence areas of *B. horridus*.

Type material. Not examined.

Additional material examined. BRASIL: DISTRITO FEDERAL: Planaltina, Embrapa Cerrados, Área Agrícola (15°35'54" S, 47°42'51" W), 18.xi.2005, luz, C. Oliveira leg. – 1♀ (CEMT); fragmento de cerrado (15°36'20" S, 47°42'26" W), 20.x.2005, luz, C. Oliveira – 1♂ (CEMT). MARANHÃO: Balsas, Serra dos Penitentes, 480 m, 30.xi.2005, C.G.C. Mielke leg. – 1♂ (EPGC). MATO GROSSO: Acorizal, 09.iv.2016, Mariani. L. leg. – 1♀ (CEMT). Araputanga, área rural, 02.iv.2015, Duarte, L.V. leg. – 1♂(CEMT). Barra das Garças, Faz. São Carlos (15°37'54" S, 52°09'42" W), 19.xi.2009, M. Aragona leg. – 1♀ 1♂ (CEMT). Chapada dos Guimarães, 05.x.2008 – 1♂ (CERPE); Parque Nacional da Chapada dos Guimarães, Vale do Eco, 17.i.2013, luz, M. Savaris & S. Lampert legs. – 1♂ (CERPE); Buriti, 6.x.1984, Dal Ponte leg. – 1♂(CERPE). Cotriguaçu, Fazenda São Nicolau, luz, xi.2007, O.P. Filho leg. – 1♂ (CEMT); i.2008, luz, O.P. Filho leg. – 1♀ (CEMT). Cuiabá, 28.x.2015, Zulli. G.A leg. – 1♂ (CEMT). C. Verde, 4.xii.2008, Vieira. M.M leg. – 1♂ (CEMT). Diamantino, Fazenda Vale da Solidão, x.2013, E. Furtado leg. – 4♂ 1♀ (CERPE); xi.2013, E. Furtado leg. – 3♀ (CERPE). Alto Rio Arinos, ix.1999, E. Furtado leg. – 1♂ (CERPE). Itanhangá, 26-29.x.2016, coleta manual, J.V. Korgut leg. – 1♂ 3♀ (CEMT). Nobres, Distrito Coqueiral, 26.vi.2010, manual, Danielle N. leg. – 1♀ (CERPE). Paranatinga, Aldeia Paikun, Manual, 11.xi.2011, O. Neto leg. – 1♂ (CERPE). P. Estrela, 24.ii.2016, Rodriguez. E.L. leg. – 1♂ (CEMT). Sapezal, 14.ii.2004, E.J. Godoi leg. – 1♀

(CEMT). Sorriso, 01.v.2003, E.P. Carboni leg. – 1♀ (CEMT). MINAS GERAIS: Belo Horizonte, x.1945 – 1♂ (CERPE); xi.1945 – 1♀ (CERPE); xii.1945 – 1♀ (CERPE). Buritis, Fazenda Querência, 03.xii.2012, luz, C.M. Oliveira leg. – 2♂ (CEMT). Ibitité, 872 m, 2-15.i.1992, A. Machado leg. – 1♂ (EPGC). Lavras, 25.iii.205, Reis. T.H.P leg. – 1♂ (CERPE); 23.ii.1999, Biasioli. G.M. leg. – 1♂ (CERPE). Tartaria, 29.x.1934, Jefferson R. leg. – 1♂ (CECL). RIO DE JANEIRO: Resende, xi.1931, Aristóteles S. leg. – 1♂ (CECL). Teresópolis, Morim, Morro da Bandeira, 1600, Torre da Petrobras, 02-10.ii.2010 – 1♂ (CERPE). SÃO PAULO: Natividade da Serra, Parque estadual Serra do Mar, Núcleo Santa Virgínia, Base Vargem Grande (23°43'76" S, 45°24'43" W), 792 m, 28.iii.2016, D.B. Muniz leg. – 1♂ (CERPE). Santo Amaro, 1938, Zikan leg. – 1♂ (IBSP).

Male redescription (Fig. 47A). **Length:** 23.7–17.09 mm. **Width:** 13.7–9.64 mm. **Color:** Head, pronotum, pro-, meso-, and metatibiae dark reddish brown; pro-, meso- and metatarsomeres dark; elytra and venter reddish brown. **Head:** Clypeus subtriangular, bidentate anteriorly; surface glabrous, rugopunctate. Frontoclypeal suture formed by a complete transverse ridge, usually convergent at middle. Interocular width equals 3.61 transverse eye diameters. Frons transversely rugose, glabrous. Ocular canthus transverse, subtriangular. **Mouthparts:** Mandibles tridentate; apical and medial teeth triangular, basal lobed. Maxillary with a small tooth at apex. Labium with a central, conic process; surface with deep, setose punctures laterally. Labrum arched, apical margin sometimes with a tooth on right side. **Thorax:** Pronotum with a middle tubercle near to anterior margin; tubercle conic shaped, moderated in size; anterior area usually with a deep concavity; posterior area strongly convex in lateral view; surface densely punctate on sides, transversely rugose on concavity, finely punctate on disc. Elytra with 9 striae (1 sutural, 4 discal, 4 lateral); interstriae II and IV smooth, others interstriae punctate; each stria with a row of

moderated, ocellate punctures, spaced about one diameter of punctures; interstriae irregularly punctate. Scutellar plate triangular, usually smooth. **Legs:** Protibiae tridentate; inner protarsal claw wider and curve than outer claw. Mesotibiae with two diagonal carinae (one basal, one medial) on external surface; discal apical surface with a small process. Metatibiae triangular, wide at apex. **Abdomen:** Tergite VII with stridulatory apparatus formed by two paired rows of finely marked carinae. Tergite VIII convex in lateral view; surface glabrous, rugose on sides and an area near to anterior margin, disc finely punctate. Ventrites I–II rugose, completely setose; III–V rugose on sides, with an incomplete row of setae, disc smooth; VI emarginated posteriorly at middle, bordered with setae, disc smooth. **Spiculum gastrale (Fig. 47C):** Y-shaped; branches substraight, subequals in length; basal sclerite from vestigial to absent. **Aedeagus (Fig. 47 D–E):** Parameres in caudal view (Fig. 47D), asymmetric, rounded shaped in overall aspect (about 1.06 times longer than wide); apex short, separated by a V-shaped emargination; inner edge of right paramere with a basal, long and recurved process; inner edge of left paramere with no process. Parameres in lateral view (Fig. 47E), bent downward ventroapically and bent upward dorsoapically.

Female redescription (Fig. 47B). Similar to male, except in the following aspects: **Length:** 23.1–21.4 mm **Width:** 12.5–11.75 mm. **Thorax:** Pronotum weakly convex in lateral view; tubercle and concavity absents; anterior middle area moderately punctate, punctures spaced about three diameters of punctures; surface from anterolateral to lateroposterior areas covered with large, dense punctures, coalescent near margins, becoming spaced less than one diameter of punctures toward disc; disc smooth. **Legs:** Protarsal inner claw subequals. **Abdomen:** Tergite VIII weakly convex in lateral view, surface completely rugose; posterior margin with a large, deeply emarginate invaginated plate (Fig. 47F). Ventrite VI triangular, densely rugopunctate. **Genitalia**

(Fig. 47G): Coxite arched, covered with irregularly scattered setae. Subcoxite oval in shape, transverse, ventral area with setae irregularly scattered near to inner margin.

Geographic distribution. Brazil (Distrito Federal, Maranhão, Mato Grosso, Minas Gerais, Rio de Janeiro, São Paulo (Fig. 57A).

***Bothynus alvarengai* Martinez, 1983 (Fig. 48 A–H; Fig. 52G; Fig. 57)**

Bothynus alvarengai Martinez 1983, p. 297

Diagnosis. *Bothynus alvarengai* differ from other species of the group by the following combination of characters: in male, pronotal tubercle subtrapezoidal shaped (truncated or bilobate apex) in frontal view (Fig. 48C), spiculum gastrale with all branches subequals in length and lateral branches upward recurved (Fig. 48D), parameres with rounded apex in lateral view (Fig. 48F); in female, invaginate plate of tergite VIII with a short and broad posterior emargination (Fig. 48G), subcoxite rhomboid-shaped (Fig. 48H).

Remarks. Until then, *B. alvarengai* is a species whose distribution was known only for its type locality: Encruzilhada, Bahia state (Martínez 1983). However, this species has its distribution expanded with two new state records: Maranhão and Minas Gerais. *Bothynus alvarengai* is related to an area known as “mata seca” from northeast Brazil. The “mata seca” is a dry forest characterized by vegetation adapted to low precipitation, losing more than 50% of their leaves during dry season, featuring a peculiar physiognomy reflecting under a particular fauna associated to it (Espírito Santo *et al.* 2008).

Type material.

Holotype (Fig. 52E). *Bothynus alvarengai*, male, at MACN, with the following labels: Encruzilhada Bahia Brazil XII.1980 [white, printed in black]/ A. Martinez e M. Alvarenga [white, printed in black]/ HOLOTYPUS [orange, printed in black]/ *Bothynus alvarengai* sp. nov. ♂ A Martinez det. 1981 [red with black margins, partially handwritten]/ MACN-En 801 [blue with black margins, printed in black]

Additional material examined. BRASIL: BAHIA, Encruzilhada (15°32'25" S, 40°50'12" W), 800, 11.xii.2007, luz, Grossi, Rafael & Parizotto legs – 1♂ 1♀ (EPGC). MARANHÃO: Mirador, Parque Estadual do Mirador, Base de Geraldina, armadilha luminosa, 11–15.xi.2007, F. Limeira-de-Oliveira leg – 1♂ (CZMA); Posto Avançado do Mel (6°43'50" S, 44°58'59" W), armadilha luminosa, 02-08.iv.2011, F. Limeira-de-Oliveira, G.A. Reis & M.S. Oliveira legs – 1♂ 1♀ (CZMA). MINAS GERAIS: Águas Vermelhas, xii.1997, Vaz-de-Mello & Belo legs – 2♂ 1♀ (CERPE); Fazenda Faceiro, 12-16.xii.2012, luz, Everardo & Paschoal Grossi legs – 6♂ 13♀ (CERPE). Berizal, Fazenda Veredão (15°39'53" S, 41°39'56" W), 15.xi.2007, coleta manual, Grossi, Rafael & Parizotto legs – 1♂ (EPGC). São Gonçalo do Rio Preto, Parque Estadual do Rio Preto, 22.xii.2011, luz negra, Oliveira & Ferreira legs – 1♂ 1♀ (EPGC).

Male redescription (Fig. 48A). **Length:** 21.8–18.59 mm. **Width:** 11.5–9.5 mm. **Color:** Nearly completely reddish brown; pro-, meso and metatarsus dark; protibial outer margins dark. **Head:** Clypeus subtriangular, rugopunctate, glabrous, bidentate on anterior margin. Frontoclypeal suture with transverse and raised ridge, convergent at middle, reaching the lateral margins. Frontal surface strongly, transversely rugose, glabrous; interocular width equals 4.16 transverse eye diameters. Ocular canthus triangular, transverse, with short setae confined on outer sides.

Mouthparts: Mandibles tridentate; apical and medial teeth triangular, basal tooth lobed; apical tooth curved. Maxillae with lobed galea, sometimes with a small tooth at apex. Labium with sides slightly constricted at middle, strongly at apex. Labrum slightly arched, transverse. **Thorax:** Pronotum with a middle tubercle near to anterior margin, followed by a rounded and shallow concavity; tubercle subtrapezoidal shaped, usually truncated at apex, sometimes bilobed (Fig. 48C); concavity surface transversely striated on tubercle basis, posteriorly with large, transverse, C-shaped punctures; pronotal sides densely covered by large punctures; punctures coalescent near margins; disc finely punctate. Elytra with 9 striae (1sutural, 4 discal, 4 lateral); last lateral stria barely marked; each stria covered by a row of ocellated punctures, usually spaced less than one diameter of punctures; interstriae irregularly punctate. **Legs:** Protibiae tridentate; inner protarsal claw apically wider than outer claw. Mesotibiae with one basal and one medial carinae, diagonally projected on outer surface. Metatibiae usually bi-carinated, transversely projected on outer surface. Meso- and metatibia with carinae and apical disc covered with spinules. **Abdomen:** Tergite VII with stridulatory apparatus formed by two paired rows of carinae, well-marked near in anterior area, becoming barely marked posteriorly. Tergite VIII convex in lateral view; surface glabrous, strongly rugose on sides and an area near basis, disc finely punctate. Ventrites I–II rugopunctate, nearly completely covered by setae; III–V with setae and rugopunctures confined to sides, disc smooth; VI emarginate posteriorly, bordered with setae. **Spiculum gastrale (Fig. 48D):** Y-shaped; lateral branches recurved upward; medial branch longer than lateral branches. **Aedeagus (Fig. 48E–F):** Parameres in caudal view (Fig. 48E), asymmetric, rounded-shaped in overall aspect (about 1.22 times longer than wide); apex truncate, separated by a deep, U-shaped emargination; inner edge of right paramere with a long, curved basal process; inner edge of left paramere with a middle, small, from triangular to lobed process. In lateral view (Fig. 48F), apex rounded.

Female redescription (Fig. 48B). Similar to male, except in the following aspects: **Length:** 22.8–19.7 mm. **Width:** 11.5–9.6 mm. **Thorax:** Pronotal tubercle and concavity absent; surface near to anterior margin from moderately striated to densely punctate; punctures becoming large, C-shaped, spaced about two diameters of punctures toward posterior area; sides densely punctate, rugose near margins; disc finely punctate. **Legs:** Inner protarsal claw similar to outer claw. **Abdomen:** Tergite VIII weakly convex in lateral view; surface strongly rugose, covered with small setae, observed under high magnifications; invaginated plate short, broadly emarginate (Fig. 48G). Ventrite VI triangular, completely rugopunctate, setose. **Genitalia (Fig. 48H):** Coxite arched, ventrally covered with setae. Subcoxite rhomboid in shape, ventral surface with setae confined near to inner area.

Geographic distribution. Brazil (Bahia, Maranhão, Minas Gerais) (Fig 57).

***Bothynus belenensis* Duarte, Grossi & Parizotto sp. nov. (Fig. 49A–H; Fig. 57)**

Diagnosis. *Bothynus belenensis* sp. nov. differ from other species of the group by the following characters: In both sexes, prosternal process with truncate apex (Fig. 49C); in male, medial branch of spiculum gastrale strongly spatulate and narrowed laterally near apex (Fig 49D), parameres with the inner left process triangular in caudal view (Fig. 49E) and visible in lateral view (Fig. 49F); in female, anterior pronotal margin sinuous (Fig. 49G), invaginated plate subtrapezoidal (Fig. 49H).

Remarks. This new species does not occur in sympatry with no other species of the group. *Bothynus belenensis* sp. nov. occurs in Amazon Rainforest areas, northward Brazil. There is a record of *B. horridus* from Belém (Pará state) according to new records from Neotropical Pentodontini in Ratcliffe and Dechambre (1983). However, this distributional information can be addressing the new species described here. Our suspicion is based on three evidence: 1) *B. horridus* is related to Brazilian areas of Cerrado (central region) and Atlantic Forest (southeast region); 2) morphological similarity among these two species may have led to a mislabeled identification; 3) labels with mislabeled distribution data.

Type material. Holotype male, dissected, labeled: “BRASIL: PARÁ: Belém, 1931, Benedicto Nogueira – 1♂ (CERPE)”. Paratypes: Two females, same data as holotype – 2♀ (CERPE); two males and one female with no data – 2♂ 1♀ (CERPE).

Etymology. The specific epithet “*belenensis*” is named after its type locality: Belém, capital of Pará (state), northern Brazil.

Holotype description (Fig. 49A). **Length:** 21.74 mm. **Width:** 11.22 mm. **Color:** Surface of head, pronotum, pro-, meso-, and metatibiae, along with pro, meso- and metatarsus dark reddish brown; other surfaces reddish brown. **Head:** Clypeus triangular, surface coarsely rugopunctate, glabrous; anterior margin with two conic teeth; setae confined to posterolateral border. Frontoclypeal suture with a transverse, complete ridge (reaching to lateral margins), convergent at middle. Frontal surface rugopunctate, glabrous. Interocular width equals 2.5 transverse eye diameter. Ocular canthus subtriangular, scarce erect setae confined at outer sides. **Mouthparts:** Mandibles tridentate; apical tooth triangular, curved; medial tooth triangular; basal tooth lobed. Labium

triangular, apex slightly narrowed on sides, disc with a conic shaped process. **Thorax:** Pronotal anterior margin with a conic tubercle at middle, followed by a concavity moderated in deep; surface densely punctate on sides, transversely striated on concavity, smooth on disc. Prosternal process truncated (Fig. 49C). Elytral surface with 9 striae (1sutural, 4 discal, 4 lateral); striae with a row of ocellated punctures; sutural stria with punctures spaced about one diameter of punctures; other striae with punctures spaced about two diameters of punctures; interstriae with irregularly scattered punctures. Scutellar plate triangular. **Legs:** Protibiae tridentate; apical tooth curved outward, medial and basal teeth triangular; basal outer margin sinuous. Meso- and metatibial outer surface with two carinae (one basal, one medial) diagonally projected. Metatibiae triangular shaped, expanded toward apex. **Abdomen:** Tergite VII with stridulatory apparatus confined at disc; stridulatory apparatus formed by two paired rows of carinae, well-marked near anteriorly, becoming barely marked posteriorly. Tergite VIII convex in lateral view; surface glabrous, rugopunctate on sides, punctate anteriorly, disc finely punctate. Ventrite I completely, densely setose; ventrites II–V setose on sides, smooth on disc; ventrite VI with posterior margin emarginate at middle, covered with setae. **Spiculum gastrale (Fig. 49D):** Y-shaped; lateral branches slightly curved; medial branch strongly spatulate in shaped, narrowing laterally near apex; medial branch wider than lateral branches. **Aedeagus (Fig. 49E–F):** Parameres in caudal view (Fig. 49E), asymmetric, rounded, 1.1 times longer than wide, short at apex, separated by a U-shaped emargination; inner edge of right paramere with a long and recurved basal process; inner edge of left paramere with a middle and triangular short process. In lateral view (Fig. 49F), left paramere with raised and visible middle process; apex curved downward

Paratypes variation. Males. Length: 23.9–20.5 mm. **Width:** 13.5–10.7 mm. **Thorax:** Pronotal concavity punctate; punctures oval shaped, large, spaced less than one dimeters of punctures,

sometimes coalescent. **Legs:** Inner protarsal claws shorter and wider than outer claws. **Female.** **Length:** 21.3–21.0 mm. **Width:** 11. 8–11.3. **Thorax:** Pronotal tubercle and concavity absent; anterior margin sinuous at middle (Fig. 49G); anterior middle area punctate. **Legs:** Inner protarsal claw similar to outer claw. **Abdomen:** Tergite VIII weakly convex in lateral view; surface rugopunctate, with small setae only observed under high magnifications; invaginated plate subtrapezoidal shape, large, weakly emarginate (Fig. 49H). Ventrite V punctate on disc; VI triangular, rugopunctate. **Genitalia:** Coxite arched, ventrally setose. Subcoxite oval shaped, with irregularly scattered setae on ventral area, confined near to inner margin.

Geographic distribution. Brazil: Pará (Fig. 57).

Species excluded from the genus *Bothynus*

Based on cladistic analysis of Chapter 2, two new combinations are proposed: *B. complexus* is moved to genus *Eremobothynus* and *B. herbivorus* is moved to *Cephaloplanum*, a new genus described here to allocate this species.

***Eremobothynus complexus* (Dechambre, 2006) comb. nov. (Fig. 50A–H; Fig. 58)**

Bothynus complexus Dechambre 2006, p. 229 (original description)

Diagnosis. *Eremobothynus complexus* com. nov. differs from other *Eremobothynus* species by the following characters: In both sexes (Fig. 50A–B), coloration dark, pronotal margin incomplete, elytral striae well-marked; in male, head tubercle flattened and bilobate at apex (Fig. 50D), inner

protarsal claw incised at apex (Fig. 50E), parameres asymmetric (Fig. 50F); in female, head with two small tubercles at frons (Fig. 50H).

Remarks. Dechambre (2006) described some characters for this species, which do not are congruent with the *Bothynus* definition, such as: clypeus with rounded anterior margins and antennae with 9 segments (bidentate anterior margin and antennae with 10 segments in *Bothynus*). Another character observed by Dechambre was the propygidium (=tergite VII) with stridulatory apparatus, however, this character is not present in this species and there are transverse punctures instead carinae. Previous phylogeny (see Chapter 2) recovered the species along with *Eremobothynus cornutus* in a sister clade of *Bothynus* formed by *B. herbivorus*, *Saccharoscapus laminifer* and *Philoscapus bonariensis*. *Eremobothynus complexus* was described based on a male specimen only, from southern Minas Gerais. Here, a population is recorded from northern Minas Gerais, in an area knowing as “mata seca”.

Type species. Not examined.

Additional material examined. BRASIL: MINAS GERAIS: Águas Vermelhas, Fazenda Faceiro, 14.xii.2001, luz, Grossi & Melo legs. – 4♂ (CERPE); Pto 05 km, 15.xii.2012, coleta manual, E. Grossi, P.C. Grossi, G.A.R Melo & J.A. Rafael legs – 1♂ (CERPE). Berizal, xii.2010. E. Abadie leg. – 1♀. Divisa Alegre, Área campo/cerrado, 12.xii.2012, E. Grossi, P.C. Grossi, G.A.R Melo & J.A. Rafael legs. – 3♂ (CERPE). Grão Mongol, 1-15.xii.2002, N. Anjos leg. – 2♂ 2♀ (EPGC).

Male redescription (Fig. 50A). **Length:** 19.5–15.3 mm. **Width:** 11.0– 9.0 mm. **Color:** Completely dark. **Head:** Clypeus subtrapezoidal, gradually constricted laterally to a truncate and raised anterior margin; surface finely punctate, scarce setae confined to sides, middle area glabrous, slightly concave. Frons with a tubercle (Fig. 50C), bilobate at apex (Fig. 50D), anterior and posterior tubercle surface scarcely setose; frontal area near eyes rugose, scarcely setose, finely punctate at middle, glabrous. Ocular canthus quadrate. **Mouthparts:** Mandibles with three, lobed teeth. Maxillae with three denticles at galea. Labium strongly convex, densely covered with deep, setose punctures. **Antennae:** Nine-segmented; club globular, short, subequal in length to antennomeres II–VI. **Thorax:** Pronotum strongly convex in lateral view, anterior middle area declivous, surface nearly completely covered with small punctures, posterior margin incomplete. Elytral surface finely punctate, longitudinally covered with 9 striae (1 sutural, 4 discal, 4 lateral), last lateral striae barely marked, other striae well-marked. Prosternal process short, confined bellow coxae. Metaventral surface moderately punctate and setose on sides; punctures shallow; discal area smooth. **Legs:** Inner protarsal weakly incised at apex (Fig. 50E). Meso- and metatibia with two carinae on outer surface (1 basal, 1 medial), medial carinae and apex crenulate. **Abdomen:** Tergite VII densely covered with transverse punctures. Tergite VIII strongly convex in lateral view, surface nearly completely finely punctate, rugopunctures confined to lateral corners. Ventrite I completely setose; ventrite II–IV with setae confined to sides; ventrite V with a complete row of setose punctures; ventrite VI smooth, with rugosity confined to corners. **Aedeagus (Fig. 50F–G):** Parameres in caudal view (Fig. 50F), asymmetric, basal half with rounded sides, apical half constricted lateroventrally, expanded laterodorsally. In lateral view (Fig. 50G), dorsal surface convex.

Female description (Fig. 50B). **Length:** 19.0–15.5 mm. **Width:** 11.1–9.0 mm. **Color:** Completely dark. **Head:** Clypeus subtrapezoidal, anterior margin truncate and raised, surface glabrous, densely covered with deep punctures. Frons convex in lateral view, with two small tubercles at middle (Fig. 50H), surface with large and coalescent punctures. Ocular canthus subquadrate. **Mouthparts:** Mandibles tridentate, teeth lobed. Labium usually convex, sometimes nearly flattened. **Antennae:** Nine-segmented. **Thorax:** Pronotum weakly convex in lateral view, anterior area moderately punctate, disc finely punctate. Elytral surface with nine deep longitudinal striae, interstriae finely punctate. **Legs:** Inner protarsal claw simple, similar to outer claw. **Abdomen:** Tergite VIII rugopunctate on sides, weakly punctate on disc. Ventricle VI triangular, rugopunctate on sides, weakly punctate on disc.

Distribution. Brazil (Minas Gerais) (Fig. 58)

***Cephaloplanum* Duarte, Grossi and Parizotto gen. nov.**

Type-species. *Ligyris herbivorus* Arrow, 1937, here designated.

Diagnosis. *Cephaloplanum* gen. nov. differ from other Neotropical genera of Pentodontini by the following combination of characters: Head with flattened dorsal surface (without tubercles, horns or carinae) (Fig. 51B), clypeus with bidentate anterior margin and with a deflexed tooth on the lateroposterior margin (Fig. 51C), antennae 10-segmented, protarsal claws simple, protibiae tridentate, meso- and metatibiae bidentate at apex and without spinules (Fig. 51E-51D), tergite VII without stridulatory apparatus.

Remarks. The type species was originally described by Arrow (1937b) in the genus *Ligyris* Burmeister, 1847 and posteriorly transferred to *Bothynus* by Endrödi (1969), where the author justified the transference based on a characteristic of pygidium (=tergite VIII emarginate anteriorly) as more related to *Bothynus*, besides this, also described the presence of stridulatory apparatus as “innumerable transverse ridges”. However, was observed by us that the “transverse ridges” are narrow and transverse punctures arranged on tergite VII, not configured a true stridulatory apparatus. The true stridulatory apparatus in *Bothynus* is formed by innumerable paired carinae arranged on tergite VII, being one of the characters that defined the genus. *Cephaloplanum* gen. nov. has a set of characters that are incongruent with *Bothynus* and *Ligyris* (=Tomarus) as the absence of frontoclypeal ridge or tubercle, presence of a deflexed tooth on each side of clypeal posterior margin, meso- and metatibial apex dentate and devoid of spinules, tergite VII without stridulatory apparatus.

Etymology. *Cephaloplanum* is the name given by the combination of the Greek word *kephale* and Latin word *planus*, in reference to dorsal surface of head without ornamentation: carinae, horns, or tubercles.

Description. **Length:** 17.1–16.2 mm. **Width:** 9.2–9.0 mm. **Color:** Nearly completely reddish brown, sometimes dark reddish brown on pronotum. **Head (Fig. 51B–C):** Dorsal surface flattened, without horns, tubercles or carina (Fig. 51B). Clypeus subtrapezoidal, bidentate on posterior margin, posterior lateral margins with a deflexed tooth in lateral view (Fig. 51C). Ocular canthus transverse, subrectangular, glabrous. **Mouthparts:** Mandibles tridentate, exposed laterally to clypeus; teeth triangular shaped. Maxillae with 4 teeth at galea; teeth increased in size toward apex; apical tooth curved. Labium triangular shaped, surrounded with long setae. **Antennae:** Ten-

segmented; club subequal in length to antennomeres II–VII combined. **Thorax:** Pronotum with a transverse tubercle near to anterior margin, tubercle small; anterior middle area with rounded, shallow concavity; anterior corners densely punctate, sides and disc moderately punctate, concavity transversely rugose. Scutellar plate with a barely marked sulcus in V shaped. Elytral surface densely covered with large, deep, ocellated punctures, spaced less than one diameter of punctures. Prosternal process globular, short, confined below coxa. **Legs:** Protarsal claws simple. Protibiae tridentate. Mesotibiae with 2 crenulate carinae on external surface (1 basal, 1 medial), apex bidentate (Fig. 51D). Mesotarsomere I with an acute process at lateroexternal apex. Metatibiae glabrous apically (Fig. 51E), with two teeth separated by a broad emargination. **Abdomen:** Tergite VII densely covered with transverse, narrow punctures. Tergite VIII glabrous, densely rugopunctate on sides, moderately punctate on disc; punctures deep, oval shaped, ocellated. Ventricle II–VI with sides densely covered with large, deep, ocellated punctures, discal area smooth. **Aedeagus (Fig. 51F–G):** In caudal view (Fig. 51F), symmetric, elongated, apical half with lateroventral area hidden under dorsal surface. In lateral view (Fig. 51G), slightly flattened dorsoventrally, basal half backward projected.

***Cephaloplanum herbivorus* (Arrow, 1937) comb. nov. (Fig. 51A, E–F; Fig. 59)**

Ligyryus herbivorus Arrow 1937, p. 44 (original description)

Bothynus herbivorus, Endrödi 1969, p. 108 (new combination)

Bothynus perforatus Arrow 1937, p. 45 (original description)

Bothynus perforatus, Endrödi 1969, p. 108 (synonymized with *B. herbivorus*)

Diagnosis. In both sexes, dorsal surface of head without ornamentations (tubercles, carinae or horn), lateroposterior margins of clypeus with a deflexed tooth on each side, metatibial apex bidentate and with no spinules; in females, discal surface of tergite VIII with a hollow.

Type material.

Syntype (Fig. 52G). *Ligyris herbivorus*, male, at NHM, with the following labels: SYNTYPE [rounded, beige with blue margins, printed in black]/ Type [rounded, beige with red margins, printed in black]/ BR. GUIANA Georgetown Golfcourse Dec. 31, 1934 C. Willians [beige, handwritten]/ Pres. by Imp.Inst.Ent. B.M.1936-61. [beige, printed in black]/ *Ligyris herbivorus* type Arrow [beige, handwritten].

Type. *Bothynus perforatus*. Not examined.

Additional material examined. COLÔMBIA: CHOCÓ: Quibdó, Pacurita, x.2016. – 1♂ (CERPE). VENEZUELA: ARAGUA, Jabillal, sur le Caura Bolivar, vi.1999, P. Rouche leg. – 1♂ (EPGC)

Male redescription (Fig. 51A). **Length:** 17.1–16.2 mm. **Width:** 9.2–9.0 mm. **Color:** Usually nearly completely reddish brown. **Head (Fig. 51 B):** Subtrapezoidal shaped, transversely rugose, glabrous, with large and deep punctures confined to posterior area between eyes. Ocular canthus transverse, subrectangular, glabrous. **Mouthparts:** Mandibles tridentate; teeth, subequal in size, apical and medial teeth triangular, basal lobed on slightly triangular. Maxillae with quadridentate galea; apical tooth, slightly curve. Labium subtriangular, densely setose, densely punctate. **Thorax:** Pronotal tubercle subtrapezoidal, transverse, located near to anterior margin; concavity moderately deep, rounded, confined on middle of anterior area; surface densely punctate on

anterior corners, sides and disc moderately punctate. Elytra densely covered with large, deep, ocellated punctures, spaced less than one diameter of punctures, striae barely marked. **Legs:** Protarsomeres I–IV subequals in length, tarsomere V twice as long as tarsomere I. Meso- and metatibiae with outer surface strongly excavated on an area between medial carina and apex. Meso- and metatarsomeres I–IV gradually decreasing in length. **Abdomen:** Tergite VII with transverse, narrow punctures, denser on disc compared to sides. Tergite VIII slightly emarginate at basal margin. **Parameres (Fig. 51F–G):** In caudal view (Fig. 51F), elongated, basal half convergent at apex, apical half with two triangular outer teeth on each side (1 medial small, 1 apical broader) (Fig. 51G). In lateral view, apical tooth projected under the ventral surface.

Female. Redescription, according to Lopez-García *et al.* (2015). **Length:** 19.5–16.0 mm. **Width:** 12.0–8.0 mm. **Pronotum:** Anterior area only with a small prominence; concavity absent; surface with large to small deep punctures evenly dispersed. **Abdomen:** Tergite VIII with a few deep punctures evenly distributed; discal area with deep, wide longitudinal hollow (see Lopez-García *et al.* 2015, Fig. 15).

Geographic distribution. Colombia (Chocó), Venezuela (Aragua).

Adult identification key to the genus *Bothynus*

1. Clypeus subtriangular with sides weakly or gradually constricted toward anterior area; frontoclypeal suture with a transverse ridge (reaching or not the lateral margins). 2

- Clypeus subpentagonal, abruptly constricted on sides near to anterior area; frontoclypeal suture with tubercles instead transverse ridge. 22
- 2. Both sexes with incomplete frontoclypeal ridge (not reaching the lateral margins), flattened labium, maxillary galea with teeth, metatibial discal apex with spinules confined to margins; males with symmetric parameres. 3
- Both sexes with complete frontoclypeal ridge (reaching the lateral margins), labium with conic process at disc, maxillary galea with no tooth, metatibial discal apex covered with spinules; males with asymmetric parameres 19
- 3. Apical and medial mandibular teeth triangular, flattened and transversely projected on outer sides of mandibles. 4
- Apical and medial mandibular teeth conic, not flattened, projected on outer sides of mandibles. 13
- 4. Clypeal anterior margin with longitudinal projected teeth. 5
- Clypeal anterior margin with transverse projected teeth. 6
- 5. Pronotum in female with shallow concavity; metafemoral ventral surface with fine punctures on disc..... ***B. leidianae* Duarte, Grossi & Parizotto sp. nov.**

- Pronotum in female with deep concavity; metafemoral ventral surface with large punctures. Male unknown. ***B. moroni* Duarte, Grossi & Parizotto sp. nov.**
- 6. Oval shaped pronotal concavity 7
- Rounded shaped pronotal concavity. 8
- 7. Metatrochanter smooth, apical half of parameres constricted lateroventrally on outer sides. Female unknown. ***B. aydanus*. Duarte, Grossi & Parizotto sp. nov.**
- Metatrochanter punctate in both sexes, apical half of parameres parallel lateroventrally on outer sides. ***B. nyx* Ratcliffe.**
- 8. Elytral surface with well-marked striae in both sexes, elytral punctures from moderate to large; male with incised inner protarsal claw. 9
- Elytral surface nearly smooth in both sexes (barely marked striae and fine punctures); inner protarsal claw not incised in male, only with a small ventromedial lobe. ***B. laevipennis* Arrow.**
- 9. Pronotal discal area covered with large punctures in both sexes. 10
- Pronotal discal area finely punctate in both sexes. ***B. ascanius* (Kirby).**
- 10. Incised protarsal claw with inner tooth subequal to outer tooth in male; discal area of tergite VIII rugose. 11

- Incised protarsal claw with inner tooth subequal to outer tooth in male; discal area of tergite VIII punctate in female ***B. sebastiani* Duarte, Grossi & Parizotto sp. nov.**
- 11. Elytral surface with discal punctures spaced from one to two punctures of diameter in both sexes; pronotal concavity with large and coalescent punctures confined to anterior area in female. 12
- Elytral surface with contiguous punctures spaced less than one puncture diameter in both sexes; pronotal concavity completely covered with large and coalescent punctures in female. ***B. tamarae* Duarte, Grossi & Parizotto sp. nov.**
- 12. Both sexes with punctate scutellar plate; male with punctate pronotal posterior corners. ***B. cylindricus* arrow.**
- Both sexes with smooth scutellar plate; male with rugopunctate pronotal posterior corners. ***B. laticifex* Burmeister.**
- 13. Male head flattened in lateral view; from median to large species (more than 17 mm in length). 14
- Male head raised at frontoclypeal area in lateral view; small species (reaching the 15 mm in length) ***B. minor* Steinheil.**
- 14. . Elytral surface glabrous in both sexes. 15

- Elytral surface setose in both sexes. ***B. thrix* Hardy.**
- 15. Protarsomere V with a small ventroapical process in male; tergite VII setose in female.
.....
16
- Protarsomere V with no ventroapical process in male; tergite glabrous in female.
18
- 16. Both sexes with shiny integument; tergite VIII weakly setose in female (surface clearly visible).
17
- Both sexes with opaque integument; tergite VIII densely setose (surface poorly visible).
..... ***B. cribrarius***
(Fairmaire).
- 17. Parameres with narrow laterodorsal apex; tergite VIII with scarce setae irregularly scattered on entire surface in female. ***B. cyclops***
(Burmeister).
- Parameres with broad dorsolateral apex; tergite VIII with setae confined to an area to posterior margin in female. ***B. andrezus* Duarte, Grossi & Parizotto sp. nov.**
- 18. Mandibular teeth separated by a deep notch and pronotal posterior area strongly convex in lateral view in both sexes. ***B. deiphobus***
(Burmeister).
- Mandibular teeth separated by a shallow notch and pronotal posterior are weakly convex in lateral. ***B. striatellus***
(Fairmaire).

19. Prosternal process with acute apex in both sexes; female with arched pronotal anterior margin. 20
- Prosternal process with truncated apex in both sexes; female with sinuous pronotal anterior margin. ***B. belenensis* Duarte, Grossi & Parizotto sp. nov.**
20. Male with acute or rounded pronotal tubercle; female with oval shaped subcoxite. 21
- Male with truncated or bilobate pronotal tubercle; female with rhomboid shaped subcoxite. ***B. alvarengai* Martinez.**
21. In male, parameres rounded shaped, with one basal process at inner margin of right paramere; in female, tergite VIII with large and broadly emarginate invaginated plate. ***B. horridus* Endrödi.**
- In male, parameres oval shaped, with one middle process at inner margin of each paramere. ***B. villiersi* Endrödi.**
22. Quadridentate protibiae. 23
- Tridentate protibiae. 24
23. In male, inner protarsal claw with absent ventromedial tooth; stridulatory apparatus with well-marked carinae on tergite VIII in both sexes. ***B. complanus* (Burmeister).**

- In male, inner protarsal claw with ventromedial tooth; in both sexes, stridulatory apparatus with barely marked carinae on tergite VII. *B. quadridens* **(Taschenberg)**.
- 24. In both sexes, clypeus with two reflexed teeth, elytral posterior border incomplete 25
- In both sexes, clypeus with four reflexed teeth, elytral posterior border complete. *B. herteli* **Endrödi**.
- 25. In both sexes, prementum fused to mentum, metatibial inner spur with spatulate apex; in male, protarsomeres thickened. 26
- In both sexes, prementum not fused to mentum, metatibial inner spur acute at apex; in male, protarsomeres not thickened. 31
- 26. In male, protarsomere IV with elongated ventroapical area (nearly reaching apically the ventrobasal process of tarsomere V); in female, pronotal apical tubercle absent and vestigial concavity. 27
- In male, protarsomere IV with short ventroapical area (not reaching the ventrobasal process of tarsomere V); in female, pronotal tubercle and concavity clearly visible. 28
- 27. In both sexes, metatrochanter with rounded apex; parameres with nearly parallel outer sides. *B. stenelus* **(Burmeister)**.
- Metatrochanter with acute apex; parameres with outer sides constricted at middle; female unknow. *B. condacki* **Duarte & Grossi**.

28. In male, rounded hypomeron (not emarginate), pronotum with two horns or only with an anterior tubercle; in female, pronotal concavity with no coalescent punctures. 29
- In male, pronotum with three horns or three tubercles instead horns, hypomeron strongly emarginate; in female, concavity strongly covered with large and coalescent punctures. *B. tricornis* Arrow.
29. In male, pronotum with small anterior tubercle, metafemora with glabrous discal area ventrally; female known. 30
- In male, pronotal anterior tubercle horn shaped, metafemoral ventral surface completely setose. *B. lancifer* Dechambre.
30. In both sexes, stridulatory apparatus with well-marked carinae near to anterior margin of tergite VII; in male, apical half of parameres with lateroventral expansion narrower than sides of basal half. *B. araya* Duarte & Grossi.
- In both sexes, stridulatory apparatus with barely marked carinae near to anterior margin of tergite VII; in male, apical half of parameres with lateroventral expansion broader than sides of basal half. *B. entellus* (LePeletier & Serville).
31. In both sexes, clypeus with angular lateral margins, pronotal margins completely rounded laterally, mesotibial inner spur with inward curved on apex. 32

- In both sexes, clypeus with sinuous lateral margins, pronotum with parallel posterolateral margins, mesotibial inner spur with outward curved apex. *B. dasypleurus* (Germar).

32. In both sexes, tridentate mandibles, labium rounded apically.
33

- In both sexes, bidentate mandibles, labium notched apically. ... *B. exaratus* (Burmeister).

33. Clypeal surface glabrous in both sexes; in male, parameres with broad apical half; in female, tergite VIII with and emarginate invaginated plate. 34

- Clypeal surface setose in both sexes; in males, parameres with narrow apical half; in females, tergite VIII with rounded invaginated. *B. medon* (Germar).

34. Stridulatory apparatus with barely marked carinae in both sexes.
35

- Stridulatory apparatus with one band of well-marked carinae in both sexes.
..... *B. simplex* Duarte, Grossi & Parizotto sp.

nov.

35. Male with incised inner protarsal claw; in female, pronotal surface densely covered with contiguous to coalescent punctures, posterior margin of ventrite VI with two weak constrictions *B. validus* (Burmeister).

- Male with simple protarsal claw (without incision); in female, pronotal surface with sparse punctures (spaced about two diameters of punctures), posterior margin of ventrite VI

complete (without constriction). *B. cunctator*
(Mannerheim).

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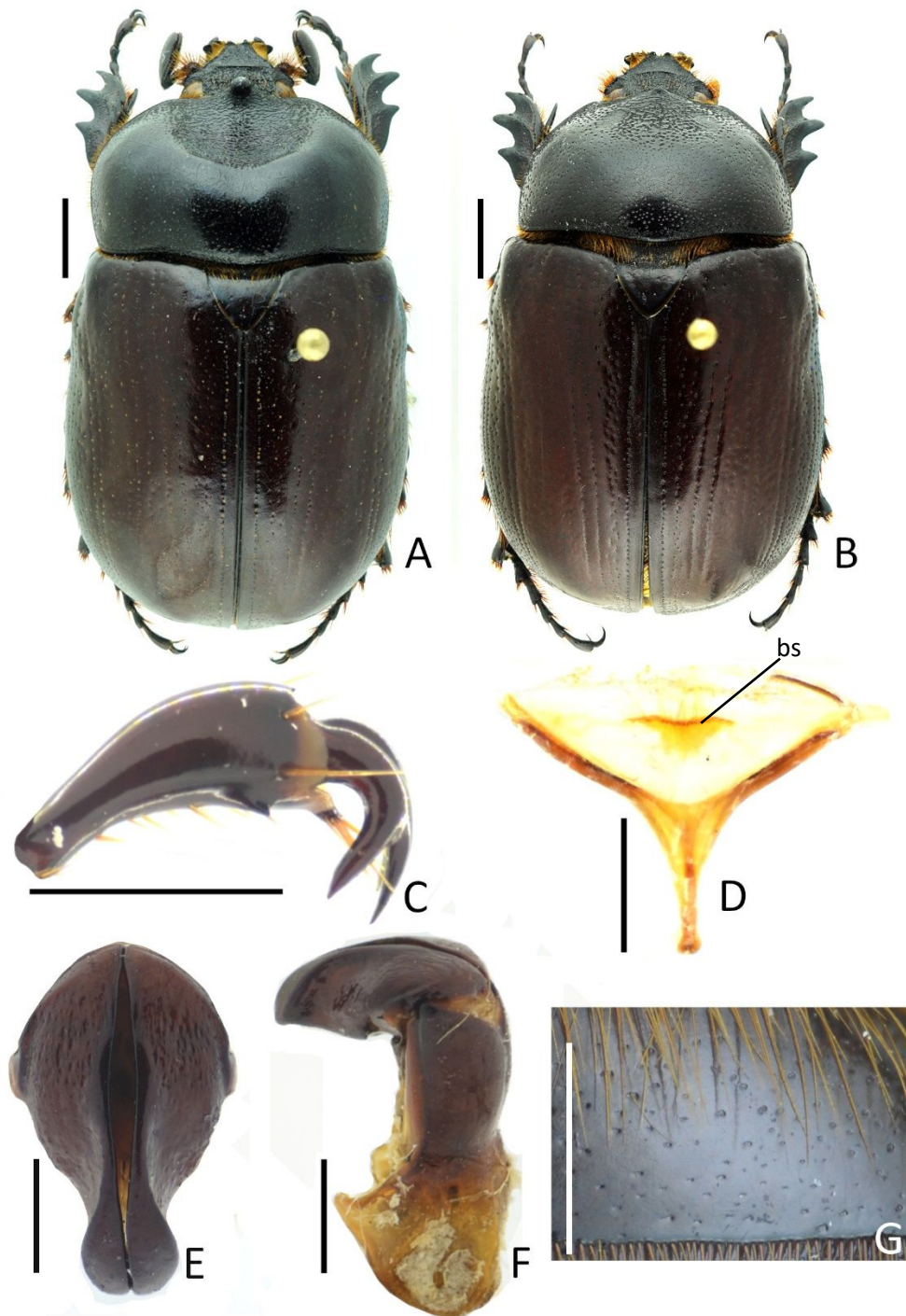


Figure 20. *Bothynus ascanius*: A) male in dorsal view; B) female in dorsal view; C) male, inner view of the last protarsomere; D) spiculum gastrale; E) parameres in caudal view; F) parameres in lateral view; G) female, discal area of metafemora. bs–basal sclerite. Scale bars = 2 mm.

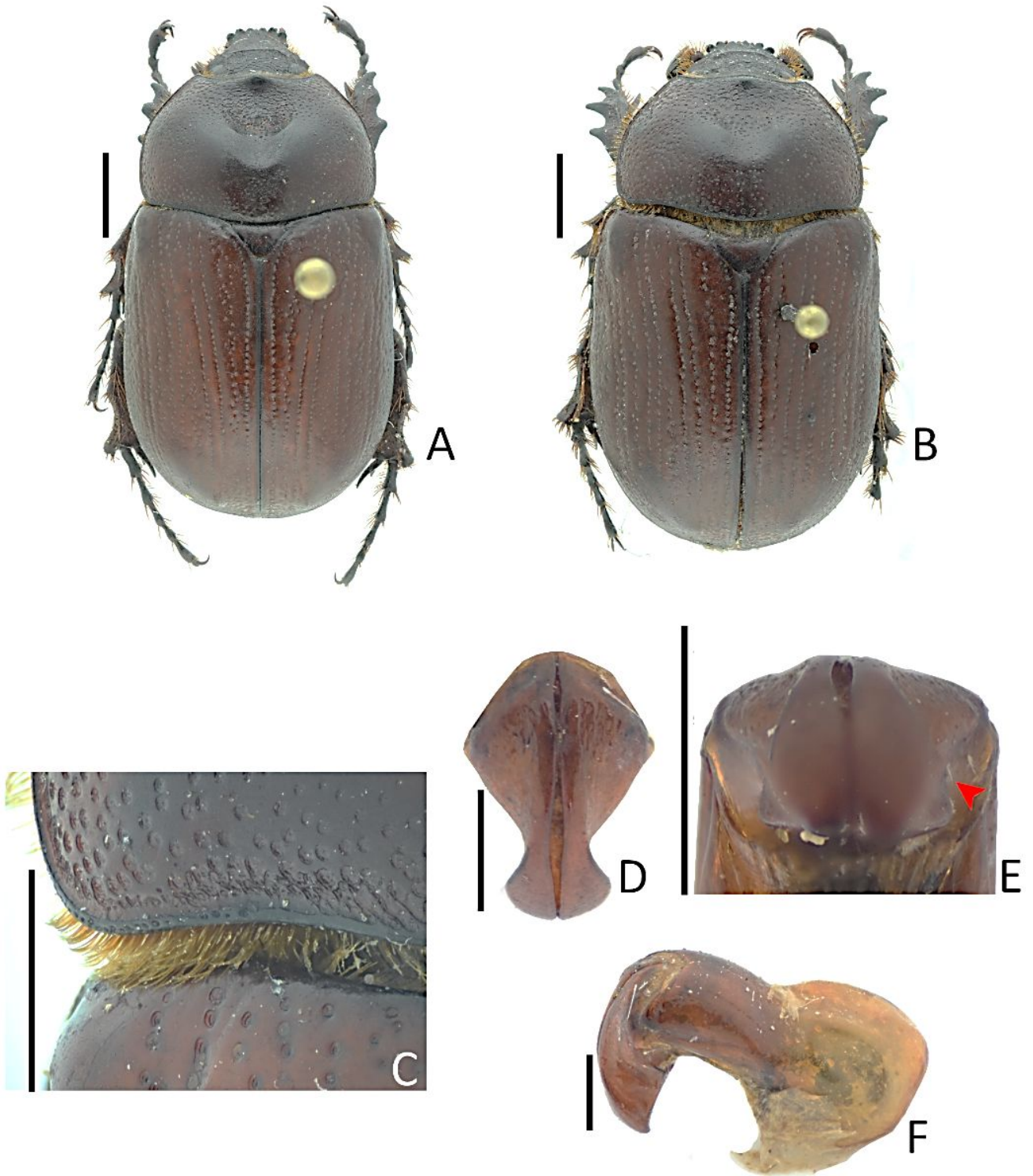


Figure 21. *Bothynus laticifex*: A) male in dorsal view; B) female in dorsal view; C) male, detail of the posterior right corner of pronotum; D) parameres in caudal view; E) parameres in frontal view; F) parameres in lateral view. Red arrow: lateral contraction in E. Scale bars = 2 mm.

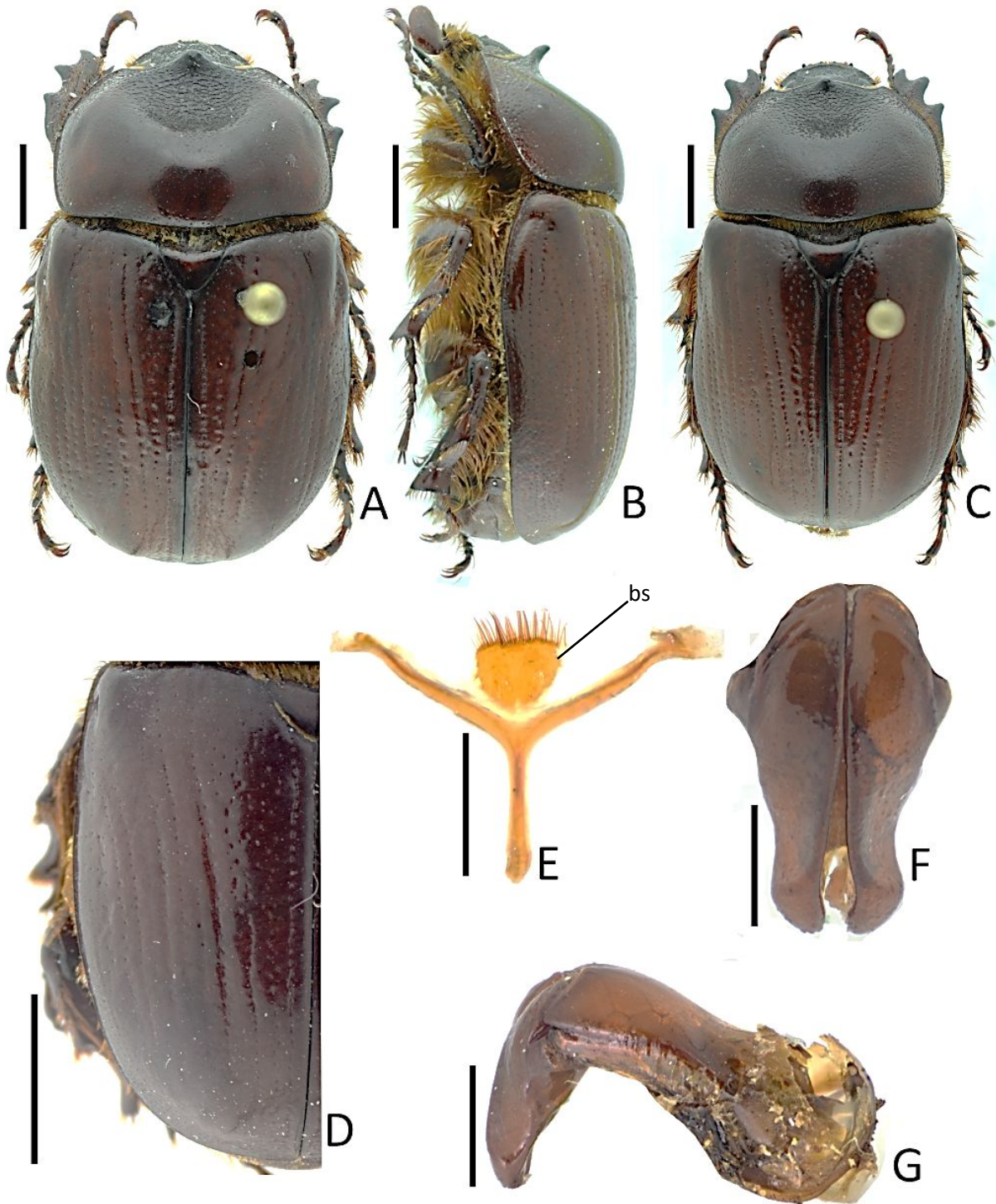


Figure 22. *Bothynus deiphobus*: A) male in dorsal view, B) male in lateral view, C) female in dorsal view, D) left elytron in dorsal view, E) spiculum gastrale, F) parameres in caudal view, G) parameres in lateral view. bs—basal sclerite. Scale bars = 2 mm.

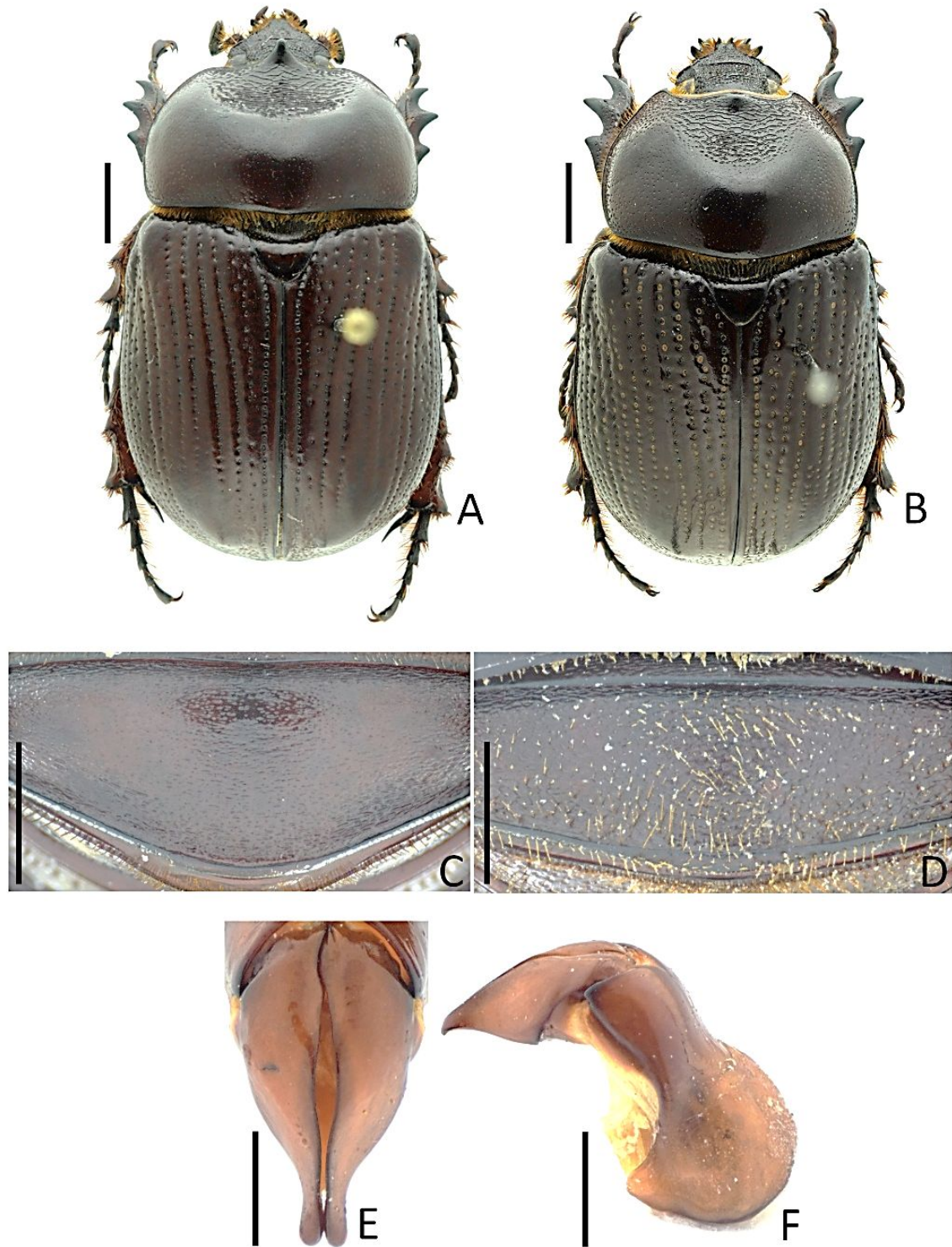


Figure 23. *Bothynus cyclops*: A) male in dorsal view; B) female in dorsal view; C) male, discal area of tergite VIII; D) female, discal area of tergite VIII; E) parameres in caudal view; F) parameres in lateral view. Scale bars = 2 mm.

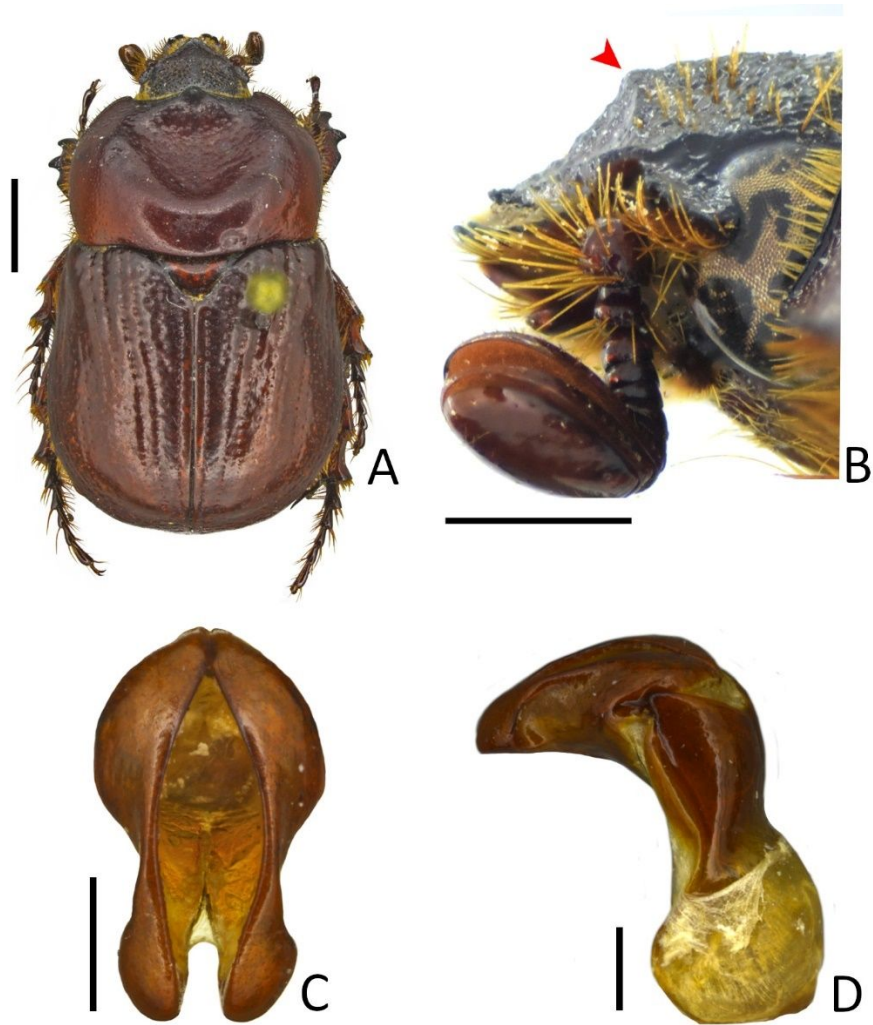


Figure 24. *Bothynus minor*: A) male in dorsal view; B) head in lateral view; C) parameres in caudal view; D) parameres in lateral view. Red arrow: raised carina in B. Scale bars = 2 mm.

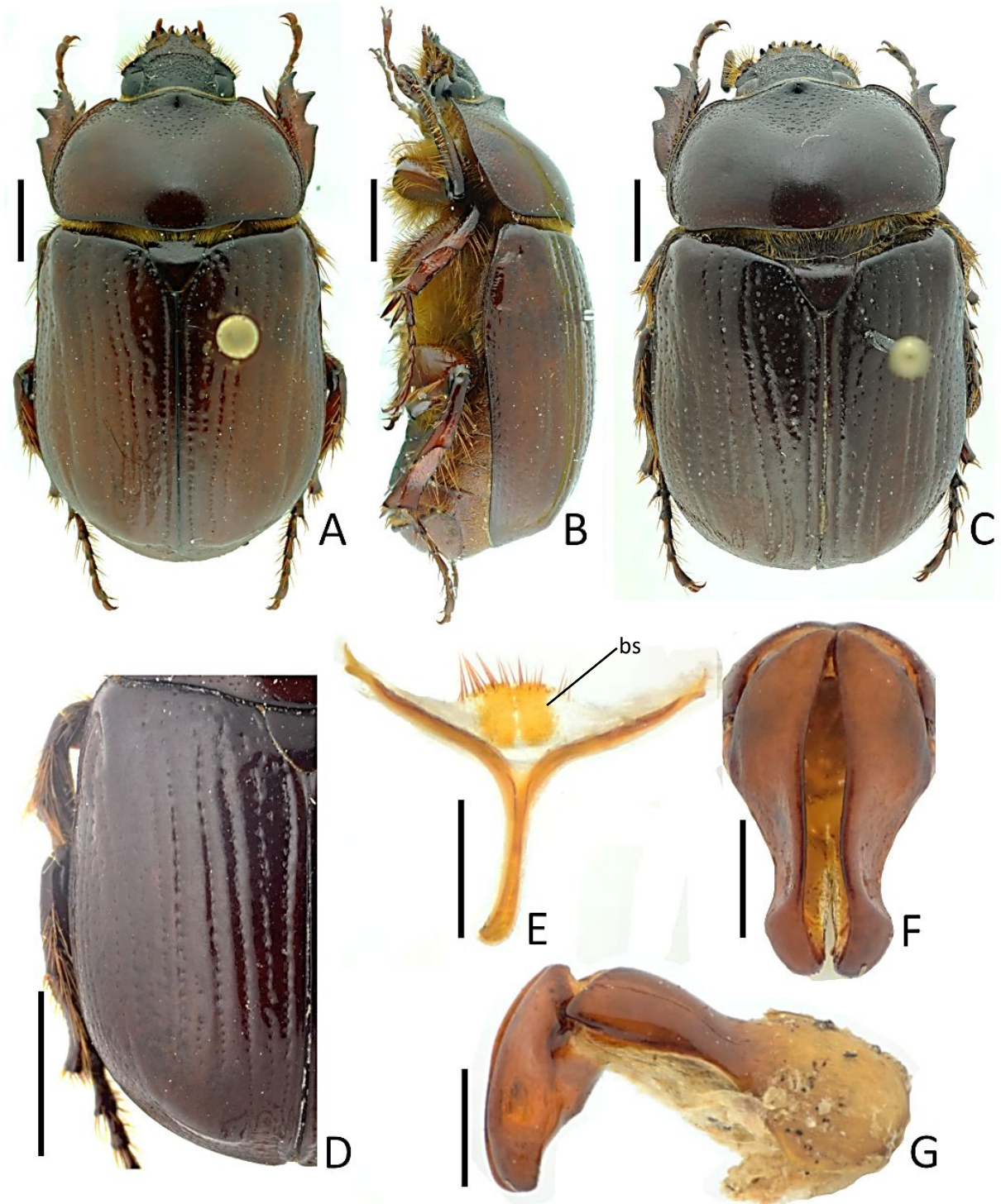


Figure 25. *Bothynus fabius*: A) male in dorsal view; B) male in lateral view; C) female in dorsal view; D) left elytron in dorsal view; E) spiculum gastral; F) parameres in caudal view; G) parameres in lateral view. bs—basal sclerite. Scale bars = 2 mm.

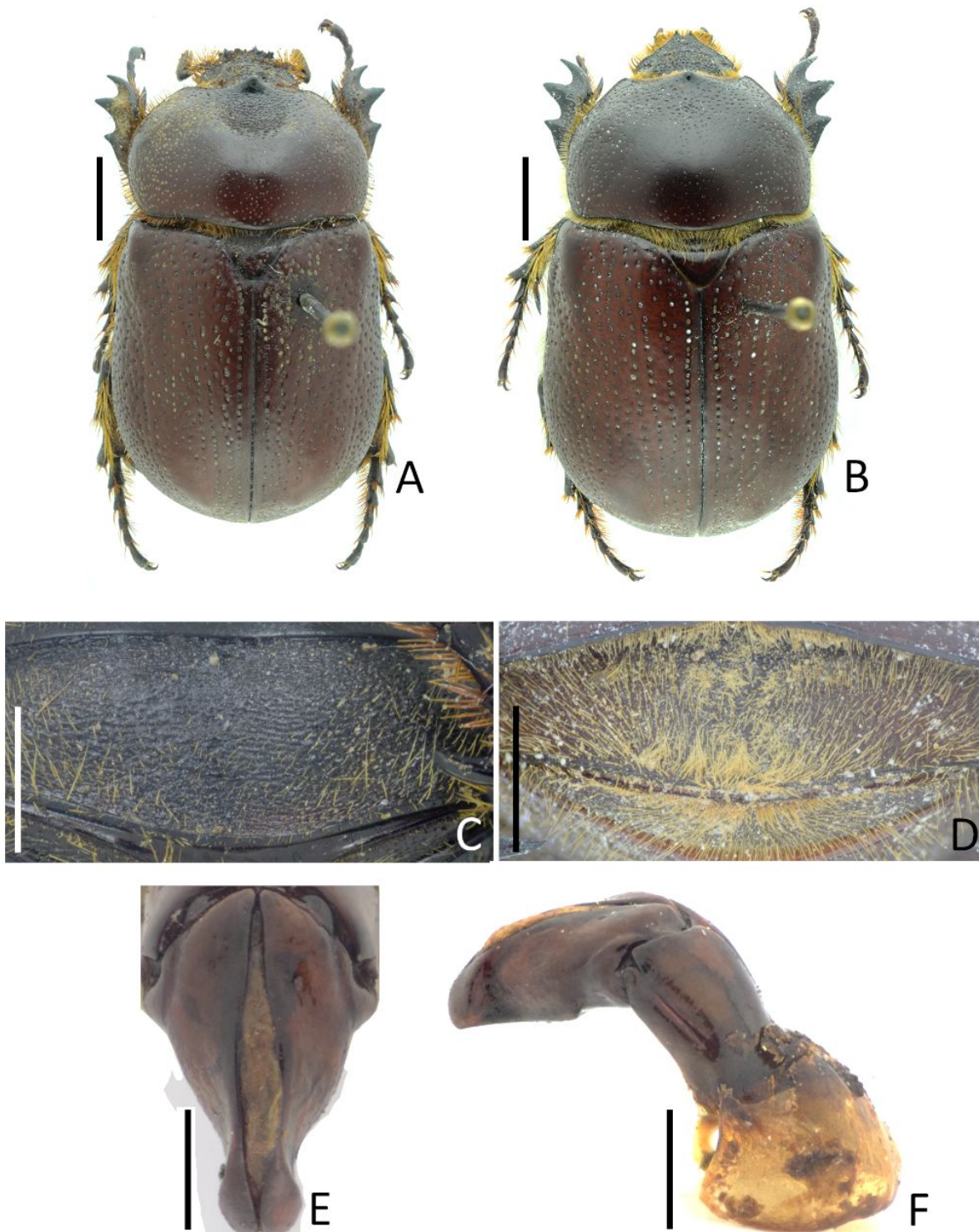


Figure 26. *Bothynus cribrarius*: A) male in dorsal view; B) female in dorsal view; C) male, discal area of tergite VIII; D) female, discal area of tergite VIII; E) parameres in caudal view; F) parameres in lateral view. Scale bars = 2 mm.

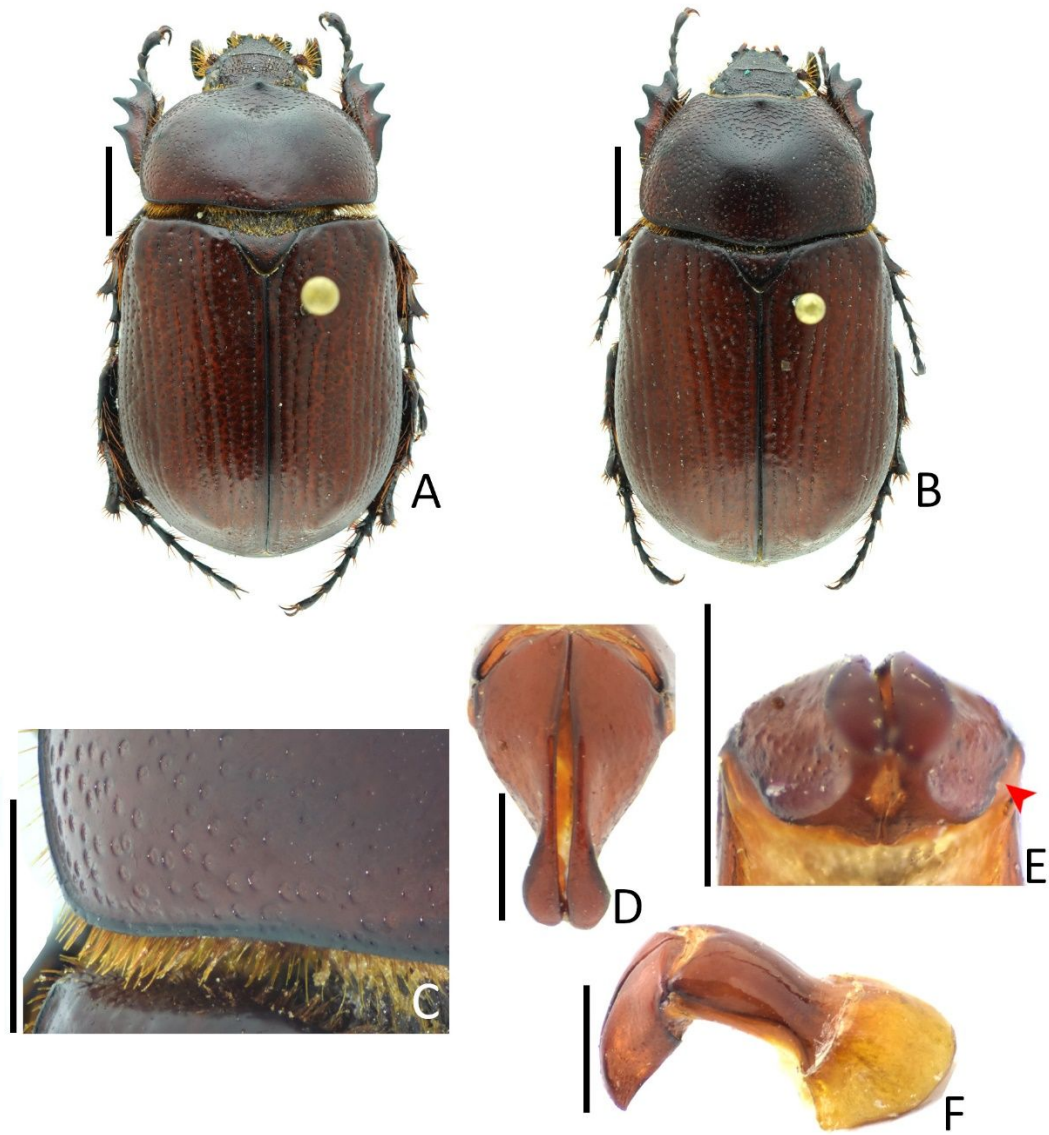


Figure 27. *Bothynus cylindricus*: A) male in dorsal view; B) female in dorsal view; C) male, detail of the posterior right corner of pronotum; D) parameres in caudal view; E) parameres in frontal view; F) parameres in lateral view. Red arrow: sides parallel in E. Scale bars = 2 mm.

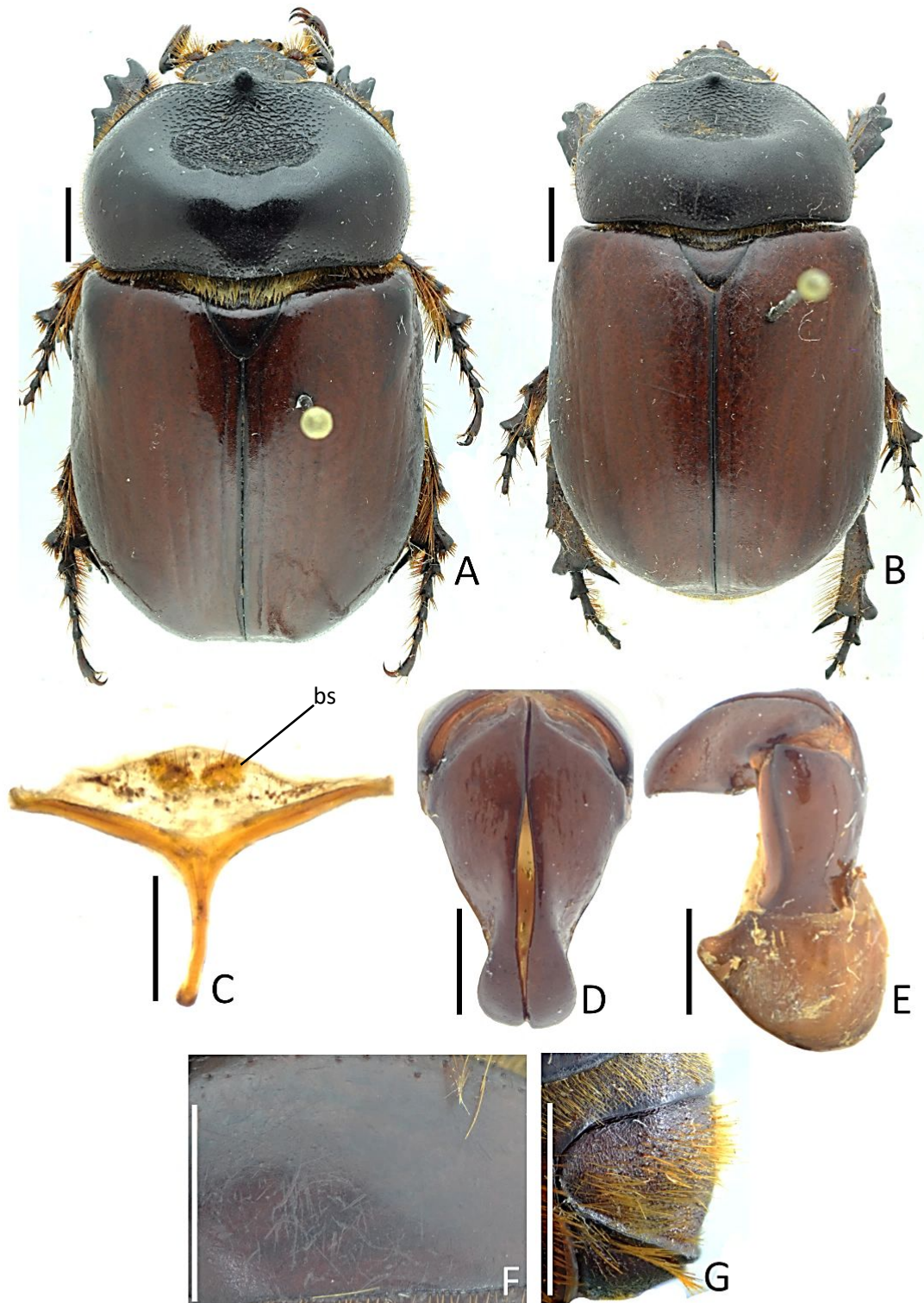


Figure 28. *Bothynus laevipennis*: A) male in dorsal view; B) female in dorsal view; C) spiculum gastrale; D) parameres in caudal view; E) parameres in lateral view; F) female, discal area of metafemora; G) female, tergite VIII in lateral view. bs—basal sclerite. Scale bars = 2 mm.

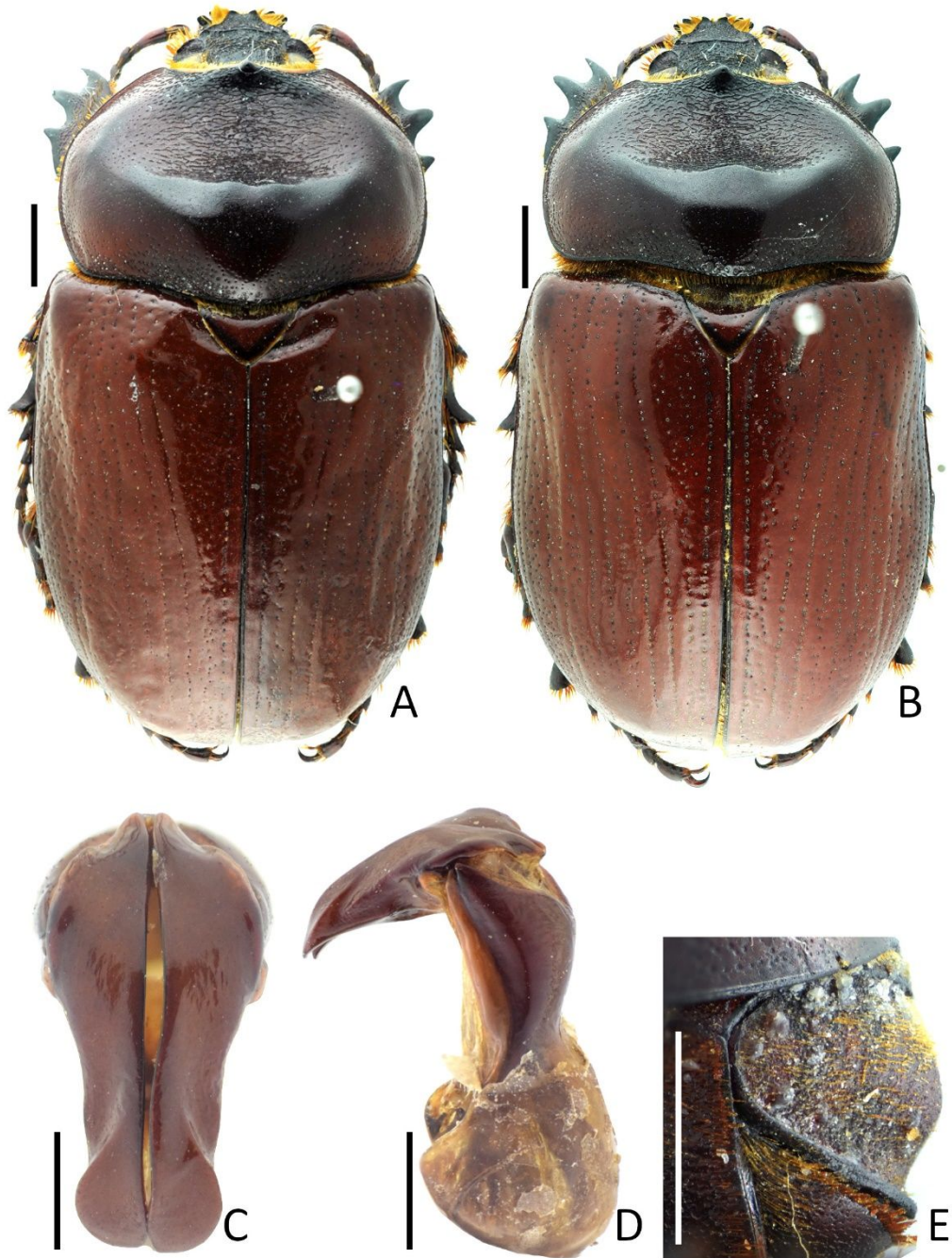


Figure 29. *Bothynus nyx*: A) male in dorsal view; B) female in dorsal view; C) parameres in dorsal view; D) parameres in lateral view; E) female, tergite VIII in lateral view. Scale bars = 2 mm.

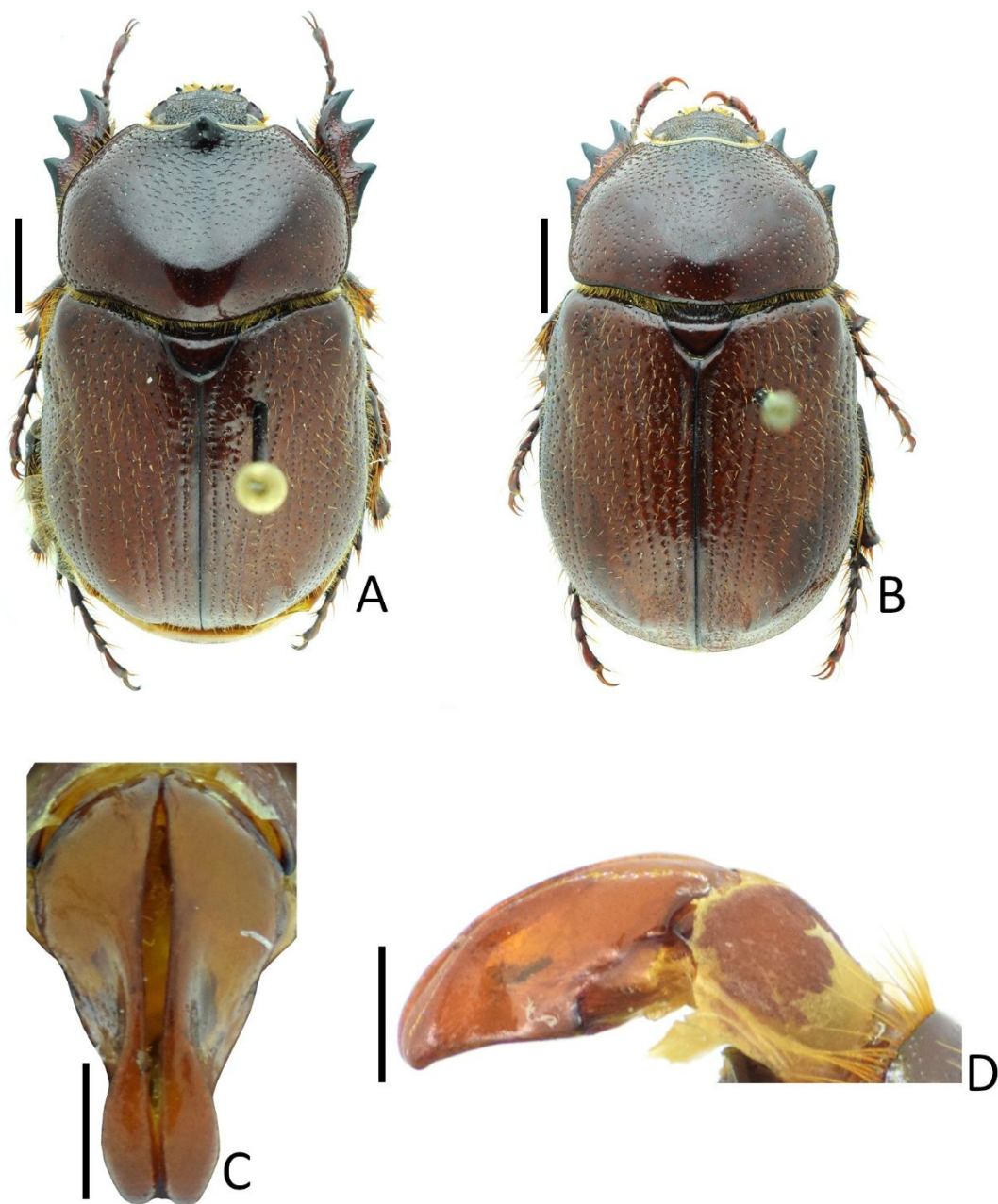


Figure 30. *Bothynus thrinx*: A) male in dorsal view; B) Female in dorsal view; C) parameres in caudal view; D) parameres in lateral view. Scale bars = 2 mm.



Figure 31. *Bothynus moroni* sp. nov.: A) male in dorsal view; B) detail of clypeus. Scale bars = 2 mm.

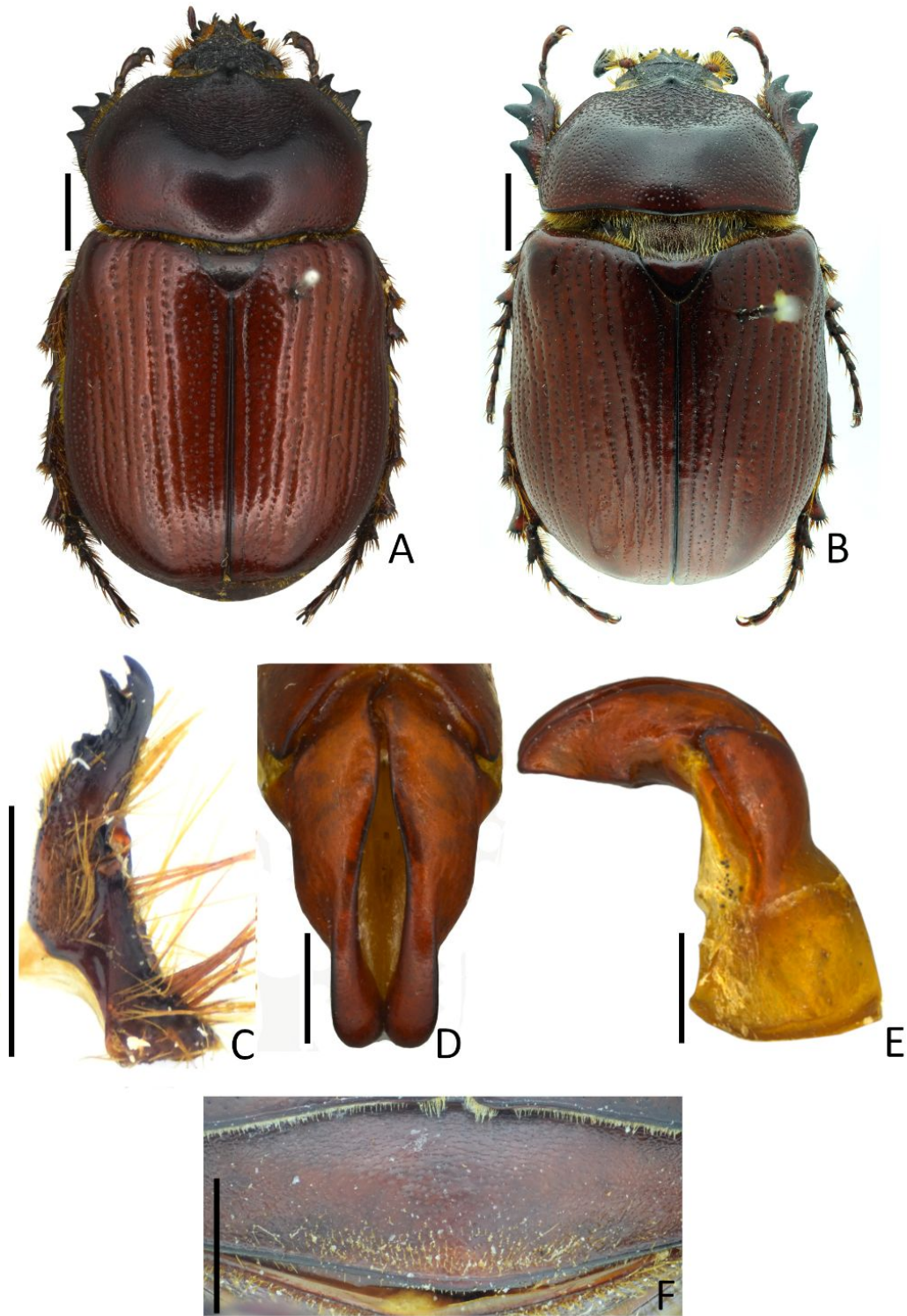


Figure 32. *Bothynus andrezus* sp. nov.: A) male in dorsal view; B) female in dorsal view; C) maxilla in ventral view; D) parameres in caudal view; E) parameres in caudal view; F) female, tergite VIII. Scale bars = 2 mm.

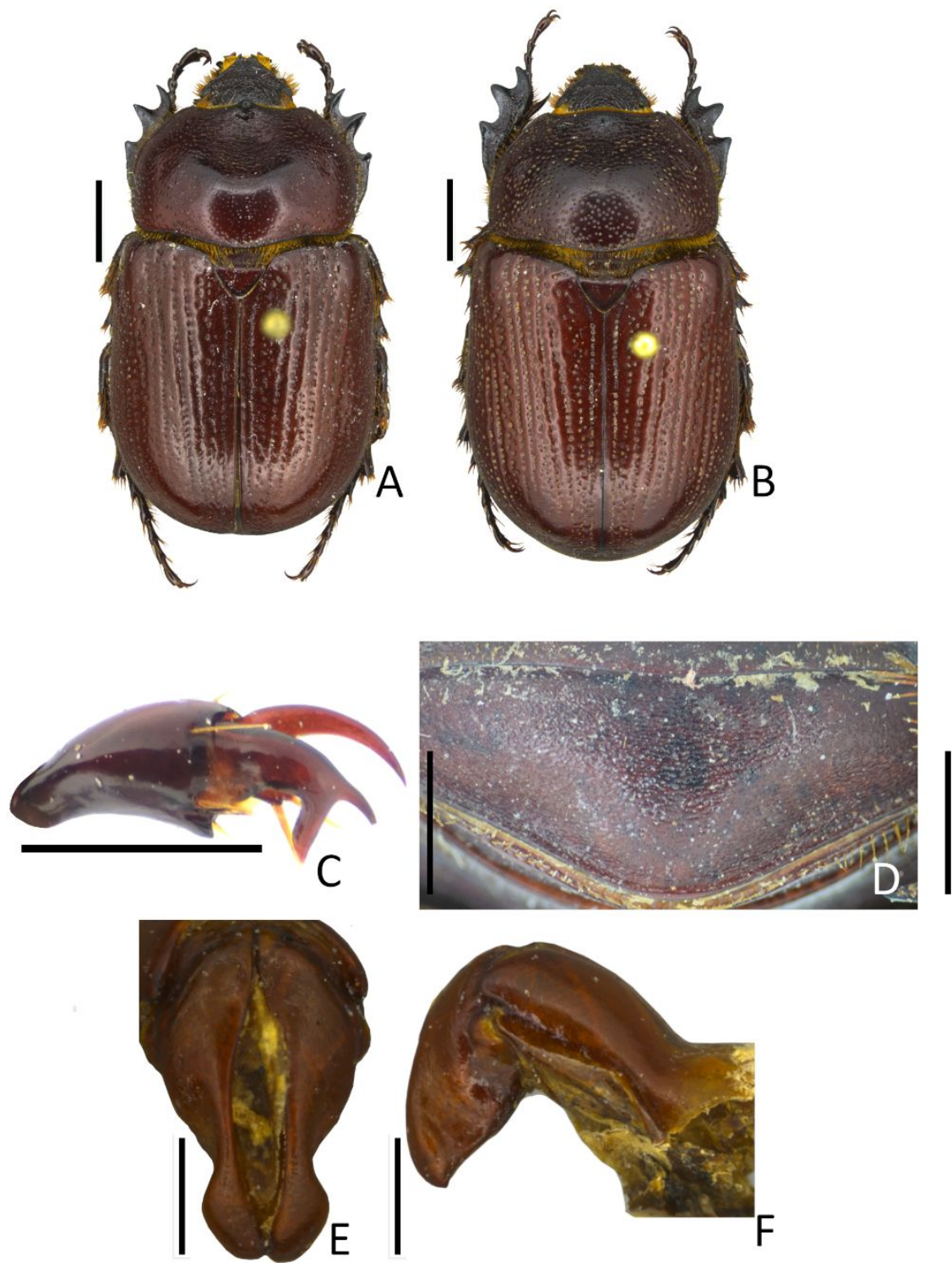


Figure 33. *Bothynus tamarae* sp. nov.: A) male in dorsal view; B) female in dorsal view; C) male, inner view of the last protarsomere; D) discal area of tergite VIII; E) parameres in caudal view; F) parameres in lateral view. Scale bars = 2 mm.

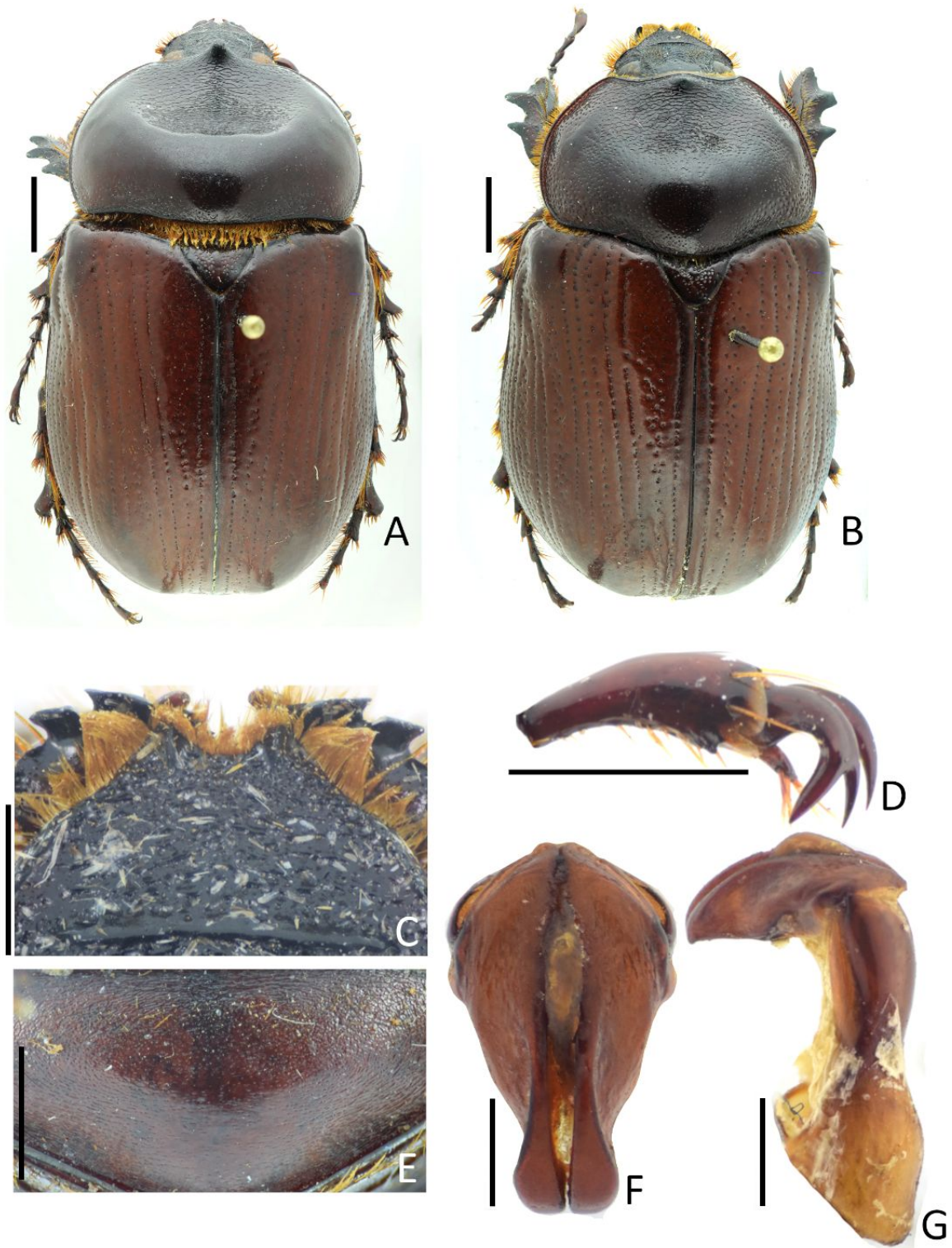


Figure 34. *Bothynus leidianoi* sp. nov.: A) male in dorsal view; B) female in dorsal view; C) detail of clypeus; D) male, inner view of the last protarsomere; E) discal area of tergite VIII; F) parameres in caudal view; G) parameres in lateral view. Scale bars = 2 mm.

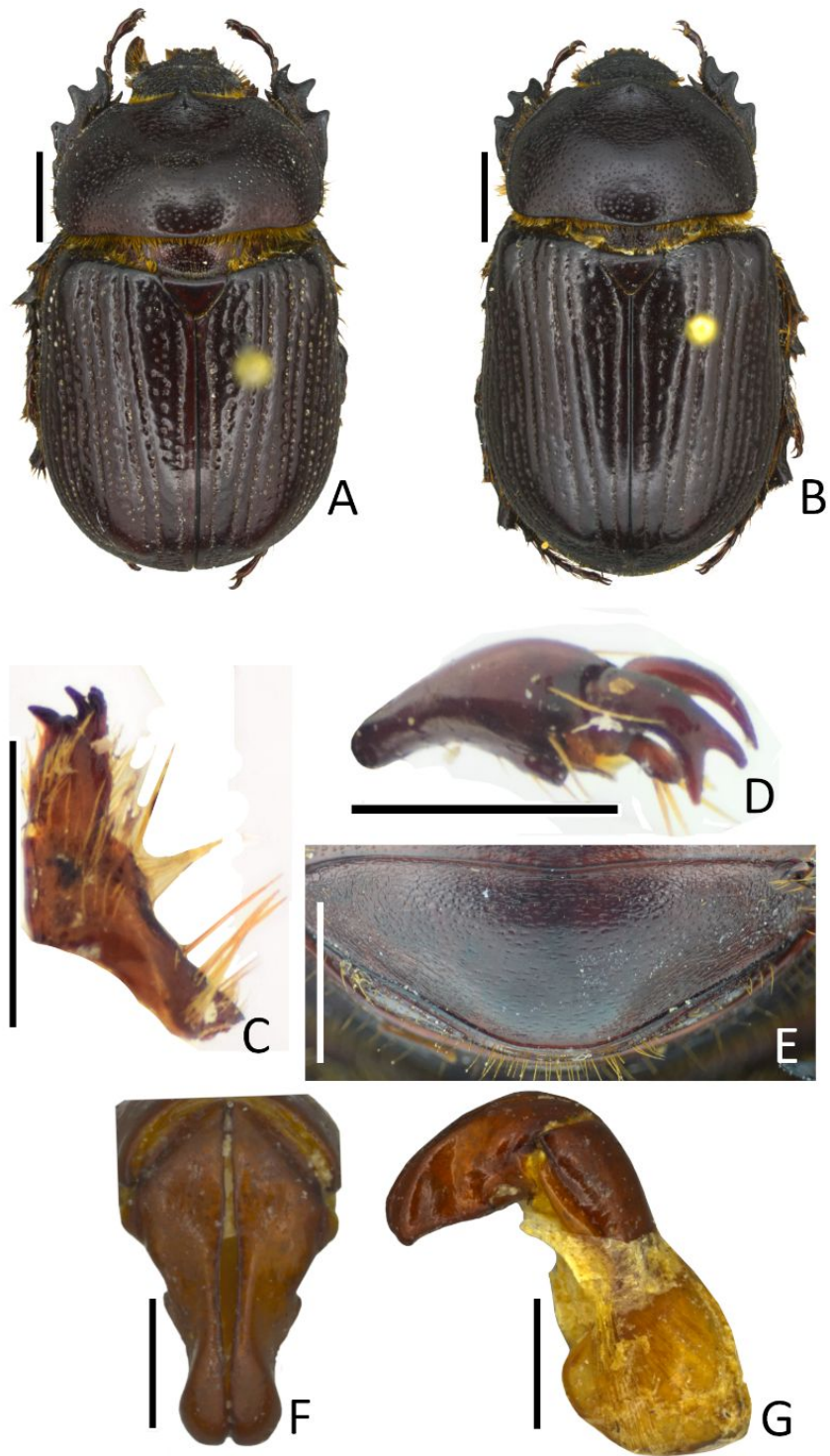


Figure 35. *Bothynus sebastiani* sp. nov.: A) male in dorsal view; B) female in dorsal view; C) maxilla in ventral view; D) male, inner view of the last protarsomere; E) discal area of tergite VIII; F) parameres in caudal view; G) parameres in lateral view. Scale bars = 2 mm.

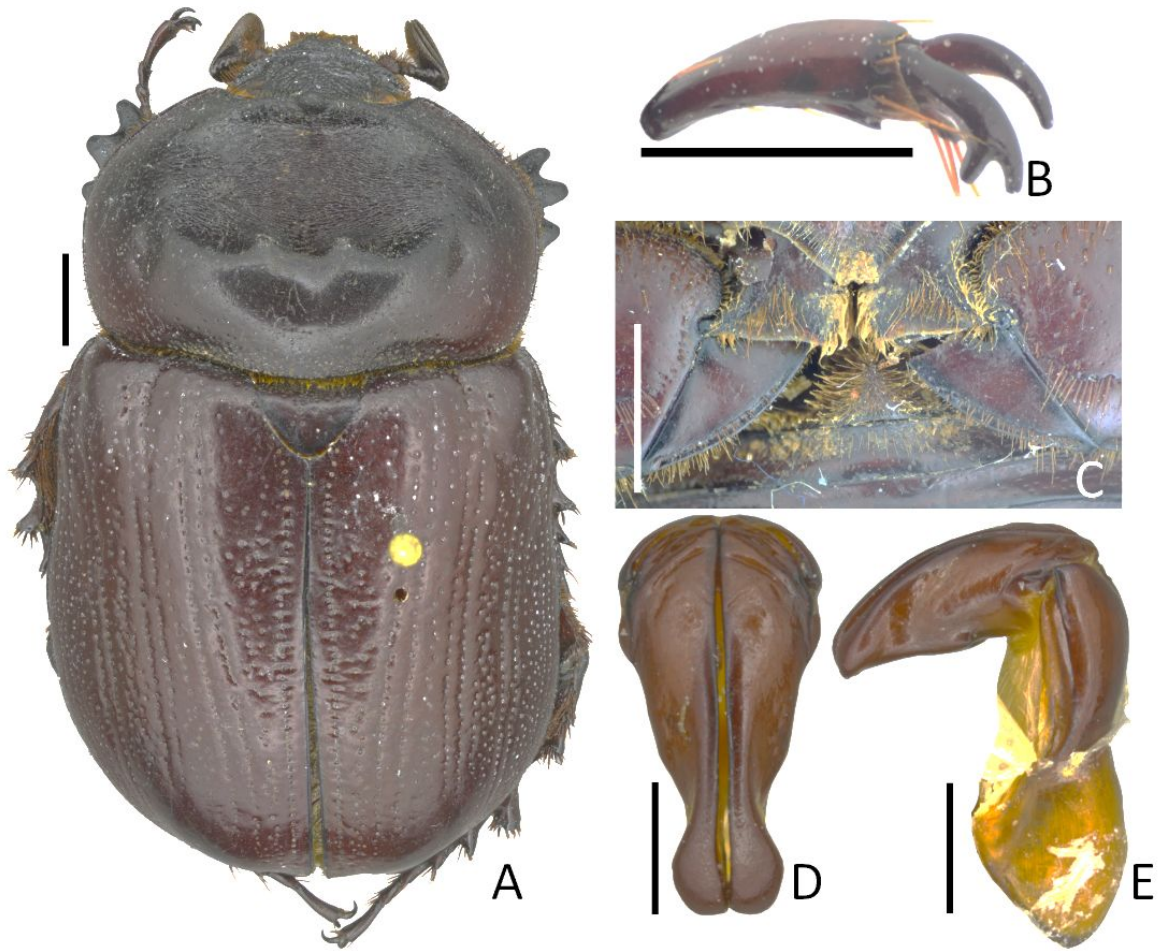


Figure 36. *Bothynus aydanus* sp. nov.: A) male in dorsal view; B) inner view of the last protarsomere; C) detail of the metatrochanter; D) parameres in caudal view; E) parameres in lateral view. Scale bars = 2 mm.

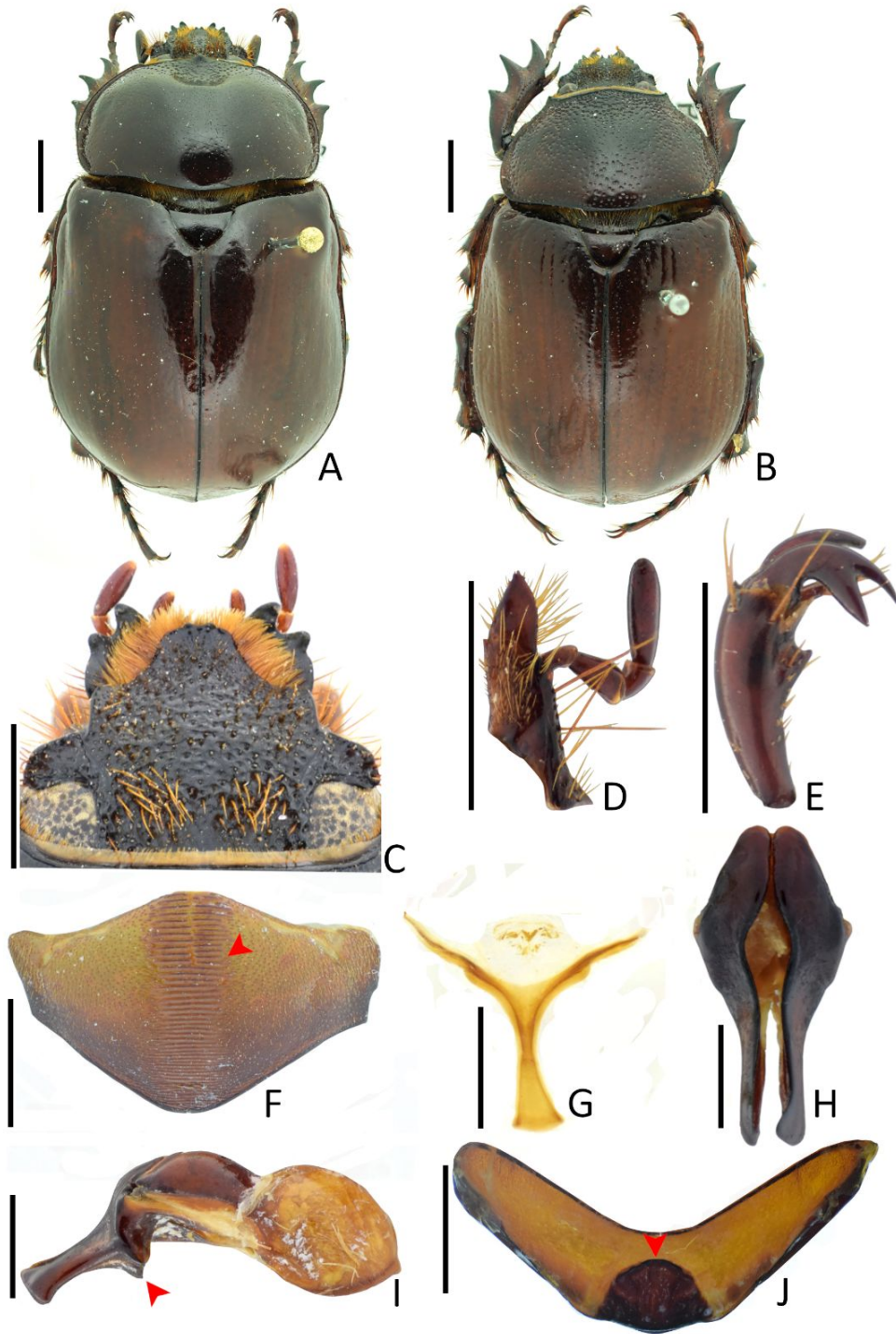


Figure 37. *Bothynus medon*: A) male in dorsal view; B) female in dorsal view; C) head in dorsal view; D) maxilla in ventral view; E) male, inner view of the last protarsomere; F) tergite VII in dorsal view; G) spiculum gastrale; H) parameres in caudal view; I) parameres in lateral view; J) female, inner view of tergite VIII. Red arrow: stridulatory apparatus in F, ventral process in I, invaginate plate in J. Scale bars = 2 mm.

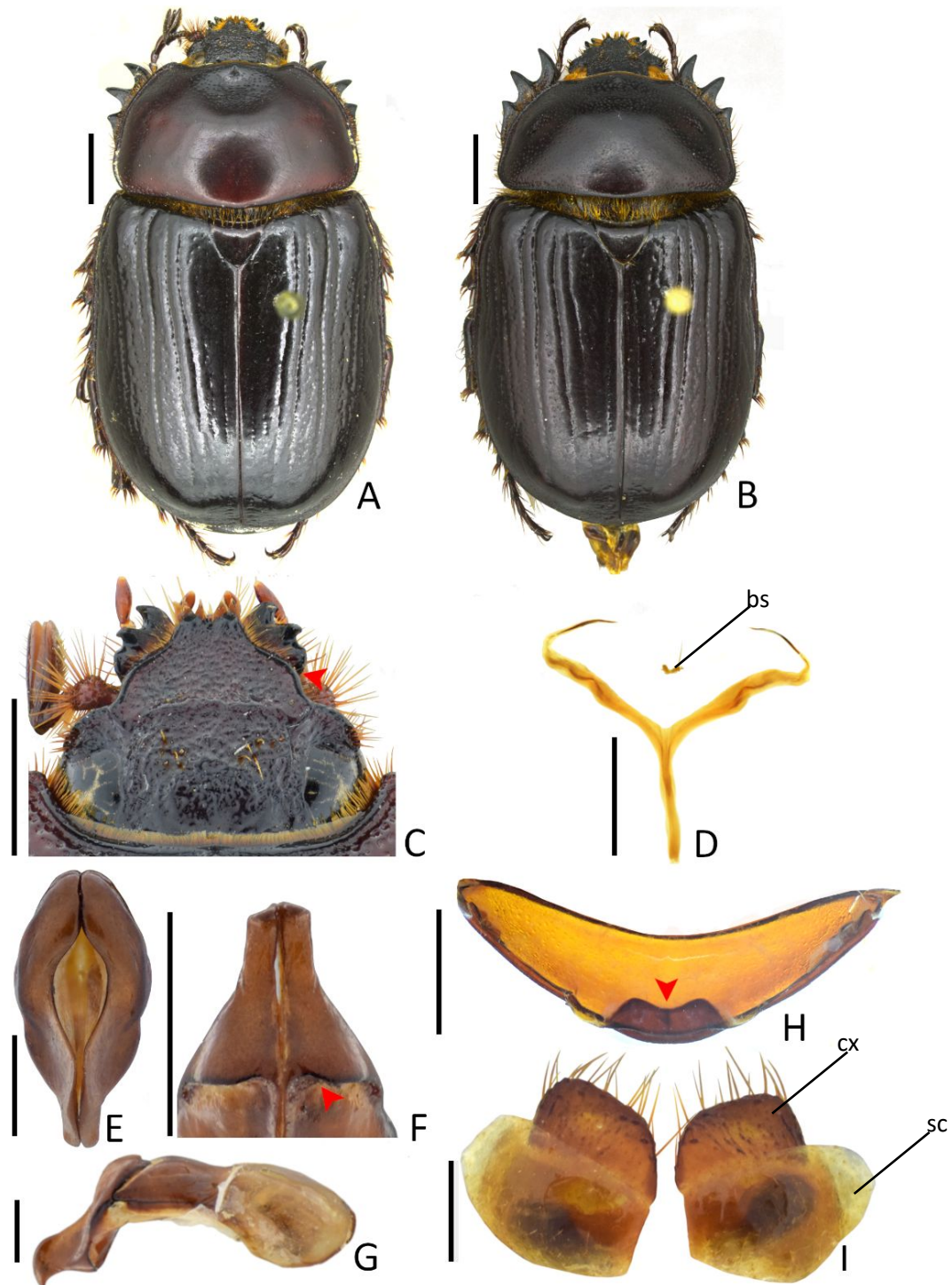


Figure 38. *Bothynus dasypleurus*: A) male in dorsal view; B) female in dorsal view; C) head in dorsal view; D) spiculum gastrale; E) parameres in caudal view; F) parameres in ventral view; G) parameres in lateral view; H) inner view of tergite VIII; I) female genitalia. bs—basal sclerite, cx—coxite, sc—subcoxite. Red arrow: sinuous lateral margin in C, ventral carina in F, invaginate plate in H. Scale bars = 2 mm.

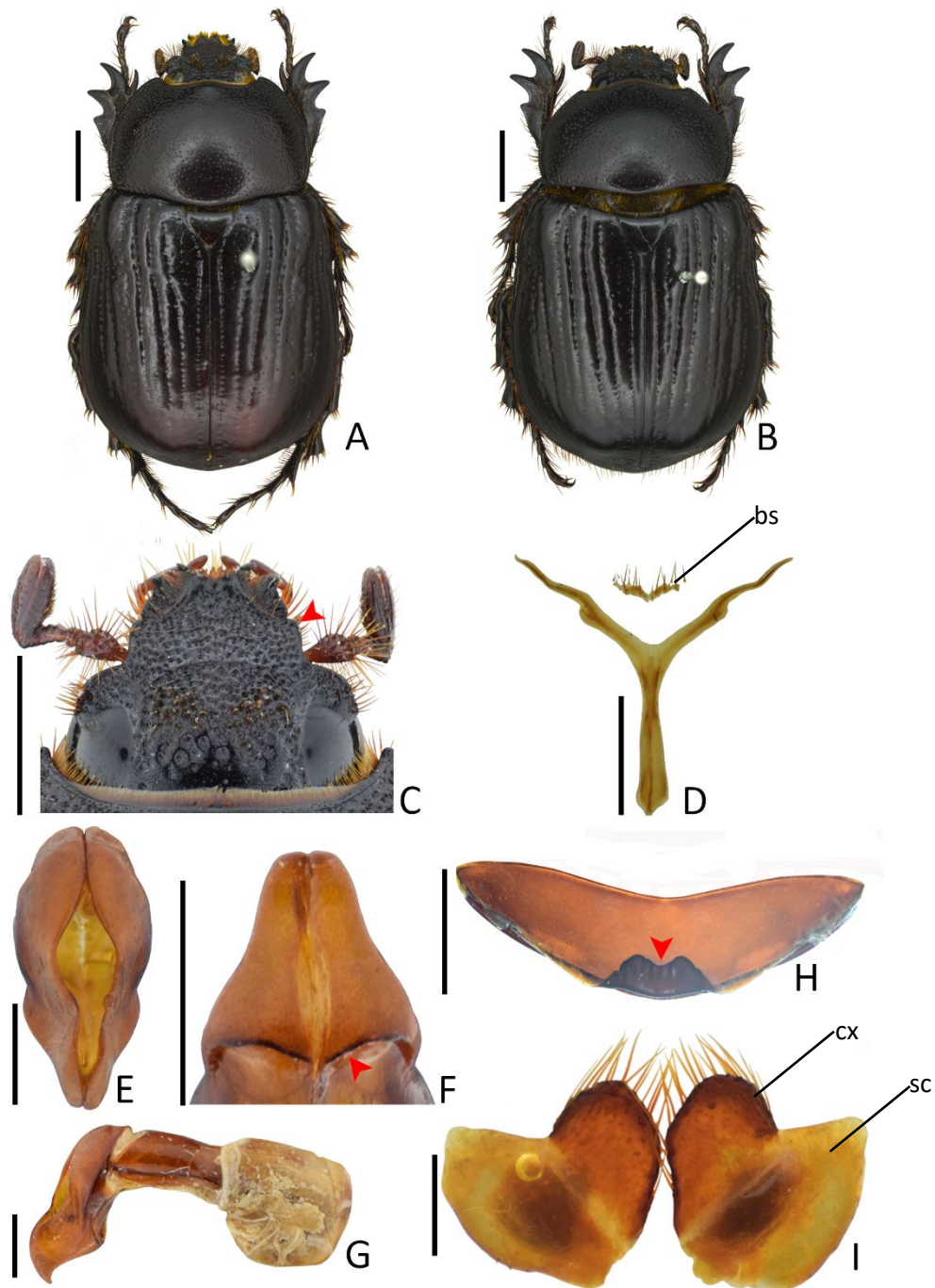


Figure 39. *Bothynus cunctator*: A) male in dorsal view; B) female in dorsal view; C) head in dorsal view; D) spiculum gastrale; E) parameres in caudal view; F) parameres in ventral view; G) parameres in lateral view; H) female, inner view of tergite VIII; I) female genitalia. bs–basal sclerite, cx–coxite, sc–subcoxite. Red arrow: angular raised margin in C, ventral carina in F, invaginate plate in H. Scale bars = 2 mm.

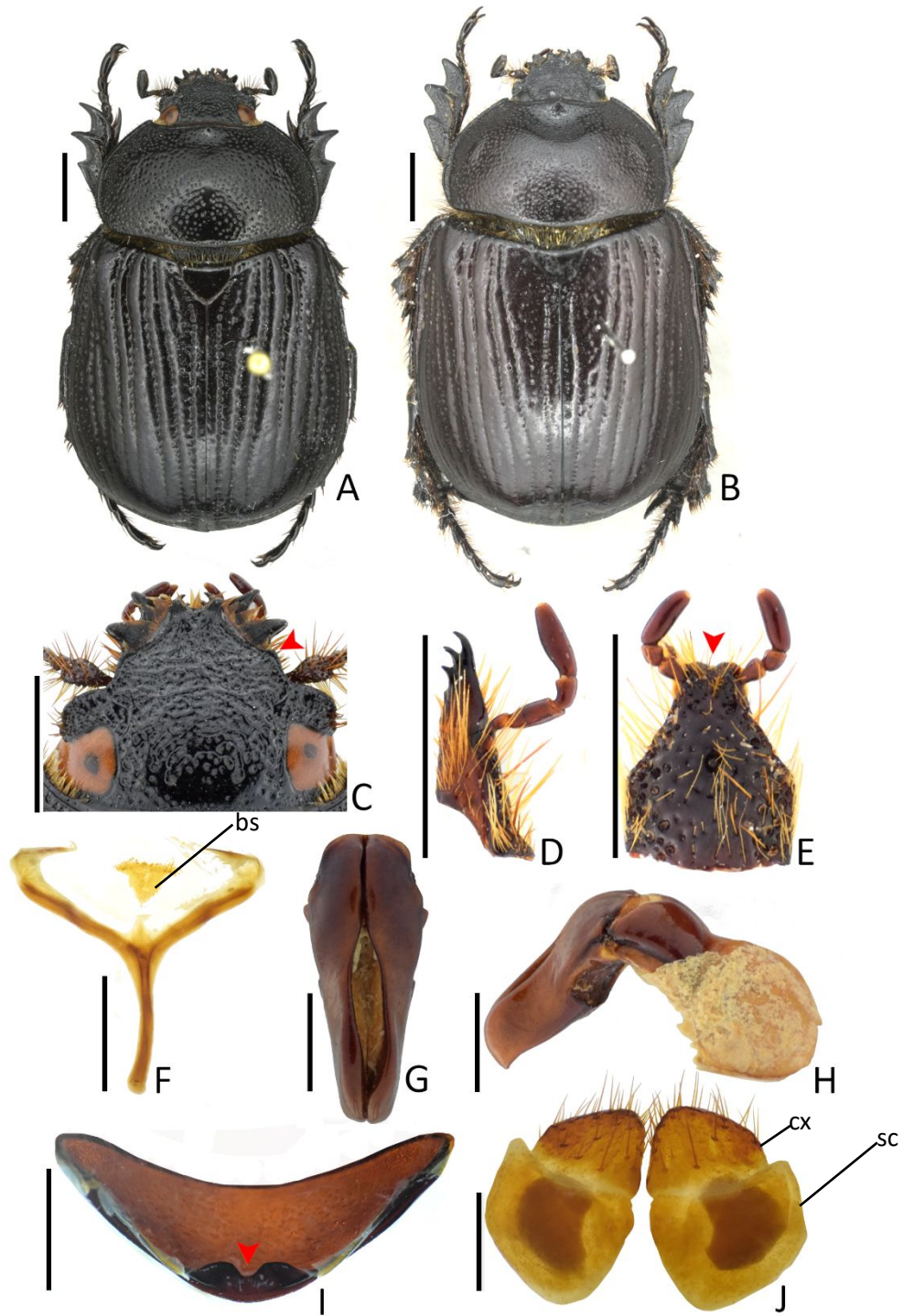


Figure 40. *Bothynus exaratus*: A) male in dorsal view; B) female in dorsal view; C) head in dorsal view; D) maxilla in ventral view; E) labium; F) spiculum gastrale; G) parameres in caudal view; H) parameres in lateral view; I) female, inner view of tergite VIII; J) female genitalia. bs—basal sclerite, cx—coxite, sc—sub coxite. Red arrow: bidentate maxilla in C, apical notch in E, invaginate plate in I. Scale bars = 2 mm.

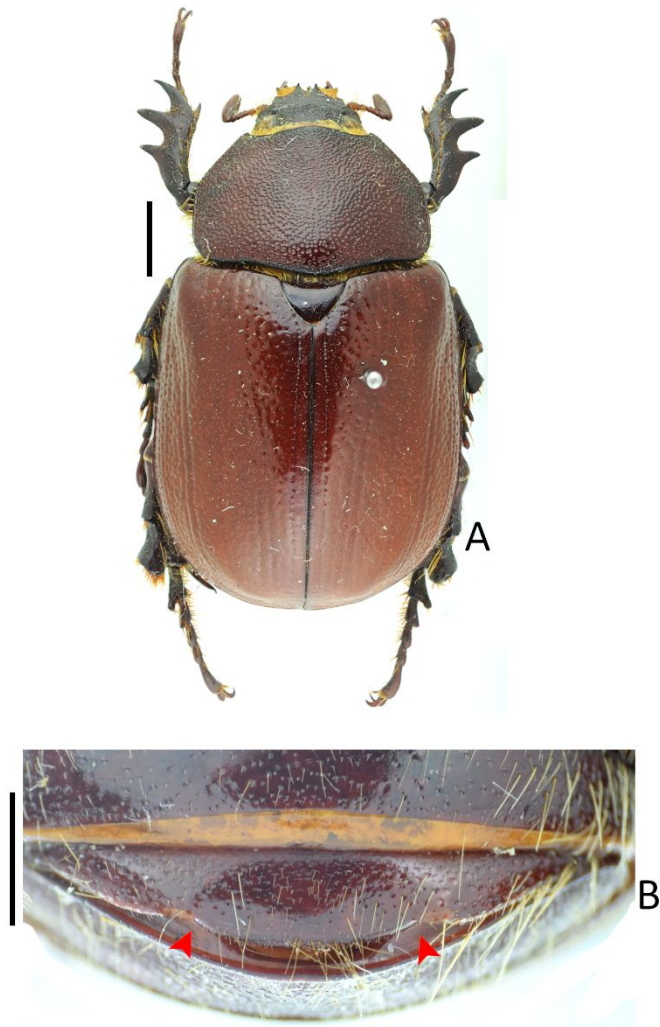


Figure 41. *Bothynus validus*: A) female in dorsal view; B) ventrite VI. Red arrow: marginal contractions in B. Scale bars = 2 mm.

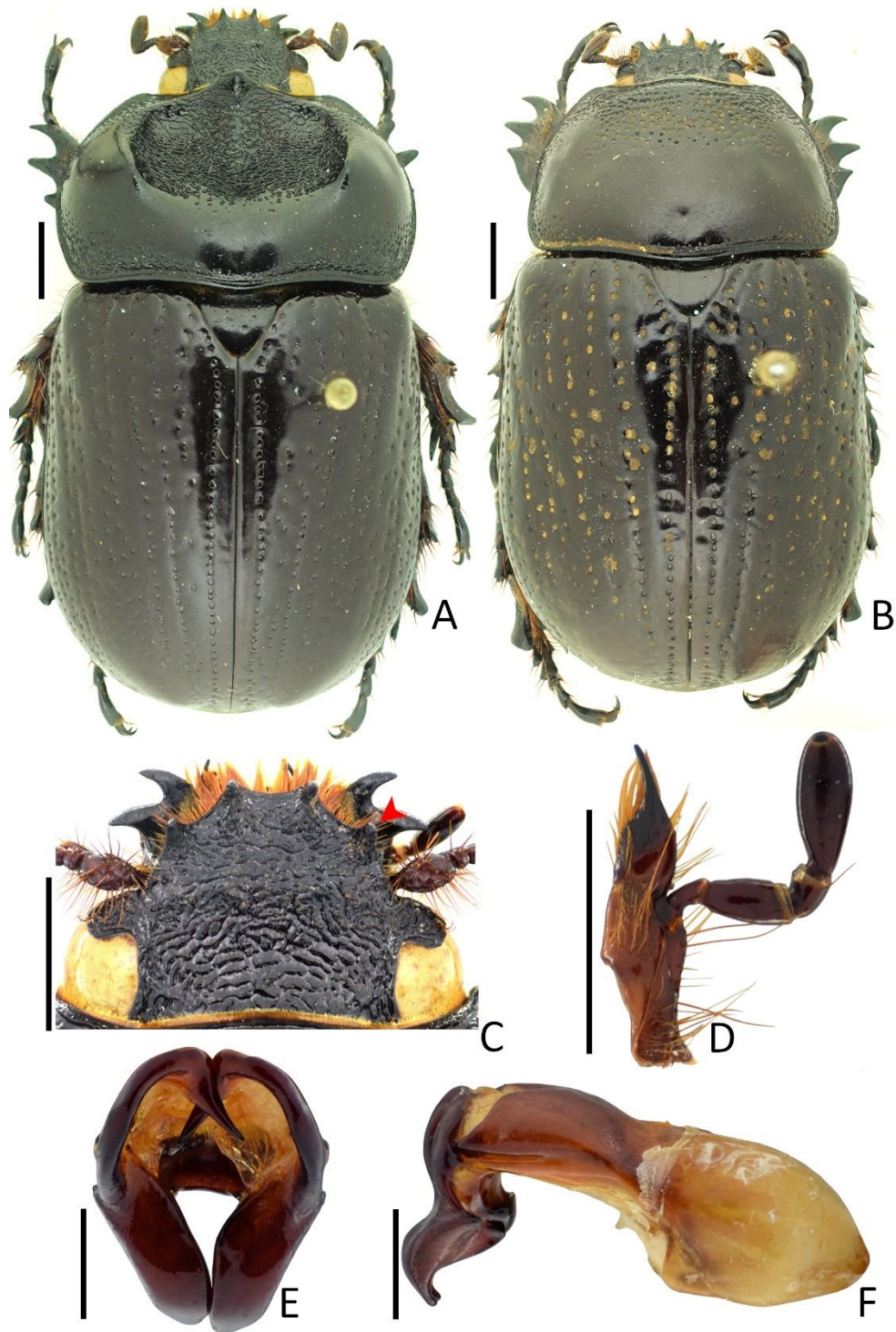


Figure 42. *Bothynus herteli*: A) male in dorsal view; B) female in dorsal view; C) head in dorsal view; D) maxilla in ventral view; E) parameres in caudal view; F) parameres in lateral view. Red arrow: lateral raised tooth in C. Scale bars = 2 mm.

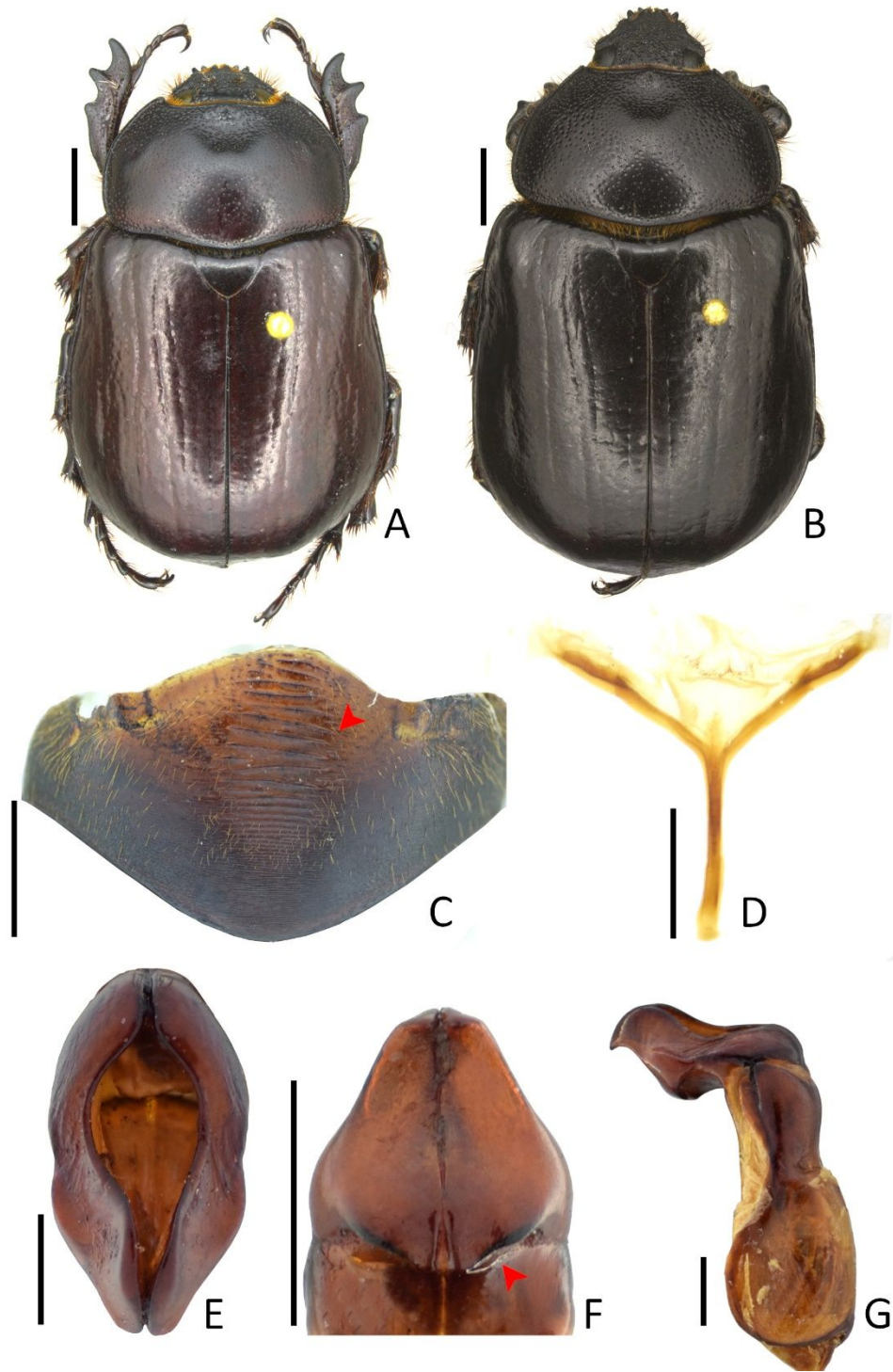


Figure 43. *Bothynus simplex* sp. nov.: A) male in dorsal view; B) female in dorsal view; C) tergite VII in dorsal view; D) spiculum gastrale; E) parameres in caudal view; F) parameres in ventral view; G) parameres in lateral view. Red arrow: stridulatory apparatus in C, ventral carina in E. Scale bars = 2 mm.

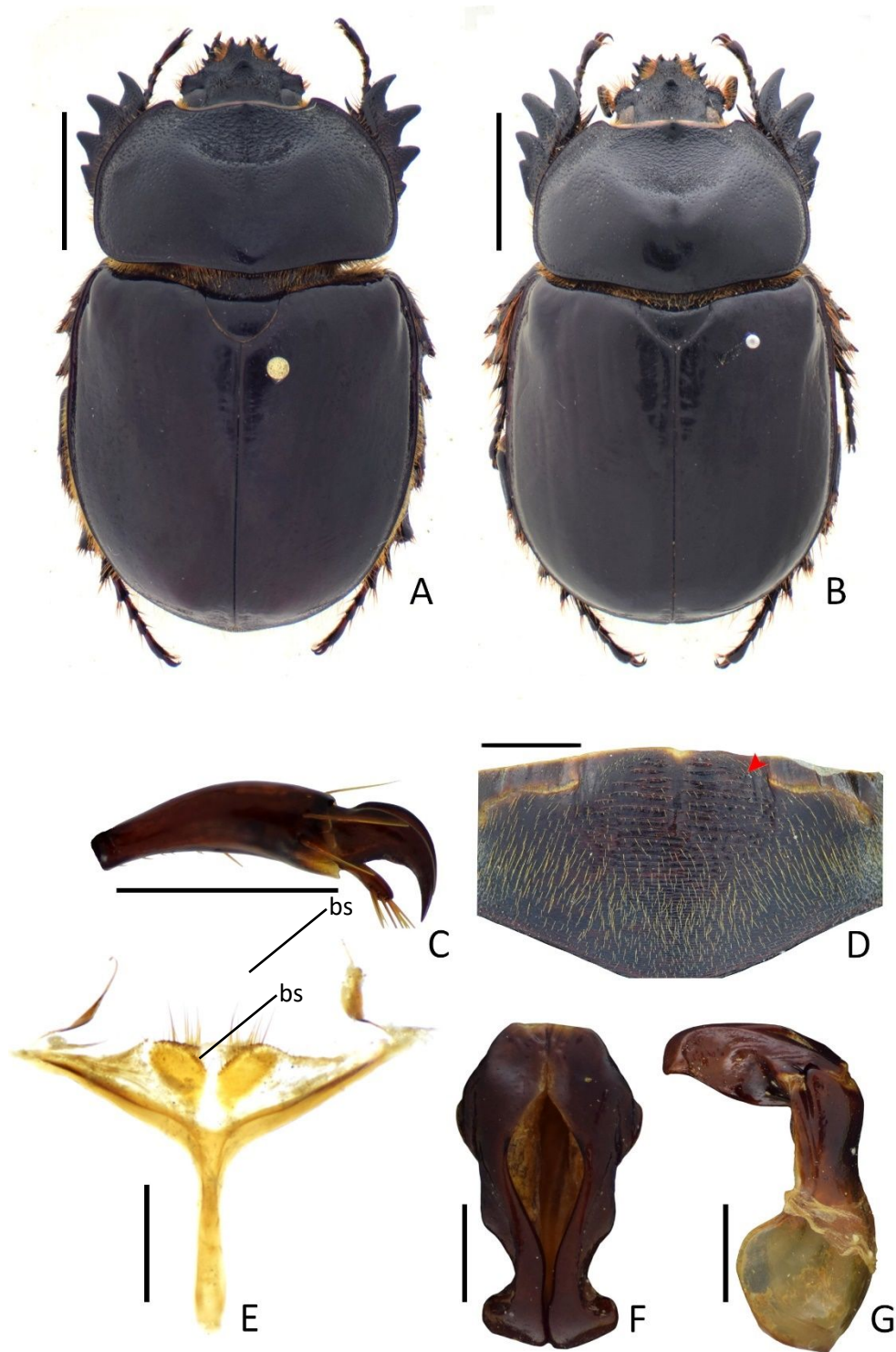


Figure 44. *Bothynus complanus*: A) male in dorsal view; B) female in dorsal view; C) male, inner view of the last protarsomere; D) tergite VIII in dorsal view; E) spiculum gastrale; F) parameres in caudal view; G) parameres in lateral view. bs—basal sclerite. Red arrow: stridulatory apparatus in D. Scale bars = 2 mm.

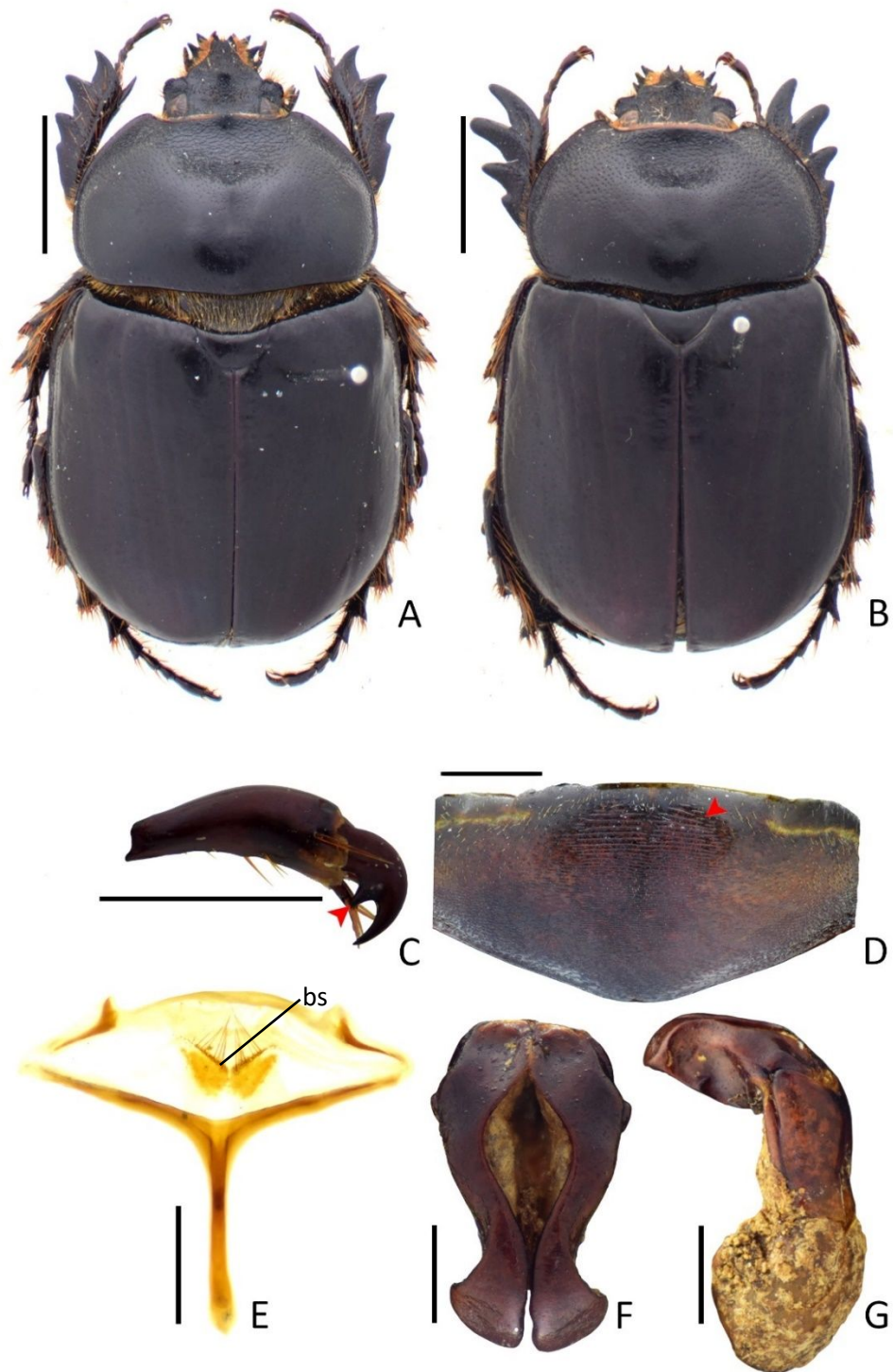


Figure 45. *Bothynus quadridens*: A) male in dorsal view; B) female in dorsal view; C) male, inner view of the last protarsomere; D) tergite VIII in dorsal view; E) spiculum gastrale; F) parameres in caudal view; G) parameres in lateral view. bs—basal sclerite. Red arrow: ventromedial tooth in C, stridulatory apparatus in D. Scale bars = 2 mm.



Figure 46. *Bothynus villiersi*: A) male in dorsal view; B) inner view of the last protarsomere; C) parameres in caudal view; D) parameres in lateral view. Scale bars = 2 mm.

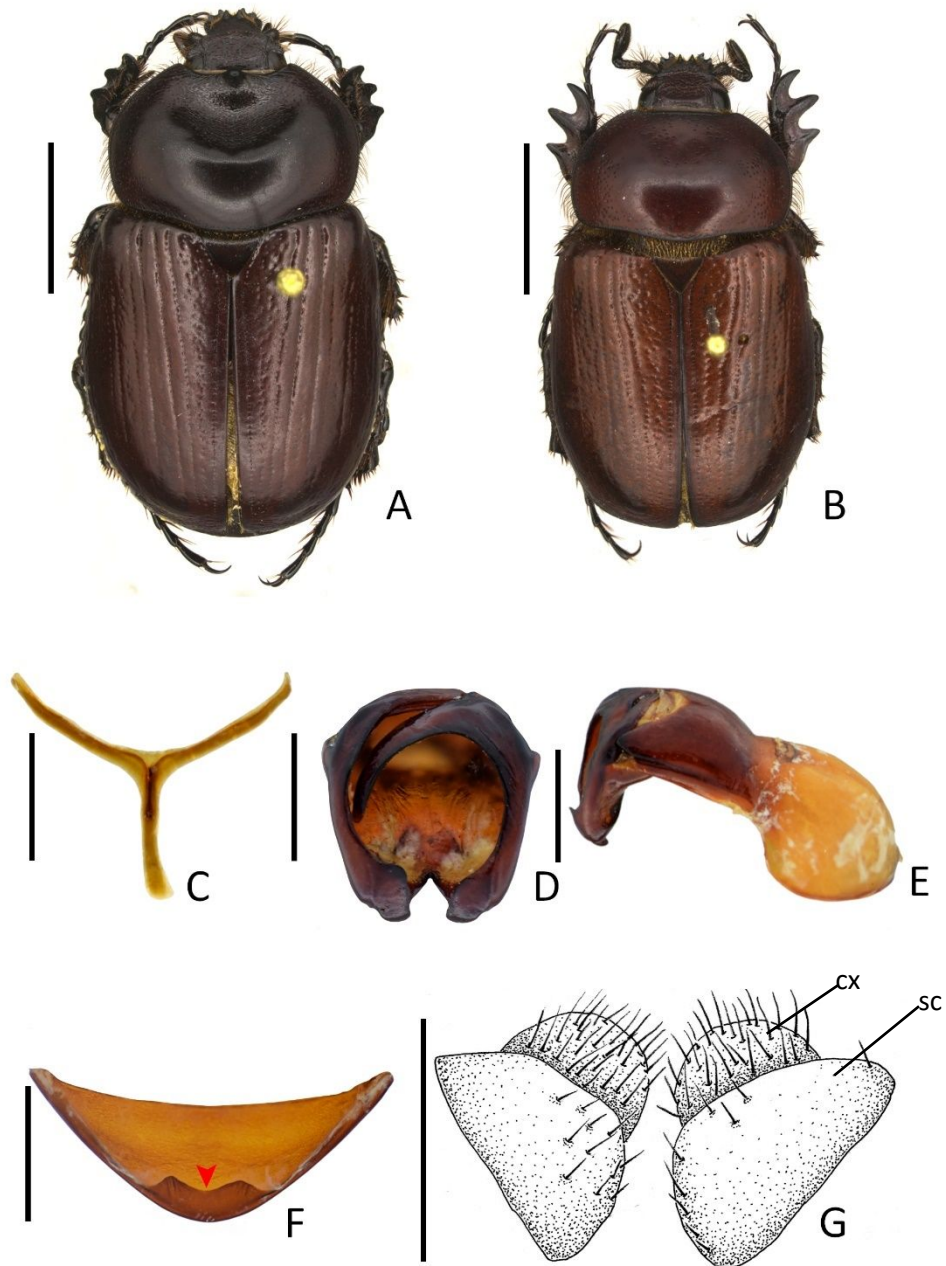


Figure 47. *Bothynus horridus*: A) male in dorsal view; B) female in dorsal view; C) spiculum gastrale; D) parameres in caudal view; E) parameres in lateral view; F) female, inner view of tergite VIII; G) female genitalia. cx–coxite, sc–subcoxite. Red arrow: invaginate apical plate in F. Scale bars = 2 mm.

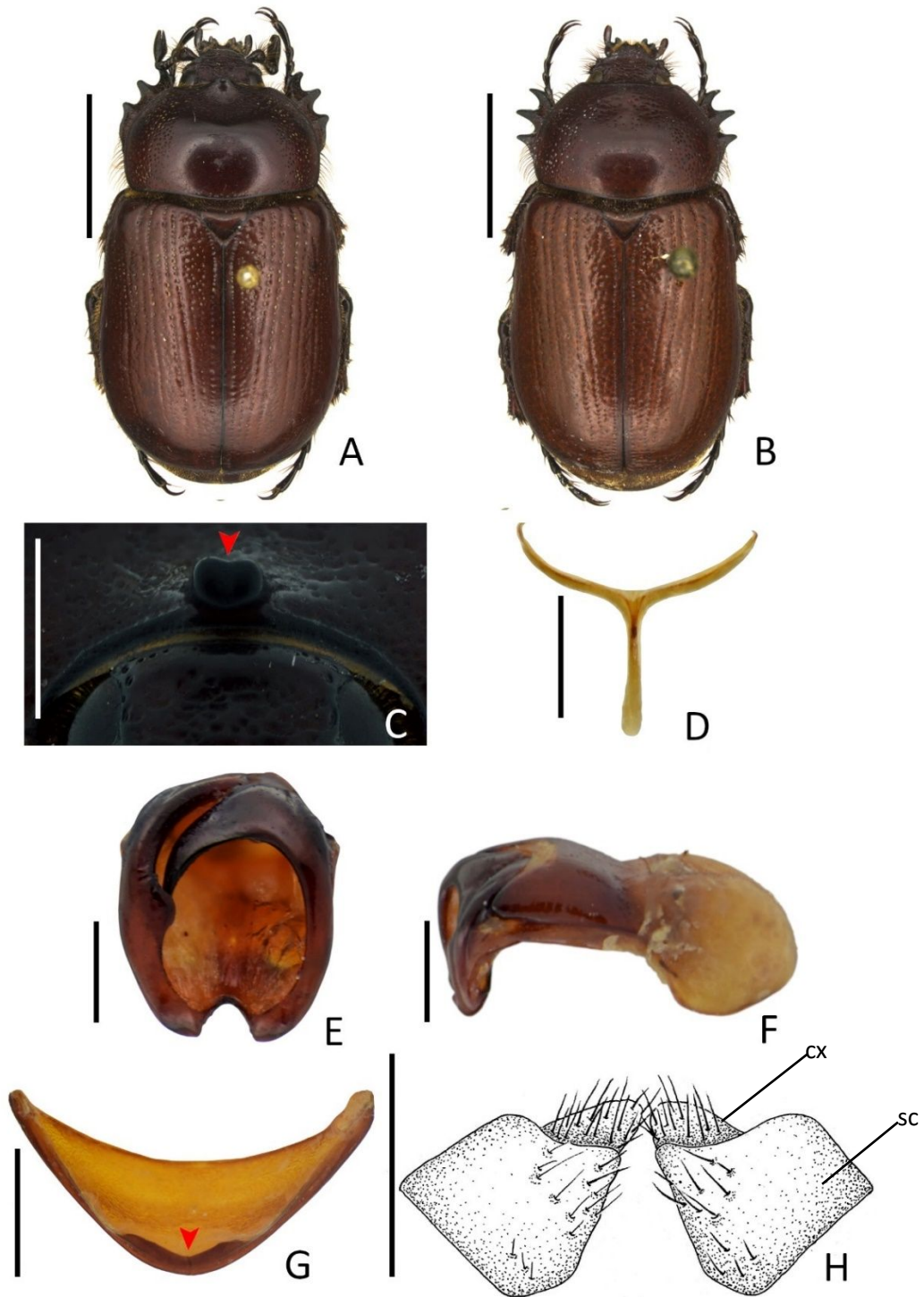


Figure 48. *Bothynus alvarengai*: A) male in dorsal view; B) female in dorsal view; C) apical tubercle in frontal view; D) spiculum gastrale; E) parameres in caudal view; F) parameres in lateral view; G) female, inner view of tergite VIII; H) female genitalia. cx–coxite, sc–subcoxite. Red arrow: apical tubercle truncated in C, invaginate plate in G. Scale bars = 2 mm.

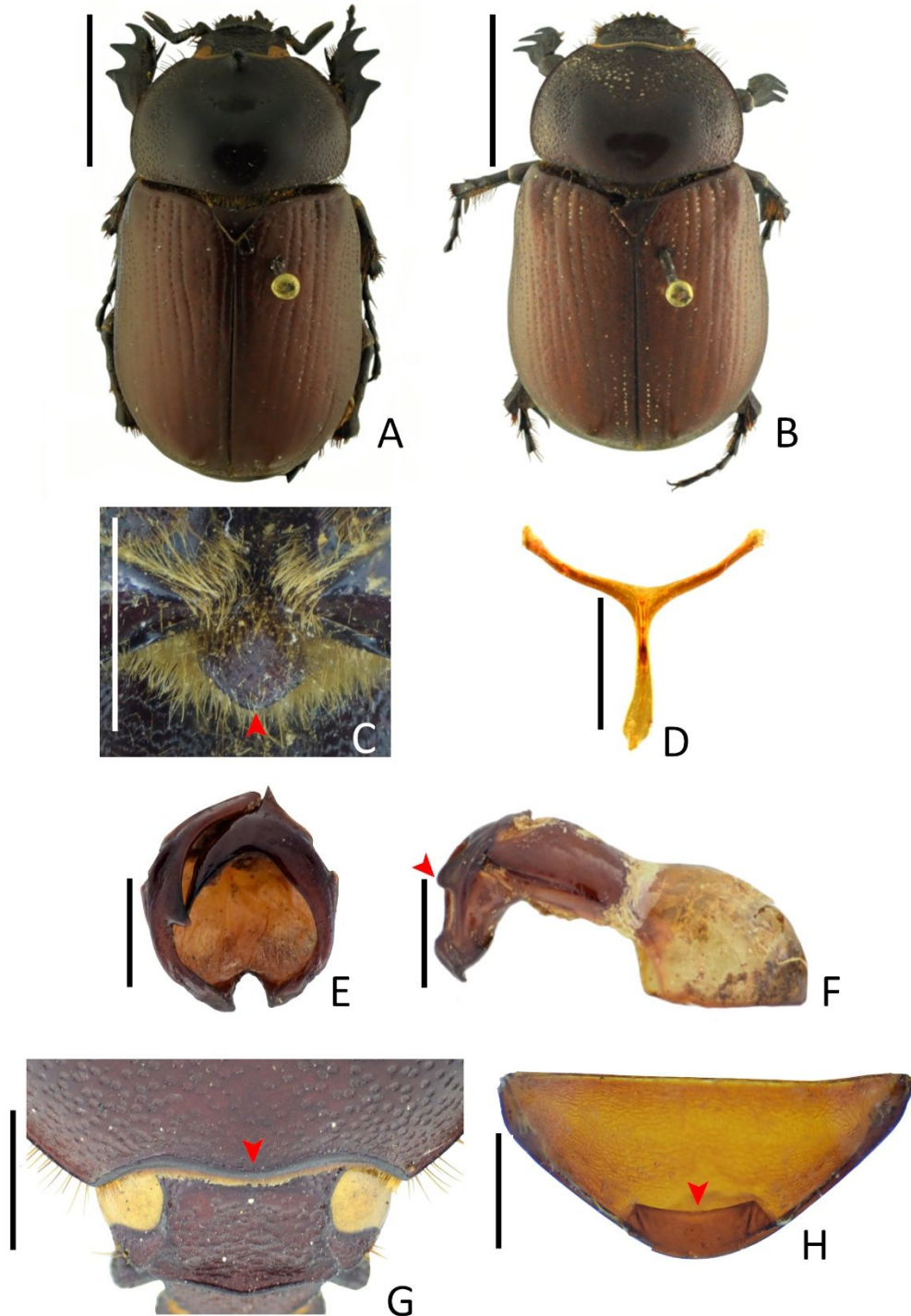


Figure 49. *Bothynus belenensis* sp. nov.: A) male in dorsal view; B) female in dorsal view; C) prosternal process; D) spiculum gastrale; E) parameres in caudal view; F) parameres in lateral view; G) female, pronotal anterior margin; H) female, inner view of tergite VIII. Red arrow: truncate apex in C, inner process raised in F, anterior pronotal margin sinuous in G, invaginate plate in H. Scale bars = 2 mm.

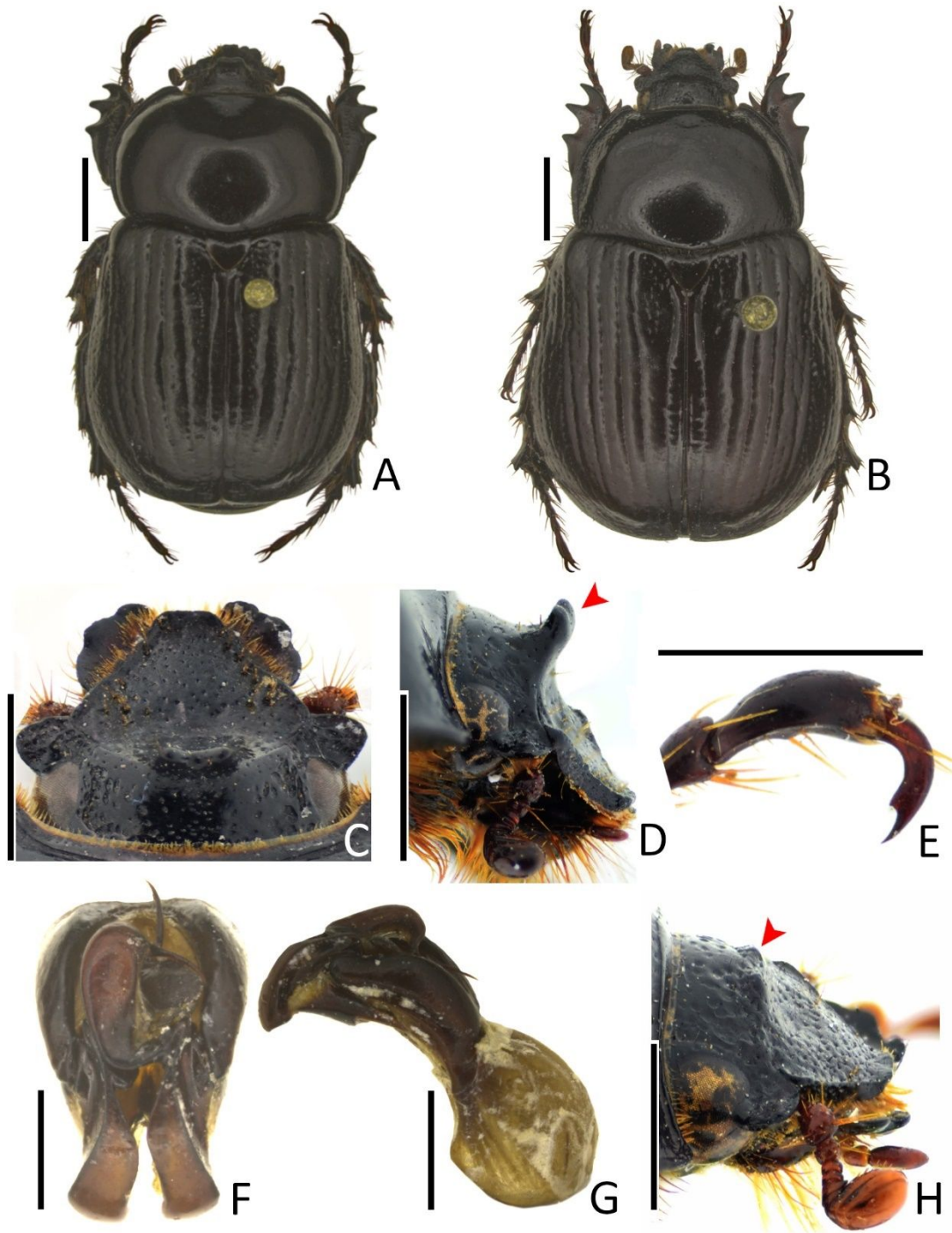


Figure 50. *Eremobothynus complexus* comb. nov.: A) male in dorsal view; B) female in dorsal view; C) male, head in dorsal view; D), male, head in lateral view; E) male, inner view of the last protarsomere; F) parameres in caudal view; G) parameres in lateral view; H) female, head in lateral view. Red arrow: frontal tubercle in D and G respectively. Scale bars = 2 mm.

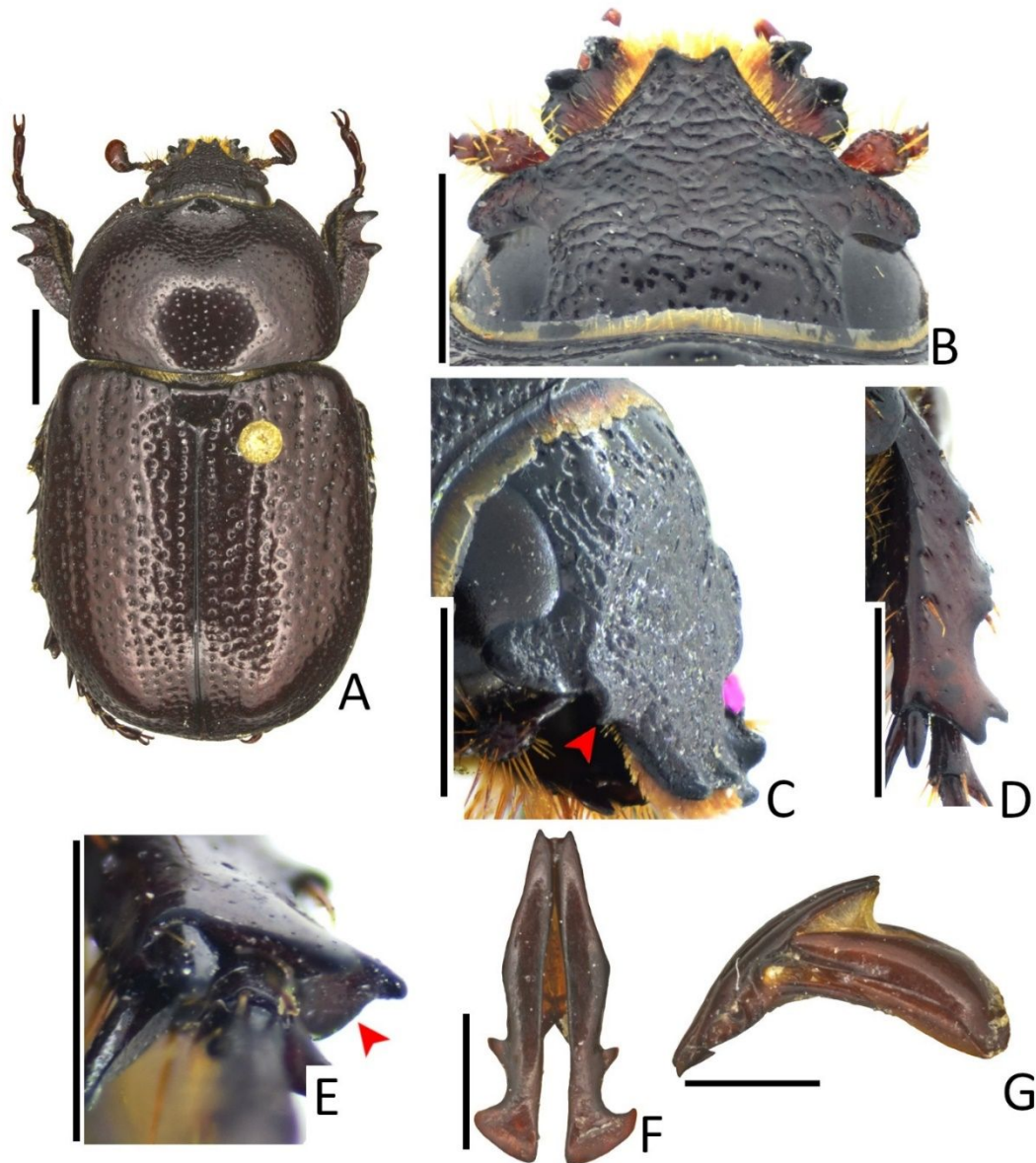


Figure 51. *Cephaloplanum herbivorus* comb. nov.: A) male in dorsal view; B) head in dorsal view; C) head in lateral view; D) mesotibia; E) metatibial apex; F) parameres in caudal view; G) parameres in lateral view. Red Arrow: deflexed lateroposterior tooth in C, apex glabrous in E. Scale bars = 2 mm.



Figure 52. Type-material: A) *Bothynus minor*; B) *Scaptophilus striatellus*; C) *Scaptophilus cribrarius*; D) *Bothynus cylindricus*; E) *Bothynus alvarengai*; F) *Bothynus simplicitaris*; G) *Ligyris herbivorus*.

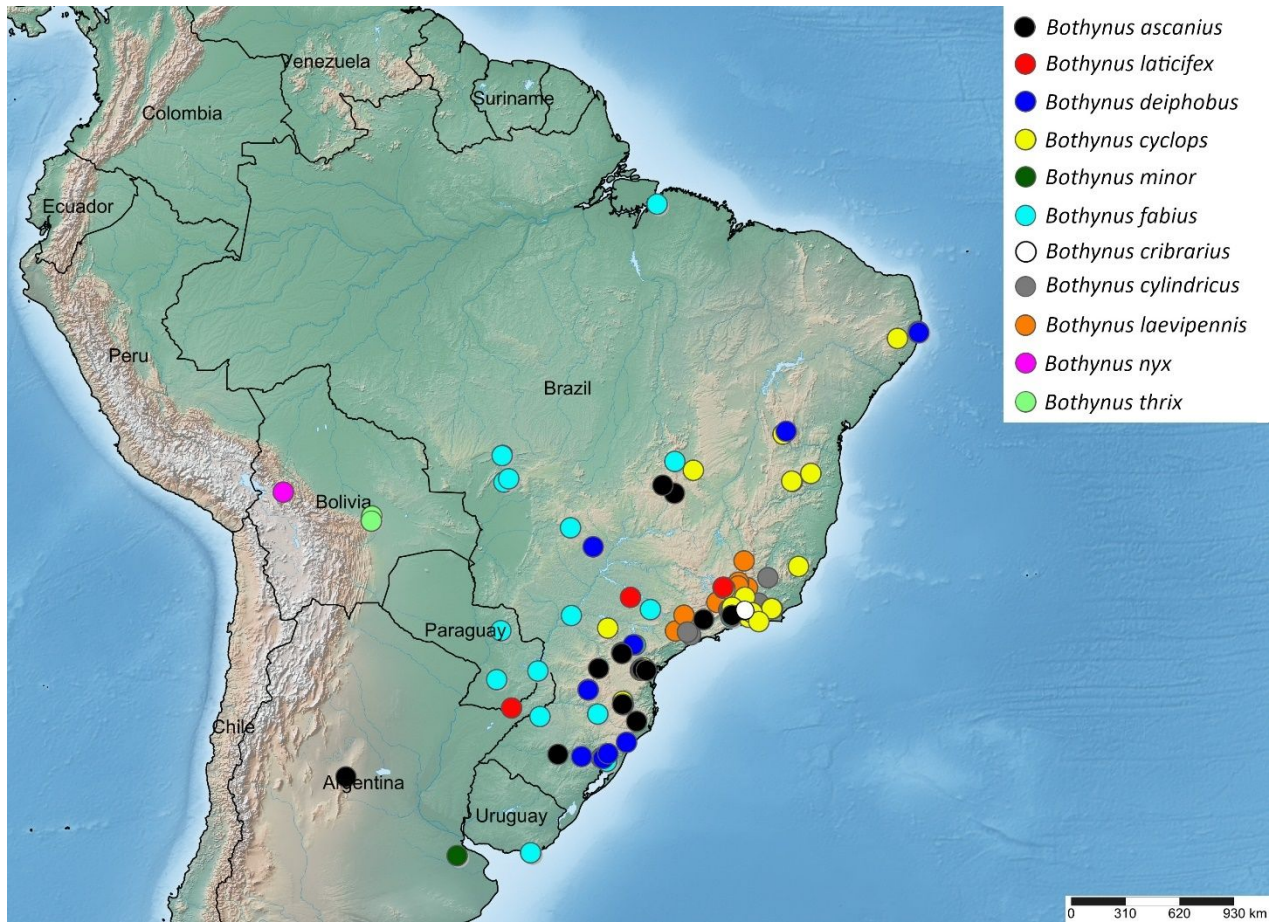


Figure 53. Distribution for the *Bothynus ascanius* species group.

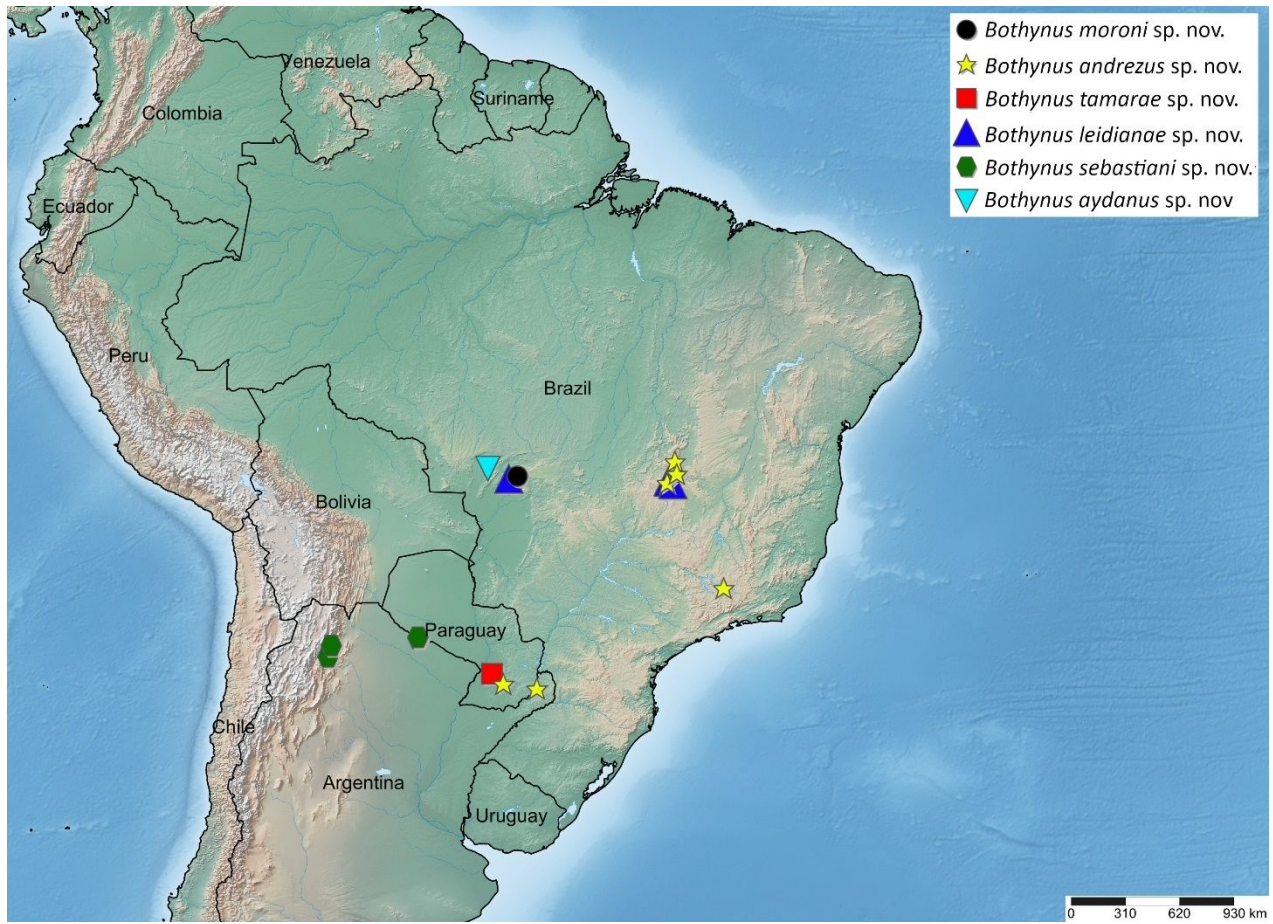


Figure 54. Distribution map for new species in the *Bothynus ascanius* species group.

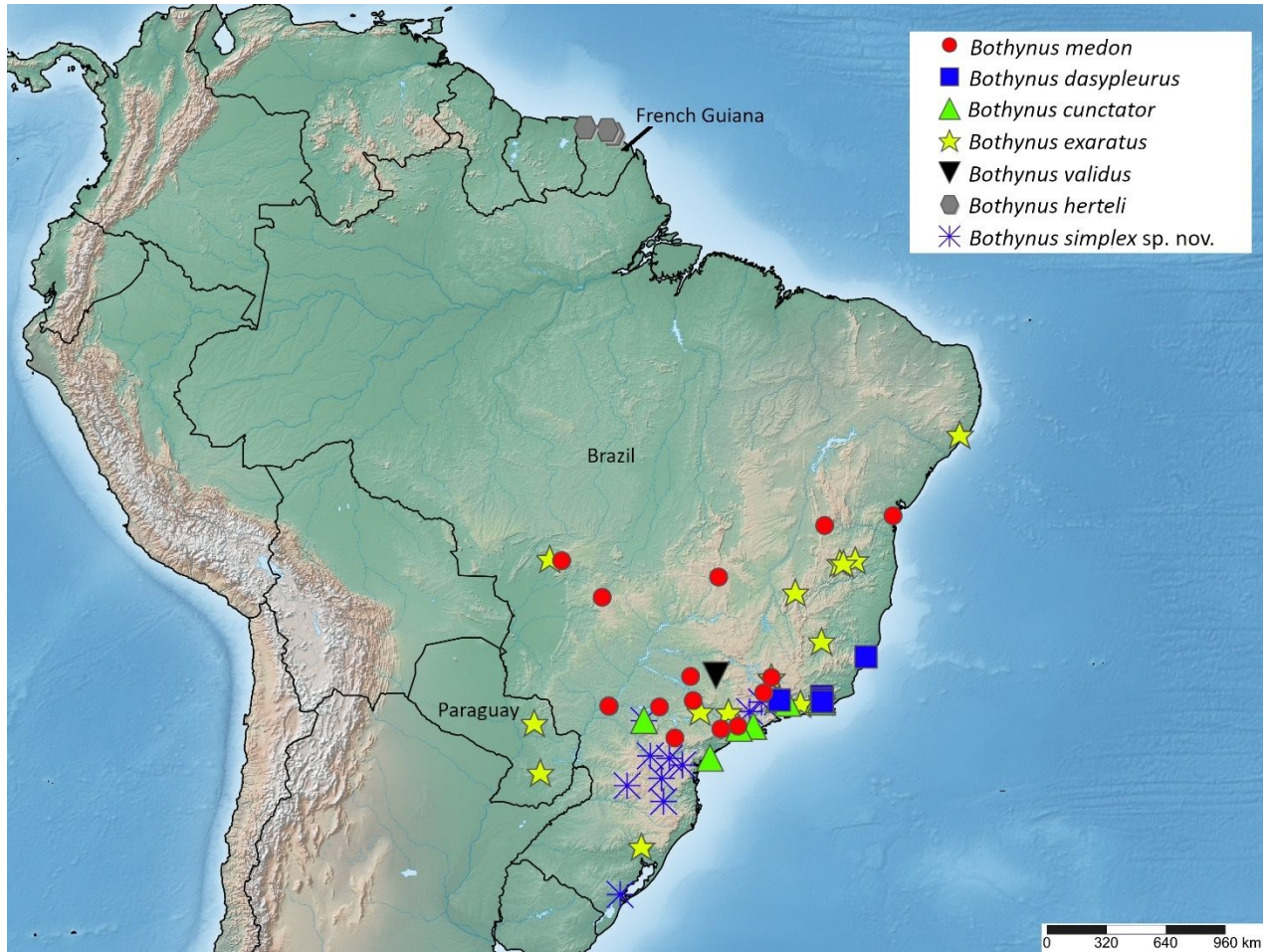


Figure 55. Distribution map for the *Bothynus medon* species group.



Figure 56. Distribution map for the *Bothynus complanus* species group.

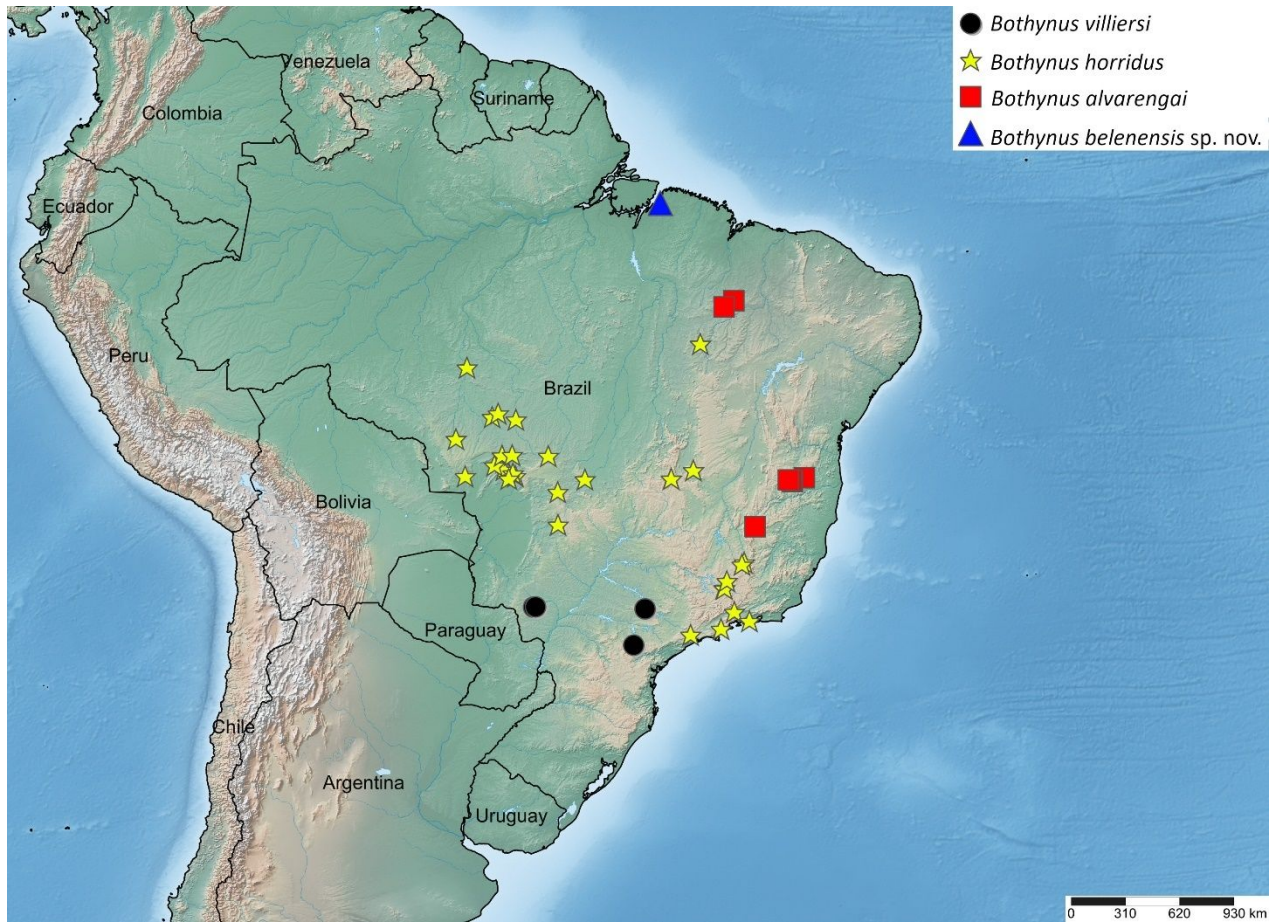


Figure 57. Distribution map for the *Bothynus villiersi* species group.



Figure 58. Distribution for the genus *Eremobothynus* in Brazil.

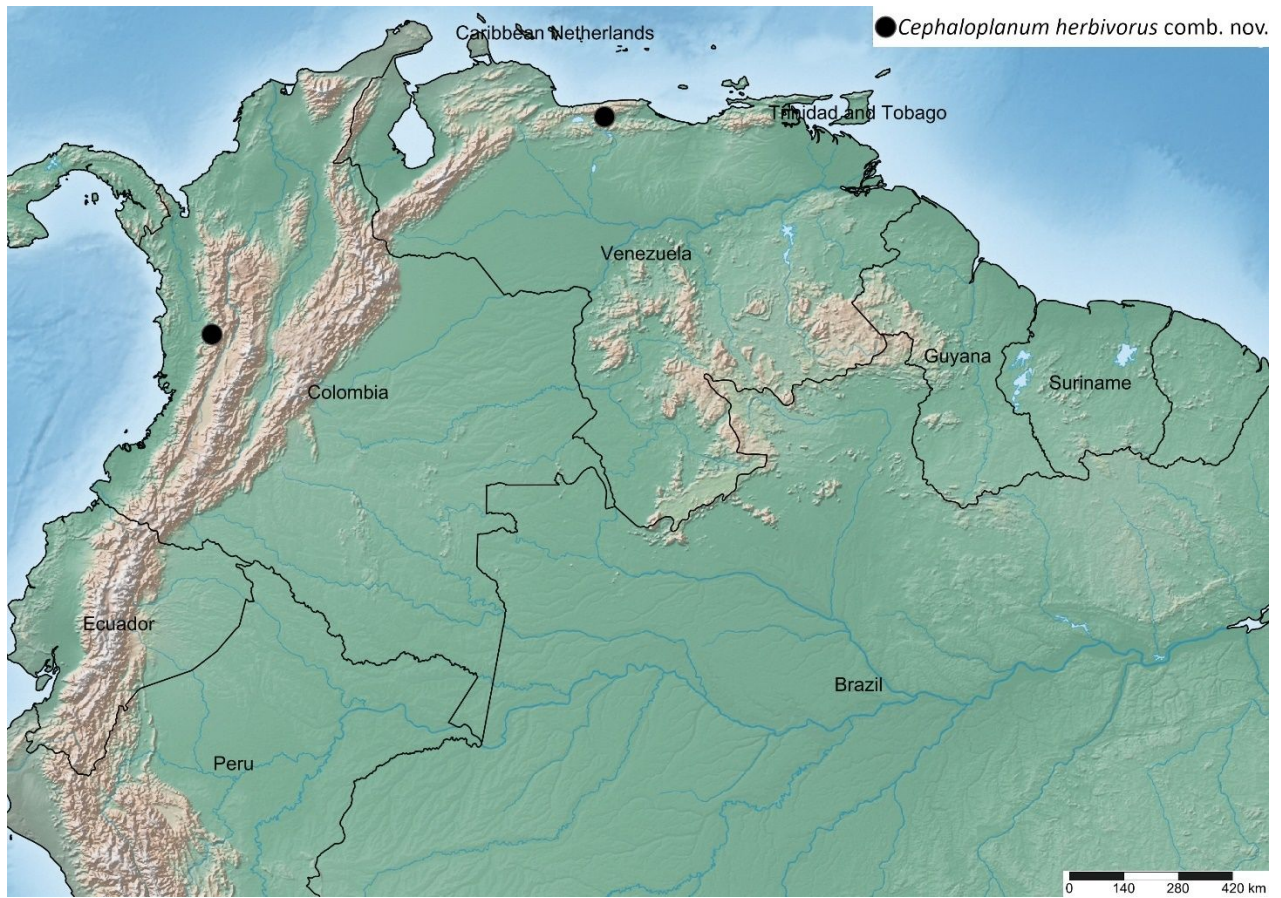


Figure 59. Distribution map for species in the genus *Cephaloplanum* gen. nov.

CHAPTER 4

FINAL CONSIDERATIONS

The phylogenetic results showed the paraphyly of *Bothynus*, and its monophyly is conditioned to the exclusion of *B. herbivorus* and *B. complexus* from the genus. The results also evidenced *Bothynus* as a lineage (excluded *B. herbivorus* and *B. complexus*) with its internal relationships formed by 36 taxa separated in five distinct clades named here of *villiersi* group, *medon* group, *complanus* group, *entellus* group, and *ascanius* group. From the five clades that compose the *Bothynus* lineage, only the *medon* and *ascanius* groups were not supported. Further studies on the *Bothynus* genus may clarify and better define these two species groups.

In the study was not possible discover the sister-genus of *Bothynus*, instead this, a clade formed by *B. herbivorus*, *B. complexus*, *S. laminifer*, *P. bonariensis*, and *E. cornutus* was recovered. *Bothynus herbivorus* is not related to any genera adopted in the analysis, being the species moved to *Planocranium* sp. nov., in CHAPTER III. Regarding *B. complexus*, it arose related to *E. cornutus*, however with low support. Despite this, biogeographic and morphological factors discussed on CHAPTER II suggest that *B. complexus* is more related to *Eremobothynus* than other Pentodontini of the New World, and for this reason, the species was moved to *Eremobothynus* in CHAPTER III.

In CHAPTER III, under the light of the phylogeny presented in CHAPTER III, the genus *Bothynus* was revised and redefined. The species diversity in the genus increased to 36 with the description of eight new: *B. moroni* sp. nov., *B. andrezus* sp. nov., *B. tamarae* sp. nov., *B. leidiana* sp. nov., *B. sebastiani* sp. nov., *B. aydanus* sp. nov., *B. simplex*, *B. belenensis* sp. nov.

Also, a nomenclatural change was made based on rules of the ICNZ, and *Bothynus fabius* was proposed as a valid name and *Bothynus striatellus* was synonymized with it.

The distribution of *Bothynus* species was expanded with new records from South America countries, with emphasis on Brazil, that assembles the most *Bothynus* species. Information from the label data also suggests the high *Bothynus* diversity in dry areas and tropical forests from central to south of South America, with few species occurring associated with tropical forest areas from northern of South America.

The present thesis was an attempt to clarify the systematics of the genus *Bothynus*, however, there are gaps in the knowledge related to the systematics for most genera of the New World Pentodontini and phylogenetic approaches and further taxonomic revisions are required to elucidate their relationships. Moreover, a phylogenetic approach is also necessary to solve the tribal definition of Pentodontini, which is currently instable, as well as the most tribes in Dynastinae.