

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ENTOMOLOGIA – PPG-ENT

Taxonomia de Agaocephalini Burmeister, 1847 (Coleoptera, Melolonthidae,
Dynastinae)

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Manaus, Amazonas

Janeiro, 2023

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Tese apresentada ao Instituto Nacional de
Pesquisas da Amazônia como parte dos
requisitos para obtenção do título de Doutor
em Ciências Biológicas, área de
concentração em Entomologia.

Manaus, Amazonas

Janeiro, 2023

Catálogo na Publicação (CIP-Brasil)

A474t Alves, Rafael Sobral
Taxonomia de Agaocephalini Burmeister, 1847 (Coleoptera,
Melolonthidae, Dynastinae) / Rafael Sobral Alves; orientador José
Wellington de Moraes; coorientador Paschoal Coelho Grossi. - Manaus: [s.l.],
2023.

16 MB
540 p. : il. color.

Tese (Doutorado - Programa de Pós-Graduação em Entomologia) -
Coordenação do Programa de Pós-Graduação, INPA, 2023.

1. Besouros-rinocerontes. 2. Taxonomia.. I. Moraes, José Wellington de.
II. Paschoal Coelho Grossi. III. Título.

CDD 595.76

Sinopse:

Foi realizada a revisão taxonômica de cinco gêneros da tribo Neotropical Agaocephalini, resultando em nove espécies novas, uma espécie revalidada, uma elevação de status para novo gênero, cinco descrições inéditas de fêmeas, um novo registro de *Lycomedes buckleyi* para o Peru, de *Minisiderus martinae* e *Colacus* para o Brasil. Foram utilizados caracteres dos aparelhos bucais e traços subutilizados da genitália masculina e feminina, quando possível, para diagnose dos táxons. Novos mapas de distribuição foram fornecidos e novas chaves de identificação foram construídas para machos e fêmeas das espécies dos gêneros revisados.

Palavras-chave: Besouros-rinoceronte, América do Sul, Neotropical, Coleoptera.

Keywords: Rhinoceros beetles, South America, Neotropical, Coleoptera.

AGRADECIMENTOS

Ao longo dessa jornada, sou muito grato a todos aqueles que me ajudaram a chegar até aqui e trilhar meu caminho como entomólogo. Agradeço a Deus pela concessão de forças nos momentos em que minha fé mais fraquejava e pela dádiva de ter ao meu lado uma ótima família e ótimos amigos.

Agradeço a Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) pela bolsa de doutorado ao longo desse tempo, bem como à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de doutorado sanduíche, sem a qual esse trabalho jamais poderia ter sido feito. Ao Instituto Nacional de Pesquisas da Amazônia (INPA) e ao Programa de Pós-Graduação em Entomologia (PPGENT) por toda a infraestrutura concedida para a pesquisa.

Aos curadores de todas as coleções das quais foram solicitados empréstimo de material, por toda a atenção e disponibilidade para fazer com que esse trabalho fosse possível. Em especial aos curadores do Natural History Museum de Londres, Max Barclay e Michael Geiser, por todo o suporte durante minha estadia no Reino Unido.

À toda equipe que faz parte do Laboratório de Sistemática e Ecologia de Artrópodes Terrestres, que se tornou uma segunda casa durante meu tempo em Manaus. Foram muitos dias, noites e madrugadas encaradas e sustentadas com doses de café, de conversas e de trabalhos produtivos. Em especial, à professora Dra. Elizabeth Franklin por me permitir usar seu laboratório todas as vezes em que foi necessário e pelas oportunidades para atuar como colaborador nas disciplinas relacionadas à Comunicação Científica no PPG-ENT e PPG-CFT.

Ao meu orientador, Dr. José Wellington de Moraes, por todo o apoio, amizade, ensinamentos, paciência e prontidão para ajudar diante de toda e qualquer dificuldade, e por toda confiança depositada para que eu pudesse realizar meu trabalho da melhor maneira possível.

Ao meu coorientador, Dr. Paschoal Coelho Grossi, pelos conselhos, orientações e muita paciência ao longo do meu treinamento para ser um taxonomista. Agradeço pela confiança, pelos ensinamentos valiosos e pela tutoria no fantástico mundo dos coleópteros.

Ao já falecido Dr. Ricardo Andrezza, meu primeiro orientador na graduação, que foi quem me apresentou à entomologia e mostrou que os insetos são criaturas fascinantes. Foram três anos de muito aprendizado, como monitor da disciplina de Entomologia Geral, que com certeza me forneceram uma base sólida nessa jornada da

vida acadêmica. Além do mais, foi quem me incentivou a sair duma pacata cidade no interior do Rio Grande do Norte para seguir jornada na selva amazônica, no INPA.

Muito obrigado, Seu Ricardo.

Agradeço ao Laboratório de Entomologia Sistemática Urbana e Forense (LESUF) e ao Dr. José Albertino Rafael pela colaboração com nosso trabalho, através de expedições de coleta e da permissão para uso da lupa de automontagem.

Aos amigos de Recife por todo o apoio logístico nas minhas estadias e pelas conversas coleopterológicas seja no ônibus Barro/Macaxeira, no Laboratório de Taxonomia ou no Bar do Bode. Um grande abraço em especial para Paulo, Andrezo e Almeida.

Aos amigos que fiz nesses anos todos de INPA, os quais estiveram sempre a disposição para ajudar e trabalhar junto comigo ao longo do mestrado e doutorado e que, certamente, levarei para vida toda. Betinho, Dieguinho, Doug, Gui, Heleodoro, Joãozinho, Renato, Larissa, Thaís, Luana, Marlus e Rayssa, muito obrigado pelas conversas produtivas sobre taxonomia, pela ajuda nos Photoshops e Illustrators da vida, pela ajuda nas dissecções dos besouros, pelas conversas produtivíssimas, pela companhia e amizade.

À Laís, minha noiva, por todos esses anos de companheirismo e amor, presente em cada momento especial dessa minha existência. Obrigado por seguir sonhando junto comigo, por toda paciência, por todo o carinho e por cada instante em que tenho o privilégio de estar ao seu lado.

Aos meus pais, Flávia e Gibson, e toda minha família, por todo amor e apoio ao longo da minha vida. Desde os 5 anos já dizia que queria ser biólogo e o que era apenas um desejo de criança se tornou realidade e meus pais sempre me incentivaram a seguir nessa profissão tão bela e exótica. O suporte de vocês foi, é, e sempre será fundamental para que eu conseguisse seguir firme com meus sonhos. Como uma vez meu pai escreveu, parafraseando Khalil Gibran, “Vós sois o arco dos quais vossos filhos são arremessados como flechas vivas. O arqueiro mira o alvo na senda do infinito e vos estica com toda a sua força para que suas flechas se projetem, rápidas e para longe. Que vosso encurvamento na mão do arqueiro seja vossa alegria, pois, assim como ele ama a flecha que voa, ama também o arco que permanece estável”. Obrigado por me fazerem alçar voos mais longos e entender que na vida nada é impossível com fé e determinação. Amo vocês!

“Se partires um dia rumo a Ítaca, faz votos de que o caminho seja longo, repleto de aventuras, repleto de saber. Nem lestrigões, nem os ciclopes, nem o colérico Poseidon te intimidem; eles no teu caminho jamais encontrarás se altivo for teu pensamento, se sutil emoção teu corpo e teu espírito tocar. Nem lestrigões, nem os ciclopes, nem o bravo Poseidon hás de ver, se tu mesmo não os lewares dentro da alma, se tua alma não os puser diante de ti.

Faz votos que o caminho seja longo. Numerosas serão as manhãs de verão nas quais, com que prazer, com que alegria, tu hás de entrar pela primeira vez em um porto para correr às lojas dos fenícios e belas mercancias adquirir: madreperolas, corais, âmbar, ébanos, e perfumes sensuais de toda a espécie, quanto houver de aromas deleitosos. A muitas cidades do Egito peregrinas para aprender, para aprender dos doutos.

Tem todo o tempo Ítaca na mente. Estás predestinado a ali chegar. Mas não apresses a viagem nunca. Melhor muitos anos lewares de jornada e fundeares na ilha velho enfim, rico de quanto ganhaste no caminho, sem esperar riquezas que Ítaca te desse. Uma bela viagem deu-te Ítaca. Sem ela não te punhas a caminho. Mais do que isso não lhe cumpre dar-te. Ítaca não te iludiu, se a achas pobre. Tu te tornaste sábio, um homem de experiência, e agora sabes o que significam Ítacas.”

Ítaca
Konstantínos Kaváfis

REJEIÇÃO PARA FINS DE NOMENCLATURA ZOOLOGICA

Este trabalho, na forma em que se apresenta (tese de doutorado), não deve ser considerado como publicação válida para fins de nomenclatura zoológica. Este é o “*disclaim and denegation*” mencionado no Código Internacional de Nomenclatura Zoológica (edição 1999), capítulo três, artigos 8.2 e 8.3.

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RESUMO

Agaocephalini Burmeister, 1847 (Scarabaeoidea, Melolonthidae, Dynastinae) é uma tribo de besouros-rinocerontes caracterizada principalmente pela pontuação irregular dos élitros e forte dimorfismo sexual, caracterizado por machos com chifres distintos na cabeça e chifre ou tubérculo no pronoto, enquanto as fêmeas possuem pronoto desarmado e cabeças com no máximo um par de tubérculos frontais. Apesar de conter alguns dos exemplares mais exuberantes de besouros-rinocerontes e atraírem a atenção de colecionadores e pesquisadores, os Agaocephalini foram revisados pela última vez por Endrödi (1970), onde foram estabelecidas todas as bases das diagnoses da tribo e dos seus gêneros. Neste trabalho foi realizado o estudo taxonômico de sete dos 10 gêneros incluídos por Endrödi (1970) na tribo, resultando na revisão de *Agacephala*, *Brachysiderus*, *Lycomedes*, *Minisiderus* e *Spodistes*, e em notas sobre *Horridocalia* e *Colacus*, promovendo a redescrição de 36 espécies, a descrição de nove espécies novas, a primeira descrição das fêmeas de cinco espécies, a redefinição de Agaocephalini, a revalidação de *Brachysiderus breyeri* **stat. rev.**, no primeiro registro de cópula de *Spodistes grandis*, na sinonimização de *Agacephala urus* **syn. nov.** com *Agacephala mannerheimi* e na elevação de status de *Lycocephala* **stat. nov.**, antigo subgênero de *Agacephala*, para gênero. Foram utilizadas características detalhadas dos aparelhos bucais e genitálias, tradicionalmente subutilizados, juntamente com traços da cabeça, pernas e esculturas cefálicas e torácicas para melhor diagnose das espécies. Novas chaves de identificação foram fornecidas para machos e fêmeas de cada um dos gêneros revisados. A distribuição geográfica dos gêneros foi atualizada e foi proposta a divisão da tribo em duas subtribos (*Agacephalina* **subtrib. nov.** e *Lycomedina* **subtrib. nov.**), além da mudança de *Colacus*, *Democrates* e *Gnathogolofa* para Pentodontini.

ABSTRACT

Agaocephalini Burmeister, 1847 (Scarabaeoidea, Melolonthidae, Dynastinae) is a tribe of rhinoceros beetles characterized mainly by the elytral irregular punctuation and strong sexual dimorphism between males and females, characterized by males with distinct horns on head, and horn or tubercle on the pronotum, while females have an unarmed pronotum and head with at most one pair of frontal tubercles. Despite containing some of the most exuberant specimens of rhinoceros beetles and attracting the attention of collectors and researchers, Agaocephalini was last reviewed by Endrödi (1970), in which all the base for the diagnosis of the tribe and its genera were established. In the current work, a taxonomic study of seven of the 10 genera included by Endrödi (1970) in the tribe was carried out, resulting in the revision of *Agacephala*, *Brachysiderus*, *Lycomedes*, *Minisiderus* and *Spodistes*, and in notes on *Horridocalia* and *Colacus*, promoting the redescription of 36 species, the description of nine new species, the first description of females of five species, the redefinition of Agaocephalini, the revalidation of *Brachysiderus breyeri* **stat. rev.**, in the first record of mating to *Spodistes grandis*, in the synonymization of *Agacephala urus* **syn. nov.** with *Agacephala mannerheimi* and in the status elevation of *Lycocephala* **stat. nov.**, a former subgenus of *Agacephala*, to genus. Detailed characters of the mouthparts and genitalia, traditionally underused, as well as traits of head, legs and cephalic and thoracic sculpture were used for a better diagnosis of the species. New identification keys were provided for males and females of each of the revised genera. The geographic distribution of the genera was updated and it was proposed to divide the tribe into two subtribes (Agacephalina **subtrib. nov.** e Lycomedina **subtrib. nov.**). Additionally, we suggest moving *Colacus*, *Democrates* and *Gnathogolofa* to Pentodontini.

SUMÁRIO

LISTA DE FIGURAS	ix
INTRODUÇÃO GERAL	1
Scarabaeoidea Latreille, 1802.....	1
Melolonthidae Leach, 1819.....	2
Dynastinae MacLeay, 1819.....	4
Agaocephalini Burmeister, 1847.....	6
OBJETIVOS	11
MATERIAL E MÉTODOS	12
CAPÍTULO I	17
CAPÍTULO II	123
CAPÍTULO III	246
CAPÍTULO IV	291
CAPÍTULO V	381
CAPÍTULO VI	473
ANEXO I	475
SÍNTESE	477
REFERÊNCIAS	479

LISTA DE FIGURAS

MATERIAL E MÉTODOS

FIGURA 1. Aparelho bucal (A-E), genitália masculina (G-I, K) e feminina (J) de *Agaocephalini*. A, Mandíbula em vista dorsal. B, Mandíbula em vista lateral. C, Mandíbula em vista ventral. D, Maxila em vista dorsal. E, Maxila em vista ventral. F, Labro em vista dorsal. G, Edeago em vista lateral. H, Parâmeros em vista lateral. I, Parâmeros em vista caudal. J, Gonocoxitos. K, Parâmeros em vista ventral.16

FIGURA 2. Cabeça (A-B, E), tórax (D), pernas (C, F-G) e abdômen (H-I) de *Agaocephalini*. A, Cabeça masculina em vista frontal. B, Cabeça feminina em vista dorsal. C, Protarso masculino em vista dorsal. D, Prosterno em vista ventral. E, Antena em vista dorsal. F, Metatíbia em vista lateral sem dentes tibiais. G, Metatíbia em vista lateral com dentes tibiais. H, Abdômen masculino em vista ventral. I, Abdômen feminino em vista ventral.17

CAPÍTULO I [Imagens no Anexo em PDF “TESE_Rafael Sobral Alves_Revisão De *Agaocephalini*_FIGURAS”]

FIGURE 1. Male and female of *Agacephala cornigera*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.2

FIGURE 2. Male head of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Head of *A. cornigera* in dorsal view. Superior white arrow pointing to lateral margin of horn; inferior white arrow pointing to connection between horns. **B**, Head of *A. cornigera* in frontal view. Superior white arrow pointing to frontal depression; inferior white arrow pointing to clypeal protuberances. **C**, Head of *A. cornigera* in dorsolateral view. White arrow pointing to connection between horns. **D**, Head of *A. cornigera* in lateral view. **E**, Head of *A. duponti* in dorsal view. **F**, Head of *A. duponti* in frontal view. Black arrows pointing to clypeal apical corners. **G**, Head of *A. duponti* in dorsolateral view. Black arrow pointing to frontal depression; white arrow pointing to punctures on cephalic horn base. **H**, Head of *A. duponti* in lateral view. White arrow showing the elevation of apex of horns. **I**, Head of *A. inermicollis* in dorsal view. Black arrow pointing to ocular canthi anterior margin. **J**, Head of *A. inermicollis*

in frontal view. **K**, Head of *A. inermicollis* in dorsolateral view. Black arrow pointing to frontal depression; white arrow pointing to sculpture of cephalic horn base. **L**, Head of *A. inermicollis* in lateral view. White arrow showing the elevation of apex of horns.

Scale bars: 1 mm.....3

FIGURE 3. Male mandible and labrum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Mandible of *A. cornigera* in ventral view. Left black arrow pointing to middle of mesal brush; right black arrow pointing to outer margin of mandible. **B**, Mandible of *A. cornigera* in lateral view. Left black arrow pointing to dorsal socket; white arrow pointing to mesal brush covering molar area; right black arrow pointing to bump anterior to condyle. **C**, Mandible of *A. cornigera* in dorsal view. White arrow pointing to apex of mesal brush. **D**, Labrum of *A. cornigera* in dorsal view. **E**, Mandible of *A. duponti* in ventral view. White arrow pointing to outer margin of mandible. **F**, Mandible of *A. duponti* in lateral view. **G**, Mandible of *A. duponti* in dorsal view. White arrows pointing to setae on outer margin of mandible. **H**, Labrum of *A. duponti* in dorsal view. Double-headed arrow comparing the length to width. **I**, Mandible of *A. inermicollis* in ventral view. White arrow pointing to the point of curvature of outer carina. **J**, Mandible of *A. inermicollis* in lateral view. White arrow pointing to outer carina reaching tooth. **K**, Mandible of *A. inermicollis* in dorsal view. Inferior white arrow pointing to outer margin of mandible. Superior white arrow pointing to mesal brush. **L**, Labrum of *A. inermicollis* in dorsal view. Scale bars: 1 mm.....4

FIGURE 4. Male maxilla and mentum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Maxilla of *A. cornigera* in ventral view. Left black arrow pointing to posterior margin of stipes; right black arrow pointing to setae on base of lateral border. **B**, Maxilla of *A. cornigera* in dorsal view. **C**, Mentum of *A. cornigera* in ventral view. **D**, Maxilla of *A. duponti* in ventral view. **E**, Maxilla of *A. duponti* in dorsal view. **F**, Mentum of *A. duponti* in ventral view. **G**, Maxilla of *A. inermicollis* in ventral view. **H**, Maxilla of *A. inermicollis* in dorsal view. **I**, Mentum of *A. inermicollis* in ventral view. Scale bars: 1 mm.....5

FIGURE 5. Male head and legs of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Ocular canthus and antennae of *A. cornigera* in dorsal view. Black arrow pointing to ocular canthus. **B**, Protarsus of *A. cornigera* in dorsal view. Superior black arrow pointing to claw tooth; inferior black arrow pointing to outer margin of protarsomere V. **C**, Mesotibia of *A. cornigera* in lateral view. Black arrow pointing to connection between metatibial apex and apical tooth. **D**, Metatibia of *A. cornigera* in lateral view. White arrows pointing to punctuation. **E**, Ocular canthus and antennae of *A. duponti* in dorsal view. Black arrow pointing to ocular canthus. **F**, Protarsus of *A. duponti* in dorsal view. Black arrow pointing to outer margin of protarsomere V. **G**, Mesotibia of *A. duponti* in lateral view. **H**, Metatibia of *A. duponti* in lateral view. **I**, Ocular canthus and antennae of *A. inermicollis* in dorsal view. **J**, Protarsus of *A. inermicollis* in dorsal view. **K**, Mesotibia of *A. inermicollis* in lateral view. **L**, Metatibia of *A. inermicollis* in lateral view. Scale bars: 1 mm.6

FIGURE 6. Male thorax and abdomen of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Pronotum of *A. cornigera* in dorsal view. White arrow pointing to pronotal tubercle. **B**, Tergite VIII of *A. cornigera* in posterior view. **C**, Abdomen of *A. cornigera* in ventral view. **D**, Pronotum of *A. duponti* in dorsal view. Black square showing shape of punctures. **E**, Tergite VIII of *A. duponti* in posterior view. **F**, Abdomen of *A. duponti* in ventral view. **G**, Pronotum of *A. inermicollis* in dorsal view. Black square showing shape of punctures. **H**, Tergite VIII of *A. inermicollis* in posterior view. **I**, Abdomen of *A. inermicollis* in ventral view. Scale bars: 5 mm.....7

FIGURE 7. Male genitalia of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Parameres of *A. cornigera* in caudal view. White arrow pointing to basal portion of parameres. **B**, Parameres of *A. cornigera* in lateral view. White arrow pointing to ventrolateral carina reaching lateral carina. **C**, Parameres of *A. cornigera* in ventral view. White arrow pointing to margin of ventral sclerite. **D**, Aedeagus of *A. cornigera* in lateral view. **E**, Parameres of *A. duponti* in caudal view. White arrow pointing to elevation of inner caudal portion of parameres; black arrows pointing to inner margin of parameres. **F**, Parameres of *A. duponti* in lateral view. White arrow pointing to lateral carina. **G**, Parameres of *A. duponti* in ventral view. Black arrow pointing to basal connection of parameres with ventral sclerite. **H**, Aedeagus of *A. duponti* in lateral view. White arrow pointing to apical corner of posterior phallobase. **I**,

Parameres of *A. inermicollis* in caudal view. **J**, Parameres of *A. inermicollis* in lateral view. Left white arrow pointing to ventrolateral carina; right white arrow pointing to lateral carina. **K**, Parameres of *A. inermicollis* in ventral view. Black arrows pointing to lateral depression of parameres; white arrow pointing to depression. **L**, Aedeagus of *A. inermicollis* in lateral view. White arrow pointing to apical corners of posterior phallobase. Scale bars: 1 mm.8

FIGURE 8. Female head of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Head of *A. cornigera* in dorsal view. **B**, Head of *A. cornigera* in lateral view. **C**, Head of *A. cornigera* in dorsolateral view. **D**, Head of *A. duponti* in dorsal view. White arrows pointing to tubercles; black arrow pointing to apex of ocular canthus. **E**, Head of *A. duponti* in lateral view. **F**, Head of *A. duponti* in dorsolateral view. White arrows pointing to lateral depressions on frons; black square showing the shape of punctures. **G**, Head of *A. inermicollis* in dorsal view. Black arrow pointing to apex of ocular canthus. **H**, Head of *A. inermicollis* in lateral view. **I**, Head of *A. inermicollis* in dorsolateral view. White arrows pointing to lateral depressions on frons; black square showing the shape of punctures. Scale bars: 1 mm.9

FIGURE 9. Female mandible and labrum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Mandible of *A. cornigera* in ventral view. Left white arrow pointing to middle of mesal brush; right white arrow pointing to outer carina. **B**, Mandible of *A. cornigera* in lateral view. **C**, Mandible of *A. cornigera* in dorsal view. Black arrow pointing to outer margin of mandibles. **D**, Labrum of *A. cornigera* in dorsal view. **E**, Mandible of *A. duponti* in ventral view. Black arrow pointing to base of inner carina. **F**, Mandible of *A. duponti* in lateral view. Black arrows pointing to mesal brush expanding to molar area. **G**, Mandible of *A. duponti* in dorsal view. Black arrows pointing to outer margin. **H**, Labrum of *A. duponti* in dorsal view. White arrow pointing to setae. **I**, Mandible of *A. inermicollis* in ventral view. Black arrow pointing to emargination between teeth. **J**, Mandible of *A. inermicollis* in lateral view. **K**, Mandible of *A. inermicollis* in dorsal view. White arrow pointing to outer margin of mandible. **L**, Labrum of *A. inermicollis* in dorsal view. Scale bars: 1 mm. ...10

FIGURE 10. Female maxilla and mentum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Maxilla of *A. cornigera* in ventral view. Black arrows

pointing to setae. **B**, Maxilla of *A. cornigera* in dorsal view. **C**, Mentum of *A. cornigera* in ventral view. **D**, Maxilla of *A. duponti* in ventral view. **E**, Maxilla of *A. duponti* in dorsal view. **F**, Mentum of *A. duponti* in ventral view. Double-headed arrows comparing maximum length to maximum width. **G**, Maxilla of *A. inermicollis* in ventral view. **H**, Maxilla of *A. inermicollis* in dorsal view. **I**, Mentum of *A. inermicollis* in ventral view. Scale bars: 1 mm.....11

FIGURE 11. Female thorax, legs and abdomen of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Pronotum of *A. cornigera* in dorsal view. **B**, Mesotibia of *A. cornigera* in lateral view. White arrow pointing to anterior carina. **C**, Metatibia of *A. cornigera* in lateral view. Black arrows pointing to anterior and posterior carina respectively. **D**, Abdomen of *A. cornigera* in ventral view. **E**, Pronotum of *A. duponti* in dorsal view. **F**, Mesotibia of *A. duponti* in lateral view. White arrows pointing to basal and apical tooth respectively. **G**, Metatibia of *A. duponti* in lateral view. White arrows pointing to setae parallel to teeth. **H**, Abdomen of *A. duponti* in ventral view. White square showing punctuation of sternite VII. **I**, Pronotum of *A. inermicollis* in dorsal view. **J**, Mesotibia of *A. inermicollis* in lateral view. **K**, Metatibia of *A. inermicollis* in lateral view. **L**, Abdomen of *A. inermicollis* in ventral view. White square showing punctuation of sternite VII. Scale bars: A,D, E,H, I,L, 5 mm; B-C, F-G, J-K, 1 mm.12

FIGURE 12. Female genitalia of *Agacephala cornigera*, *Agacephala duponti*, *Agacephala inermicollis*, *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Gonocoxites of *A. cornigera* in ventral view. Left black arrow pointing to posterior corners; superior black arrow pointing to distal coxites; white arrows pointing to setae on inner margin. **B**, Gonocoxites of *A. duponti* in ventral view. Black double-headed arrows comparing length to width. **C**, Gonocoxites of *A. inermicollis* in ventral view. Left regular arrows pointing to setae on inner apical corner; black double-headed arrows comparing length to width. **D**, Gonocoxites of *A. bicuspis* in ventral view. Black arrows pointing to setae. **E**, Gonocoxites of *A. margaridae* in ventral view. Black arrows downward pointing to distal coxites; black arrows pointing upward to apical margin; white arrows showing ventral depression. **F**, Gonocoxites of *A. mannerheimi* in ventral view. White arrows showing the divergent position of distal coxites; left black arrow pointing to connection between distal and proximal coxites; right arrows pointing to setae.

Scale bars: 1 mm.....13

FIGURE 13. Male and female of *Agacephala duponti*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Black arrow pointing to lateral posterior margin. Scale bars: 10 mm.....14

FIGURE 14. Male of *Agacephala duponti* from Argentina. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. Scale bars: 10 mm.15

FIGURE 15. Male and female of *Agacephala inermicollis*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Black arrow pointing to lateral posterior margin. Scale bars: 10 mm.....16

FIGURE 16. Male and female of *Agacephala bicuspis*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. White arrow pointing to lateral posterior margin. Scale bars: 10 mm.....17

FIGURE 17. Male head of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Head of *A. bicuspis* in dorsal view. Black arrow pointing to connection between horns. **B**, Head of *A. bicuspis* in frontal view. **C**, Head of *A. bicuspis* in dorsolateral view. **D**, Head of *A. bicuspis* in lateral view. Black arrow pointing to anterior margin of pronotum. **E**, Head of *A. margaridae* in dorsal view. **F**, Head of *A. margaridae* in frontal view. **G**, Head of *A. margaridae* in dorsolateral view. **H**, Head of *A. margaridae* in lateral view. Black arrows pointing to dorsal protuberances on horns. **I**, Head of *A. mannerheimi* in dorsal view. White arrow pointing to lateral margin of horn. **J**, Head of *A. mannerheimi* in frontal view. White arrow pointing to connection between horns; black arrow pointing to clypeal apical corner. **K**, Head of *A. mannerheimi* in dorsolateral view. **L**, Head of *A. mannerheimi* in lateral view. Scale bars: 1 mm.....18

FIGURE 18. Male mandible and labrum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Mandible of *A. bicuspis* in ventral view. White arrow pointing to outer carina; black arrow pointing to outer margin. **B**, Mandible of *A. bicuspis* in lateral view. **C**, Mandible of *A. bicuspis* in dorsal view. Black arrows pointing to carinae. **D**, Labrum of *A. bicuspis* in dorsal view. Black arrow pointing to emargination of anterior margin. **E**, Mandible of *A. margaridae* in ventral view. White arrow pointing to inner carina; black arrow pointing to outer margin. **F**, Mandible of *A. margaridae* in lateral view. Black arrow pointing to bump near socket; white arrow pointing to concavity on basal portion of molar area. **G**, Mandible of *A. margaridae* in dorsal view. Black arrow pointing to protuberance near tooth. **H**, Labrum of *A. margaridae* in dorsal view. **I**, Mandible of *A. mannerheimi* in ventral view. Black arrow pointing to outer margin. **J**, Mandible of *A. mannerheimi* in lateral view. Black arrow pointing to bump near condyle. **K**, Mandible of *A. mannerheimi* in dorsal view. Black arrow pointing to apex of mesal brush. **L**, Labrum of *A. mannerheimi* in dorsal view. Scale bars: 1 mm.....19

FIGURE 19. Male maxilla and mentum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Maxilla of *A. bicuspis* in ventral view. White arrows pointing to short teeth. **B**, Maxilla of *A. bicuspis* in dorsal view. **C**, Mentum of *A. bicuspis* in ventral view. **D**, Maxilla of *A. margaridae* in ventral view. White arrow pointing to emargination of palpifer; black arrow pointing to posterior margin of stipes. **E**, Maxilla of *A. margaridae* in dorsal view. **F**, Mentum of *A. margaridae* in ventral view. **G**, Maxilla of *A. mannerheimi* in ventral view. Black arrow pointing to outer margin of lateral border of stipes. **H**, Maxilla of *A. mannerheimi* in dorsal view. **I**, Mentum of *A. mannerheimi* in ventral view. Scale bars: 1 mm.....20

FIGURE 20. Male head and legs of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Ocular canthus and antennae of *A. bicuspis* in dorsal view. Black arrow pointing to ocular canthus. **B**, Protarsus of *A. bicuspis* in dorsal view. **C**, Mesotibia of *A. bicuspis* in lateral view. **D**, Metatibia of *A. bicuspis* in lateral view. **E**, Ocular canthus and antennae of *A. margaridae* in dorsal view. **F**, Protarsus of *A. margaridae* in dorsal view. **G**, Mesotibia of *A. margaridae* in lateral view. White arrow pointing to inner tooth. **H**, Metatibia of *A. margaridae* in lateral view. Black arrow pointing to metatibial apex. **I**, Ocular canthus and antennae of *A. mannerheimi* in dorsal

view. **J**, Protarsus of *A. mannerheimi* in dorsal view. Left black arrow pointing to basal tooth of claw; right black arrow pointing to outer margin of protarsomere V. **K**, Mesotibia of *A. mannerheimi* in lateral view. Black arrow pointing to apical outer corner. **L**, Metatibia of *A. mannerheimi* in lateral view. Scale bars: 1 mm.....21

FIGURE 21. Male thorax and abdomen of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Pronotum of *A. bicuspis* in dorsal view. **B**, Tergite VIII of *A. bicuspis* in posterior view. **C**, Abdomen of *A. bicuspis* in ventral view. **D**, Pronotum of *A. margaridae* in dorsal view. **E**, Tergite VIII of *A. margaridae* in posterior view. **F**, Abdomen of *A. margaridae* in ventral view. **G**, Pronotum of *A. mannerheimi* in dorsal view. White arrow showing apex of thoracic horn. **H**, Tergite VIII of *A. mannerheimi* in posterior view. White arrows pointing to setae on tergite VIII. **I**, Abdomen of *A. mannerheimi* in ventral view. Scale bars: 5 mm.22

FIGURE 22. Male genitalia of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Parameres of *A. bicuspis* in caudal view. Left black arrow pointing to basal angulation of lateral margin; white arrow pointing to lateral margin on apex; right black arrow pointing to inner margin. **B**, Parameres of *A. bicuspis* in lateral view. White arrow pointing to ventrolateral carina. **C**, Parameres of *A. bicuspis* in ventral view. **D**, Aedeagus of *A. bicuspis* in lateral view. **E**, Parameres of *A. margaridae* in caudal view. Black arrow pointing to tooth. **F**, Parameres of *A. margaridae* in lateral view. Black arrow pointing to apex of parameres. **G**, Parameres of *A. margaridae* in ventral view. White arrow pointing to tooth; black arrow pointing to inner margin of parameres. **H**, Aedeagus of *A. margaridae* in lateral view. **I**, Parameres of *A. mannerheimi* in caudal view. Black arrow pointing to apex of parameres; white arrow pointing to lateral margin. **J**, Parameres of *A. mannerheimi* in lateral view. Left white arrow pointing to ventrolateral tooth; right white arrow pointing to dorsal margin of parameres. **K**, Parameres of *A. mannerheimi* in ventral view. White arrows pointing to ventrolateral teeth. **L**, Aedeagus of *A. mannerheimi* in lateral view. Scale bars: 1 mm. 23

FIGURE 23. Female head of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Head of *A. bicuspis* in dorsal view. White arrows pointing to tubercles; left black arrow pointing to clypeal depression; right black arrow pointing to canthus. **B**, Head of *A. bicuspis* in lateral view. Black arrow pointing to tubercles. **C**,

Head of *A. bicuspis* in dorsolateral view. **D**, Head of *A. margaridae* in dorsal view. Left black arrow pointing to ocular canthus base; right black arrow pointing to clypeal apex. **E**, Head of *A. margaridae* in lateral view. Black arrow pointing to protuberance on frons. **F**, Head of *A. margaridae* in dorsolateral view. **G**, Head of *A. mannerheimi* in dorsal view. **H**, Head of *A. mannerheimi* in lateral view. Black arrow pointing to tubercles; left white arrow pointing to clypeal base; right white arrow pointing to carina near eye. **I**, Head of *A. mannerheimi* in dorsolateral view. White arrows pointing to tubercles. Scale bars: 1 mm.24

FIGURE 24. Female mandible and labrum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Mandible of *A. bicuspis* in ventral view. White arrow pointing to outer carina. **B**, Mandible of *A. bicuspis* in lateral view. Black arrow pointing to outer carina. **C**, Mandible of *A. bicuspis* in dorsal view. Black arrow pointing to outer margin; white arrow pointing to setae. **D**, Labrum of *A. bicuspis* in dorsal view. Black arrow pointing to emargination on anterior margin. **E**, Mandible of *A. margaridae* in ventral view. Superior white arrow pointing to inner carina; inferior white arrow pointing to basal protuberance. **F**, Mandible of *A. margaridae* in lateral view. **G**, Mandible of *A. margaridae* in dorsal view. Left white arrow pointing to setae; right white arrow pointing to apical tooth. **H**, Labrum of *A. margaridae* in dorsal view. **I**, Mandible of *A. mannerheimi* in ventral view. Left white arrow pointing to outer carina; right white arrow pointing to outer margin. **J**, Mandible of *A. mannerheimi* in lateral view. **K**, Mandible of *A. mannerheimi* in dorsal view. Left black arrow pointing to outer margin; right black arrow pointing to mesal brush. **L**, Labrum of *A. mannerheimi* in dorsal view. Scale bars: 1 mm.25

FIGURE 25. Female maxilla and mentum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Maxilla of *A. bicuspis* in ventral view. Black arrow pointing to outer margin of lateral border base. **B**, Maxilla of *A. bicuspis* in dorsal view. **C**, Mentum of *A. bicuspis* in ventral view. **D**, Maxilla of *A. margaridae* in ventral view. **E**, Maxilla of *A. margaridae* in dorsal view. **F**, Mentum of *A. margaridae* in ventral view. **G**, Maxilla of *A. mannerheimi* in ventral view. Superior black arrow pointing to apex of galea; inferior black arrow pointing to outer margin of lateral border base. **H**, Maxilla of *A. mannerheimi* in dorsal view. **I**, Mentum of *A. mannerheimi* in ventral view. Scale bars: 1 mm.26

FIGURE 26. Female thorax, legs and abdomen of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Pronotum of *A. bicuspis* in dorsal view. **B**, Mesotibia of *A. bicuspis* in lateral view. White arrow pointing to round thick setae. **C**, Metatibia of *A. bicuspis* in lateral view. **D**, Abdomen of *A. bicuspis* in ventral view. Black arrows pointing to transverse row of setae; white arrows pointing to setae on posterior margin. **E**, Pronotum of *A. margaridae* in dorsal view. **F**, Mesotibia of *A. margaridae* in lateral view. White arrow pointing to inner tooth. **G**, Metatibia of *A. margaridae* in lateral view. **H**, Abdomen of *A. margaridae* in ventral view. **I**, Pronotum of *A. mannerheimi* in dorsal view. **J**, Mesotibia of *A. mannerheimi* in lateral view. Superior white arrow showing absence of anterior carina; inferior white arrow pointing to thick setae. **K**, Metatibia of *A. mannerheimi* in lateral view. White arrow pointing to sculpture. **L**, Abdomen of *A. mannerheimi* in ventral view. Scale bars: A,D, E,H, I,L, 5 mm; B-C, F-G, J-K, 1 mm.....27

FIGURE 27. Male and female of *Agacephala margaridae*. **A**, Habitus of male in dorsal view. Black arrow pointing to mesotibia. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.28

FIGURE 28. Male and female of *Agacephala mannerheimi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.29

FIGURE 29. Male and female of *Agacephala mineira*. **A**, Habitus of male in dorsal view; **B**, habitus of female in dorsal view. Scale bars: 10 mm.....30

FIGURE 30. Male and female of *Agacephala alvarengai*. **A**, Habitus of male in dorsal view; **B**, habitus of female in dorsal view. Scale bars: 10 mm.....31

FIGURE 31. Male head, thorax and proleg of *Agacephala mineira* and *Agacephala alvarengai*. **A**, Ocular canthus of *A. mineira* in dorsal view. **B**, Ocular canthus of *A. alvarengai* in dorsal view. **C**, Pronotum of *A. mineira* in frontolateral view. **D**, Pronotum of *A. alvarengai* in frontolateral view. **E**, Protarsus of *A. mineira* in dorsal view. **F**, Protarsus of *A. alvarengai* in dorsal view. Scale bars: 1 mm.....32

FIGURE 32. Genitalia of *Agacephala mineira* and *Agacephala alvarengai*. **A**, Parameres of *A. mineira* in caudal view. **B**, Parameres of *A. alvarengai* in caudal view. Scale bars: 1 mm.....33

FIGURE 33. Male and female of *Lycocephala brasiliiana*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.34

FIGURE 34. Male head, thorax, legs and genitalia of *Lycocephala brasiliiana*. **A**, Head of *L. brasiliiana* in dorsal view. **B**, Ocular canthus of *L. brasiliiana* in dorsal view. **C**, Protarsus of *L. brasiliiana* in dorsal view. **D**, Pronotum of *L. brasiliiana* in dorsal view. **E**, Pronotal lateral margin of *L. brasiliiana* in dorsal view. **F**, Metatibia of *L. brasiliiana* in ventral view. **G**, Parameres of *L. brasiliiana* in caudal view. **H**, Parameres of *L. brasiliiana* in lateral view. **I**, Aedeagus of *L. brasiliiana* in lateral view. Scale bars: A-C, G-E, I, 1 mm; D, F, 5 mm.....35

FIGURE 35. Distribution map of *Agacephala* and *Lycocephala*.....36

FIGURE 36. Male and female of *Aegopsis*. **A**, Habitus of *Aegopsis curvicornis* in dorsal view. **B**, Habitus of *Aegopsis curvicornis* in lateral view. Black arrow pointing to thoracic horn. **C**, Head of *Aegopsis curvicornis* in dorsolateral view. Black arrow pointing to clypeal apex. **D**, Head of *Aegopsis curvicornis* in frontal view. Black arrow pointing to clypeal sides. **E**, Habitus of female *Aegopsis bolboceridus* in dorsal view. **F**, Habitus of female *Aegopsis bolboceridus* in lateral view. Black arrow pointing to tergite VII. **G**, Head of female *Aegopsis bolboceridus* in dorsal view. **H**, Head of female *Aegopsis curvicornis* in dorsal view. Black arrow pointing to clypeal base. Scale bars: 1 mm.37

FIGURE 37. Diagnostic traits of head and thorax of Agaocephalini. **A**, Head and pronotum of *Agacephala* sp. **B**, Head and pronotum of *Spodistes* sp. **C**, Head and pronotum of *Minisiderus* sp. **D**, Head and pronotum of *Brachysiderus* sp.38

FIGURE 38. Diagnostic traits of appendages, head, thorax and mouthparts of Agaocephalini. **A**, Protarsus of male *Agacephala* sp. in dorsal view. **B**, Protarsus of

female *Agacephala* sp. in dorsal view. **C**, Head of *Agacephala* sp. in dorsolateral view. White arrows pointing to tubercles. **D**, Head and pronotum of *Minisiderus* sp. in dorsolateral view. **E**, Elytra of male *Agacephala* sp. in dorsal view. **F**, Mandible of *Agacephala* sp. in dorsal view. **G**, Mandible of *Agacephala* sp. in lateral view. White arrow pointing to molar area. **H**, Metatarsomere I of *Agacephala* sp. in ventral view. **I**, Prosternum of *Lycomedes* sp. in ventral view. White arrow pointing to prosternal process. **J**, Prosternum of *Aegopsis* sp. in ventral view.39

FIGURE 39. Comparison between Agaocephalini and *Colacus*, *Democrates* and *Gnathogolofa*. **A**, Mandible of *Colacus* sp. in dorsal view. **B**, Protibia of *Democrates* sp. in ventral view. White arrow pointing to base of protarsomere I; black arrow pointing to inner corner of protibia. **C**, Metatarsomere I of *Gnathogolofa* sp. in lateral view. **D**, Head and pronotum of *Gnathogolofa* sp. in lateral view. **E**, Mandible of *Agacephala* sp. in dorsal view. **F**, Protibia of *Agacephala* sp. in ventral view. White arrow pointing to base of protarsomere I; black arrow pointing to inner corner of protibia. **G**, Metatarsomere I of *Agacephala* sp. in ventrolateral view. **H**, Head and pronotum of *Minisiderus* sp. in lateral view.....40

FIGURE 40. Diagnostic traits of Agaocephalina **subtrib. nov.** **A**, Protarsus of *Agacephala duponti* in dorsal view. **B**, Protarsus of *Agacephala mannerheimi* in dorsal view; **C**, Protarsomere IV of *Agacephala mannerheimi* in dorsal view. **D**, Ocular canthus of *Agacephala* sp. in dorsal view. **E**, Head of *Minisiderus* sp. in dorsal view. **F**, Head of female *Minisiderus* sp. in dorsal view. **G**, Head and pronotum of female *Minisiderus* sp. in dorsal view. **H**, Head of *Agacephala* sp. in dorsal view.....41

FIGURE 41. Diagnostic traits of Lycomedina **subtrib. nov.** **A**, Protarsus of *Brachysiderus* sp. in dorsal view. **B**, Protarsomere IV of *Brachysiderus* sp. in dorsal view; **C**, Head of *Brachysiderus* sp. in dorsal view. **D**, Head of *Lycomedes* sp. in dorsal view. **E**, Head of female *Lycomedes* sp. in dorsal view. **F**, Pronotum of female *Lycomedes* sp. in dorsal view. **G**, Head of female *Brachysiderus* sp. in dorsal view.42

FIGURE 42. Habitus of *Antodon goryi*. **A**, Male of *Antodon goryi* in dorsal view. **B**, Female of *Antodon goryi* in dorsal view. Scale bars: 10 mm.43

FIGURE 43. Habitus of *Mitracephala humboldti*. **A**, Male of *Mitracephala humboldti* in dorsal view. **B**, Female of *Mitracephala humboldti* in dorsal view. **C**, Head of male *Mitracephala humboldti* in frontal view. **D**, Legs and part of thorax of female *Mitracephala humboldti* in ventral view. **E**, Elytra and tergite VIII of female *Mitracephala humboldti* in posterior view. Scale bars: A-B, D-E, 10 mm; C, 5 mm.....44

CAPÍTULO II [Imagens no Anexo em PDF “TESE_Rafael Sobral Alves_Revisão De Agaocephalini_FIGURAS”]

FIGURE 1. Male of *Minisiderus paranensis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm. Photo: Natural History Museum Data Portal46

FIGURE 2. Male of *Minisiderus lenorae*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.....47

FIGURE 3. Head and pronotum of *Minisiderus lenorae* and *Minisiderus paranensis*. **A**, Head of *M. lenorae* in dorsal view. White arrows pointing to wrinkles. **B**, head of *M. lenorae* in frontal view. Double-headed white arrows showing width of horns and clypeal apex; black arrow pointing to lateral margin of clypeus. **C**, head of *M. lenorae* in lateral view. White arrow pointing to concavity on anterior margin. **D**, head of *M. lenorae* in frontolateral view. White arrows pointing to pronotal tubercles; black arrow pointing to clypeal apex. **E**, head of *M. paranensis* in dorsal view. Downside black arrow pointing to anterior margin of canthus; upside black arrow pointing to canthus apex. **F**, head of *M. paranensis* in frontal view. Double-headed white arrows showing width of horns and clypeal apex; black arrow pointing to lateral margin of clypeus. **G**, head of *M. paranensis* in lateral view. Black arrow showing apex of horn upturned; white arrow pointing to pronotal anterior margin. **H**, head of *M. paranensis* in frontolateral view. White arrows pointing to pronotal tubercles; black arrow pointing to clypeal apex. Scale bars: 1 mm.48

FIGURE 4. Mandible and Labrum of *Minisiderus lenorae*, *Minisiderus paranensis*. **A**, Mandible of *M. lenorae* in ventral view. Left black arrow pointing to lateral margin of molar area; right black arrow pointing to depression. **B**, Mandible of *M. lenorae* in dorsal view. White arrow pointing to limit of mesal brush; double-headed black arrows

comparing sizes. **C**, Mandible of *M. lenorae* in lateral view. **D**, Labrum of *M. lenorae* in dorsal view. **E**, Mandible of *M. paranensis* in ventral view. Left black arrow pointing to lateral margin of molar area; right black arrow pointing to depression. **F**, Mandible of *M. paranensis* in dorsal view. White arrow pointing to limit of mesal brush; double-headed black arrows comparing sizes. **G**, Mandible of *M. paranensis* in lateral view. **H**, Labrum of *M. paranensis* in dorsal view. Scale bars: 1 mm.49

FIGURE 5. Maxilla and Mentum of *Minisiderus lenorae*, *Minisiderus paranensis*. **A**, Maxilla of *M. lenorae* in ventral view. Left black arrow pointing to apex of galea; double-headed white arrows comparing length to width of palpomere II. **B**, Maxilla of *M. lenorae* in dorsal view. Black arrow pointing to sensorial area in palpomere IV. **C**, Mentum of *M. lenorae* in ventral view. **D**, Maxilla of *M. paranensis* in ventral view. Left black arrow pointing to apex of galea; right black arrow pointing to lateral border of stipes; white arrows pointing to sinuosities on lateral border; double-headed black arrows comparing length to width of palpomere II. **E**, Maxilla of *M. paranensis* in dorsal view. Black arrow pointing to sensorial area in palpomere IV. **F**, Mentum of *M. paranensis* in ventral view. Scale bars: 1 mm.50

FIGURE 6. Male genitalia of *Minisiderus lenorae*, *Minisiderus paranensis*. **A**, Parameres of *M. lenorae* in caudal view. Upper white arrow pointing to carina on parameres; lower white arrow pointing to posterior base; upper black arrows pointing to ridges; lower black arrow pointing to depression of posterior phallobase. **B**, Parameres of *M. lenorae* in lateral view. Black arrow pointing to apex of depression. **C**, Parameres of *M. lenorae* in ventral view. Upper black arrow pointing to apex of parameres; lower black arrow pointing to ventral carina. **D**, Microscopy vision of parameres of *M. lenorae* in caudal view. White arrows pointing to ridges. **E**, Parameres of *M. paranensis* in caudal view. Left white arrow showing the lack of carina on parameres; right white arrows pointing to ridges; left black arrows pointing to posterior base; right black arrow pointing to depression of posterior phallobase. **F**, Parameres of *M. paranensis* in lateral view. Black arrow pointing to apex of depression. **G**, Parameres of *M. paranensis* in ventral view. Upper black arrow pointing to apex of parameres; lower black arrow pointing to ventral carina. **H**, Microscopy vision of parameres of *M. paranensis* in caudal view. White arrows pointing to ridges. Scale bars: 1 mm.51

FIGURE 8. Male of *Minisiderus minicola*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. White lines comparing length to width of outer margin of metatibia; black arrow pointing to connection between apical margin to apical tooth. Scale bars: 10 mm.....52

FIGURE 9. Head of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Head of *M. minicola* in dorsal view. White arrow pointing to protuberance on canthus base. **B**, Head of *M. minicola* in frontal view. Upper white arrow pointing to carina on anterior margin; lower white arrow pointing to connection between horns. **C**, Head of *M. minicola* in frontolateral view. **D**, Head of *M. benjamini* in dorsal view. Black arrow pointing to protuberance on canthus base. **E**, Head of *M. benjamini* in frontal view. White arrow pointing to connection between horns. **F**, Head of *M. benjamini* in frontolateral view. White arrow showing limits of frontal depression. **G**, Head of *M. bertolossiorum* in dorsal view. Black arrow pointing to protuberance on clypeal base. **H**, Head of *M. bertolossiorum* in frontal view. Upper black arrow pointing to tubercles; lower black arrow pointing to base of cephalic horns; white arrow pointing to sides of horns. **I**, Head of *M. bertolossiorum* in frontolateral view. Scale bars: 1 mm.....53

FIGURE 10. Mandible and Labrum of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Mandible of *M. minicola* in ventral view. **B**, Mandible of *M. minicola* in dorsal view. **C**, Mandible of *M. minicola* in lateral view. **D**, Labrum of *M. minicola* in dorsal view. **E**, Mandible of *M. benjamini* in ventral view. Left black arrow pointing to apex of mesal brush; right black arrow pointing to tooth. **F**, Mandible of *M. benjamini* in dorsal view. White arrow pointing to emargination of tooth; black arrows pointing to outer margin. **G**, Mandible of *M. benjamini* in lateral view. White arrow pointing to apex of molar area. **H**, Labrum of *M. benjamini* in dorsal view. **I**, Mandible of *M. bertolossiorum* in ventral view. White arrow pointing to inner carina; black arrow pointing to tooth. **J**, Mandible of *M. bertolossiorum* in dorsal view. Black arrow pointing to tooth; white arrow pointing to base of mesal brush. **K**, Mandible of *M. bertolossiorum* in lateral view. Black arrow pointing to ventral condyle. **L**, Labrum of *M. bertolossiorum* in dorsal view. Black arrow pointing to middle of anterior margin. Scale bars: 1 mm.....54

FIGURE 11. Maxilla and Mentum of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Maxilla of *M. minicola* in ventral view. **B**, Maxilla of *M. minicola* in dorsal view. **C**, Mentum of *M. minicola* in ventral view. **D**, Maxilla of *M. benjamini* in ventral view. White arrow pointing to posterior projection of ventral stipes. **E**, Maxilla of *M. benjamini* in dorsal view. Black arrow pointing to cardum. **F**, Mentum of *M. benjamini* in ventral view. Upper white arrow pointing to mentum apex; lower white arrows pointing to apical corners of mentum. **G**, Maxilla of *M. bertolossiorum* in ventral view. **H**, Maxilla of *M. bertolossiorum* in dorsal view. Black arrow pointing to subgalea crossing margin of stipes. **I**, Mentum of *M. bertolossiorum* in ventral view. Scale bars: 1 mm.....55

FIGURE 12. Male genitalia of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Parameres of *M. minicola* in caudal view. Black arrow pointing to outer margin. **B**, Parameres of *M. minicola* in lateral view. Left red arrow pointing to ventral carina. Right red arrow pointing to dorsal emargination. **C**, Parameres of *M. minicola* in ventral view. **D**, Parameres of *M. benjamini* in caudal view. Right black arrow pointing to outer margin; left black arrow pointing to notch at inner margin. **E**, Parameres of *M. benjamini* in lateral view. Black arrow pointing to lateral margin; white arrow pointing to apical margin of posterior phallobase. **F**, Parameres of *M. benjamini* in ventral view. Red arrow pointing to ventral depression. **G**, Parameres of *M. bertolossiorum* in caudal view. Black arrow pointing to outer margin; upper white arrow pointing to notch at inner margin; lower white arrow pointing to inner margin of basal portion. **H**, Parameres of *M. bertolossiorum* in lateral view. Left black arrow pointing to ventral carina; right black arrow pointing to lateral margin; white arrow pointing to basal carina. **I**, Parameres of *M. bertolossiorum* in ventral view. Black arrows pointing to anterior corners of ventral sclerite; white arrow pointing to lateral margin of ventral sclerite. Scale bars: 1 mm.....56

FIGURE 13. Male of *Minisiderus minicola* with antennal anomaly. **A**, Head in dorsal view. **B**, Head in ventral view. **C**, in ventral view, long-clubed left antennae. **C**, in ventral view, short-clubed right antennae. White arrows in C-D showing antennal insertion. Scale bars: 1 mm.....57

FIGURE 14. Head and metatibia of *Minisiderus benjamini*. **A**, Head of *M. benjamini* in dorsal view. Double-headed black arrow comparing clypeal length to width. **B**, Head of *M. benjamini* in lateral view. Black arrows pointing to frontal tubercles. **C**, Ocular canthus of *M. benjamini* in dorsal view. Black arrow pointing to canthus apex. **D**, Metatibia of *M. benjamini* in ventral view. Scale bars: A-C, 1 mm, D, 2 mm.....58

FIGURE 15. Male and female of *Minisiderus benjamini*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. White arrows pointing to pronotal wrinkles; Upper black arrow pointing to pronotal side flattened; lower black arrows showing elytral rugosities. **D**, habitus of female in lateral view. Black arrow pointing to posterior margin of tergite VIII. Scale bars: 10 mm.....59

FIGURE 16. Male and female of *Minisiderus mielkeorum*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.60

FIGURE 17. Male head, pronotum, metatibia and genitalia of *Minisiderus mielkeorum* and *Minisiderus elyanae*. **A**, Head and pronotum of *M. mielkeorum* in frontal view. White arrow pointing to space between tubercles. **B**, Head and pronotum of *M. mielkeorum* in lateral view. Black arrow pointing to horn carina; red arrow pointing to frontal tubercle; white arrow pointing to pronotal tubercles. **C**, Head and pronotum of *M. mielkeorum* in dorsal view. **D**, Metatibia of *M. mielkeorum* in ventral view. Upper white arrow pointing to anterior carina; lower white arrow pointing to posterior carina. **E**, Genitalia of *M. mielkeorum* in lateral view. **F**, Head and pronotum of *M. elyanae* in frontal view. Red arrow pointing to apex of pronotal tubercles. **G**, Head and pronotum of *M. elyanae* in lateral view. Red arrow pointing to frontal tubercles; white arrow pointing to pronotal tubercle. **H**, Head and pronotum of *M. elyanae* in dorsal view. **I**, Metatibia of *M. elyanae* in ventral view. Upper white arrow pointing to anterior carina; lower white arrow pointing to posterior carina; black arrow pointing to medial tooth. **J**, Genitalia of *M. elyanae* in lateral view. Scale bars: 1 mm.61

FIGURE 18. Mandible and Labrum of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Mandible of *M. mielkeorum* in ventral view. Black arrow pointing to tooth. **B**, Mandible of *M. mielkeorum* in dorsal view. Black arrow pointing to outer margin. **C**,

Mandible of *M. mielkeorum* in lateral view. Black arrow pointing to ventral bump. **D**, Labrum of *M. mielkeorum* in dorsal view. **E**, Mandible of *M. elyanae* in ventral view. Upper white setae pointing to tooth; lower white setae pointing to lateral angulation of molar area margin. **F**, Mandible of *M. elyanae* in dorsal view. Black arrow pointing to outer margin. **G**, Mandible of *M. elyanae* in lateral view. Black arrow pointing to ventral bump. **H**, Labrum of *M. elyanae* in dorsal view. Scale bars: 1 mm.....62

FIGURE 19. Maxilla and Mentum of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Maxilla of *M. mielkeorum* in ventral view. Black arrow pointing to inner margin of stipes. **B**, Maxilla of *M. mielkeorum* in dorsal view. Black arrow pointing to inner margin of stipes. **C**, Mentum of *M. mielkeorum* in ventral view. White arrow pointing to punctures. **D**, Maxilla of *M. elyanae* in ventral view. Black arrow pointing to lateral border. **E**, Maxilla of *M. elyanae* in dorsal view. Black arrow pointing to inner margin of stipes. **F**, Mentum of *M. elyanae* in ventral view. White arrow pointing to punctures. Scale bars: 1 mm.....63

FIGURE 20. Male genitalia of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Parameres of *Minisiderus mielkeorum* in caudal view. White arrow pointing to outer margin; red arrow pointing to protrusion of inner margin at basal portion. **B**, Parameres of *Minisiderus mielkeorum* in lateral view. White arrow pointing to ventral carina; black arrow pointing to apical margin of posterior phallobase. **C**, Parameres of *Minisiderus mielkeorum* in ventral view. White arrow pointing to basal portion of margin of parameres; red arrow pointing to anterior emargination of ventral sclerite; black arrow pointing to apical inner margin. **D**, Parameres of *Minisiderus elyanae* in caudal view. White arrow pointing to notch at outer margin; red arrow pointing to inner margin at basal portion. **E**, Parameres of *Minisiderus elyanae* in lateral view. Upper white arrow pointing to ventral carina; lower white arrow pointing to apical margin of posterior phallobase. **F**, Parameres of *Minisiderus elyanae* in ventral view. White arrow pointing to basal portion of margin of parameres; red arrow pointing to emargination of ventral sclerite. Scale bars: 1 mm.....64

FIGURE 21. Female head, metatibia and genitalia of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Head of *Minisiderus mielkeorum* in dorsal view. Black arrow pointing to canthus anterior margin; double-headed black arrows comparing clypeal

length to width; white arrows pointing to punctures on clypeal apical portion. **B**, Coxites of *M. mielkeorum* in ventral view. Black arrows pointing to apical emargination. **C**, Head of *M. mielkeorum* in lateral view. Black arrow pointing to frontal tubercle; left white arrow pointing to clypeal base elevated; right white arrow pointing to pronotal anterior corner. **D**, Metatibia of *M. mielkeorum* in ventral view. **E**, Head of *Minisiderus elyanae* in dorsal view. Black arrows pointing to wrinkles on frons and vertex; double-headed arrows comparing clypeal length to width; white arrows pointing to clypeal apical portion. **F**, Coxites of *M. elyanae* in ventral view. Black arrows pointing to apical emargination. **G**, Head of *M. elyanae* in lateral view. Black arrow pointing to frontal tubercle; white arrow pointing to clypeal base. **H**, Metatibia of *M. elyanae* in ventral view. Scale bars: 1 mm.....65

FIGURE 22. Male and female of *Minisiderus elyanae*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. Black arrow pointing to elytral apex. **D**, habitus of female in lateral view. Black arrow pointing to posterior margin of tergite VIII. Scale bars: 10 mm.66

FIGURE 23. Male of *Minisiderus veadeirensis*. **A**, Habitus in dorsal view. Upper white arrow pointing to outer margin of humeral umbone; lower white arrow pointing to lateral margin of elytra. **B**, habitus in lateral view. Upper white arrow pointing to anterior carina of mesotibia; white stripes comparing length of outer margin of metatibia to width. Scale bars: 10 mm.67

FIGURE 24. Male head and pronotum of *Minisiderus veadeirensis* and *Minisiderus rondoniensis*. **A**, Head of *M. veadeirensis* in dorsal view. White arrow pointing to connection between canthus and horn. **B**, Head of *M. veadeirensis* in frontal view. **C**, Head and pronotum of *M. veadeirensis* in lateral view. White arrow pointing to area between anterior margin of pronotum and pronotal tubercles. **D**, Head of *M. rondoniensis* in dorsal view. **E**, Head of *M. rondoniensis* in frontal view. White arrow pointing to connection between cephalic horns. **F**, Head and pronotum of *M. rondoniensis* in frontoateral view. Black arrow pointing to limit of depression on frons. Scale bars: 1 mm.....68

FIGURE 25. Male genitalia of *Minisiderus veadeirensis* and *Minisiderus rondoniensis*. **A**, Parameres of *M. veadeirensis* in caudal view. White arrow pointing to outer margin; black arrow pointing to notch at inner margin; red arrow pointing to inner margin at basal portion. **B**, Parameres of *M. veadeirensis* in lateral view. Upper white arrow pointing to end of lateral margin; lower white arrow pointing to end of ventral margin; black arrows pointing to basal carina; green arrow pointing to depression on posterior phallobase. **C**, Parameres of *M. veadeirensis* in ventral view. White arrows pointing to apex of ventral depression. **D**, Parameres of *M. rondoniensis* in caudal view. White arrow pointing to emargination at outer margin; red arrow pointing to medial notch; black arrow pointing to inner margin at basal portion. **E**, Parameres of *M. rondoniensis* in lateral view. Upper black arrow pointing to end of lateral margin; lower black arrow pointing to end of ventral margin; white arrow pointing to dorsal margin of basal portion; upper red arrow pointing to apex of posterior phallobase corner; lower red arrow pointing to apical margin of posterior phallobase. **F**, Parameres of *M. rondoniensis* in ventral view. White arrows pointing to anterior corners of ventral sclerite; black arrow pointing to basal portion of lateral margin. Scale bars: 1 mm.69

FIGURE 26. Male of *Minisiderus bertolossiorum*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Upper white arrows pointing to outer teeth of mesotibia; lower white arrow pointing to metatibial apex in connection to apical tooth; black arrow pointing to posterior carina of metatibia. Scale bars: 10 mm.70

FIGURE 27. Male of *Minisiderus rondoniensis*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Upper black arrow pointing to medial tooth; lower black arrow pointing to metatibial apex in connection to apical tooth. Scale bars: 10 mm.71

FIGURE 28. Male head, pronotum and tergite VIII of *Minisiderus rondoniensis* and *Minisiderus benjamini*. **A**, Head of *M. rondoniensis* in lateral view. White arrow pointing to apical portion of lateral margin. **B**, Head and pronotum of *M. rondoniensis* in dorsal view. White arrows pointing to wrinkles of pronotal disc. **C**, Tergite VIII of *M. rondoniensis* in posterior view. **D**, Head of *M. benjamini* in lateral view. **E**, Head and pronotum of *M. benjamini* in dorsal view. **F**, Tergite VIII of *M. benjamini* in posterior view. Scale bars: A, D, 1 mm, B-C, E-F, 5 mm.72

FIGURE 29. Male mouthparts of *Minisiderus rondoniensis*. **A**, Mandible in ventral view. White arrow pointing to tooth; black arrow pointing to short carina near tooth. **B**, Mandible in dorsal view. Upper black arrow pointing to emargination of tooth; lower black arrow pointing to mandibular depression. **C**, Mandible in lateral view. Left black arrow pointing to margin of socket; right black arrow pointing to condyle. **D**, Labrum in dorsal view. Black arrow pointing to bump on anterior margin. **E**, Maxilla in ventral view. Upper black arrow pointing to galea; lower black arrow pointing to cardum. **F**, Maxilla in dorsal view. Black arrow pointing to margin of palpomere III; white arrow pointing to outer margin of subgalea. **G**, Mentum in ventral view. Scale bars: 1 mm....73

FIGURE 30. Female of *Minisiderus* sp. **A**, Habitus in dorsal view. Black arrow pointing to pronotal lateral margin; white arrows pointing to regular rows of setae on elytra. **B**, habitus in lateral view. White arrow pointing to basal tooth of metatibia. Scale bars: 10 mm.74

FIGURE 31. Head, abdomen, metatibia and genitalia of female of *Minisiderus* sp. **A**, Head in dorsal view. White arrows pointing to thin punctures near tubercles. **B**, Head in dorsolateral view. Left white arrow pointing to clypeal base elevated; right arrows pointing to tubercles. **C**, Head in lateral view. Black arrow pointing to projected wrinkle. **D**, Abdomen in ventral view. **E**, Mesotibia in ventral view. White arrow pointing to medial tooth. **F**, Coxites in ventral view. White arrow pointing to emargination. Scale bars: 1 mm.75

FIGURE 32. Male and female of *Minisiderus matogrossensis*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. White arrow pointing to pronotal anterior horn. **C**, habitus of female in dorsal view. Black arrow pointing to elytral apex. **D**, habitus of female in lateral view. Double-headed white arrows comparing the length between metatibial anterior and medial tooth to length between medial and apical tooth; black arrow pointing to connection between apical margin and apical tooth. Scale bars: 10 mm.76

FIGURE 33. Male head, pronotum, canthus and mesotibia of *Minisiderus matogrossensis*, *Minisiderus cyclofoveatus*. **A**, Pronotal fovea of *M. matogrossensis* in dorsal view. **B**, Head of *M. matogrossensis* in frontal view. Double-headed red arrows

showing clypeal length. **C**, Ocular canthus of *M. matogrossensis* in dorsal view. White arrow pointing to connection between canthus and horn. **D**, Mesotibia of *M. matogrossensis* in ventral view. White arrow pointing to space between anterior carina and basal tooth; red arrow pointing to metatibial apex. **E**, Pronotal fovea of *M. cyclofoveatus* in dorsal view. **F**, Head of *M. cyclofoveatus* in frontal view. Double-headed red arrows showing clypeal length. **G**, Ocular canthus of *M. cyclofoveatus* in dorsal view. Red arrow pointing to connection between canthus and horn. **H**, Mesotibia of *M. cyclofoveatus* in ventral view. Black arrow pointing to carina on inner margin. Scale bars: A, E, 5 mm, B-D, F-H, 1 mm.....77

FIGURE 34. Mandible and Labrum of *Minisiderus matogrossensis*, *Minisiderus furtadoi*, *Minisiderus martinae*. **A**, Mandible of *M. matogrossensis* in ventral view. White arrow pointing to tooth; upper black arrow pointing to mesal brush apex; lower black arrow pointing to lateral margin near molar area. **B**, Mandible of *M. matogrossensis* in dorsal view. Upper black arrow pointing to emargination of tooth; lower black arrow pointing to protuberance of outer margin; white arrow pointing to end of mesalbrush. **C**, Mandible of *M. matogrossensis* in lateral view. Black arrow pointing to bump near condyle. **D**, Labrum of *M. matogrossensis* in dorsal view. **E**, Mandible of *M. furtadoi* in ventral view. Black arrow pointing to tooth. **F**, Mandible of *M. furtadoi* in dorsal view. Upper black arrow pointing to apex of mesal brush; lower black arrow pointing to basal insertion of mesal brush. **G**, Mandible of *M. furtadoi* in lateral view. Left black arrow pointing to base of mesal brush; right black arrow pointing to bump. **H**, Labrum of *M. furtadoi* in dorsal view. **I**, Mandible of *M. martinae* in ventral view. Left white arrow pointing to emargination on tooth; right white arrow pointing to round outer margin of tooth. **J**, Mandible of *M. martinae* in dorsal view. Black arrow pointing to base of outer margin; upper white arrow pointing to apex of mesal brush; lower white arrow pointing to basal insertion of mesal brush. **K**, Mandible of *M. martinae* in lateral view. Upper black arrow pointing to lateral margin of molar area; lower black arrow pointing to ventral condyle. **L**, Labrum of *M. martinae* in dorsal view. Black arrow pointing to middle of anterior margin. Scale bars: 1 mm.78

FIGURE 35. Maxilla and Mentum of *Minisiderus matogrossensis*, *Minisiderus furtadoi*, *Minisiderus martinae*. **A**, Maxilla of *M. matogrossensis* in ventral view. Left black arrow pointing to galea; right black arrow pointing to constriction of palpomere

II. **B**, Maxilla of *M. matogrossensis* in dorsal view. Black arrow pointing to outer margin of subgalea. **C**, Mentum of *M. matogrossensis* in ventral view. Double-headed white arrows comparing width of base to apical corners. **D**, Maxilla of *M. furtadoi* in ventral view. **E**, Maxilla of *M. furtadoi* in dorsal view. **F**, Mentum of *M. furtadoi* in ventral view. **G**, Maxilla of *M. martinae* in ventral view. Black arrow pointing to inner margin of galea **H**, Maxilla of *M. martinae* in dorsal view. Black arrow pointing to subgalea crossing margin of stipes. **I**, Mentum of *M. martinae* in ventral view. White arrow pointing to apex. Scale bars: 1 mm.79

FIGURE 36. Genitalia of *Minisiderus matogrossensis*, *Minisiderus cyclofoveatus*. **A**, Parameres of *M. matogrossensis* in caudal view. Black arrows pointing to notch at inner margin. **B**, Parameres of *M. matogrossensis* in dorsolateral view. Black arrow pointing to end of lateral margin. **C**, Parameres of *M. matogrossensis* in lateral view. Upper black arrow pointing to lateral margin; lower black arrow pointing to ventral carina. **D**, Parameres of *M. matogrossensis* in ventral view. White arrow pointing to ventral depression. **E**, Genitalia of *M. matogrossensis* in lateral view. White arrow pointing to apical corner of posterior phallobase; double-headed white arrow showing thickness of posterior phallobase. **F**, Parameres of *M. cyclofoveatus* in caudal view. **G**, Parameres of *M. cyclofoveatus* in dorsolateral view. Black arrow pointing to end of lateral margin. **H**, Parameres of *M. cyclofoveatus* in lateral view. Upper black arrow pointing to lateral margin; lower black arrow pointing to ventral carina. **I**, Parameres of *M. cyclofoveatus* in ventral view. Black arrow pointing to ventral depression. **J**, Genitalia of *M. cyclofoveatus* in lateral view. White arrow pointing to apical corner of posterior phallobase; double-headed white arrow showing thickness of posterior phallobase. Scale bars: 1 mm.....80

FIGURE 37. Head, abdomen, metatibia and genitalia of female of *Minisiderus matogrossensis*. **A**, Head in dorsal view. Black arrow pointing to apical corner of ocular canthus. **B**, Head in dorsolateral view. **C**, Head in lateral view. Black arrow pointing to frontal tubercles. **D**, Abdomen in ventral view. Black arrow pointing to sternite VIII covering elytra. **E**, Mesotibia in ventral view. Black arrow pointing to posterior carina. **F**, Coxites in ventral view. Scale bars: 1 mm.81

FIGURE 38. Male of *Minisiderus cyclofoveatus*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Black arrow pointing to pronotal horn on anterior margin. Scale bars: 10 mm.....82

FIGURE 39. Male of *Minisiderus goyanus*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Scale bars: 10 mm.....83

FIGURE 40. Head and pronotum of *Minisiderus goyanus*, *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Head of *M. goyanus* in lateral view. White arrow pointing to area between pronotal anterior margin and pronotal tubercles; upper black arrow pointing to pronotal tubercles; lower black arrow pointing to anterior portion of lateral margin. **B**, Ocular canthus of *M. goyanus* in dorsal view. Left white arrow pointing to basal protuberance of ocular canthus; right white arrow pointing to canthus carina. **C**, Head of *M. goyanus* in dorsal view. **D**, Head of *M. martinae* in lateral view. White arrow pointing to area between pronotal anterior margin and pronotal tubercles; black arrow pointing to tubercles. **E**, Ocular canthus of *M. martinae* in dorsal view. White arrow pointing to canthus carina **F**, Head of *M. martinae* in dorsal view. **G**, Head of *M. furtadoi* in lateral view. Black arrow pointing to lateral margin of pronotal tubercles. **H**, Ocular canthus of *M. furtadoi* in dorsal view. Left white arrow pointing to basal connection between canthus and horns; right white arrow pointing to canthus carina **I**, Head of *M. furtadoi* in dorsal view. Black arrow pointing to side of pronotal tubercles; upper white arrows showing margins of frontal depression; lower white arrow pointing to horn base in frontal view. **J**, Head of *M. parecisensis* in lateral view. **K**, Ocular canthus of *M. parecisensis* in dorsal view. Black arrow pointing to basal protuberance of ocular canthus. **L**, Head of *M. parecisensis* in dorsal view. Double-headed black arrows comparing width of pronotal tubercles and eye; white arrow pointing emargination of horn; lower black arrows pointing base of horn. Scale bars: 1 mm.....84

FIGURE 41. Pronotum, prosternum and metatibia of *Minisiderus goyanus*, *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Head and pronotum of *M. goyanus* in dorsal view. White arrows pointing to punctures shagrinated on posterior corners of pronotum. **B**, Prosternum and part of proleg of *M. goyanus* in ventral view. White arrows pointing to wrinkles on procoxa. **C**, Metatibia of *M. goyanus* in lateral

view. White arrows pointing to outer teeth; black arrow pointing to setae on tergite VIII. **D**, Head and pronotum of *M. martinae* in dorsal view. **E**, Prosternum and part of proleg of *M. martinae* in ventral view. Upper black arrow pointing to prosternal anterior margin; lower black arrow pointing to femoral connection to protrocantheri. **F**, Metatibia of *M. martinae* in lateral view. Black arrows pointing to metatibial outer teeth. **G**, Head and pronotum of *M. furtadoi* in dorsal view. **H**, Prosternum and part of proleg of *M. furtadoi* in ventral view. **I**, Metatibia of *M. furtadoi* in lateral view. Upper black arrow pointing to basal tooth; lower basal tooth pointing to apical tooth. **J**, Head and pronotum of *M. parecisensis* in dorsal view. **K**, Prosternum and part of proleg of *M. parecisensis* in ventral view. Upper black arrows pointing to medial carina. **L**, Metatibia of *M. parecisensis* in lateral view. White arrows pointing to C-punctures on outer margin; black arrow pointing to connection between apical margin and apical tooth. Scale bars: A, D, G, J, 5 mm, B-C, D-E, H-I, K-L, 1 mm.....85

FIGURE 42. Mouthparts of *Minisiderus goyanus*. **A**, Mandible in dorsal view. Upper black arrow pointing to emargination of tooth; lower black arrow pointing to mesal brush; white arrows pointing to rows of short thin setae. **B**, Maxilla in dorsolateral view. Left black arrow pointing to palpomere III; right black arrow pointing to emargination at apex of galea. **C**, Mentum in ventral view. Double-headed white arrows comparing width of base to apican corners of mentum. Scale bars: 1 mm.86

FIGURE 43. Male genitalia of *Minisiderus goyanus*, *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Parameres of *M. goyanus* in caudal view. Black arrow pointing to notch on outer margin; upper white arrow pointing to notch at medial inner margin; lower white arrow pointing to basal inner margin. **B**, Parameres of *M. goyanus* in lateral view. Upper white arrow showing apex elongated; lower white arrow pointing to lateral margin. **C**, Parameres of *M. goyanus* in caudal view. Black arrow pointing to margin of ventral sclerite; white arrow pointing to posterior phallobase apical corner. **D**, Parameres of *M. martinae* in caudal view. Red arrow pointing to angulation at apical inner margin; black arrow pointing to outer margin; white arrow pointing to posterior projection. **E**, Parameres of *M. martinae* in lateral view. Black arrow pointing to lateral margin. **F**, Parameres of *M. martinae* in ventral view. Upper black arrow pointing to apex of parameres; lower black arrow pointing to emargination of anterior margin of ventral sclerite. **G**, Parameres of *M.*

furtadoi in caudal view. White arrow pointing to notch at medial inner margin; upper black arrow pointing to inner margin basally; lower black arrow pointing to posterior projection. **H**, Parameres of *M. furtadoi* in lateral view. Upper white arrow pointing dorsal surface of basal portion; lower white arrow pointing posterior projection. **I**, Parameres of *M. furtadoi* in ventral view. Left white arrow pointing to ventral depression; right white arrow pointing to lateral margin. **J**, Parameres of *M. parecisensis* in caudal view. White arrow pointing to notch at inner margin; upper black arrow pointing to basal inner margin; lower black margin pointing to posterior projection. **K**, Parameres of *M. parecisensis* in lateral view. Black arrow pointing to lateral margin. **L**, Parameres of *M. parecisensis* in ventral view. Black arrow pointing to apex of parameres; white arrow pointing to lateral margin. Scale bars: 1 mm.87

FIGURE 44. Male and female of *Minisiderus martinae*. **A**, Habitus of male in dorsal view. Black arrows pointing to fissures on elytra. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. Black arrows pointing to rugose surface of elytra. **D**, habitus of female in lateral view. Double-headed white arrows comparing the length between metatibial anterior and medial tooth to length between medial and apical tooth; black arrow pointing to connection between apical margin and apical tooth. Scale bars: 10 mm.88

FIGURE 45. Female head and genitalia of *Minisiderus martinae*, *Minisiderus furtadoi*. **A**, Head of *M. martinae* in dorsal view. Left black arrow pointing to frontal wrinkles; right black arrow pointing to connection between canthus and clypeus; white arrow pointing to vertex. **B**, Head of *M. martinae* in dorsolateral view. Left white arrow pointing to clypeal base elevation; right white arrows pointing to tubercles. **C**, Ocular canthus of *M. martinae* in dorsal view. Black arrow pointing to apex. **D**, Coxites of *M. martinae* in ventral view. Black arrow pointing to V-shaped emargination. **E**, Head of *M. furtadoi* in dorsal view. Left black arrows pointing to frontal wrinkles; right black arrow pointing to connection between canthus and clypeus; white arrow pointing to vertex. **F**, Head of *M. furtadoi* in dorsolateral view. Left white arrow pointing to clypeal base elevation; right white arrows pointing to tubercles. **G**, Ocular canthus of *M. furtadoi* in dorsal view. Left black arrow pointing to apex; right black arrow pointing to carina. **H**, Coxites of *M. furtadoi* in ventral view. Scale bars: 1 mm.89

FIGURE 46. Male and female of *Minisiderus furtadoi*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Black arrow pointing to connection between metatibial apical margin and apical tooth. Scale bars: 10 mm.....90

FIGURE 47. Antennal anomaly in male of *Minisiderus furtadoi*. **A**, Antennae and part of head in ventral view. Black arrow pointing to elongate projection from antenomere II; white arrow pointing to circular depression on apex of projection. **B**, Antennae and part of head slightly in ventrolateral view. Black arrows pointing to the two distal antenomeres. Scale bars: 1 mm.91

FIGURE 48. Male of *Minisiderus parecisensis*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. Scale bars: 10 mm.92

FIGURE 49. Male abdomen of *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Abdomen of male of *M. martinae* in ventroposterior view. Black arrows pointing to punctures on anterior margin of tergite VIII. **B**, Abdomen of male of *M. furtadoi* in ventroposterior view. Black arrows pointing to microsetae on posterior margin of tergite VIII. **C**, Abdomen of male of *M. parecisensis* in ventroposterior view. Black arrows pointing to wrinkles on anterior margin of tergite VIII. Scale bars: 5 mm.....93

FIGURE 50. Distribution map of *Minisiderus*.94

FIGURE 51. Comparison between male and female of *Minisiderus* and *Brachysiderus*. **A**, Head of *M. lenorae* in dorsal view. Black arrow pointing to apex of ocular canthus; white arrow pointing to apex of horns; lower white arrow pointing to anterior corner of ocular canthi. **B**, Head of *Brachysiderus* in dorsal view. Black arrow pointing to apex of ocular canthus; upper white arrow pointing to apex of horns; lower white arrow pointing to anterior corner of ocular canthi. **C**, Head of *M. benjamini* in dorsal view. Black arrow pointing to apex of ocular canthus; white arrow pointing to apex of horns; lower white arrow pointing to anterior corner of ocular canthi. **D**, Head and pronotum of female of *Minisiderus*. Black arrow pointing to connection between clypeal base and ocular canthus; upper white arrow pointing to apex of clypeus; lower white arrow pointing to

base of ocular canthi. **E**, Head and pronotum of female of *Brachysiderus*. Left black arrow pointing to connection between clypeal base and ocular canthus; white arrow pointing to apex of clypeus; right black arrow pointing to base of ocular canthi. **F**, Elytra of female of *Minisiderus*. **G**, Elytra of female of *Brachysiderus*. **H**, Protarsus of male *Minisiderus*. Upper black arrow pointing to protarsal claw; lower black arrow pointing to inner margin of protarsomere V. **I**, Protarsus of male *Brachysiderus*. Upper black arrows pointing to protarsal claws; lower black arrow pointing to inner margin of protarsomere V. Scale bars: A-C, F-I, 1 mm, D-E, 5 mm.95

FIGURE 52. Comparison between male and female of *Minisiderus* and *Aegopsis*. **A**, Head and pronotum of male *Minisiderus* in dorsal view. Upper white arrows pointing to cephalic horns; lower white arrow pointing to pronotal tubercles. **B**, Head and pronotum of male *Aegopsis* in dorsal view. Upper black arrows pointing to cephalic horns; lower black arrow pointing to pronotal horn. **C**, Parameres of *Minisiderus* in ventral view. Left black arrow pointing to margin of ventral sclerite; right black arrow pointing to ventral margin of parameres. **D**, Parameres of *Aegopsis* in ventral view. Black arrow pointing to margin of ventral sclerite fused to ventral parameres. **E**, Head of female *Minisiderus* in dorsal view. Upper white arrow pointing to anterior margin of ocular canthus; lower white arrow showing apex of canthus elongated. **F**, Head of female *Aegopsis* in dorsal view. Upper white arrow pointing to anterior margin of ocular canthus; lower white arrow showing apex of canthus short. **G**, Head of female *Minisiderus* in frontal view. Double-headed white arrow showing thickness of anterior margin of clypeus. **H**, Head of female *Aegopsis* in frontal view. Double-headed white arrow showing thickness of anterior margin of clypeus. **I**, Elytral apex of female *Minisiderus* in dorsal view. Black arrow pointing to tergite VIII hidden under elytral apex. **J**, Elytral apex of female *Aegopsis* in dorsal view. Black arrow pointing to tergite VIII crossing elytral apex. Scale bars: A-B, 5 mm, C-J, 1 mm.96

CAPÍTULO III [Imagens no Anexo em PDF “TESE_Rafael Sobral Alves_Revisão De Agaocephalini_FIGURAS”]

FIGURE 1. Male of *Brachysiderus quadrimaculatus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.98

FIGURE 2. Male head of *Brachysiderus quadrimaculatus* and *Brachysiderus andinus*. **A**, Head of *B. quadrimaculatus* in dorsal view. White arrow pointing to fovea. **B**, Head of *B. quadrimaculatus* in frontal view. Simple white arrow pointing to apex of horn; double-headed white arrows comparing clypeal base width with clypeal apex. **C**, Head of *B. quadrimaculatus* in lateral view. White arrows pointing to foveal protuberances. **D**, Head of *B. quadrimaculatus* in dorsolateral view. White arrow pointing to emargination near anterior corner of clypeus. **E**, Head of *B. andinus* in dorsal view. White arrow pointing to fovea. **F**, Head of *B. andinus* in frontal view. Superior simple white arrow pointing to apex of horn; inferior simple white arrow pointing to lateral protuberance of clypeus; double-headed white arrows comparing clypeal base width with clypeal apex; simple black arrow pointing to concavity on clypeal base; double-headed black arrows comparing width of cephalic horn middle with apex. **G**, Head of *B. andinus* in lateral view. Black arrows pointing to foveal protuberances. **H**, Head of *B. andinus* in dorsolateral view. Superior white arrow pointing to depression on horn; inferior white arrow pointing to emargination near anterior corner of clypeus. Scale bars: 1 mm.99

FIGURE 3. Male ocular canthus, thorax and legs of *Brachysiderus quadrimaculatus* and *Brachysiderus andinus*. **A**, Canthus of *B. quadrimaculatus* in dorsal view. **B**, Protarsus of *B. quadrimaculatus* in dorsal view. White arrow pointing to mesobasal tooth. **C**, Protibia of *B. quadrimaculatus* in ventral view. White arrow pointing to V-shaped margin; black arrow pointing to apical concavity of protibia. **D**, Pronotum of *B. quadrimaculatus* in dorsal view. **E**, Prosternum of *B. quadrimaculatus* in ventral view. White arrows pointing to setae. **F**, Canthus of *B. andinus* in dorsal view. Black arrow showing direction of ocular canthi tooth. **G**, Protarsus of *B. andinus* in dorsal view. Superior white arrow pointing to protuberance on distal inner claw; inferior white arrow pointing to basal tooth. **H**, Protibia of *B. andinus* in ventral view. Left white arrow pointing to U-shaped margin; right white arrow pointing to carena. **I**, Pronotum of *B. andinus* in dorsal view. **J**, Prosternum of *B. andinus* in ventral view. White arrow pointing to medial elevation of prosternum. Scale bars: A-C, E, F-H, J, 1 mm; D, I, 5 mm.100

FIGURE 4. Male genitalia of *Brachysiderus quadrimaculatus* and *Brachysiderus andinus*. **A**, Parameres of *B. quadrimaculatus* in caudal view. Black arrows pointing to bump on medial portion of parameres; double-headed white arrows comparing distal part to proximal part of basal portion of parameres. **B**, Parameres of *B. quadrimaculatus* in lateral view. White arrow pointing to carina. **C**, Parameres of *B. quadrimaculatus* in ventral view. Left white arrow pointing to ventrolateral carina; right white arrow pointing to projection of posterior margin; simple black arrow pointing to concavity of posterior margin of parameres; double-headed arrows comparing width of apical and basal portions. **D**, Aedeagus of *B. quadrimaculatus* in lateral view. **E**, Parameres of *B. andinus* in caudal view. White arrow pointing to corner expanded. **F**, Parameres of *B. andinus* in lateral view. **G**, Parameres of *B. andinus* in ventral view. Simple black arrow pointing to ventrolateral carina; left white arrow showing posterior margin not touching carina; right white arrow pointing to projection of posterior margin; double-headed black arrows comparing width of apical and basal portions. **H**, Aedeagus of *B. andinus* in lateral view. Black arrow pointing to ventrobasal margin. Scale bars: 1 mm.101

FIGURE 5. Male and female of *Brachysiderus andinus*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, Habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.102

FIGURE 6. Female head of *Brachysiderus andinus* and *Brachysiderus tridentiger*. **A**, Head of *B. andinus* in dorsal view. Superior simple white arrows pointing to lateral protuberances of clypeal apex; inferior white arrows pointing to fovea; double-headed white arrows comparing width of clypeal apex to basal protuberance of ocular canthi. **B**, Head of *B. andinus* in lateral view. White arrows pointing to foveal protuberances. **C**, Canthus of *B. andinus* in dorsal view. Simple white arrow pointing to basal protuberance of canthus; double-headed white arrow showing thickness of canthus. **D**, Head of *B. andinus* in dorsolateral view. White arrows pointing to foveal protuberances. **E**, Head of *B. andinus* in frontal view. Double-headed white arrows for comparisons. **F**, Head of *B. tridentiger* in dorsal view. White arrow pointing to fovea; double-headed red arrows comparing width of clypeal apex to basal protuberance of ocular canthi. **G**, Head of *B. tridentiger* in lateral view. White arrows pointing to foveal protuberances. **H**, Canthus of *B. tridentiger* in dorsal view. Double-headed white arrow showing thickness of canthus. **I**, Head of *B. tridentiger* in dorsolateral view. White arrows pointing to

foveal protuberances. **J**, Head of *B. tridentiger* in frontal view. Double-headed white arrows for comparisons. Scale bars: 1 mm.....103

FIGURE 7. Female thorax and legs of *Brachysiderus andinus* and *Brachysiderus tridentiger*. **A**, Pronotum of *B. andinus* in dorsal view. **B**, Mesotibia of *B. andinus* in lateral view. **C**, Mesotibia of *B. andinus* in lateral view. Black arrow pointing to apical tooth of outer margin. **D**, Prosternum of *B. andinus* in ventral view. **E**, Pronotum of *B. tridentiger* in dorsal view. **F**, Mesotibia of *B. tridentiger* in lateral view. Black arrow pointing to anterior carina. **G**, Metatibia of *B. tridentiger* in lateral view. Black arrow pointing to apical tooth of outer margin. **H**, Prosternum of *B. tridentiger* in ventral view. Black arrow pointing to transverse row of setae near posterior margin of prosternum. Scale bars: A, E, 5 mm; B-D, F-H, 1 mm.....104

FIGURE 8. Male and female of *Brachysiderus tridentiger*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, Habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.105

FIGURE 9. Male head of *Brachysiderus tridentiger* and *Brachysiderus breyeri*. **A**, Head of *B. tridentiger* in dorsal view. White arrow pointing to fovea. **B**, Head of *B. tridentiger* in frontal view. Simple white arrow pointing to apex of horn; simple black arrow pointing to medial portion of clypeal lateral margin; double-headed white arrows comparing width of horn middle to horn apex. **C**, Head of *B. tridentiger* in lateral view. Black arrows pointing to foveal protuberances. **D**, Head of *B. tridentiger* in dorsolateral view. **E**, Head of *B. breyeri* in dorsal view. White arrow pointing to fovea. **F**, Head of *B. breyeri* in frontal view. White arrow pointing to apex of horn; black arrow pointing to medial portion of clypeal lateral margin. **G**, Head of *B. breyeri* in lateral view. White arrow pointing to posterior tooth of cephalic horn; black arrow pointing to vertex elevated. **H**, Head of *B. breyeri* in dorsolateral view. White arrow showing the elevation of apex of horns. Scale bars: 1 mm.106

FIGURE 10. Male ocular canthus, thorax and legs of *Brachysiderus tridentiger* and *Brachysiderus breyeri*. **A**, Canthus of *B. tridentiger* in dorsal view. Black arrow showing direction of ocular canthi basal tooth; white arrows pointing to carina. **B**, Protarsus of *B. tridentiger* in dorsal view. White arrow pointing to protuberance of

distal inner claw; black arrow pointing to mesobasal tooth. **C**, Protibia of *B. tridentiger* in ventral view. Black arrow pointing to apical portion of protibia. **D**, Pronotum of *B. tridentiger* in dorsal view. **E**, Prosternum of *B. tridentiger* in ventral view. White arrow pointing to medial elevation on prosternum. **F**, Canthus of *B. breyeri* in dorsal view. White arrow pointing to emargination on canthus. **G**, Protarsus of *B. breyeri* in dorsal view. Left black arrow pointing to distal inner claw disarmed; right black arrow pointing to basal tooth. **H**, Protibia of *B. breyeri* in ventral view. Black arrow pointing to apical concavity of protibia. **I**, Pronotum of *B. breyeri* in dorsal view. **J**, Prosternum of *B. breyeri* in ventral view. Simple white arrow pointing to depression near prosternal posterior margin; double-headed arrow showing thickness of medial portion of prosternum. Scale bars: A-C, E, F-H, J, 1 mm; D, I, 5 mm.107

FIGURE 11. Male genitalia of *Brachysiderus tridentiger* and *Brachysiderus breyeri*. **A**, Parameres of *B. tridentiger* in caudal view. Double-headed arrows comparing distal and proximal parts of basal portion. **B**, Parameres of *B. tridentiger* in lateral view. Black arrow pointing to ventrolateral projection. **C**, Parameres of *B. tridentiger* in ventral view. Superior black arrow pointing to ventrolateral carina; inferior black arrow pointing to outer edge of posterior margin; simple white arrow pointing to posterior margin projection; double-headed white arrow showing width of medial portion of parameres. **D**, Aedeagus of *B. tridentiger* in lateral view. White arrow pointing to outer edge of anterior phallobase. **E**, Parameres of *B. breyeri* in caudal view. **F**, Parameres of *B. breyeri* in lateral view. Black arrow pointing to ventrolateral projection. **G**, Parameres of *B. breyeri* in ventral view. Black arrow pointing to emargination of posterior margin; simple white arrow pointing to posterior margin projection; double-headed white arrow showing width of medial portion of parameres. **H**, Aedeagus of *B. breyeri* in lateral view. White arrow pointing to outer edge of anterior phallobase. Scale bars: 1 mm.108

FIGURE 12. Male of *Brachysiderus breyeri*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.109

FIGURE 13. Distribution map of *Brachysiderus*.110

FIGURE 14. Male and female of *Brachysiderus*, *Lycomedes* and *Spodistes*. **A**, Habitus of *Brachysiderus tridentiger* male in dorsal view. **B**, Habitus of *Lycomedes buckleyi* male in dorsal view. **C**, Habitus of *Spodistes hopei* male in dorsal view. **D**, Habitus of *Brachysiderus tridentiger* female in dorsal view. **E**, Habitus of *Lycomedes buckleyi* female in dorsal view. **F**, Habitus of *Spodistes hopei* female in dorsal view. Scale bars: 10 mm.111

CAPÍTULO IV [Imagens no Anexo em PDF “TESE_Rafael Sobral Alves_Revisão De Agaocephalini_FIGURAS”]

FIGURE 1. Male of *Spodistes hopei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm. Photo by: Keita Matsumoto.113

FIGURE 2. Head of *Spodistes hopei*, *Spodistes grandis*, *Spodistes angulicollis*. **A**, Ocular canthus of *S. grandis*; **B**, ocular canthus of *S. angulicollis*; **C**, head of *S. hopei* in frontal view; **D**, head of *S. grandis* in frontal view; **E**, head of *S. angulicollis* in frontal view; **F**, mouthparts of *S. angulicollis* in ventral view. White arrow pointing to outer edge of mandible. Scale bars: 1 mm.114

FIGURE 3. Aedeagus of *Spodistes hopei*, *Spodistes grandis*, *Spodistes angulicollis*. **A**, Parameres of *S. hopei* in caudal view; **B**, aedeagus of *S. hopei* in lateral view; **C**, parameres of *S. hopei* in ventral view; **D**, parameres of *S. grandis* in caudal view; **E**, aedeagus of *S. grandis* in lateral view; **F**, parameres of *S. grandis* in ventral view; **G**, parameres of *S. angulicollis* in caudal view; **H**, aedeagus of *S. angulicollis* in lateral view; **I**, parameres of *S. angulicollis* in ventral view. Scale bars: 1 mm.115

FIGURE 4. Mandibles of male *Spodistes* in ventral view. **A**, Mandible of *S. hopei*; **B**, mandible of *S. grandis*; **C**, mandible of *S. mnischechi*; **D**, mandible of *S. batesi*; **E**, mandible of *S. monzoni*. White arrows pointing to the apical corner of outer edge in D and E. Scale bars: 1 mm.116

FIGURE 5. Female of *Spodistes hopei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.117

FIGURE 6. Females of *Spodistes hopei*, *Spodistes grandis* and *Spodistes beltianus*. **A**, Head of *S. hopei* in dorsal view; **B**, head of *S. grandis* in dorsal view; **C**, head of *S. beltianus* in dorsal view; **D**, abdomen of *S. grandis* in ventral view; **E**, abdomen of *S. beltianus* in ventral view. White arrows indicating for comparisons the width of clypeal apex, the distance between cephalic tubercles and diameter of the eye, in A–C; white arrows indicating the width of sternite VII related to the length of sternite VIII in D–E. Scale bars: A-C, 1 mm, D-E, 5 mm.....118

FIGURE 7. Mentum of female *Spodistes* in ventral view. **A**, Mentum of *S. hopei*; **B**, mentum of *S. grandis*; **C**, mentum of *S. mniszehci*; **D**, mentum of *S. batesi*; **E**, mentum of *S. monzoni*; **F**, mentum of *S. beltianus*. Pair of white arrows indicating the length of apical half and basal half of mentum in A and D; white arrows pointing to the apical region of mentum in C and E. Scale bars: 1 mm.119

FIGURE 8. Mandibles of female *Spodistes*. **A**, Mandible of *S. hopei* in dorsal view; **B**, mandible of *S. grandis* in dorsal view; **C**, mandible of *S. mniszehci* in dorsal view; **D**, mandible of *S. batesi* in dorsal view; **E**, mandible of *S. monzoni* in dorsal view; **F**, mandible of *S. beltianus* in ventral view. White arrows pointing to indetantion of outer edge in A and D; white arrow pointing to carina of apical tooth in B; black arrows pointing to apical corner of outer edge in A and D. Scale bars: 1 mm.....120

FIGURE 9. Male of *Spodistes grandis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.....121

FIGURE 10. Female of *Spodistes grandis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.....122

FIGURE 11. Mating of *Spodistes grandis*. Image by: YouTube Channel “AKIRA RISING”.123

FIGURE 12. Male of *Spodistes angulicollis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.....124

FIGURE 13. Male of *Spodistes mniszehi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.125

FIGURE 14. **A**, Labrum of *S. mniszehi* male in dorsal view; **B**, labrum of *S. batesi* male in dorsal view; **C**, mentum of *S. batesi* male in ventral view; **D**, mentum of *S. mniszehi* male in ventral view. Scale bars: 1 mm.126

FIGURE 15. Aedeagus of *Spodistes mniszehi*, *Spodistes batesi*, *Spodistes monzoni*. **A**, Parameres of *S. mniszehi* in caudal view; **B**, aedeagus of *S. mniszehi* in lateral view; **C**, parameres of *S. mniszehi* in ventral view; **D**, parameres of *S. batesi* in caudal view; **E**, aedeagus of *S. batesi* in lateral view; **F**, parameres of *S. batesi* in ventral view; **G**, parameres of *S. monzoni* in caudal view; **H**, aedeagus of *S. monzoni* in lateral view; **I**, parameres of *S. monzoni* in ventral view. Black arrows pointing to basal protuberance at outer edge of parameres in F and I. Scale bars: 1 mm.127

FIGURE 16. Head, abdomen and maxilla of female *Spodistes mniszehi*, *Spodistes batesi*, *Spodistes monzoni*. **A**, Head of *S. mniszehi* in dorsal view; **B**, head of *S. batesi* in dorsal view; **C**, head of *S. monzoni* in dorsal view; **D**, tergite VIII of *S. mniszehi* in lateral view; **E**, tergite VIII of *S. batesi* in lateral view; **F**, tergite VIII of *S. monzoni* in lateral view; **G**, maxilla of *S. mniszehi* in ventral view; **H**, maxilla of *S. batesi* in ventral view; **I**, maxilla of *S. monzoni* in ventral view. White arrows indicating for comparisons the width of clypeal apex, the distance between cephalic tubercles and diameter of the eye, in A–C; black arrows indicating the anterior margin of tergite VIII in D–E; white lines contouring base of galea in G–I. Scale bars: 1 mm.128

FIGURE 17. Female of *Spodistes mniszehi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.129

FIGURE 18. Male of *Spodistes batesi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.130

FIGURE 19. Feale of *Spodistes batesi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.131

- FIGURE 20.** Minor male of *Spodistes batesi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.132
- FIGURE 21.** Male of *Spodistes monzoni*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.133
- FIGURE 22.** Female of *Spodistes monzoni*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.134
- FIGURE 23.** Male of *Spodistes beltianus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.135
- FIGURE 24.** Aedeagus and ocular canthus of *Spodistes beltianus*, *Spodistes armstrongi*. **A**, Parameres of *S. beltianus* in caudal view; **B**, aedeagus of *S. beltianus* in lateral view; **C**, parameres of *S. beltianus* in ventral view; **D**, parameres of *S. armstrongi* in caudal view; **E**, aedeagus of *S. armstrongi* in lateral view; **F**, ocular canthus of *S. beltianus* in dorsal view; **G**, ocular canthus of *S. armstrongi* in dorsal view. Scale bars: 1 mm.136
- FIGURE 25.** Female of *Spodistes beltianus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.137
- FIGURE 26.** Male of *Spodistes armstrongi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm. Photo by: Antoine Mantilleri.138
- FIGURE 27.** **A**, Metatibial apex of female *S. monzoni* in ventral view; **B**, metatibial apex of female *S. mniszewski* in ventral view; **C**, hypopygium and procoxa of female *S. mniszewski* in ventral view; **D**, hypopygium and procoxa of female *S. beltianus* in ventral view; **E**, protibia of female *S. mniszewski* in ventral view; **F**, protibia of female *S. hopei* in ventral view. Black arrows pointing to thick setae on metatibial apex in A–B; white arrows pointing to the hypopygial protuberance and to punctures on procoxa in C–D; white arrows pointing to apex of protibial carina in E–F. Scale bars: 1 mm.139

FIGURE 28. *Lycomedes buckleyi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view; **E**, mentum in ventral view. Scale bars A–D: 10 mm; scale bar E: 1 mm.140

FIGURE 29. Distribution map of the species of *Spodistes*.141

FIGURE 30. Zoomed distribution of *Spodistes*. **A**, Species from Southern Mexico to Costa Rica; **B**, species from Panama to southern Ecuador. Question mark referring to a dubious distribution in A; black ellipsis zooming the distribution in western Panama in B.142

FIGURE 31. Female of *Spodistes angulicollis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.143

FIGURE 32. Head of *Spodistes hopei* and *Spodistes angulicollis*. **A**, Head of *S. hopei* in dorsal view; **B**, head of *S. hopei* in frontal view; **C**, head of *S. hopei* in lateral view; **D**, head of *S. angulicollis* in dorsal view; **E**, head of *S. angulicollis* in frontal view; **F**, head of *S. angulicollis* in lateral view. Scale bars: 1 mm.144

FIGURE 33. Thorax, leg and antenna of *Spodistes hopei* and *Spodistes angulicollis*. **A**, Prosternum of *S. hopei* in ventral view; **B**, proleg of *S. hopei* in ventral view; **C**, antenna of *S. hopei* in frontal view; **D**, prosternum of *S. angulicollis* in ventral view; **E**, proleg of *S. angulicollis* in ventral view; **F**, antenna of *S. angulicollis* in frontal view. Scale bars: 1 mm.145

CAPÍTULO V [Imagens no Anexo em PDF “TESE_Rafael Sobral Alves_Revisão De Agaocephalini_FIGURAS”]

FIGURE 1. Male of *Lycomedes reichei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.147

FIGURE 2. Male head of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Head of *L. reichei* in dorsal view. White arrow pointing to emargination of posterior branch of horn; black arrow pointing to ocular canthus. **B**, Head of *L. reichei* in dorsolateral view. White arrow pointing to keel between anterior and posterior branches of horn. **C**, Head of *L. reichei* in frontal view. **D**, Head of *L. reichei* in lateral view. **E**, Head of *L. ramosus* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **F**, Head of *L. ramosus* in dorsolateral view. Superior black arrows pointing to apical corners of clypeus; inferior black arrow pointing to carina of ocular canthus. **G**, Head of *L. ramosus* in lateral view. **H**, Head of *L. ramosus* in lateral view. Superior black arrow pointing to apex of posterior branch of cephalic horn; inferior black arrow pointing to frontal concavity of horn. Scale bars: 1 mm.....148

FIGURE 3. Male thorax of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Pronotum of *L. reichei* in dorsal view. **B**, Pronotum of *L. reichei* in frontolateral view. Black arrow pointing to emargination of horn. **C**, Pronotum of *L. reichei* in lateral view. Black arrows pointing to lateral carinae of thoracic horn. **D**, Pronotum of *L. ramosus* in dorsal view. Lateral black arrows pointing to pronotal depressions; central black arrow pointing to emargination of horn. **E**, Pronotum of *L. ramosus* in lateral view. Black arrow pointing to posterior depression. Scale bars: 1 mm.149

FIGURE 4. Male thorax, leg and abdomen of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Prosternum of *L. reichei* in ventral view. White arrow pointing to prosternal process. **B**, Protibia of *L. reichei* in dorsal view. **C**, Protarsus of *L. reichei* in dorsal view. **D**, Abdomen of *L. reichei* in ventral view. Superior white arrow pointing to medial projection of sternite III; inferior white arrow pointing to setae on posterior margin of tergite VIII. **E**, Prosternum of *L. ramosus* in ventral view. Superior white arrow pointing to medial projection of anterior margin; inferior white arrow pointing to prosternal process. **F**, Protibia of *L. ramosus* in dorsal view. **G**, Protarsus of *L. ramosus* in dorsal view. White arrow pointing to basal tooth of protarsal claw. **H**, Abdomen of *L. ramosus* in ventral view. Superior white arrow pointing to medial projection of sternite III. Scale bars: 1 mm.....150

FIGURE 5. Male genitalia of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Parameres of *L. reichei* in caudal view. Black arrow pointing to basal carina. **B**,

Parameres of *L. reichei* in lateral view. Black arrow pointing to lateral carina. **C**, Parameres of *L. reichei* in ventral view. **D**, Aedeagus of *L. reichei* in lateral view. Black arrow pointing to posterior phallobase. **E**, Parameres of *L. ramosus* in caudal view. **F**, Parameres of *L. ramosus* in lateral view. Black arrow pointing to apex of parameres. **G**, Parameres of *L. ramosus* in ventral view. **H**, Aedeagus of *L. ramosus* in lateral view. Scale bars: 1 mm.....151

FIGURE 6. Male of *Lycomedes ramosus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.....152

FIGURE 7. Male and female of *Lycomedes buckleyi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.153

FIGURE 8. Male head of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Head of *L. buckleyi* in dorsal view. Superior white arrows pointing to apex of cephalic horn; inferior white arrow pointing to posterior tooth of horn; black arrow pointing to basal projection of ocular canthus. **B**, Head of *L. buckleyi* in dorsolateral view. Black arrow pointing to shallow depression of frons. **C**, Head of *L. buckleyi* in frontal view. Black arrows pointing to anterior corners of clypeus. **D**, Head of *L. buckleyi* in lateral view. **E**, Head of *L. hirtipes* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **F**, Head of *L. hirtipes* in dorsolateral view. Black arrow pointing to fovea. **G**, Head of *L. hirtipes* in frontal view. Superior white arrow pointing to apex of cephalic horn; inferior white arrows pointing to anterior corners of clypeus. **H**, Head of *L. hirtipes* in lateral view. Black arrow pointing to frontal portion of cephalic horn. **I**, Head of *L. velutipes* in dorsal view. Black arrows pointing to carinae; white arrow pointing to anterior margin of ocular canthus. **J**, Head of *L. velutipes* in dorsolateral view. Black arrow pointing to fovea. **K**, Head of *L. velutipes* in frontal view. Black arrow pointing to apex of cephalic horn; white arrows pointing to clypeal carinae. **L**, Head of *L. velutipes* in lateral view. Scale bars: 1 mm.....154

FIGURE 9. Male mouthparts of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Mandible of *L. buckleyi* in ventral view. Black arrows pointing to inner and medial carina respectively from left to right. **B**, Mandible of *L. buckleyi* in

dorsal view. Double-headed black arrow showing width of mesal brush apically; simple black arrow pointing to base of inner margin laterally. **C**, Maxilla of *L. buckleyi* in ventral view. Superior black arrow pointing to medial tooth of galea; inferior black arrow pointing to outer margin of lateral border. **D**, Labrum of *L. buckleyi* in dorsal view. Double-headed arrows comparing medial length to lateral width. **E**, Mandible of *L. hirtipes* in ventral view. White arrow pointing to inner carina; black arrow pointing to apical outer margin. **F**, Mandible of *L. hirtipes* in dorsal view. Black arrow pointing to apex of inner tooth. **G**, Maxilla of *L. hirtipes* in ventral view. Superior black arrow pointing to medial tooth of galea; inferior black arrow pointing to outer margin of lateral border. **H**, Labrum of *L. hirtipes* in dorsal view. **I**, Mandible of *L. velutipes* in ventral view. Left black arrow pointing to medial carina; right black arrow pointing to outer carina. **J**, Mandible of *L. velutipes* in dorsal view. Simple black arrow pointing to molar protuberance area; double-headed black arrow showing width of mesal brush. **K**, Maxilla of *L. velutipes* in ventral view. Black arrow pointing to outer margin of galea base. **L**, Labrum of *L. velutipes* in dorsal view. Scale bars: 1 mm.155

FIGURE 10. Male thorax of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Pronotum of *L. buckleyi* in dorsal view. **B**, Pronotum of *L. buckleyi* in frontolateral view. **C**, Pronotum of *L. buckleyi* in lateral view. Black arrow pointing to posterior depression. **D**, Pronotum of *L. hirtipes* in dorsal view. **E**, Pronotum of *L. hirtipes* in frontolateral view. **F**, Pronotum of *L. hirtipes* in lateral view. Black arrow pointing to posterior depression. **G**, Pronotum of *L. velutipes* in dorsal view. **H**, Pronotum of *L. velutipes* in frontolateral view. Black arrow pointing to medial carina. **I**, Pronotum of *L. velutipes* in lateral view. Scale bars: 5 mm.156

FIGURE 11. Male thorax, leg and abdomen of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Prosternum of *L. buckleyi* in ventral view. Black arrow pointing to carina; white arrow pointing to prosternal process. **B**, Protibia of *L. buckleyi* in dorsal view. **C**, Protarsus of *L. buckleyi* in dorsal view. Black arrow pointing to basal tooth of protarsal claw; white arrow pointing to mesobasal portion of claw. **D**, Abdomen of *L. buckleyi* in ventral view. **E**, Prosternum of *L. hirtipes* in ventral view. Black arrow pointing to prosternal process. **F**, Protibia of *L. hirtipes* in dorsal view. **G**, Protarsus of *L. hirtipes* in dorsal view. **H**, Abdomen of *L. hirtipes* in ventral view. Superior white arrow pointing to medial projection of sternite III. **I**, Prosternum of *L.*

velutipes in ventral view. White arrow pointing to prosternal process. **J**, Protibia of *L. velutipes* in dorsal view. **K**, Protarsus of *L. velutipes* in dorsal view. White arrow pointing to mesobasal tooth of protarsal claw. **L**, Abdomen of *L. velutipes* in ventral view. Scale bars: C, G, K, 1 mm; A-B, D, E-F, H, I-J, L, 5 mm.....157

FIGURE 12. Male genitalia of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Parameres of *L. buckleyi* in caudal view. **B**, Parameres of *L. buckleyi* in lateral view. Left black arrow pointing to ventral margin; right black arrow pointing to lateral carina. **C**, Parameres of *L. buckleyi* in ventral view. **D**, Aedeagus of *L. buckleyi* in lateral view. Black arrow pointing to apical corner of posterior phallobase. **E**, Parameres of *L. hirtipes* in caudal view. Left black arrow pointing to setae; right black arrow pointing to apex of parameres. **F**, Parameres of *L. hirtipes* in lateral view. White arrow pointing to lateral carina; black arrow pointing to apical depression. **G**, Parameres of *L. hirtipes* in ventral view. **H**, Aedeagus of *L. hirtipes* in lateral view. White arrow pointing to apical corner of posterior phallobase. **I**, Parameres of *L. velutipes* in caudal view. Double-headed black arrows comparing width of apical and basal portions; simple black arrow pointing to outer margin medially. **J**, Parameres of *L. velutipes* in lateral view. Left black arrow pointing to ventral carina; right black arrow pointing to basal carina. **K**, Parameres of *L. velutipes* in ventral view. Left black arrow pointing to base of parameres; right black arrow pointing to ventral carina. **L**, Aedeagus of *L. velutipes* in lateral view. White arrow pointing to apical corner of posterior phallobase; black arrow pointing to apical margin of posterior phallobase. Scale bars: 1 mm.....158

FIGURE 13. Female head of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Head of *L. buckleyi* in dorsal view. Black arrow pointing to basal protuberance of ocular canthus. **B**, Head of *L. buckleyi* in frontal view. Double-headed black arrows comparing clypeal apex with base. **C**, Head of *L. buckleyi* in lateral view. Black arrows pointing to clypeal apical horns and clypeal base projections. **D**, Head of *L. hirtipes* in dorsal view. Black arrow pointing to anterior margin of ocular canthus. **E**, Head of *L. hirtipes* in frontal view. White arrows pointing to depression on vertex; double-headed black arrows comparing clypeal apex with base; simple black arrow pointing to lateral margin of clypeus. **F**, Head of *L. hirtipes* in lateral view. Black arrows pointing to clypeal base. **G**, Head of *L. velutipes* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **H**, Head of *L. velutipes* in frontal view.

White arrows pointing to depression on vertex; double-headed black arrows comparing clypeal apex with base. **I**, Head of *L. velutipes* in lateral view. Black arrows pointing to protuberance on vertex. Scale bars: 1 mm.....159

FIGURE 14. Female mouthparts of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Mandible of *L. buckleyi* in ventral view. Black arrow pointing to outer margin. **B**, Mandible of *L. buckleyi* in dorsal view. **C**, Maxilla of *L. buckleyi* in ventral view. Black arrows pointing to maxillar teeth. **D**, Labrum of *L. buckleyi* in dorsal view. Black arrow pointing to anterior margin. **E**, Mandible of *L. hirtipes* in ventral view. Double-headed black arrow showing distance from inner margin to inner carina; simple black arrow pointing to outer margin. **F**, Mandible of *L. hirtipes* in dorsal view. Double-headed black arrows showing distance between teeth; simple black arrow pointing to inner margin basally. **G**, Maxilla of *L. hirtipes* in ventral view. Simple black arrow pointing to tooth; double-headed black arrow showing thickness of lateral border. **H**, Labrum of *L. hirtipes* in dorsal view. **I**, Mandible of *L. velutipes* in ventral view. White arrow pointing to medial carina; simple black arrow pointing to outer carina; superior double-headed black arrow showing distance between inner and medial carina; inferior double-headed black arrow showing distance between inner margin and inner carina basally. **J**, Mandible of *L. velutipes* in dorsal view. Black arrow pointing to outermost portion of mesal brush. **K**, Maxilla of *L. velutipes* in ventral view. Simple black arrow pointing to base of galea; double-headed black arrow showing thickness of lateral border. **L**, Labrum of *L. velutipes* in dorsal view. Scale bars: 1 mm.160

FIGURE 15. Female thorax and abdomen of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Pronotum of *L. buckleyi* in dorsal view. **B**, Prosteronum of *L. buckleyi* in ventral view. Black arrow pointing to medial elevation of prosteronum; superior white arrow pointing to medial keel; inferior white arrow pointing to prosteronum process. **C**, Abdomen of *L. buckleyi* in ventral view. **D**, Pronotum of *L. hirtipes* in dorsal view. **E**, Prosteronum of *L. hirtipes* in ventral view. Superior white arrow pointing to medial elevation; inferior white arrow pointing to prosteronum process. **F**, Abdomen of *L. hirtipes* in ventral view. Black arrow pointing to tergite VIII. **G**, Pronotum of *L. velutipes* in dorsal view. **H**, Prosteronum of *L. velutipes* in ventral view. Superior black arrows pointing to prosteronum depression; inferior black arrow pointing to prosteronum process. **I**, Abdomen of *L. velutipes* in ventral view. Scale bars: 5 mm.161

FIGURE 16. Male and female of *Lycomedes hirtipes*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.162

FIGURE 17. Male and female of *Lycomedes velutipes*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.163

FIGURE 18. Male and female of *Lycomedes ohausi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.164

FIGURE 19. Male head of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Head of *L. ohausi* in dorsal view. Black arrow pointing to anterior margin of ocular canthus. **B**, Head of *L. ohausi* in dorsolateral view. Black arrow pointing to shallow depression of frons. **C**, Head of *L. ohausi* in frontal view. Black arrows pointing to anterior corners of clypeus. **D**, Head of *L. ohausi* in lateral view. **E**, Head of *L. enigmaticus* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **F**, Head of *L. enigmaticus* in dorsolateral view. Superior black arrow pointing to clypeal apex; inferior black arrow pointing to fovea. **G**, Head of *L. enigmaticus* in frontal view. Black arrows pointing to anterior corners of clypeus. **H**, Head of *L. enigmaticus* in lateral view. Black arrow pointing to frontal portion of cephalic horn. **I**, Head of *L. burmeisteri* in dorsal view. **J**, Head of *L. burmeisteri* in dorsolateral view. **K**, Head of *L. burmeisteri* in frontal view. Black arrows pointing to clypeal anterior corners. **L**, Head of *L. burmeisteri* in lateral view. Scale bars: 1 mm.165

FIGURE 20. Male mouthparts of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Mandible of *L. ohausi* in ventral view. Left black arrow pointing to carina on tooth; right black arrow pointing to molar protuberance; white arrow pointing to ventral depression. **B**, Mandible of *L. ohausi* in dorsal view. White arrow pointing to outermost portion of mesal brush; black arrow pointing to base of inner margin. **C**, Maxilla of *L. ohausi* in ventral view. Black arrows pointing to maxillar teeth. **D**, Labrum of *L. ohausi* in dorsal view. Black arrow pointing to setae insertion. **E**,

Mandible of *L. enigmaticus* in ventral view. Black arrow pointing to molar protuberance. **F**, Mandible of *L. enigmaticus* in dorsal view. Black arrow pointing to concavity on outer margin. **G**, Maxilla of *L. enigmaticus* in ventral view. Black arrows pointing to maxillar teeth; white arrow pointing to lateral border outer margin. **H**, Labrum of *L. enigmaticus* in dorsal view. **I**, Mandible of *L. burmeisteri* in ventral view. Left black arrow pointing to inner margin; right black arrow pointing to area of molar protuberance. **J**, Mandible of *L. burmeisteri* in dorsal view. Simple black arrow pointing to outermost portion of mesal brush; double-headed black arrow showing length of molar area. **K**, Maxilla of *L. burmeisteri* in ventral view. Black arrows pointing to maxillar teeth; red arrow pointing to outer margin of lateral border. **L**, Labrum of *L. burmeisteri* in dorsal view. Scale bars: 1 mm.166

FIGURE 21. Male thorax of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Pronotum of *L. ohausi* in dorsal view. **B**, Pronotum of *L. ohausi* in frontolateral view. **C**, Pronotum of *L. ohausi* in lateral view. **D**, Pronotum of *L. enigmaticus* in dorsal view. Black arrow pointing to emargination of thoracic horn. **E**, Pronotum of *L. enigmaticus* in frontolateral view. Black arrow pointing to medial line of thoracic horn. **F**, Pronotum of *L. enigmaticus* in lateral view. Left black arrow pointing to anterior depression; right black arrow pointing to posterior depression. **G**, Pronotum of *L. burmeisteri* in dorsal view. Black arrow pointing to posterior depression of horn. **H**, Pronotum of *L. burmeisteri* in frontolateral view. Black arrow pointing to lateral carina; white arrow pointing to tomentum. **I**, Pronotum of *L. burmeisteri* in lateral view. Left black arrow pointing to lateral carina at base; right black arrow pointing to posterior depression. Scale bars: 1 mm.167

FIGURE 22. Male thorax, leg and abdomen of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Prosternum of *L. ohausi* in ventral view. White arrow pointing to keel; black arrow pointing to prosternal process. **B**, Protibia of *L. ohausi* in dorsal view. **C**, Protarsus of *L. ohausi* in dorsal view. Black arrow pointing to mesobasal protuberance of protarsal claw. **D**, Abdomen of *L. ohausi* in ventral view. **E**, Prosternum of *L. enigmaticus* in ventral view. Black arrow pointing to prosternal process. **F**, Protibia of *L. enigmaticus* in dorsal view. **G**, Protarsus of *L. enigmaticus* in dorsal view. White arrow pointing to basal tooth of protarsus; black arrow pointing to mesobasal protuberance of protarsal claw. **H**, Abdomen of *L. enigmaticus* in ventral

view. Superior white arrow pointing to medial projection of sternite III. **I**, Prosternum of *L. burmeisteri* in ventral view. Black arrow pointing to medial elevation. **J**, Protibia of *L. burmeisteri* in dorsal view. **K**, Protarsus of *L. burmeisteri* in dorsal view. Black arrow pointing to basal tooth of protarsal claw; white arrow pointing to mesobasal protuberance of protarsal claw. **L**, Abdomen of *L. burmeisteri* in ventral view. Scale bars: C, G, K, 1 mm; A-B, D, E-F, H, I-J, L, 5 mm.168

FIGURE 23. Male genitalia of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Parameres of *L. ohausi* in caudal view. Black arrows pointing to lateral protuberances of basal portion. **B**, Parameres of *L. ohausi* in lateral view. Double-headed black arrow showing thickness of apical portion. **C**, Parameres of *L. ohausi* in ventral view. Left black arrow pointing to ventral suture; right black arrow pointing to ventrolateral portion of parameres. **D**, Aedeagus *L. ohausi* in lateral view. Black arrow pointing to apical corner of posterior phallobase. **E**, Parameres of *L. enigmaticus* in caudal view. Superior black arrow pointing to apex of inner margin; inferior black arrows pointing to carinae on basal portion. **F**, Parameres of *L. enigmaticus* in lateral view. Superior black arrow pointing to apex of parameres; white arrow pointing to carina; inferior black arrow pointing to basal margin. **G**, Parameres of *L. enigmaticus* in ventral view. Black arrow pointing to lateral margin of base; black square showing wrinkles. **H**, Aedeagus of *L. enigmaticus* in lateral view. Left black arrow pointing to apical corner of posterior phallobase; right black arrow pointing to apical margin of posterior phallobase. **I**, Parameres of *L. burmeisteri* in caudal view. **J**, Parameres of *L. burmeisteri* in lateral view. Black arrow pointing to lateral carina; white arrow pointing to dorsal depression. **K**, Parameres of *L. burmeisteri* in ventral view. Superior black arrow pointing to apical portion of lateral margin; inferior black arrow pointing to medial concavity. **L**, Aedeagus of *L. burmeisteri* in lateral view. White arrow pointing to apical corner of posterior phallobase. Scale bars: 1 mm.169

FIGURE 24. Female head of *Lycomedes ohausi* and *Lycomedes burmeisteri*. **A**, Head of *L. ohausi* in dorsal view. Black arrow pointing to anterior margin of ocular canthus. **B**, Head of *L. ohausi* in frontal view. Double-headed black arrows comparing clypeal apex with base; simple black arrow pointing to clypeal apex. **C**, Head of *L. ohausi* in lateral view. Black arrows pointing to clypeal base projections. **D**, Head of *L. burmeisteri* in dorsal view. Black arrow pointing to tomentum. **E**, Head of *L.*

burmeisteri in frontal view. **F**, Head of *L. burmeisteri* in lateral view. Black arrows pointing to clypeal base projections. Scale bars: 1 mm.170

FIGURE 25. Female mouthparts of *Lycomedes ohausi*. **A**, Mandible in ventral view. Black arrow pointing to molar protuberance. **B**, Mandible in dorsal view. Black arrow pointing to outer basal projection. **C**, Maxilla in ventral view. Black arrow pointing to tooth. **D**, Labrum in dorsal view. Scale bars: 1 mm.171

FIGURE 26. Female thorax, legs and abdomen of *Lycomedes ohausi* and *Lycomedes burmeisteri*. **A**, Pronotum of *L. ohausi* in dorsal view. Black arrow pointing to anterior border. **B**, Prosternum of *L. ohausi* in ventral view. Black arrow pointing to medial portion of prosternum. **C**, Part of abdomen, metafemur and metatibia of *L. ohausi* in ventral view. Black arrows pointing to tomentose areas; white arrows pointing to setae insertion. **D**, Pronotum of *L. burmeisteri* in dorsal view. **E**, Prosternum of *L. burmeisteri* in ventral view. White arrow pointing to prosternal process. **F**, Part of abdomen, metafemur and metatibia of *L. burmeisteri* in ventral view. Black arrows pointing to setae insertion. Scale bars: 5 mm.171

FIGURE 27. Male of *Lycomedes enigmaticus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.172

FIGURE 28. Male and female of *Lycomedes burmeisteri*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.173

FIGURE 29. Male and female of *Horridocalia peruviana*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.174

FIGURE 30. Male head and thorax of *Horridocalia delislei* and *Horridocalia peruviana*. **A**, Head of *H. delislei* in dorsal view. Black arrow pointing to keel. **B**, Pronotum of *H. delislei* in dorsal view. Black arrow pointing to apex of horn. **C**, Head and thorax of *H. delislei* in lateral view. Superior black arrow pointing to horn carina; inferior black arrow pointing to prosternal process; black square showing pronotal

punctures. **D**, Head of *H. peruviana* in dorsal view. Black arrow pointing to small fovea; white arrows pointing to carinae. **E**, Pronotum of *H. peruviana* in dorsal view. Black arrow pointing to apex of horn. **F**, Head and thorax of *H. peruviana* in lateral view. Black arrow pointing to prosternal process; black square showing pronotal punctures. Scale bars: A-B, D-E, 5 mm; C,F, 10 mm.175

FIGURE 31. Male and female mouthparts of *Horridocalia peruviana*. **A**, Mandible of male *H. peruviana* in ventral view. Black arrow pointing to carina on inner tooth. **B**, Mandible of male *H. peruviana* in dorsal view. Black arrow pointing to apical outer margin. **C**, Maxilla of male *H. peruviana* in ventral view. Black arrow pointing to carina. **D**, Labrum of male *H. peruviana* in dorsal view. **E**, Mandible of female *H. peruviana* in ventral view. Left black arrow pointing to basal inner depression; right black arrow pointing to molar protuberance. **F**, Mandible of female *H. peruviana* in dorsal view. Black arrow pointing to carina between teeth. **G**, Maxilla of female *H. peruviana* in ventral view. **H**, Labrum of female *H. peruviana* in dorsal view. Scale bars: 1 mm.176

FIGURE 32. Male genitalia of *Horridocalia peruviana*. **A**, Parameres in caudal view. **B**, Parameres in lateral view. Left black arrow pointing to ventral slight protuberance; right black arrow pointing to apical protuberance; white arrow pointing to lateral carina. **C**, Parameres in ventral view. Superior black arrow pointing to apical emargination; inferior black arrow pointing to ventrolateral carina; white arrow pointing to basal ventral carina. **D**, Aedeagus *L. ohausi* in lateral view. Scale bars: 1 mm.176

FIGURE 33. Female head of *Horridocalia peruviana*. **A**, Head in dorsal view. Simple black arrow pointing to anterior corner of clypeus; double-headed arrows comparing clypeal apex with base. **B**, Head in frontal view. Black arrows pointing to tomentum. **C**, Head in lateral view. **D**, Pronotum in dorsal view. **E**, Prosternum in ventral view. Black arrow pointing to prosternal process. **F**, Part of abdomen, metafemur and metatibia in ventral view. Scale bars: 5 mm.177

FIGURE 34. Male of *Horridocalia delislei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.178

FIGURE 35. Distribution map of *Lycomedes*.179

FIGURE 36. Distribution map of *Horridocalia*.180

INTRODUÇÃO GERAL

Scarabaeoidea Latreille, 1802

Essa superfamília da ordem Coleoptera é um grupo de besouros conhecidos popularmente como escaravelhos, estando comumente presentes na cultura pop moderna e fazendo parte da cultura histórica de vários povos ao redor do mundo, como é o caso do escaravelho como representação divina para os egípcios ou dos besouros rutelíneos, cujos élitros de brilho metálico são usados como ornamentos de colares e cocares pelo povo Jivaro do Equador e Peru (Ratcliffe, 2006; Moore *et al.* 2017). Scarabaeoidea é um grupo diverso e cosmopolita, ocorrendo nos mais diferentes tipos de habitats e possuindo uma gama diversa de hábitos alimentares, podendo ser fungívoros, predadores, herbívoros, polinizadores, decompositores de matéria orgânica, entre outros (Jameson & Ratcliffe, 2002). Em geral, os Scarabaeoidea são solitários, mas, alguns grupos possuem um certo grau de socialidade, como é o caso dos passalídeos, que constroem galerias em madeira em decomposição, onde passam a viver em grupos familiares, havendo cuidado parental (Jameson & Ratcliffe, 2002; Ulyshen, 2018). Algumas espécies podem ser termitófilas, vivendo dentro de cupinzeiros e até mesmo manipulando os cupins para carregá-las dentro das colônias, como é o caso de espécies de *Termitotrox* Reichensperger, ou mirmecófilas, sendo encontradas dentro de formigueiros, como espécies de *Phileurus* Latreille e *Cyclidius* McLeay (Jameson & Ratcliffe, 2002; Alves-Oliveira *et al.* 2015; Kakizoe *et al.* 2020).

Scarabaeoidea é um grupo monofilético, principalmente caracterizado pelos adultos com protórax robusto, procoxas largas – características de adaptação para escavação – e protíbias geralmente denteadas com um esporão na parte interna do ápice; asas posteriores com venação reduzida e mecanismo de dobramento no terço apical; clava antenal lamelada; placas metacoxais ausentes; presença de quatro túbulos de Malpighi; tergito VIII não coberto pelos élitros, nem oculto pelo tergito VII; e pelas larvas escarabeiformes, com formato de C, corpo cilíndrico, pernas e antenas desenvolvidas, ausência de urogonfos no segmento terminal do abdômen, e presença de espiráculos geralmente cribiformes (Lawrence & Britton, 1991). Apesar da monofilia bem consolidada de Scarabaeoidea, as relações dessa superfamília com outras superfamílias de Coleoptera ainda não estão completamente esclarecidas. Entre os principais candidatos a grupo-irmão de Scarabaeoidea estão Staphylinoidea, recuperado recentemente por Zhang *et al.* (2018) e McKenna *et al.* (2019) através de análise molecular com genes

codificadores de proteínas nucleares (NPCs), e Dascilloidea, recuperado recentemente por Lawrence *et al.* (2011) utilizando caracteres morfológicos de larvas e adultos.

Atualmente, é estimado que existam cerca de 40000 espécies de Scarabaeoidea descritas no mundo (Schoolmeesters, 2021). Porém, a classificação interna das famílias que compõem Scarabaeoidea ainda é incerta para alguns grupos e tem sido tópico de discussão por muito tempo, desde Sharp & Muir (1912) que consideravam 6 famílias, até Bouchard *et al.* (2011), que consideram 12 famílias dentro de Scarabaeoidea. Para este estudo, estamos utilizando a classificação de Bouchard *et al.* (2011), porém considerando Melolonthidae e Cetoniidae como famílias separadas de Scarabaeidae (Cherman & Morón, 2014). Assim sendo, consideramos Scarabaeoidea possuindo 14 famílias, sendo elas: Belohinidae Paulian, 1959; Diphylosomatidae Holloway, 1972; Geotrupidae Latreille, 1802; Glaresidae Shanski & Medvedev, 1932; Glaphyridae MacLeay, 1819; Hybosoridae Erichson, 1802; Lucanidae Latreille, 1804; Ochodaeidae Mulsant & Rey, 1871; Passalidae Leach, 1815; Pleocomidae Le Conte, 1861; Trogidae MacLeay, 1819; Scarabaeidae Latreille, 1802; Cetoniidae Leach, 1815; Melolonthidae Leach, 1819.

Melolonthidae Leach, 1819

Melolonthidae é um grupo de escaravelhos que tem gerado um debate intenso por pesquisadores, ao longo dos tempos, sobre sua posição como família dentro de Scarabaeoidea. Endrödi (1966) foi o primeiro a sugerir que Melolonthidae deveria ser considerada como uma família separada de Scarabaeidae. À época, os Scarabaeidae eram subdivididos em dois grupos (chamados de séries) – Pleurosticti e Laparosticti – com características morfológicas tão distintas entre si que Endrödi considerou que deveriam ser tratadas como famílias independentes. Os Laparosticti, onde estavam incluídos os escaravelhos clássicos, tinham os espiráculos dos três últimos segmentos abdominais localizados na membrana pleural e possuíam hábitos alimentares majoritariamente coprófagos e necrófagos e, portanto, foram mantidos dentro de Scarabaeidae. Já os Pleurosticti, com os espiráculos terminais localizados na parte superior dos esternitos e hábitos alimentares majoritariamente fitófagos e fitosaprófagos foram considerados uma nova família por Endrödi, que escolheu o gênero *Melolontha* Fabricius como gênero-tipo, surgindo assim Melolonthidae (Endrödi, 1966; Cherman & Morón, 2014).

Essa classificação de Melolonthidae *sensu* Endrödi (1966) vem sendo bastante usada principalmente pelos pesquisadores latino-americanos. Em contrapartida, em outras partes do mundo, especialmente na América do Norte, os pesquisadores adotam a

classificação de acordo com Lawrence & Newton (1995), que considera os Melolonthidae *sensu* Endrödi como várias subfamílias distintas dentro de Scarabaeidae. Além disso, de acordo com Jameson & Ratcliffe (2002), o nome Melolonthidae seria incorreto para se referir a esse grupo. Isso porque dentre as subfamílias que fazem parte de Melolonthidae *sensu* Endrödi está Cetoniinae, que teve o nome estabelecido por Leach em 1815, enquanto que Melolonthinae teve o nome estabelecido por Samouelle em 1819. Portanto, seguindo o princípio da prioridade do Código de Nomenclatura Zoológica, o nome da família deveria ser Cetoniidae, por ser mais antigo, ao invés de Melolonthidae (Jameson & Ratcliffe, 2002).

A fim de validar Melolonthidae *sensu* Endrödi, Cherman & Morón (2014) realizaram um compilado de informações das principais análises filogenéticas que incluíam as relações entre grupos de Scarabaeoidea. Para isso, foram considerados estudos filogenéticos desde a década de 1990 que incluíam análises morfológicas de larvas e adultos ou só adultos, e análises moleculares a partir de DNAr 18S e 28S, RNAr 18S, RNAr 16S mitocondrial e subunidade I do citocromo oxidase (Browne & Scholtz, 1998; Howden, 1982; Smith *et al.* 2006; Hunt *et al.* 2007; Micó *et al.* 2008; Lawrence *et al.* 2011). Em todas as análises, os táxons fitófagos (Cetoniinae, Dynastinae, Rutelinae e Melolonthinae) aparecem como um grupo separado dos táxons copro-necrófagos (Scarabaeinae e Aphodinae) e, na maioria das vezes, como seu grupo-irmão. Dessa forma, Cherman & Morón (2014) estabeleceram Melolonthidae *sensu* Endrödi como o clado que agrupa Dynastinae, Rutelinae e Melolonthinae, enquanto que a antiga subfamília Cetoniinae foi elevada para o nível de família (Cetoniidae), ambas sendo monofiléticas (Smith *et al.* 2006; Micó *et al.* 2008; Cherman & Morón, 2014). Apesar disso, ainda há muita incerteza quanto às relações desses clados com outras famílias de Scarabaeoidea.

Os Melolonthidae divergem dos Scarabaeidae pelas seguintes características dos adultos: clipeo estreito, com mandíbulas geralmente expostas; mandíbulas fortemente esclerosadas, adaptadas para o hábito alimentar fitófago e fitosaprófago; e espiráculos abdominais, em sua maioria, localizados na porção superior dos esternitos, enquanto que os Scarabaeidae são caracterizados pelo clipeo largo, com mandíbulas geralmente ocultas em vista dorsal; mandíbulas pouco esclerosadas, muito membranosas, adaptadas para o hábito alimentar coprófago, necrófago e saprófago; e espiráculos abdominais, em sua maioria, localizados na membrana pleural. Os Cetoniidae podem ser diferenciados de Melolonthidae pelo labro membranoso e presença de entalhe preocular nos adultos (labro esclerosado e entalhe preocular ausente nos adultos de Melolonthidae), ausência de

epizígio na epifaringe e tamanho similar dos três pares de pernas nas larvas (epizígio presente na epifaringe e tamanhos distintos dos três pares de pernas nas larvas de Melolonthidae) (Endrödi, 1966; Micó *et al.* 2008; Cherman & Morón, 2014).

Nesse trabalho, optamos por seguir a classificação proposta por Cherman & Morón (2014), que considera Melolonthidae formada por seis subfamílias: Melolonthinae Leach, 1819; Sericinae Kirby, 1837; Hopliinae Latreille, 1829; Euchirinae Hope, 1840; Rutelinae MacLeay, 1819 e Dynastinae MacLeay, 1819.

Dynastinae MacLeay, 1819

Os Dynastinae são popularmente conhecidos como besouros-rinocerontes devido aos chifres cefálicos presentes nos machos das espécies mais conhecidas dessa subfamília, como é o caso do *Dynastes hercules* (Linnaeus, 1758) e *Megasoma actaeon* (Linnaeus, 1758) nas Américas. Esses besouros vem sendo objeto de fascínio de colecionadores do mundo todo e possuem um certo destaque na cultura de vários povos ao redor do mundo. Na Ásia é comum a realização de eventos de lutas clandestinas de insetos nos quais os dinastíneos estão sempre entre os participantes, especialmente aqueles com chifres mais exuberantes, como é o caso de *Xylotrupes gideon* (Linnaeus, 1767) e *Trypoxylus dichotomus* (Linnaeus, 1771). De forma convergente, existem vários registros de povos na África e nas Américas que usam ou usaram partes de besouros-rinocerontes, especialmente o protórax e a cabeça, como adornos corporais ou de vestimentas. O consumo de larvas e até mesmo de adultos está presente em muitos povos indígenas da América latina, África e Ásia (Endrödi, 1985; Ratcliffe, 2006). No Japão existem lojas especializadas na venda de besouros-rinocerontes nativos e exóticos como bichos de estimação, gerando um mercado interno que inclui a criação dessas espécies desde os estágios larvais até a venda de gaiolas, substrato e geleias específicas para alimentação desses besouros. Além disso, espécies de Dynastinae são frequentemente utilizadas na cultura pop japonesa, em animações, jogos e filmes (Takada, 2013).

As principais características usadas na identificação dos adultos de Dynastinae são: mandíbula geralmente visível em vista dorsal; antenas com 9 a 10 segmentos, tendo a base do escapo oculta em vista dorsal; procoxa transversa; base do pronoto com largura similar à base do élitro; metatíbia com dois esporões no ápice; garras do meso- e metatarso simples, não-bifurcadas; escutelo visível; mesepímero oculto e esternitos sem constrição medial. Apesar dessa subfamília ser popularmente conhecida pelos chifres dos machos de algumas espécies, a maior parte dos dinastíneos não possui chifres ou possui outras

formas de ornamentos cefálicos e torácicos, como tubérculos e depressões (Endrödi, 1985; Ratcliffe, 2003). Estimativas recentes indicam que existam um pouco mais de 2000 espécies descritas de Dynastinae, ocorrendo em quase todas as regiões biogeográficas, exceto na polar. A região Neotropical é a que possui a maior riqueza de besouros-rinocerontes, com cerca de 700 espécies (Gasca-Álvarez & Amat-García, 2010; Schoolmeesters, 2021).

Essa subfamília possui um papel fundamental na degradação da serapilheira, especialmente pela ação de suas larvas que se alimentam da matéria orgânica vegetal e a fragmenta, proporcionando assim uma maior susceptibilidade da serapilheira à decomposição bacteriana. Os adultos pouco são vistos se alimentando, mas, geralmente consomem frutas maduras ou em decomposição, raízes e seiva. Os adultos de algumas espécies da tribo Cyclocephalini se alimentam ou se abrigam em flores de diversas angiospermas, como Annonaceae, Araceae, Arecaceae, Magnoliaceae e Nymphaeaceae, sendo importantes polinizadores destas. Tanto larvas quanto adultos servem de alimento para diversos outros grupos de animais, como aves, aracnídeos, anfíbios, répteis, etc. As larvas, de vida edáfica, contribuem para a aeração do solo e facilitação da drenagem de água, através da construção de túneis, e para o aumento das concentrações de carbono e nitrogênio no solo, através de suas fezes. Entretanto, as larvas de algumas espécies são consideradas pragas agrícolas, podendo atacar cultivos de arroz, cana-de-açúcar, mandioca, banana, entre outros (Morón, 1985; Morón-Rios, 2008; Oliveira *et al.* 2012; Parizotto & Grossi, 2018).

Estudos filogenéticos recentes, tanto moleculares quanto morfológicos, têm mostrado Dynastinae como grupo-irmão de Rutelinae, apesar das relações entre as outras subfamílias de Melolonthidae ainda não estarem tão claras. Até então, Melolonthinae é o principal candidato a grupo-irmão do clado (Dynastinae + Rutelinae), porém, Cetoniidae também aparece como uma possibilidade em dois cenários: o primeiro, como grupo irmão do clado ((Dynastinae + Rutelinae) + Melolonthinae)) (Hunt *et al.* 2007); e o segundo como grupo irmão do clado (Dynastinae + Rutelinae), com a posição de Melolonthinae ainda incerta (Smith *et al.* 2006). As relações filogenéticas internas de Dynastinae são ainda mais escassas, de forma que a relação entre as tribos e seu monofiletismo ainda é incerta. Atualmente apenas uma proposta filogenética para a tribo Dynastini foi publicada (Rowland & Miller, 2012). As tribos que compõem Dynastinae são: Phileurini,

Pentodontini, Oryctoderini, Oryctini, Hexodontini, Dynastini, Cyclocephalini e Agaocephalini (Endrödi, 1985).

Agaocephalini Burmeister, 1847

A tribo Agaocephalini foi originalmente descrita como Agaocephalidae por Burmeister (1847) para agrupar os gêneros *Aegopsis* Burmeister, 1847, *Agaocephala* Lepeletier de Saint-Fargeau & Audinet-Serville, 1825, *Lycomedes* Brême, 1844 e *Antodon* Brême, 1844. No trabalho, Burmeister descreve a diagnose de Agaocephalidae como “Lamelicórneos xilófagos, fronte e pronoto com dimorfismo sexual, fronte dos machos com dois ou um chifre, fêmeas sempre sem chifres; processo prosternal não-tuberculado; tarso anterior com dimorfismo sexual, primeiro artículo tarsal dos tarsos posteriores pontiagudo”. Nessa época, alguns entomólogos, como Pierre Dejean e Pierre-André Latreille, achavam que alguns desses gêneros incluídos posteriormente em Agaocephalidae por Burmeister poderiam fazer parte dos “Rutelidae”, como era conhecida a subfamília Rutelinae na época, especialmente por serem encontrados em flores e pelo distinto brilho metálico de seus corpos (em *Aegopsis*, *Agaocephala* e *Antodon*), características muito comuns em alguns gêneros de rutelíneos, como *Chrysina* Kirby, 1828 e *Pelidnota* MacLeay, 1819. Entretanto, somente essas duas características poderiam ser compartilhadas entre esses besouros e, levando em conta as demais características morfológicas presentes na diagnose do grupo, estava claro para Burmeister que Agaocephalidae era mais próximo de Dynastidae (que na época incluía apenas os grandes besouros-rinocerontes, tais como *Dynastes* Kirby, 1825, *Golofa* Hope, 1837 e *Xylotrupes* Hope, 1837).

Ao longo da segunda metade do século XIX e início do século XX, o grupo foi tratado por nomes distintos: Agaocephalides (Lacordaire, 1856), Agaocephalitae (Thomson, 1860), Agaocephalinae (Bates, 1888). Foi Casey (1915), todavia, quem classificou o grupo como uma tribo de Dynastinae pela primeira vez. Passaram-se 123 anos até que uma revisão desse grupo fosse feita por Endrödi (1970) em sua “*Monographie der Dynastinae (Coleoptera)*”. Ao longo desses 123 anos desde a criação de Agaocephalidae, cinco novos gêneros foram descritos e incluídos no grupo, sendo eles *Brachysiderus* Waterhouse, 1881, *Colacus* Ohaus, 1910, *Gnathogolofa* Arrow, 1914, *Mitracephala* Thomson, 1859 e *Spodistes* Burmeister, 1847. Endrödi ainda incluiu em Agaocephalini o gênero *Democrates* Burmeister, 1847 que havia sido descrito por Burmeister (1847) como membro de Oryctomorphidae e depois transferido

por Lacordaire (1856) para Cyclocephalides, mas, sem dar maiores explicações sobre o porquê de ter considerado esse gênero como um Agaocephalini. Endrödi (1970) expandiu um pouco mais as descrições dos gêneros e das espécies e forneceu chaves dicotômicas para todos estes táxons.

Na sua descrição da tribo, Endrödi (1970) acrescenta alguns caracteres além dos já pontuados por Burmeister (1847), tais como: “fêmeas podendo ter 1 a 2 tubérculos na cabeça e pronoto sem protuberâncias; mandíbulas cobertas pelo clípeo, com dentes no ápice; propigídio (tergito VII) sem aparato estridulatório; tíbias médias e posteriores levemente ou moderadamente expandindo em direção ao ápice, com duas quilhas oblíquas, ápice truncado ou curvado com um anel de cerdas esparsas ou densas”. Apesar da busca por caracteres que fossem diagnósticos para todos os gêneros da tribo, algumas daquelas características não estavam de fato presentes em todos os gêneros que Endrödi (1970) incluiu em Agaocephalini, como é o caso de *Colacus*, *Democrates* e *Gnathogolofa*. *Colacus* possui a pontuação elitral disposta em fileiras, ao invés de irregular; *Democrates* tem cabeça e pronoto sem chifres ou tubérculos; e os três gêneros não possuem dentes nas mandíbulas. O próprio Endrödi já havia percebido isso e pontuado essas exceções na descrição da tribo, mas, não comenta mais a fundo sobre as razões pelas quais ele havia decidido agrupar esses três gêneros junto dos outros. Pouco tempo depois, Endrödi (1974) descreveu um novo gênero para a tribo: *Horridocalia* Endrödi, 1974, gênero monotípico descrito com base em um único espécime presente na coleção do entomólogo francês Melchior de Lisle, amigo do autor. Por muito tempo as principais novidades descobertas em Agaocephalini foram a nível de espécie, até que Milani (2019) propôs a mudança de status de *Minisiderus* Endrödi, 1970 de subgênero de *Brachysiderus* para gênero. Dessa forma, atualmente Agaocephalini é composta por 12 gêneros, sendo eles: *Agaocephala*, *Aegopsis*, *Antodon*, *Brachysiderus*, *Colacus*, *Democrates*, *Gnathogolofa*, *Horridocalia*, *Lycomedes*, *Minisiderus*, *Mitracephala* e *Spodistes*.

Os 12 gêneros de Agaocephalini estão representados por 44 espécies, todas Neotropicais, com distribuição que vai desde o sul do México até o noroeste da Argentina. Dentre os gêneros de Agaocephalini, *Horridocalia* e *Colacus* foram revisados recentemente por Pardo-Locarno *et al.* (2014) e Neita-Moreno (2015) respectivamente. Pardo-Locarno *et al.* (2014) fez a redescrição de *Horridocalia delislei* Endrödi, 1974, única espécie do gênero até aquele momento, com base em machos

maiores e menores, além da primeira descrição da fêmea. Além disso, os autores também forneceram a primeira nota de história natural dessa espécie, observando que os espécimes possuíam atividade noturna, se alimentavam de frutos em cativeiro, eram atraídos por luzes artificiais e podiam ser encontrados sob epífitas no sub-bosque da região do Chocó, na Colômbia. Neita-Moreno (2015), em sua revisão de *Colacus*, redescreveu o gênero, sinonimizou *Colacus endroedii* Martínez, 1988 com *Colacus morio* Ohaus, 1910, redescreveu as duas espécies existentes, *C. morio* e *C. bicolor* Ohaus, 1910, e ainda descreveu uma nova espécie, *Colacus moroni* Neita-Moreno, 2015, fazendo uma minuciosa comparação morfológica envolvendo os caracteres tradicionalmente utilizados na taxonomia de Dynastinae, como a genitália masculina e estruturas da cabeça, juntamente com caracteres não tão utilizados, como as peças do aparelho bucal e escleritos genitais femininos. Outro gênero que passou por uma revisão recente foi *Aegopsis*, que foi iniciada por Sobral *et al.* (em prep.) como parte de sua dissertação de mestrado, o que resultou em um trabalho já publicado com duas novas espécies para o Cerrado brasileiro (Sobral *et al.* 2018) (ver Anexo I).

Ao longo da história taxonômica, as descrições de espécies de Agaocephalini foram majoritariamente centradas nos espécimes machos adultos, algo comum em Dynastinae como um todo. As fêmeas das espécies de Agaocephalini, quando conhecidas, foram geralmente descritas com pouca minúcia nos caracteres, de tal forma que os detalhes da escultura da cabeça e tórax, do aparelho bucal, do tegumento das pernas, abdômen e escleritos genitais não estão presentes nas descrições desses espécimes. Algumas das possíveis razões para esse subestudo são que as fêmeas são mais difíceis de serem coletadas do que os machos e menos vistosas. Portanto, quando os colecionadores conseguiam uma fêmea de uma espécie conhecida, normalmente eles não tinham interesse em dissecá-la, pois, devida a sua raridade, era preferível conservá-la intacta do que dissecá-la para fins taxonômicos. Além disso, em certos gêneros de Agaocephalini, como *Spodistes* e *Lycomedes* por exemplo, as fêmeas são muito parecidas entre si na morfologia externa, o que tornava difícil distingui-las com os equipamentos de até meados do século XX, algo que certamente contribuiu para que muitos espécimes de espécies diferentes fossem guardados nas mesmas gavetas como sendo da mesma espécie (o que aconteceu com *Spodistes mniszewski* (Thomson, 1860) e *Spodistes monzoni* Warner, 1992, por exemplo).

Quanto aos imaturos de Agaocephalini, os registros são ainda mais escassos, somente havendo a descrição de larvas e pupas de três espécies: *Lycomedes hirtipes* Arrow, 1902, *Aegopsis bolboceridus* (Thomson, 1860) e *Aegopsis curvicornis* Burmeister, 1847 (Pardo-Locarno & Morón, 2006; Neita-Moreno *et al.* 2014). A biologia desse grupo também é vagamente conhecida e, em geral, é generalizada com base nas observações feitas com *A. bolboceridus*, *L. hirtipes* e *H. delislei*. O ciclo de vida é univoltino, resultando em uma geração por ano; as larvas são encontradas enterradas no solo, abaixo da serapilheira ou se alimentando das raízes de plantas (especialmente arbustivas); no último estágio larval, os espécimes constroem uma câmara pupal misturando saliva, fezes e matéria orgânica do solo, onde irão permanecer até que se tornem adultos e atinjam a maturação sexual; o estágio de pupa dura cerca de três meses e os adultos emergem do solo durante a estação chuvosa (Pardo-Locarno & Morón, 2006; Oliveira *et al.* 2008; Oliveira & Frizzas, 2013; Pardo-Locarno *et al.* 2014).

Agaocephalini é uma das tribos menos estudadas de Dynastinae, provavelmente pela raridade de muitas de suas espécies, assim como pela sua restrição à região Neotropical e à dificuldade em reunir o material histórico e recente disperso por coleções da Europa e das Américas. As descrições e diagnoses para os táxons que não tiveram revisões feitas desde Endrödi (1970) ainda permanecem as mesmas. Embora Endrödi (1970) tenha dado um passo importante no avanço taxonômico dos gêneros e espécies de Agaocephalini, suas descrições específicas não tinham uma diagnose, de forma que as chaves dicotômicas acabavam exercendo o papel da diagnose do ponto de vista comparativo. Além disso, táxons com fêmeas muito similares (*Spodistes*, *Lycomedes*, *Minisiderus* e *Agaocephala*) são difíceis de se identificar quando somente espécimes fêmeas são coletadas na natureza ou encontradas em coleções sem um espécime macho correspondente. Devido a ausência de chaves dicotômicas detalhadas para as fêmeas desses gêneros, a maioria das identificações é feita com base em aproximação pelo local de coleta, comparando-as com machos já identificados de locais o mais aproximados possíveis, o que acaba ocasionando em erros e nublando a real distribuição das espécies. Com base nos resultados obtidos por Sobral *et al.* (2018) na descrição de espécies novas semelhantes à *Aegopsis bolboceridus*, com fêmeas incluídas, e por Neita-Moreno (2015) na revisão de *Colacus*, foi percebido que as peças do aparelho bucal e traços subutilizados da morfologia externa, podem servir como

traços marcantes na diagnose das espécies. Dos 12 gêneros de Agaocephalini, apenas *Colacus*, *Aegopsis* e *Horridocalia* tiveram revisões recentes que incluíssem tais caracteres nas suas descrições e diagnoses. Considerando a distribuição das espécies de mesmo gênero em regiões orográficas próximas, como ocorre em *Minisiderus* e *Agaocephala* no Cerrado e áreas de transição com Mata Atlântica, e em *Brachysiderus*, *Spodistes* e *Lycomedes* nos Andes, uma descrição esmiuçada desses caracteres permite maior robustez na sua delimitação, principalmente entre espécies muito similares. Dessa forma, o uso de novos caracteres masculinos e femininos nas descrições e diagnoses são necessários para auxiliar em uma acurada delimitação dos gêneros, subgêneros e espécies da tribo.

OBJETIVOS

Objetivo geral

Fazer um estudo taxonômico de *Agaocephalini* Burmeister, 1847 (Coleoptera, Melolonthidae, Dynastinae).

Objetivos específicos

- a) Revisar os gêneros *Agaocephala* Lepeletier de Saint-Fargeau & Audinet-Serville, 1825, *Brachysiderus* Waterhouse, 1881, *Minisiderus* Endrödi, 1970, *Lycomedes* Brême, 1844, e *Spodistes* Burmeister, 1847;
- b) Redescrever os táxons conhecidos, quando necessário, e descrever os possíveis táxons novos de forma padronizada, utilizando traços morfológicos subutilizados como aparelho bucal, falobase e vista ventral dos parâmeros;
- c) Revisar as diagnoses de gêneros, subgêneros e espécies dentro da tribo;
- d) Ilustrar os caracteres morfológicos utilizados para a identificação dos táxons;
- e) Atualizar os registros de distribuição geográfica;
- f) Elaborar uma chave dicotômica atualizada para os gêneros e espécies de *Agaocephalini*.

MATERIAL E MÉTODOS

Material examinado

Foram examinados cerca de 400 exemplares, obtidos através de empréstimos, visitas presenciais ou fotos fornecidas pelas seguintes coleções:

BMNH – Naturhistorisches Museum Basel, Basel, Suíça (Cristoph Germann)

CEMT – Coleção Zoológica, Seção de Entomologia da Universidade Federal do Mato Grosso, Cuiabá, MT, Brasil (Fernando Vaz-de-Mello);

EPGC – Coleção Entomológica Particular Everardo e Paschoal Grossi, Nova Friburgo, RJ, Brasil (Everardo Grossi);

CERPE – Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, PE, Brasil (Paschoal Grossi);

CMNC – Canadian Museum of Nature, Ottawa, Canadá (François Geniér)

DZUP – Coleção Entomológica Padre Jesús Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brasil (Lúcia Massutti de Almeida)

HNHM – Hungarian Natural History Museum, Budapeste, Hungria (Otto Merkl)

IFML – Colección de Entomologia del Instituto e Fundación Miguel Lillo, Tucumán, Argentina (Emília Perez)

INPA – Coleção de Invertebrados do Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brasil (Márcio Oliveira);

MNHN – Muséum National d’Histoire Naturelle, Paris, França (Antoine Mantillieri);

MNRJ – Museu Nacional do Rio de Janeiro, Rio de Janeiro, RJ, Brasil (Marcela L. Monné);

MSUC – Michigan State University Albert J. Cook Arthropod Research Collection (Anthony Cognato, Gary Parsons);

MZLU – Lund Museum of Zoology, Lund, Suécia (Christoffer Fägerström);

MZUSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (Sônia Casari);

NHM – The Natural History Museum, Londres, Reino Unido (Max Barclay);

NMPC – National Museum of Natural History, Praga, República Tcheca (Jiří Hájek);

OUMNH – Oxford University Museum of Natural History, Oxford, Reino Unido (Zoë Simmons);

RBINS – Royal Belgian Institute of Natural Sciences, Bruxelas, Bélgica (Alain Drumont);

UFRN – Coleção Entomológica Adalberto Antônio Varela Freire, Natal, RN, Brasil (Ricardo Andreazze);

ZMNB – Zoological Museum für Naturkunde, Berlim, Alemanha (Johannes Frisch).

Estudo morfológico

Para análise da morfologia externa da cabeça, tórax, pernas e abdômen, os espécimes foram examinados secos e alfinetados. Já para as análises da morfologia de peças internas, como o aparelho bucal e a genitália, foram realizadas disseções. O protocolo para disseção foi estabelecido da seguinte maneira: os espécimes foram colocados em água fervida por cerca de 20 a 30 minutos para amolecimento dos tecidos. A disseção da genitália masculina (edeago) foi realizada com o auxílio de uma pinça de ponta fina através de uma incisão transversal entre os tergitos VI e VII para remoção da peça, enquanto que a genitália feminina (gonocoxitos) foi extraída com o mesmo tipo de pinça através de incisão da membrana entre o esternito VIII e o tergito VIII. Para disseção das peças do aparelho bucal, foi utilizado um estilete entomológico com ponta de agulha hipodérmica afiada. Visando preservar ao máximo a integridade dos espécimes dissecados, nos casos das peças bucais pareadas – mandíbulas e maxilas – somente as do lado direito, em vista ventral, foram removidas. Para remoção, foram feitas incisões juntamente de movimentos de alavanca nas bases de cada peça bucal. Após a disseção, cada estrutura foi colada em uma etiqueta de papel-cartão, adaptando o método de Ohaus (1934), e cada etiqueta foi alfinetada abaixo do espécime. Os espécimes dissecados foram colocados por cerca de um dia na estufa para total secagem.

Identificação e Terminologia

As identificações foram feitas com base nas descrições originais dos gêneros e das espécies, detalhes dos autores estão destacados na Introdução e no Material e Métodos de cada um dos gêneros nos capítulos subsequentes. Além disso, os espécimes foram comparados com os espécimes-tipo de cada táxon, exceto quando tipo desaparecido ou destruído. Também foram utilizadas fotografias para comparação com o material-tipo e material adicional examinados.

A terminologia utilizada no presente trabalho seguiu Snodgrass (1993) e Endrödi (1985) para as estruturas gerais do corpo (Fig. 2A-I), Nel & Scholtz (1990) para as peças do aparelho bucal, Cristóvão & Vaz-de-Mello (2020) para estruturas do abdômen e peças da genitália (Fig. 1A-K) e Führmann (2010) para as pontuações corporais.

Mensuração

As medidas de cada espécime foram feitas com o auxílio de um paquímetro digital para as estruturas maiores e uma lente ocular milimetrada para estruturas menores. As medidas foram feitas tendo como base o intervalo mínimo ao máximo, sendo elas:

1. Comprimento corporal (Body length): distância entre o ápice do clípeo e o ápice do tergito VIII;
2. Comprimento da cabeça (Head length): distância entre a base do vértice e o ápice do clípeo;
3. Comprimento do chifre cefálico (Cephalic horn length): distância entre a base e o ápice dos chifres cefálicos;
4. Comprimento elitral (Elytral length): distância entre a base e o ápice do élitro;
5. Largura elitral (Elytral width): largura entre as extremidades externa e interna de um élitro;
6. Largura pronotal (Pronotal width): largura entre as extremidades laterais do pronoto;
7. Comprimento protibial (Protibial length): distância entre a base e o ápice da protíbia;
8. Comprimento do chifre torácico (Thoracic horn length): distância entre a base e o ápice do chifre pronotal.

Fotografias

As fotografias foram feitas em parte com câmera fotográfica LEICA DFC 295 acoplada ao estereomicroscópio LEICA M205C, através do software Leica Application Suite LAS V3.6, e em parte com câmera fotográfica de celular Xiaomi Remi Note8 Pro acoplada ao estereomicroscópio Digilab DI 106-T com posterior montagem em vários focos no software Helicon Focus 7. Fotografias de estruturas grandes foram feitas em partes e unidas posteriormente através da função *Photomerge* do Adobe Photoshop CS6. As edições das imagens e montagem das pranchas foram feitas nesse mesmo software.

Mapas de distribuição

A elaboração dos mapas de distribuição geográfica da tribo, gêneros e espécies foi feita através dos dados de locais de coleta presentes nas etiquetas de cada espécime examinado. Para os espécimes cujos dados de latitude e longitude estavam ausentes nas etiquetas, foi estabelecido com uso do *GoogleMaps* um ponto dentro dos limites da mais restrita informação de local disponível na etiqueta (reserva, parque, distrito, município, etc.). Para registros de distribuição em literatura cujos espécimes não foram encontrados ou passíveis de serem examinados, foi considerada a informação original. A confecção dos mapas foi feita no programa *SimpleMapp* (<http://www.simmplemapp.net>) (Shorthouse, 2010).

Ecorregiões e habitats

Para as discussões acerca da distribuição geográfica das espécies e gêneros de Agaocephalini, foram levadas em conta a regionalização biogeográfica do Neotrópico proposta por Morrone (2014) e as ecorregiões globais propostas por Dinerstein *et al.* (2017). As fitofisionomias do Cerrado citadas seguiram as seguintes bibliografias: Ribeiro & Walter (1998), Vasconcelos (2011) e Carvalho *et al.* (2011).

Dados de etiquetas

A citação das etiquetas foi feita de acordo com o seguinte padrão: sexo do exemplar examinado; sigla da instituição de origem do espécime entre parênteses; nome do país de origem, nome de estados, cidades e outros locais com apenas a primeira letra maiúscula; data de coleta com o mês representado por algarismo romano; nome do método de coleta; coordenadas geográficas; letras minúsculas seguidas por parênteses indicando a ordem das etiquetas (a, b, c – primeira, segunda e terceira etiqueta); símbolo de barra (/) separando as linhas de cada etiqueta; informações entre chaves ({}) sobre dados abreviados ou correções nas etiquetas; nome dos coletores seguidos pela sigla “leg.”; nome dos identificadores seguidos ou precedidos pela sigla “det.”.

Nomenclatura

De acordo com o Código Internacional de Nomenclatura Zoológica (ICZN, 2000, cap. 3, art. 8), a nomenclatura dos táxons proposta nessa tese não é considerada válida enquanto não for publicada em periódicos científicos. Contudo, os nomes das espécies novas foram aqui utilizados como prática para o ato nomenclatural e para facilitar as comparações entre as espécies.

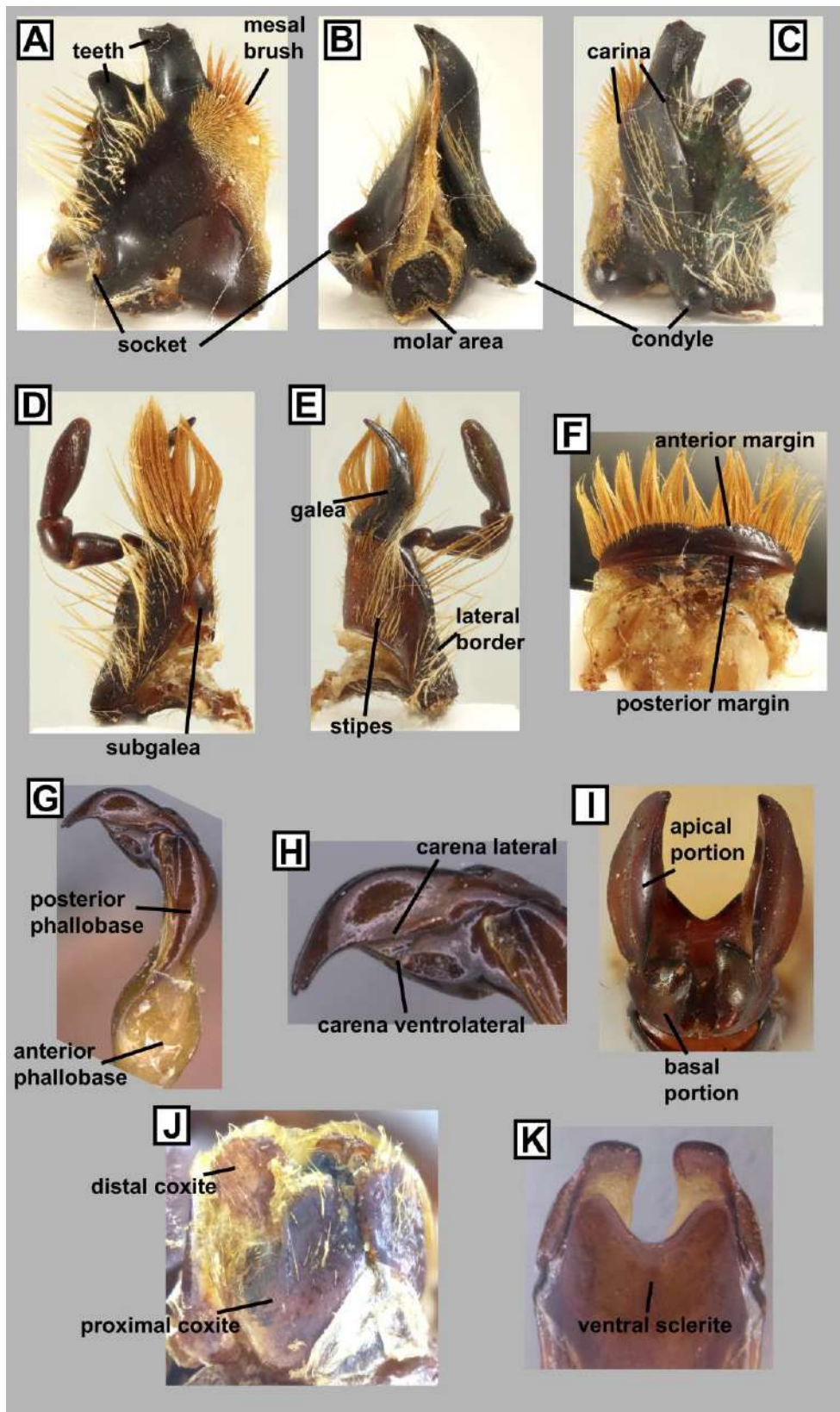


FIGURA 1. Aparelho bucal (A-F), genitália masculina (G-I, K) e feminina (J) de Agaocephalini. A, Mandíbula em vista dorsal. B, Mandíbula em vista lateral. C, Mandíbula em vista ventral. D, Maxila em vista dorsal. E, Maxila em vista ventral. F, Labro em vista dorsal. G, Edeago em vista lateral. H, Parâmeros em vista lateral. I, Parâmeros em vista caudal. J, Gonocoxitos. K, Parâmeros em vista ventral.

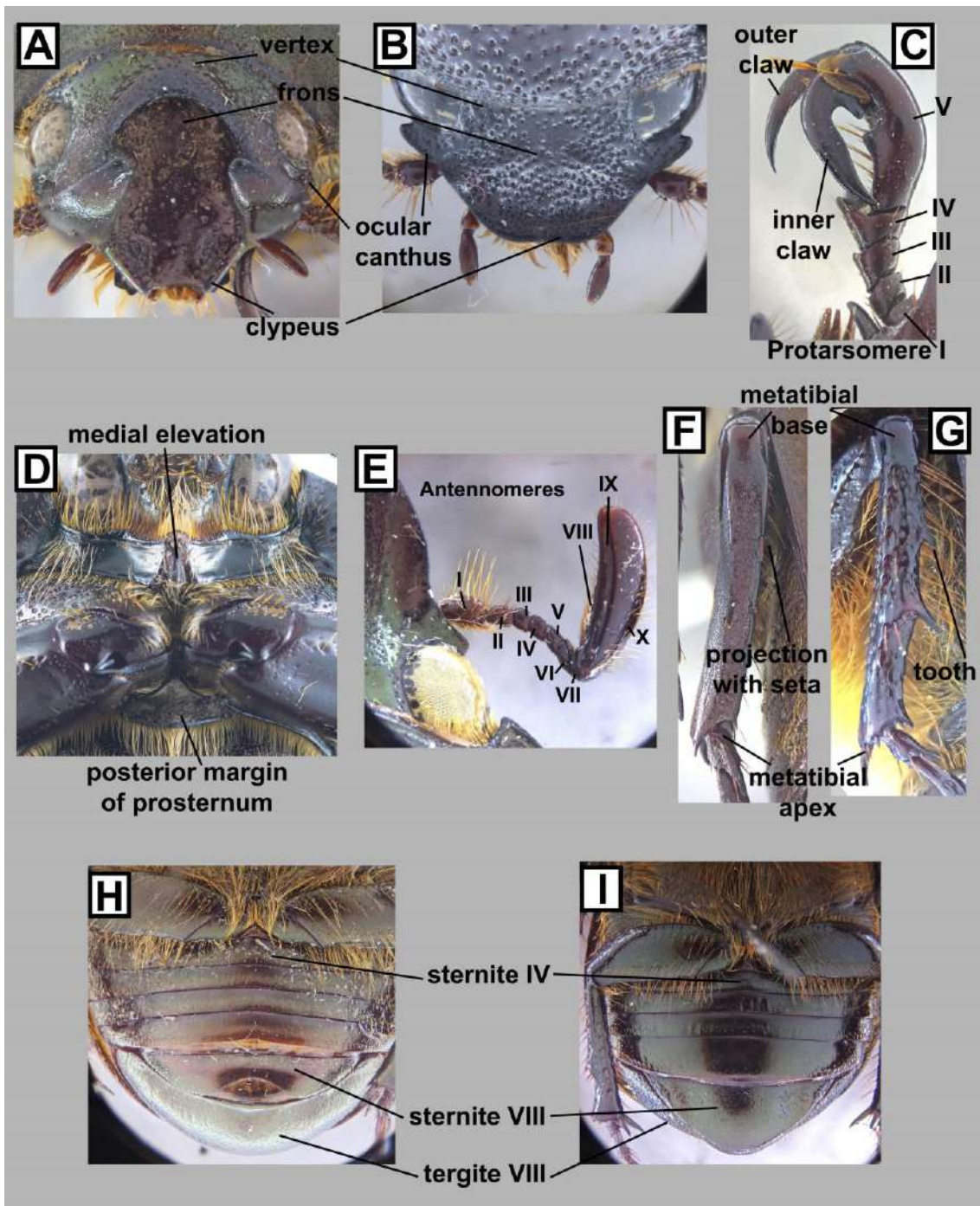


FIGURA 2. Cabeça (A-B, E), tórax (D), pernas (C, F-G) e abdômen (H-I) de Agaocephalini. A, Cabeça masculina em vista frontal. B, Cabeça feminina em vista dorsal. C, Protarso masculino em vista lateral interna. D, Prosterno em vista ventral. E, Antena em vista dorsal. F, Metatíbia em vista lateral sem dentes tibiais. G, Metatíbia em vista lateral com dentes tibiais. H, Abdômen masculino em vista ventral. I, Abdômen feminino em vista ventral.

CAPÍTULO I

Sobral, R., Duarte, P.R.M. & Grossi, P.C. Review of *Agacephala* Lepeletier de Saint-Fargeau & Audinet-Serville, 1825 (Coleoptera, Scarabaeoidea, Dynastinae), with two new species described from Brazil and notes on Agaocephalini with description of two new subtribes. Manuscrito em preparação para submeter à revista *Zootaxa*.

Review of *Agacephala* Lepeletier de Saint-Fargeau & Audinet-Serville, 1825 (Coleoptera, Scarabaeoidea, Dynastinae), with two new species described from Brazil and notes on Agaocephalini with description of two new subtribes

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Abstract

Agacephala mineira sp. nov. and *Agacephala alvarengai* sp. nov are described from East and Northeast of Minas Gerais State, Brazil, respectively. The new species are compared with similar species from which they differ mainly in the pronotum punctuation, body shape and ocular canthi. After studying the holotype of *Agacephala urus* (Thomson, 1860), we synonymize it with *Agacephala mannerheimi* Laporte, 1832, **new synonym**. The subgenus *Agacephala* (*Lycocephala*) Martínez is erected to the generic status *Lycocephala* Martínez, **new status**, and its diagnostic characters discussed. A known distribution map and a key to species are given, as new collection records for other *Agacephala* species. Notes on Agaocephalini are provided and three genera previously in the tribe – *Democrates*, *Colacus* and *Gnathogolofa* – are transferred to Pentodontini. Also two new subtribes are created: Lycomedina subtrib. nov. and Agacephalina subtrib. nov. based on morphological and geographical similarities among the genera of the tribe. Key to genera and subtribes of Agaocephalini are provided.

Key words: Agaocephalini, Melolonthidae, new combination, Scarabaeidae.

Introduction

Agacephala Saint-Fargeau & Audinet-Serville, 1828 is a genus distributed in the Neotropical Region from Venezuela to Argentina and currently includes eight valid species (Endrödi 1985; Lachaume 1992; Abadie *et al.* 2008). This genus is very distinctive among most of the genera of the Agaocephalini and is usually distinguished

by a combination of characters as the evident sexual dimorphism, with males possessing a pair of frontal horns, pronotum often with a tubercle or projection, missing in three species, body with metallic reflexes, mainly on head, pronotum, legs and venter, with elytra light to dark brown. Species of the genus can be found in distinct biomes, but almost all are restricted to Atlantic Forest from Bahia to Rio Grande do Sul states in Brazil. One species is restricted to Venezuela, *A. bicuspis*, which has been collected near open areas of South American Savanna (Joly 1992). The most distinctive species within the genus is probably *A. margaridae*, by the bifurcated frontal horns of males and enlarged size when compared with other species of *Agacephala*, and the only species occurring in Amazon region, but in open areas (Alvarenga 1968). All species can be collected with light traps usually flying during a few days along the year and are considered an uncommon group in collections, represented by few specimens. Almost nothing is known about their biology, instead that adults are attracted by artificial lights, and immature stages are unknown.

In this present contribution, we review the species of *Agacephala* and describe two new species from southern and northeastern Minas Gerais state, one of them commonly collected and wrongly identified as *A. urus* (Thomson) in all collections studied. *Agacephala urus* is placed into synonymy with *Agacephala mannerheimi*, **syn. nov.**, after the study of the holotype specimen in MNHN, France. With our findings, now *Agacephala* comprises nine valid species. Additionally, the subgenera *Agacephala* (*Lycocephala*) Martínez & Alvarenga is raised to generic status and its species has a new combination. For each genus, the main diagnostic characters are discussed. We also provide the description of two new subtribes to accommodate the two distinct groups within Agaoccephalini. A key is provided to Agaoccephalini genera and to species of *Agacephala*.

Materials and methods

More than a hundred specimens were studied from the following collections (acronyms according Evenhuis (2009) when available).

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

CEMT Seção de Entomologia da Coleção Zoológica da Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso, Brazil (Fernando Z. Vaz-de-Mello)

CMNC Canadian Museum of Nature, Ottawa, Canada (François Génier)

HNHM	Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl)
DZUP	Coleção Entomológica Padre Jesús Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (Lúcia Massutti de Almeida)
EPGC	Everardo and Paschoal Grossi Collection, Nova Friburgo, Rio de Janeiro, Brazil (Everarado J. Grossi)
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (Marcio L. Oliveira)
MNRJ	Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (Marcela L. Monné)
MNHN	Muséum National d’Histoire Naturelle, Paris, France (Antoine Mantillieri)
MSUC	Michigan State University Albert J. Cook Arthropod Research Collection, East Lansing, USA (Anthony Cognato & Gary Parsons)
MZLU	Lund Museum of Zoology, Lund, Sweden (Christoffer Fägerström)
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Sônia Casari)
NHM	Natural History Museum, London, United Kingdom (Max Barclay)

Terminology follows in part Endrödi (1985) for the general characters. The aedeagi were dissected after boiling specimens for a few minutes in warm water with neutral soap, and then glued in card mount, and pinned just below each specimen. Images were obtained with a Leica DFC295 attached at a stereoscopic microscope M205 and a smartphone Xiaomi Redmi Note8 Pro attached at a stereoscopic microscope Digilab DI 106-T with stacked images made on software Helicon Focus 7. Images were edited using Adobe Photoshop CS6.

Results

Taxonomy

Agaocephalini Burmeister, 1847

Type genus: *Agacephala* Saint-Fargeau & Audinet-Serville, 1825: 370.

Diagnosis. Agaocephalini can be distinguished from the other tribes of Dynastinae by the combination of the following characters. **Males:** Head armed with distinct horn (Fig. 37B) or pair of horns (Fig. 37A). Pronotum armed with one distinct horn (Fig.

37B) or one pair of tubercles (Fig. 37C), only in *Brachysiderus* and in *Agacephala bicuspis* pronotum not armed but with shape distinctly globose in lateral view (Fig. 37D). Protarsi distinctly thick (Fig. 38A). **Females:** Sexual dimorphism strong, distinct on head, pronotum and protarsi (Fig. 38B). Head unarmed or armed with tubercles (Fig. 38C). Pronotum unarmed, shape convex (Fig. 38D). **Males and females** with elytra irregularly punctate, with large or thin punctures not distributed in a pattern of regular rows (Fig. 38E), except in *Horridocalia* and *Lycomedes velutipes*. Mandibles with teeth on outer margin (Fig. 38F). Prosternum with (Fig. 38I) or without prosternal process (Fig. 38J). Molar area short, surface slightly concave (Fig. 38G). Metatarsomere I subtriangular with long projection (Fig. 38H). Tergite VII densely covered by short thin setae, stridulatory apparatus absent. Occurrence in mainland and islands of Central and South America.

Composition. Agaocephalini is formed by 10 genera: *Agacephala* Saint-Fargeau & Audinet-Serville, 1825, *Aegopsis* Burmeister, 1847, *Antodon* Brême, 1844, *Brachysiderus* Waterhouse, 1881, *Horridocalia* Endrödi, 1974, *Lycocephala* Martínez & Alvarenga, 1987, *Lycomedes* Brême, 1844, *Minisiderus* Endrödi, 1970, *Mitracephala* Thomson, 1859 and *Spodistes* Burmeister, 1847.

Geographic distribution. Argentina, Bolivia, Belize, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Peru, Trinidad and Tobago, Venezuela.

Remarks. After examining specimens of *Democrates* Burmeister, 1847, *Colacus* Ohaus, 1910, and *Gnathogolofa* Arrow, 1914, we decided to remove these genera from Agaocephalini and change them to Pentodontini. The reason is that they do not have the diagnostic characteristics of the tribe that are shared by the other 10 genera, instead they fit in the diagnosis of Pentodontini by Endrödi (1985): “Anterior tarsi of males rarely thickened, sexual dimorphism not very distinct, apex of posterior tibiae slightly truncated (...)”. Endrödi (1970) included them in Agaocephalini but did not give a detailed discussion about it. These three genera differ from the Agaocephalini by: mandibles toothless, with apex round (Fig. 39A), protibia with insertion of spur posterior to insertion of protarsomere I (Fig. 39B), inner anterior corner of protibia smooth (Fig. 39B), metatarsomere I smooth on outer margin (Fig. 39C), sexual dimorphism almost indistinct, females with short cephalic horns in *Colacus* and *Gnathogolofa* (Fig. 39D) whereas in Agaocephalini mandibles toothed, with apex prominent (Fig. 39E), protibia with insertion of protarsomere I posterior to insertion of spur (Fig. 39F), inner anterior corner of protibia toothed (Fig. 39F), metatarsomere I

with strong projection on outer margin (Fig. 39G), sexual dimorphism distinct, females hornless (Fig. 39H).

It was possible to observe that among the genera of Agaocephalini there is a set of morphological characteristics and geographical distribution robust enough to indicate that there are two groups with genera more similar to each other than the other group. These differences may indicate there was some process of separation of ancestral populations that, although it preserved the diagnostic traits of Agaocephalini, provided shared morphological variations between smaller groups. The genera of Agaocephalini that occur in the Andes and Central America have more morphological similarities to each other than to the genera that occur in the Guiana and Brazilian shields. For this reason, we are proposing the division of these genera into two subtribes.

Agacephalina Sobral & Grossi new subtribe

Type genus: *Agacephala* Lepeletier de Saint-Fargeau & Audinet-Serville, 1825: 370.

Diagnosis. Agacephalina is characterized by the combination of the following characters. **Males:** Protarsal claws symmetric and simple (Fig. 40A) or, when asymmetric, presence of short protuberance on inner claw (Fig. 40B). Protarsomere V thick and curved, ventral margin smooth (Fig. 40A-B). Protarsomere IV with basal portion pedunculated, inner margin of apical portion angulated and simple (Fig. 40C). Ocular canthi vertical or slightly transverse, protuberances absent on transverse canthi (Figs. 40D-E). Pronotum, elytra and appendages lustrous, presence of metallic shine on pronotum or appendages (in *Aegopsis*, *Agacephala*, *Lycocephala*, *Mitracephala*).

Females: Clypeus round (Fig. 40F) or subtrapezoidal simple (Fig. 40H). Clypeal anterior margin devoid teeth (Fig. 40F, 40H). Pronotum glabrous (Fig. 40G). Prosternal process absent. Main distribution through the Brazilian highlands and lowlands, the Guiana shield and eastern foothills of southern Andes (except by two species of *Aegopsis* with records in northern Andes).

Composition. Agacephalina is composed by *Agacephala* Lepeletier de Saint-Fargeau & Audinet-Serville, 1825, *Aegopsis* Burmeister, 1847, *Lycocephala* Martínez & Alvarenga, 1987, *Minisiderus* Endrödi, 1970 and *Mitracephala* Thomson, 1859.

Lycomedina Sobral & Grossi new subtribe

Type genus: *Lycomedes* Brême, 1844: 299.

Diagnosis. Lycomedina is characterized by the combination of the following characters.

Males: Protarsal claws asymmetric, inner claw pincer-like shaped with basal tooth and one weak or strong protuberance distally near claw tip (Fig. 41A). Protarsomere V distinctly thick, inner margin distinctly excavated on apex, presence of medial tooth (Fig. 41A). Protarsomere IV with basal portion flat, inner margin of apical portion projected and elongated (Fig. 41B). Ocular canthi transverse, presence of strong or weak protuberances on apical or basal portions of anterior margins (Figs. 41C-D).

Pronotum, elytra and appendages tomentose (in *Spodistes*, *Lycomedes* and *Horridocalia*), or glabrous, devoid tomentum (in *Brachysiderus*), or pronotum and appendages covered with yellowish, long, thin setae (in *Antodon*). **Females:** Clypeus campaniform (Fig. 41E). Clypeal anterior margin with weak or strong pair of tooth on corners (Fig. 41E, 41G). Pronotum with tomentose punctures (Fig. 41F). Prosternal process present. Main distribution through the Cordillera of the Andes and mainland Central America (except by *Antodon* with occurrence in Brazilian Atlantic forest).

Composition. Lycomedina is composed by *Lycomedes* Brême, 1844, *Antodon* Brême, 1844, *Brachysiderus* Waterhouse, 1881, *Horridocalia* Endrödi, 1974, *Spodistes* Burmeister, 1847.

Key to subtribes and genera of Agaocephalini Burmeister, 1847 (modified from Endrödi, 1985)

1. Males with protarsal claws symmetric and simple (Fig. 40A) or, when asymmetric, presence of short protuberance on inner claw (Fig. 40B). Protarsomere V thick and curved, inner margin not excavated (Fig. 40A-B). Protarsomere IV with basal portion pedunculated, inner margin of apical portion angulated and simple (Fig. 40C). Females with clypeus round (Fig. 40F) or subtrapezoidal simple (Fig. 40H). Clypeal apex simple (Fig. 40F, 40H). Pronotum glabrous (Fig. 40G) [Agaocephalina **subtrib. nov.**]..... 2
- Males with protarsal claws asymmetric, inner claw pincer-like shaped with basal tooth and one weak or strong protuberance distally near claw tip (Fig. 41A). Protarsomere V distinctly thick, inner margin distinctly excavated on apex, presence of medial tooth (Fig. 41A). Protarsomere IV with basal portion flat, inner margin of apical portion projected and elongated (Fig. 41B). Females with clypeus campaniform (Fig. 41E). Clypeal apex with weak or strong pair of protuberances on corners (Fig. 41E, 41G). Pronotum with

- tomentose punctures (except *Brachysiderus*) (Fig. 41F) [*Lycomedina* **subtrib. nov.**]... 11
2. Head armed with horns . Pronotum armed with horn or tubercles (only disarmed in *Agacephala duponti*, *A. inermicollis* and *A. bicuspis*) [males]..... 3
- Head disarmed or with tubercles. Pronotum disarmed [females]..... 7
3. Body robust, big size (ca. 35 – 45 mm of length) (Fig. 43A). Head with one cephalic horn, shape thick with base almost covering entire frons (Fig. 43C)..... ***Mitracephala Thomson, 1859***
- Body not robust, small to medium size (ca. 15 – 30 mm of length). Head with two cephalic horns (either distinctly separated or partially fusionated), base of horns not covering entire frons..... 4
4. Pronotum with margins crenulated (Fig. 34E). Pronotal disc completely rugose (Fig. 34D)..... ***Lycocephala (Martínez & Alvarenga, 1987)***
- Pronotum with margins smooth. Pronotal disc not rugose..... 5
5. Cephalic horns partially fusionated medially (Fig. 52A [in Cap. II]). Pronotum with pair of tubercles (Fig. 52A [in Cap. II])..... ***Minisiderus (Endrödi, 1970)***
- Cephalic horns distinctly separated. Pronotum with horn or disarmed..... 6
6. Pronotum black or with shades of brown (Fig. 36A-B). Elytra black or with shades of brown (Fig. 36A-B)..... ***Aegopsis Burmeister, 1847***
- Pronotum green or red metallic (Fig. 1A). Elytra yellowish or light brown with dark patches on humeral and apical umbones (Fig. 1A)..... ***Agacephala Saint-Fargeau & Audinet-Serville, 1825***
7. Body robust, big size (Fig. 43B). Elytral apex widely expanded, covering tergite VIII like a hood (Fig. 43E). Protibiae and protarsi distinctly thick (Fig. 43D)... ***Mitracephala Thomson, 1859***
- Body moderate to small (except in *Agacephala margaridae*). Elytral apex not as widely expanded, discretely covering tergite VIII. Protibiae and protarsi slender..... 8
8. Pronotum rugose and completely hirsute (Fig. 33C). Lateral margins of pronotum crenulated (Fig. 33C)..... ***Lycocephala (Martínez & Alvarenga, 1987)***
- Pronotum not rugose and glabrous. Lateral margins of pronotum smooth..... 9
9. Pronotum and abdomen with greenish or reddish metallic shine (Fig. 1C, 11L). Elytra yellowish with dark patches on at least one pair of the umbones (Fig. 1C)..... ***Agacephala Saint-Fargeau & Audinet-Serville, 1825***
- Pronotum and abdomen without metallic shine or, when present, not green or red. Elytra black or in shades of brown, when yellowish not with dark patches on

umbones.....	9
10. Clypeus in frontal view distinctly thickened (Fig. 52G [in Cap. II]). Tergite VIII hidden by elytral apex in dorsal view (Fig. 52I [in Cap. II]). Ocular canthi elongated with base not elevated (Fig. 52E [in Cap. II]).....	Minisiderus (Endrödi, 1970)
- Clypeus in frontal view distinctly narrow (Fig. 52H [in Cap. II]). Tergite VIII exceeding elytral apex in dorsal view (Fig. 52J [in Cap. II]). Ocular canthi short and slightly protruded basally (Fig. 52F [in Cap. II]).....	Aegopsis Burmeister, 1847
11. Head armed with one distinct horn. Pronotum with horn or tubercles (except in <i>Brachysiderus</i>). Protarsal claws asymmetric, inner claw pincer-like shaped [males].....	12
- Head disarmed. Pronotum disarmed. Protarsal claws symmetric, inner claw simply curved [females].....	16
12. Pronotum disarmed (Fig. 1B [in Cap. III]). Pronotum glabrous (Fig. 3D [in Cap. III]). Ocular canthi with distinct horn-like projection on apical anterior corner (Fig. 3A [in Cap. III]).....	Brachysiderus Waterhouse, 1881
- Pronotum armed with horn or tubercle. Pronotum tomentose or hirsute. Ocular canthi not as above.....	13
13. Pronotum hirsute (Fig.). Pronotal lateral margins crenulated (Fig.). Elytra smooth and lustrous (Fig.).....	Antodon Brême, 1844
- Pronotum tomentose or with tomentose punctures. Pronotal lateral margins smooth. Elytra tomentose.....	14
14. Pronotum not completely tomentose, densely covered by tomentose punctures (Fig. 30B [in Cap. V]). Pronotal horn wide and short (Figs. 30C, 30F [in Cap. V]). Elytra with regular rows of punctures (Fig. 29A [in Cap. V]).....	Horridocalia Endrödi, 1974
- Pronotum completely tomentose. Pronotal horn thin and long in major males. Elytra with elytral punctures irregular (when punctures regular, galea with paired teeth).....	15
15. Pronotal horn directed forward (Fig. 1B [in Cap. IV]). Prosternal process absent.....	Spodistes Burmeister, 1847
- Pronotal horn directed upward (Fig. 1B [in Cap. V]). Prosternal process present (Fig. 4A [in Cap. V]).....	Lycomedes Brême, 1844
16. Pronotum hirsute (Fig.). Pronotal lateral margins crenulated (Fig.). Elytra smooth and yellow with umbones not marked (Fig.).....	Antodon Brême, 1844
- Pronotum not hirsute. Pronotal lateral margins smooth. Elytra tomentose or, when not	

- tomentose, orange with umbones marked by dark patches..... 17
17. Pronotum with regular punctures (Fig. 7A [in Cap. III]). Head with fovea (Fig. 6F [in Cap. III]). Elytra not tomentose, presence of dark patches on umbones (Fig. 5C [in Cap. III])..... ***Brachysiderus* Waterhouse, 1881**
- Pronotum with tomentose punctures. Head without fovea. Elytra tomentose, umbones not patched..... 18
18. Head without oblique tomentose stripes from clypeal base to vertex (Fig. 13A [in Cap. V]). Mentum drop-like shaped (Fig. 28E [in Cap. IV])..... ***Lycomedes* Brême, 1844**
- Head with oblique tomentose stripes from clypeal base to vertex. Mentum pear-like shaped..... 19
19. Elytra with big tomentose punctures distributed in regular rows (Fig. 29C [in Cap. V]) ***Horridocalia* Endrödi, 1974**
- Elytra with thin tomentose punctures distributed irregularly on disc (Fig. 5A [in Cap. IV]) ***Spodistes* Burmeister, 1847**

***Agacephala* Lepeletier de Saint-Fargeau & Audinet-Serville**

(Figs. 1-35)

Agacephala Saint-Fargeau & Audinet-Serville 1825: 370 (original description); Latreille 1829: 549 (cited); Laporte 1832: 404 (description of new species); Alvarenga 1958: 47 (description of new species); Lachaume 1992: 23 (catalogue); Smith 2006: 176

Agaocephala Mannerheim 1829: 59 (subsequent description); Burmeister 1847: 282 (cited); Erichson 1848: 560 (description of new species); Lacordaire 1856: 451 (cited); Thomson 1860: 15 (description of new species); Arrow 1914: 276 (description of new species); Prell 1934: 58 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 42 (revision); Endrödi 1985: 210 (catalogue); Joly 1992: 51 (description of female)

Aegecephala syn. Prell 1934: 58 (description)

Type species: *Agacephala cornigera* Lepeletier de Saint-Fargeau & Audinet-Serville, 1825: 370.

Diagnosis. *Agacephala* differs from other genera of Agaocephalini by the combination of the following characters. **Males:** Body lustrous, head, pronotum, appendages and venter with metallic shine reddish or greenish (Figs. 1A-B, 13A-B, 14, 15A-B, 16A-B, 27A-B, 28A-B, 29A, 30A); elytra testaceous in the majority of species (Fig. 1A) with metallic shine in *A. bicuspis* (Fig. 16A). Head with pair of cephalic horns sharp mainly

without dorsal protuberances (Figs. 2A, 2E, 2I), with dorsal protuberances in *A. margaridae* (Figs. 27A). Protarsi slender, protarsomere V slightly thickened, protarsal claws symmetric (Figs. 5F, 5J, 20B), or with a ventrobasal, small, tooth lobe-like on anterior claw (Figs. 5B, 20J). Pronotum mainly with anterior armature present either as protuberance or as horn (Figs. 1B, 27B, 28B), armature absent in *A. bicuspis*, *A. duponti* and *A. inermicollis* (Figs. 13B, 15B, 16B). **Females:** Head with (Figs. 23D, 23G) or without metallic shine (Fig. 8G, 23A). Clypeus subtrapezoidal simple (Figs. 8A, 8D, 8G, 23G) or slightly round (Figs. 23A, 23D). Mandibles subtriangular with two teeth and two ventral carinae (Fig. 9A, 9E, 9I). Mandibles in lateral view with molar area excavated and broad, mesal brush distinctly covering sides of molar area (Fig. 9B, 9F, 9J). Mentum distinctly round (Fig. 10C), strongly round basally with apex slightly narrow (Figs. 10I, 25C, 25F, 25I) or distinctly elongated (Fig. 10F). Pronotum convex, horn absent, disc distinctly punctate or wrinkled, pronotal lateral margins round or slightly acute (Figs. 11A, 11E, 11I, 26A, 26E, 26I).

Male description. Color: Body lustrous, head, pronotum, appendages and venter with metallic shine reddish or greenish (Figs. 1A-B, 13A-B, 14, 15A-B, 16A-B, 27A-B, 28A-B, 29A, 30A). **Head:** Shape subquadrate, ocular canthi transverse (Fig. 2A) or longitudinal (Figs. 2E). Cephalic horns paired and elongated, with or without carinae connecting them posteriorly, in dorsal view (Figs. 2A, 2E, 2I); in *A. margaridae*, presence of strong dorsolateral protuberance (Fig. 27A). Clypeus subtrapezoidal or subrectangular, corners protruded or flattened (Figs. 2B, 2F, 2J, 17B, 17F, 17J).

Mouthparts: Mandibles subtriangular with two teeth and two ventral carinae, mandibular size elongated (Fig. 3E, 3I) or thickened (Fig. 18A, 18E); presence of long thick setae on outer margin, pale thin setae densely distributed medially and basally (Fig. 9A, 9E, 9I); in lateral view, molar area excavated and broad (Fig. 9B, 9F, 9J), dorsal socket slightly projected (Fig. 3B) or distinctly projected (Fig. 18B); in dorsal view, base near molar area distinctly elongated (Fig. 9C, 9G, 9K). Maxillae with galea falciform (Figs. 10D, 25A, 25D, 25G) or subtriangular (Figs. 10A, 10G). Mentum distinctly round (Fig. 10C), strongly round basally with apex slightly narrow (Figs. 10I, 25C, 25F, 25I) or distinctly elongated (Fig. 10F). **Thorax:** Pronotum mainly with anterior armature present either as protuberance or as horn (Figs. 1B, 27B, 28B), armature absent in *A. duponti*, *A. inermicollis* and *A. bicuspis* (Fig. 2G, 2K, 17C); pronotal disc convex and distinctly punctate (Figs. 6D, 6G) or wrinkled (Figs. 21A,

21D, 21G). Prosternal process absent. Elytra slightly rugose with surface irregularly punctate, usually with presence of longitudinal dark stripe on elytral suture and dark spots on apical and humeral umbones (Figs. 1A, 13A), rarely absent (Figs. 28A, 30A), apical umbones smooth and round. **Legs:** Protibiae with three (Fig. 1A) or four teeth (Fig. 27A) on outer margin, inner apical corner distinctly acute near protibial spur. Protarsi slender, protarsomere V slightly thickened, protarsal claws symmetric (Figs. 5F, 5J, 20B), or with short protuberance on superior claw (Figs. 5B, 20J). Metatibiae with three pairs of teeth oblique and sharp on outer edge (Figs. 26C, 26G, 26K). **Abdomen:** Tergite VII with stridulatory apparatus absent. Tergite VIII convex, posterior margin bordered with middle thick (Fig. 6B, 6E, 6H); in ventral view, tergite VIII distinctly surrounding sternite VIII (Fig. 6C, 6F, 6I). **Aedeagus:** Parameres asymmetric basally, with right basal portion prominent internally superposing left basal portion (Figs. 7A, 7E, 22A, 22E, 22I) except in *A. inermicollis* with left basal portion superposing right basal portion (Fig. 7I). In lateral view, parameres with dorsal margin distinctly convex (Fig. 7B, 7F, 7J, 22B, 22F, 22J). Shape of apical portion dilated (Figs. 7I, 22E) or narrow (Figs. 7A, 7E, 22I).

Female description. Body as in males with metallic shine on head, thorax, venter and appendages, and elytra testaceous (Figs. 1C-D, 13C-D, 15C-D, 16C-D, 27C-D, 28C-D, 29B, 30B). **Head:** Cephalic horns absent. Surface distinctly punctate, frons slightly flat (Figs. 8B, 8E, 8H) or protruded (Fig. 23E). Clypeus subtrapezoidal simple (Figs. 8A, 8D, 8G, 23G) or slightly round (Figs. 23A, 23D), borders slightly deflected, apex slightly emarginated or truncate. Ocular canthi transverse, thin (Fig. 8D) or broad (Fig. 8A) with basal protuberance in *A. margaridae* (Fig. 23D), presence of oblique carinae from base to frons. **Mouthparts:** Mandibles subtriangular with two teeth and two ventral carinae; presence of long thick setae on outer margin, pale thin setae medially and basally (Fig. 9A, 9E, 9I); in lateral view, molar area excavated and broad (Fig. 9B, 9F, 9J); in dorsal view, base near molar area distinctly elongated (Fig. 9C, 9G, 9K). Maxillae with galea falciform (Figs. 10D, 25A, 25D, 25G) or subtriangular (Figs. 10A, 10G). Mentum distinctly round (Fig. 10C), strongly round basally with apex slightly narrow (Figs. 10I, 25C, 25F, 25I) or distinctly elongated (Fig. 10F). **Thorax:** Pronotum convex, horn absent, disc distinctly punctate, pronotal lateral margins round or slightly acute (Figs. 11A, 11E, 11I, 26A, 26E, 26I). Elytra as in males (Figs. 1C-D, 13C-D, 15C-D, 16C-D, 27C-D, 28C-D, 29B, 30B). **Legs:** Protibiae with three (Fig. 1C) or four external teeth (Fig. 27C). Protarsi shorter and slender than in males, protarsal

claws shorter and more curved than in males. Metatibiae with three pairs of teeth oblique and sharp on outer edge, shorter than in males (Fig. 11C, 11G, 11K, 26C, 26G, 26K). **Abdomen:** Tergite VIII with posterior margin acute, sides slightly depressed. Sternites with metallic shine strong (Figs. 11D, 11H, 11L, 26D, 26H, 26L).

Geographical distribution. South America, in the following countries: Argentina, Brazil and Venezuela (Fig. 35).

Remarks. *Agacephala* is the type genus of Agaocephalini and one of the most remarkable genus in the tribe due to the vivid metallic color of males ranging from green to copperish. The only genera which resemble *Agacephala* are *Aegopsis* and *Lycocephala* **stat. nov.** as both have males with a pair of cephalic horns emerging from sides of frons and strong sexual dimorphism with hornless females. However male *Agacephala* can be distinguished by the metallic color of head (Fig. 2A), elytra coloration dark yellow with brown stripes on elytral suture and brown patches sometimes present on humeral and apical umbones (Fig. 1A), thoracic horn when present generally short [except in *A. mannerheimi* and *A. margaridae*], not reaching frons (Fig. 1B), clypeus subtrapezoidal with apical corners strongly or slightly protruded (Figs. 2B, 2J), parameres asymmetric basally, with right basal portion prominent internally superposing left basal portion (Figs. 7A, 7E, 22A, 22E, 22I) except in *A. inermicollis* with left basal portion superposing right basal portion (Fig. 7I). In contrast, *Aegopsis* can be distinguished by an entirely black or brown body with metallic shine or lustrous surface (Fig. 36A), elytra coloration black or brown with the same pattern as the rest of body (Fig. 36A), thoracic horn in major males strong and elongated, exceeding frons (Fig. 36B), clypeus parabolic or subretangular wide with apical corners simply round (Figs. 36C-D), parameres symmetric. Finally, *Lycocephala* can be distinguished from *Agacephala* and *Aegopsis* by its rugose pronotum, with crenulate sides, as well as the elytral surface completely tomentose, gray (Fig. 33A-B). Females of these three genera can be distinguished by: *Agacephala* with elytra coloration dark yellow with brown stripe on elytral suture and brown patches sometimes present on humeral and apical umbones (Fig. 1C), clypeus subtrapezoidal simple (Figs. 8A, 8D, 8G, 23G) or slightly round (Figs. 23A, 23D), tergite VII covered by elytral apex in lateral view (Fig. 1D) whereas in *Aegopsis* elytra coloration black or brown with no patches on humeral and apical umbones (Fig. 36E), clypeus parabolic or rounded (Fig. 36G), subtrapezoidal in *A. curvicornis* but with base projected (Fig. 36H), tergite VII not covered by elytral apex in lateral view (Fig. 36F). *Lycocephala* differ from the

other two genera by the lateral margins of pronotum crenulated, the rugose texture of pronotum with moderately long thin setae on disc and elytral surface tomentose and yellowish with thin black stripes on umbones (Fig. 33C-D).

Agacephala is the valid name instead of *Agaocephala* because Serville, who was the author of the name, described the genus with this spelling (more of it will be discussed in the **remarks** section of *A. cornigera*). Our first thought was that since *Agacephala* must be the correct spelling of the generic name so the name of the tribe should be Agacephalini. However, according to the article 29.5 of The International Code of Zoological Nomenclature “If a spelling of a family-group name was not formed in accordance with Article 29.3 (the stem of a family group-name based on the name of its type genus) but is in prevailing usage, that spelling is to be maintained, whether or not it is the original spelling and whether or not its derivation from the name of the type genus is in accordance with the grammatical procedures (...)” (ICZN, 2012). Therefore, the name of the tribe remains Agaocephalini.

***Agacephala cornigera* Saint-Fargeau & Audinet-Serville, 1825**

(Figs. 1-12, 35)

Agacephala cornigera Saint-Fargeau & Audinet-Serville 1825: 370 (original description); Latreille 1829: 549 (cited); Laporte 1832: 404 (cited); Alvarenga 1958: 47 (cited); Lachaume 1992: 23 (cited)

Agaocephala cornigera Mannerheim 1829: 59 (subsequent description); Burmeister 1847: 282 (cited); Erichson 1848: 560 (cited); Lacordaire 1856: 451 (cited); Thomson 1860: 18 (cited); Prell 1934: 58 (cited); Blackwelder 1944: 260 (checklist); Alvarenga 1958: 48 (synonymization); Endrödi 1970: 42 (revision, neotype designation); Endrödi 1985: 210 (catalogue).

Diagnosis. Male: Clypeus with corners sharp and acute, middle concave. Protarsomere V with dorsal surface slightly emarginated near base (Fig. 5B). Ocular canthi longitudinal, lateral margin convex (Fig. 5A). Cephalic horns with base connected by strong carinae (Fig. 2C). Strong depression between cephalic horns (Fig. 2B). Antennal club shorter than antennomeres I-VII (Fig. 5A). Pronotal protuberance short, not reaching line of pronotal anterior margin (Fig. 6A). Protarsal claws asymmetric, superior claw with short tooth basally (Fig. 5B). Elytral spots short on humeral umbones, absent on apical umbones (Fig. 1A).

Female: Clypeus subtrapezoidal, apex truncate 2.7 times narrower than clypeal base (Fig. 8A). Ocular canthi short and transverse, anterior margin round (Fig. 8A). Antennae with short club, length shorter than antennomeres I-VII combined (Fig. 8C). Mentum subcircular and broad with thick C-punctures medially (Fig. 10C). Maxilla with galea subtriangular (Fig. 10A). Mandible, in lateral view, with socket short and outer carina near apical tooth straight and not projected (Fig. 9B). Mandible, in dorsal view, with outer margin oblique with distinct projection near base (Fig. 9C). Pronotal disc with punctures large and dense, becoming denser near corners (Fig. 11A). Metatibial apex crenulated and not projected medially (Fig. 11C).

Redescription. Male. Color: Surface lustrous; head, pronotum, appendages and venter with metallic red shine, some greenish shine on pronotum; elytra testaceous (Fig. 1A-B). **Head:** Vertex densely covered by thin and moderate punctures. Frons distinctly excavated, punctures bigger than on vertex, punctures sparser medially and denser laterally towards horns. Cephalic horns with distinct dorsal carinae convergent basally towards vertex, presence of wrinkles near carinae basally (Fig. 2A), surface medially and apically with punctures moderate and dense. Clypeus subtrapezoidal with corners protruded, apex truncate (Fig. 2B); clypeal punctures thin and sparse medially, coalescent laterally. Ocular canthi longitudinal, outer shape convex, surface smooth near horn and punctate basally (Fig. 5A). Antennae with 10 segments, lamellae short, shorter than segments I-VII (Fig. 5A). **Mouthparts:** Labrum transversely slender, anterior margin truncate, lateral sides oblique, setae reaching anterior half medially (Fig. 3D). Mandibles subtriangular with two apical teeth and two ventral carinae; in ventral view, teeth connected apically, outer margin distinctly projected mesobasally with thick long setae on it (Fig. 3A), area between carinae densely setose with thin long setae, mesal brush with medial portion distinctly emarginated (Fig. 3A); in inner view, margin of dorsal socket weakly projected (Fig. 3B), molar area as long as wide with mesal brush covering part of lateral margin of molar area (Fig. 3B), inner carina forming an angulation near condyle (Fig. 3B); in dorsal view, apical portion of mesal brush distinctly round, mandibular medial and basal portions distinctly depressed, presence of continuous row of thin setae near outer margin (Fig. 3C). Maxillae with galea subtriangular, stipes short with posterior margin slightly concave in ventral view, basal portion of lateral border densely setose, with inner margin truncate (Fig. 4A); in dorsal view, galea densely setose, subgalea with inner margin short and round, not crossing

stipes (Fig. 4B); outer edge of cardo thin and blunt, slightly crossing line of stipes externally, in ventral view. Mentum broad, almost globose, apex evenly blunt, ventral surface with long thin setae erected, surface distinctly punctate, punctures coalescent, C-shaped (Fig. 4C). **Thorax:** Pronotum with disc thick, presence of short protuberance anteriorly not crossing anterior margin (Fig. 6A). Pronotal surface densely wrinkled, presence of coalescent punctures distinct near protuberance. Hypomerum slightly excavated towards middle. Scutellum densely punctate, punctures ocellate and coalescent near apex. **Elytra:** Form 2.5 times longer than wide. Surface glabrous, slightly rugose, covered by ocellate punctures surrounded by dark borders (Fig. 1A). Elytral margins darker than disc. Humeral umbone with disform brown patch, presence of punctures thinner than on disc. Apical umbone finely punctate, patch absent (Fig. 1A). **Legs:** Protibia with three external teeth, medial tooth longer than others. Protibial surface densely punctate, thin and moderate punctures intertwined. Protarsal claws asymmetric, inner claw with a distinct round tooth basally (Fig. 5B). Mesotibia with apex excavated near apical tooth, outer margin with C-punctures densely distributed between teeth (Fig. 5C). Metatibial apex truncate near spur; metatibial surface with C-punctures moderate and dense (Fig. 5D). Metatarsomere I with projection short barely reaching metatarsomere II basally; metatarsomere V less than two times longer than metatarsomere IV. **Abdomen:** Tergite VIII broadly convex, 2.8 times wider than long; surface completely covered by sculpture densely rugose, presence of microsetae sparse on disc (Fig. 6B). Sternites IV–VIII densely rugose, sternite VIII less rugose than others. Pair of transverse rows of short and sparse setae laterally on sternites V–VII. Sternite VIII with short setae on posterior margin (Fig. 6C). **Aedeagus:** Parameres asymmetric, slender in dorsal view, basal portion with sclerite prominent towards inner region, basal prominent sclerite with hook-shaped tip (Fig. 7A); in lateral view, apex distinctly downturned, ventrolateral portion with oblique short carina reaching lateral carina medially, base excavated (Fig. 7B, D); in ventral view, ventral sclerite U-shaped and long, border thick (Fig. 7C).

Measurements. Body length: 22.8–27.7 mm. Elytral length: 15.2–19.1 mm. Elytral width: 6.9–8.8 mm. Head length: 3.1–4.5 mm. Pronotal width: 10.9–13.6 mm. Pronotal length: 8.1–9.3 mm. Protibial length: 5.9–6.2 mm.

Female. Females as males in general aspect (Fig. 1C-D), except by the following. **Head:** Cephalic horns absent. Frons with two inconspicuous oblique protuberances, surface slightly excavated medially (Fig. 8B-C); punctures coalescent on

vertex and frons. Clypeus subtrapezoidal, apex truncate, punctures coalescent dorsally and thin on borders (Fig. 8A). Ocular canthi short and transverse, anterior margin round, few large punctures dorsally; presence of a thick carinae from base of ocular canthi to vertex (Fig. 8A). **Mouthparts:** Labrum as in males, but not slender, setae densely distributed on anterior corners (Fig. 9D). Mandibles similar to males; in ventral view, outer carina reaching outer tooth (Fig. 9A), mesal brush not dilated on inner margin (Fig. 9A); in lateral view, equal as in male (Fig. 9B); in dorsal view, outer margin straight with distinct projection near base, setae scarce (Fig. 9C). Maxillae with galea subtriangular, densely hirsute in dorsal view (Fig. 10B); in ventral view, maxilla with long thin setae densely distributed on inner portion of stipes and palpifer (Fig. 10A). Mentum subcircular and broad, ventral surface with large and sparse punctures medially, puncture smaller and denser on sides (Fig. 10C). **Thorax:** Pronotum more flattened than in male. Disc with punctures large and dense, becoming denser near corners, presence of coalescent punctures on sides and near anterior margin (Fig. 11A). Prosternum with medial portion of anterior margin short and convex, almost at the same level as adjacent protuberances, prosternal disc with medial keel thin. Metasternum hirsute, surface with punctures thin and sparse, setae dense laterally on outer edge and sparse near inner edge. Scutellum with apex slightly truncate, disc with large and dense punctures intertwined by thin micropunctures. **Elytra:** Disc with large ocellate punctures with dark borders. Brown patches on humeral and apical umbones evanescent, when present (Fig. 1C-D). **Legs:** Protibial punctures large and sparse dorsally, becoming thinner and denser near protibial teeth. Protarsal claw thin, basal tooth absent. Mesotibia with outer margins punctate by C-punctures denser near anterior carina and sparser between posterior carina and mesotibial apex (Fig. 11B). Metatibial apex truncate near spur, metatibia densely punctate with short and long punctures intertwined, presence of two oblique carinae distinct from outer edge (Fig. 11C). **Abdomen:** Tergite VIII slightly concave posteriorly, apex slightly protruded; punctures thin and dense on entire surface. Sternite VIII with apex truncate, lateral margins with thin setae longer than discal setae, disc with microsetae. Sternites VI–VII with moderate and sparse punctures, thin punctures only close to anterior margin; presence of rows of setae laterally, not reaching middle. Sternites IV–V with thin punctures reaching medial area intertwined with bigger punctures (Fig. 11D). **Genitalia:** Gonocoxites with proximal coxites blunt on posterior outer corner, presence of thin setae on inner margin (Fig. 12A), distal coxites strongly projected dorsally (Fig. 12A).

Measurements of females. Body length: 29.4–30.4 mm. Elytral length: 18.3–19.5 mm. Elytral width: 7.5–8.8 mm. Head length: 3.1–3.4 mm. Pronotal width: 12.7–13.6 mm. Pronotal length: 8.8–9.3 mm. Protibial length: 6.1–6.3 mm.

Geographic distribution. Brazil: Distrito Federal, Minas Gerais (Fig. 35).

Material examined. Non-type specimens: 52 males and 6 females. 2 males (RBINS) labeled: a) “Brésil”, b) “Collection/ E. Candeze”, c) “*Agaocephala/ cornigera* Mann./ det. L. Candeze”; 5 males (RBINS): a) “Barbacena”, b) “Coll. Camille/ Van Voixem”, c) “10146”, d) “*Agaocephala/ cornigera* Mann./ det.”; 8 males and 3 females (RBINS): a) “Coll. R.I.Sc.N.B./ Brazil/ Le Moults vendit”, b) “*Agaocephala/ cornigera*”; 1 male (RBINS): a) “Coll. Thirot/ Barbacena/ Brésil”, b) “*cornigera* Mann.”; 4 males (MNHN): a) “Brasilia (District fédéral)/ Brésil/ XI.1993”, b) “*Agaocephala/ cornigera* Serville/ F. Dupuis det. 2014”, c) “MNHN/ EC11709”; 4 males (MNHN): a) “Pogas {Poços} de Caldas (Etat de Minas Gerais)/ Brésil/ XI.1991”, b) “*Agaocephala/ cornigera* Serville/ F. Dupuis det. 2014”, c) “MNHN/ EC11708”; 5 males (MNHN): a) “Brésil (Minas)/ Sertão de Diamantina/ Faz. De melancias/ E. Gounelle 10-11 {X-XI}.1902”, b) “*Agaocephala/ cornigera* Serville/ F. Dupuis det. 2011”, c) “MNHN/ EC11707”; 4 males (MNHN): a) “Brésil/ Diamantina/ Abbé Torgues {collector}”, b) “*Agaocephala/ cornigera* Serville/ F. Dupuis det. 2011”, c) “MNHN/ EC11706”; 1 male (NHM): a) “Minas/ Geraes”, b) “Fry Coll./ 1905.100”, c) “*Agaocephala/ Duponti* Casteln./ Brasilien”, d) “NHMUK 014560320”; 5 males (NHM) with same data as previous specimen except: c) “NHMUK 014560309”; c) “NHMUK 014560306”; c) “NHMUK 014560321”; c) “NHMUK 014560325”; c) “NHMUK 014560316”; 1 male (NHM): a) “Minas/ Geraes”, b) “Fry Coll./ 1905.100”, c) “E.Y. Western Coll./ B.M. 1924-176”, d) “*Agaocephala/ cornigera* Serville/ R.-P. Dechambre det. 1976”, e) “NHMUK 014560329”; 1 male (NHM): a) “*Agaocephala/ cornigera* Serville/ R.-P. Dechambre det. 1976”, b) “NHMUK 014560310”; 1 male (NHM): a) “Brazil”, b) “NHMUK 014560308”; 1 male (NHM): a) “Brazil”, b) “NHMUK 014560311”; 1 male (NHM): a) “Brazil”, b) “*cornigera* Mannerh.”, c) “*Agaocephala/ cornigera* Serville/ Det E.J. Grossi 2011”, d) “NHMUK 014560324”; 1 male (NHM): a) “Nevinson Coll./ 1918-14”, b) “*Agaocephala/cornigera*/Serville/ det. B.C. Ratcliffe 2001”, c) “NHMUK 014560332”; 1 male (NHM): a) “Nevinson Coll./ 1918-14”, b) “NHMUK 014560336”; 1 male (NHM): a) “*Agaocephala/ cornigera* Mannerh./ Brazil”, b) “Nevinson Coll./ 1918-14”, c) “NHMUK 014560334”; 1 male (NHM): a) “Brazil/ 90.79”, b) “NHNMUK 014560318”; 1 male (NHM): a) “BRAZIL:/ Sabara-Bello Horizonte/ Rio das Velhas/

A.G.N. Chaimers/ B.M. 1932-11”, b) “NHNMUK 014560328”; 1 female (NHM): a) “Pascoe/ Coll./ 93-60”, b) “NHMUK 014560331”; 1 male (NHM): a) “S{outhern}. Brazil/ Rio Grande/ c. 1880. Dimes/ B.M. 1966-8”, b) “*Agaocephala/ cornigera/ Serville/ Det. E.J. Grossi 2011*”, c) “NHMUK 014560322”; 1 male (NHM) with same data as previous specimen except: c) “NHMUK 014560313”; 1 male (NHM): a) “Nevinson Coll./ 1918-14”, b) “*Agaocephala/ cornigera Serville/ R.-P. Dechambre det. 1976*”, c) “*Agaocephala/ cornigera/ Serville/ Det E.J. Grossi 2011*”, d) “NHMUK 014560323”; 1 male (NHM): a) “Nevinson Coll. 1918-14”, b) “NHMUK 014560335”; 1 male (MZLU): a) “Insecta exotica/ Collectio/ Johan Wilh{elm} Zetterstedt”, b) “Brasil interior”, c) “MZLU/ 00161085”, d) “*Agacephala/ cornigera Serville/ R. Sobral det. 2021*”; 1 male (MZLU): a) “Insecta exotica/ Collectio/ Johan Wilh Zetterstedt”, b) “*Agacephala*”, c) “*A. cornigera/ MG. Bra{zi}l. Greco {collector’s name probably}*”, d) “MZLU/ 00161082”; ”; e) “*Agacephala/ cornigera Serville/ R. Sobral det. 2021*”; 1 male (MZLU): a) “Brasilia/ Mus. Reg. Swe.”, b) “Coll. Ver.”, c) “*Agaocephala/ cornigera. Mann{for some time Mannerheimi was considered the author of the species}./ Descript. De/ Scarab. Du Brasil. P. 31. F.l.g. 1–3.*”, d) “MZLU/ 00161084”; e) “*Agacephala/ cornigera Serville/ R. Sobral det. 2021*”; 1 male (MZLU): a) “Brasil/Oscar”, b) “Coll. Ver.”, c) “*Agaocephala/ cornigera Serv./ det. Dr. Endrödi 1981*”, d) “MZLU/ 00161083”; e) “*Agacephala/ cornigera Serville/ R. Sobral det. 2021*”; 1 male (CERPE): a) “BRASILIA, DF/ BRASIL XI.90”, b) “COLEÇÃO/ E. & P. GROSSI”; 1 female (CERPE): a) “BRASILIA, DF/ BRASIL XI.92”, b) “COLEÇÃO/ E. & P. GROSSI”; 1 female (MSUC): a) “Planaltina, DF/ BRASIL – 1000m/ 15°35’S/ 47°42’W/ 17 Feb{ruary} 1996/ F.W. Stehr”, b) “*Agaocephala/ inermicollis/ Arrow/ det. G. Parsons 2008*”.

Remarks. *Agacephala cornigera* can be mistaken with *Agacephala mannerheimi* as they are both species with pronotum armed, share the distribution in Brasilia (Brazilian central plateau) and have close occurrences in the Serra do Espinhaço, a distinct mountain range in the eastern Brazil. However, these species can be distinguished by the following characters of males: *A. cornigera* has cephalic horns with a strong depression between them (Fig. 2B), cephalic horns with lateral margins exposed in dorsal view (Fig. 2A), clypeus subtrapezoidal with apical corners protruded (Fig. 2B), pronotal protuberance short, not reaching line of pronotal anterior margin (Fig. 6A), tergite VIII with disc bare (Fig. 6B) whereas in *A. mannerheimi* cephalic horns not depressed between them (Fig. 17J), cephalic horns with lateral margins

concealed in dorsal view (Fig. 17I), clypeus subretangular with apical corners discrete (Fig. 17J), pronotal horn elongated and bifid, reaching line of pronotal anterior margin (Fig. 21G), tergite VIII with disc densely setose (Fig. 21H). Females of these species differs by: *A. cornigera* with mesotibial anterior carina connected to basal tooth (Fig. 11B) [in *A. mannerheimi* mesotibial anterior carina absent (Fig. 26J)], mandibles with ventral outer carina connecting to lateral tooth (Fig. 9A) [in *A. mannerheimi* connecting to apical tooth (Fig. 24I)], mandibular outer margin oblique with basal protuberance (Fig. 9C) [in *A. mannerheimi* outer margin round (Fig. 24K)], frons with lateral carina absent near eyes (Fig. 8B) [in *A. mannerheimi* carina present and sharp (Fig. 23H)], apex of clypeus shorter in *A. cornigera* (Fig. 8A) than in *A. mannerheimi* (Fig. 23G).

The original description of *A. cornigera* is a curious case. The species was first described in the literature by Saint-Fargeau & Audinet-Serville (1825) but in the text they mentioned that new species was named by the count Carl Gustaf Mannerheim, a renowned Finnish entomologist and coleopterist. Also, he told that the specimen he was basing the description on his work was given to him by count Dejean who, in turn, had received it from Mannerheim himself. Only four years later Mannerheim (1829) would publish his description of *Agacephala* and its type-species *Agacephala cornigera*. Perhaps in that time it was a well known knowledge among the entomologists that that new genus and species was “discovered” by Mannerheim and that he was preparing a manuscript with the description of it. This fact can be supported by all articles published during the 19th century that credited the authorship of *Agacephala* to Mannerheim, i.e.: Laporte (1832), Burmeister (1847) and Thomson (1860). However, from Endrödi (1970) onwards the authorship has been credited to Serville and recently to Saint-Fargeau & Audinet-Serville. Endrödi (1970) did not provide details on why he changed the authorship but we believe that he followed the article 50.1 from the International Code of Zoological Nomenclature, which states that “The author of a name or nomenclatural act is the person who first publishes it in a way that satisfies the criteria of availability (...)”. Thus, we have opted to follow Endrödi’s decision and kept the authorship to Saint-Fargeau & Audinet-Serville (1825).

***Agacephala bicuspis* (Erichson, 1848)**

(Figs. 12, 16-26, 35)

Agacephala bicuspis Lachaume 1992: 24 (cited)

Agaocephala bicuspis Erichson 1848: 560 (original description); Lacordaire 1856: 451 (cited);

Thomson 1860: 18 (cited); Prell 1934: 58 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 42 (revision); Endrödi 1985: 210 (catalogue); Joly 1992: 51 (description of female).

Diagnosis. Male: Protibiae with four external teeth (Fig. 16B). Cephalic horns with dorsal carinae connected posteriorly on frons, connection smooth (Fig. 17A). Ocular canthi round (Fig. 20A). Clypeus broad, apex truncate, apical corners slightly angulated (Fig. 17B). Protarsal claws symmetrical (Fig. 20B). Pronotal area near anterior margin distinctly prominent and blunt, horn or protuberance absent (Fig. 17D). Pronotal disc densely wrinkled, green metallic shine conspicuous (Fig. 21A). Elytral disc densely and irregularly punctate, major punctures intertwined by dense micropunctures (Fig. 16A). Parameres asymmetric, in dorsal view, basal portion with sclerite prominent towards inner region, sclerite shape round, inner edges distinctly concave, lateral carinae distinctly protruded converging slightly towards apex (Fig. 22A)

Female: Frons strongly rugose, punctures large (Fig. 23A). Ocular canthi short, anterior margin curved, apex round (Fig. 23A). Clypeus with lateral margins slightly curved (Fig. 23A). Clypeus, in lateral view, with protuberances short but distinct (Fig. 23B). Antennal club short, slightly longer than antennomeres II-VII (Fig. 23C). Labrum slender, anterior margin slightly emarginated medially (Fig. 24D). Mandibles, in ventral view, with apical tooth distinctly thick, lateral tooth almost parabolic, outer carina reaching apical tooth (Fig. 24A). Maxilla with galea falciform (Fig. 25A). Pronotal disc with anterior half covered by large and dense punctures, posterior half with sparser punctures (Fig. 26A). Sternite VIII densely setose on posterior margin and with transverse row of setae on anterior margin (Fig. 26D). Sternites IV-VI distinctly punctate, punctures stronger laterally than medially (Fig. 26D).

Redescription. Male. **Color:** Surface lustrous; head, pronotum, scutellum and venter with metallic green shine; elytra testaceous with some greenish shine (Fig. 16A-B).

Head: Frons less punctate than vertex. Vertex densely covered by moderate punctures, punctures denser and more slender near horns (Fig. 17B). Frons inconspicuously excavated compared to vertex, punctures moderate and sparse. Cephalic horns slightly angulated on outer edge, dorsal carinae abruptly ending before reaching apical portion of horn; surface of horns densely punctate, punctures moderate and coalescent basally intertwined with few wrinkles, punctures less coalescent and slightly sparser on apex than on base. Clypeus subtrapezoidal with corners protruded, apex slightly concave,

dorsal surface elevated medially and excavated on both sides (Fig. 17B); clypeal punctures moderate and dense especially on sides, punctures medially with same shape as lateral punctures but slightly sparser. Ocular canthi distinctly semicircular, presence of curve shallow furrow near base of cephalic horn (Fig. 20A); surface punctate, thin and dense punctures on outer edge, moderate and dense punctures dorsally. Antennae with 10 segments, lamellae short, shorter than segments I–VII (Fig. 20A). **Mouthparts:** Labrum thin, anterior margin emarginated medially with sides lobated (Fig. 18D). Mandibles short, with two apical teeth, inner tooth stronger than outer tooth, outer edge round, outer carina reaching base of outer tooth, in ventral view (Fig. 18A); in lateral view mandible with molar area concave basally, surface near condyle smooth (Fig. 18B); in dorsal view, presence of carinae near molar area (Fig. 18C). Maxillae with galea falciform; galea with dorsal carina on apex not reaching middle, outer edge with 3-4 short denticules sparse (Fig. 19A); in dorsal view, (Fig. 19B). Mentum broad, apex slightly acuminate; in ventral view, surface hirsute and with punctures large and dense (Fig. 19C); in dorsal view, presence of pair of oblique carinae on apical corners.

Thorax: Pronotum round, apical portion near anterior margin slightly elevated, armature absent (Fig. 17D). Pronotal surface densely wrinkled intertwined with coalescent punctures on disc and sides, punctures sparser near anterior margin (Fig. 21A). Hypomerum slightly excavated near anterior corners. Prosternal sides densely punctate, setae sparse. Metepisternum distinctly wrinkled and hirsute. Metasternum hirsute and densely punctate, punctures moderate and dense, wrinkles near posterior corners. Scutellum densely punctate, punctures of different sizes on entire disc, larger punctures coalescent, smaller punctures condensed between the larger. **Elytra:** Form 2.2 times longer than wide. Surface glabrous, slightly rugose, covered by ocellate punctures, micropunctures densely filling the spaces between the ocellate punctures on entire surface (Fig. 16A). Elytral margins darker than disc. Humeral umbone with big disform patch, apical umbone with short brown patch slender than humeral patch. **Legs:** Protibia with four external teeth, increasing in size anteriorly. Protibial surface densely punctate, punctures coalescent basally, punctures large and short intertwined medially and apically. Protarsal claws symmetric, thin, tooth absent (Fig. 20B). Profemora punctate with irregular pattern of punctures. Meso- and metafemora densely punctate, punctures short and micropunctures intertwined. Mesotibia with three outer teeth distinct and increasing in size distally, apical tooth bigger than other, presence of short thick setae basally (Fig. 20C). Metatibial apex concave near spur; metatibial surface

with thin and dense punctures on entire surface, surface shagrinated on outer margin from base to area between medial and apical teeth (Fig. 20D). Metatarsomere I with projection short barely reaching metatarsomere II basally; metatarsomere V more than two times longer than metatarsomere IV. **Abdomen:** Tergite VIII convex, not protruded, almost 3 times wider than long; surface densely covered by microsculpture, microsetae absent (Fig. 21B). Sternites IV–VIII densely covered by short punctures. Sternite VIII with posterior margin V-shaped (Fig. 21C), presence of short and dense punctures laterally, sparser punctures medially. Sternite VII completely covered by short punctures. Sternites IV–VI with punctures on posterior half slightly sparser and bigger than on anterior half. **Aedeagus:** Parameres asymmetric, in dorsal view, basal portion with sclerite prominent towards inner region, sclerite shape round, inner edges distinctly concave, lateral carinae distinctly protruded converging slightly towards apex (Fig. 22A); in lateral view, dorsal edge semicircular, presence of short angulate carina below lateral carinae, ventrolateral area mainly excavated with a basal slightly elevated area with short and dense punctures (Fig. 22B, D); in ventral view, basal margin U-shaped divergent, apical half two times shorter than basal half (Fig. 22C).

Measurements. Body length 26.2–28.4 mm. Elytral length: 13.4–19.3 mm. Elytral width: 8.4–8.8 mm. Head length: 3.1–3.6 mm. Pronotal width: 12.9–13.6 mm. Pronotal length: 8.3–9.3 mm. Protibial length: 5.8–7.1 mm.

Female. Females are similar to males but hornless (Fig. 16C-D). **Head:** Cephalic horns absent. Frons with inconspicuous elevation near clypeus (Fig. 23A-B); punctures on vertex and frons moderate and coalescent. Clypeus subtrapezoidal, borders slightly elevated, clypeal surface excavated laterally reaching base of ocular canthi (Fig. 23A); clypeal punctures coalescent as in frons. Ocular canthi transverse and thick, shape slightly subrectangular, tip round; carinae inconspicuous, shape short and curved (Fig. 23A). Antennal segments III–VII more compact than in male (Fig. 23C). **Mouthparts:** Labrum slender, anterior margin slightly emarginated medially, sides projected with anterior corners round, setae only on anterior half in dorsal view (Fig. 24D). Mandibles subtriangular, with two outer teeth and two ventral carinae. Mandibles, in ventral view, with apical tooth distinctly thick, lateral tooth almost parabolic, outer carina reaching apical tooth (Fig. 24A); in lateral view, outer carina distinctly projected, molar area densely covered by mesal brush on sides (Fig. 24B); in dorsal view, outer margin almost straight, presence of dense aggregation of pale thin setae on outer margin as dense on base as on apex reaching lateral tooth (Fig. 24C). Maxillae with cardo setose

on borders, not distinctly setose on ventral surface. Galea falciform, with apex distinctly sharp, palpifer bare, with no setae on it in ventral view, stipes slightly acuminate on outer side covering lateral border, base of lateral border straight on outer margin and densely setose, setae bigger than on stipes (Fig. 25A); in dorsal view, maxilla with galea hirsute, subgalea with short thin setae only on outer margin (Fig. 25B). Mentum globose, sides distinctly round, apex slightly acuminate, ventral surface sparsely punctate, sides hirsute (Fig. 25C). **Thorax:** Pronotum more flattened and lateral margins more angulate than in male. Metallic shine copperish. Disc densely punctate, wrinkles absent; discal punctures intertwined by micropunctures strongly distributed anteriorly and near corners (Fig. 26A); presence of few coalescent punctures near anterior margin medially. Prosternum with medial portion of anterior margin short and parabolic, with curved connection to adjacent protuberances. Prosternal disc medially thick and blunt. Metasternum setose, setae erected thin and sparse, surface punctate, punctures conspicuous and bigger near anterior margins. Metepisternum with large and dense punctures covered by erected long thin setae. Scutellum with short ocellate punctures densely distributed on entire surface. **Elytra:** Shape short, apex slightly truncate showing part of middle portion of tergite VIII in dorsal view. Elytra with ocellate punctures intertwined by thinner punctures on disc (Fig. 16C). Color testaceous with no metallic shine. **Legs:** Protibial punctuation less dense than in male, punctures decreasing in size laterally towards teeth. Protrocantheri densely punctate and with short thin setae basally. Mesotibia with basal tooth almost inconspicuous, medial and apical teeth elongated, posterior carina with thick round setae almost parallel to medial tooth (Fig. 26B). Metafemora thick, surface less punctate than in male but yet densely punctate near anterior and posterior margins. Metatibial apex with round thick setae on outer edge, apex concave near spur, surface covered by wide ellipsoid punctures and thin coalescent punctures, presence of two oblique carinae distinctly elevated from outer edge (Fig. 26C). **Abdomen:** Tergite VIII slightly concave posteriorly, in lateral view; presence of smooth carina medially near posterior margin; surface densely punctate, punctures denser and thinner near corners. Sternites IV-VII densely punctate, punctures on sternite IV agglomerated near anterior margin (Fig. 26D). Sternite VII with lateral setae longer and thicker than those on sternites IV-VI. Sternite VIII densely hirsute on margins; disc mainly glabrous, only with transverse row of setae near anterior margin, wrinkles near anterior margin, punctures thin and sparse towards posterior margin. **Genitalia:** Gonocoxites with proximal coxites emarginated on apical portion, posterior

corner oblique on outer margin, presence of sparse setae near inner margin but absent on inner corners (Fig. 12D), distal coxites projected dorsally, surface covered by sparse long thin setae.

Measurements of females. Body length: 26.7–30.2 mm. Elytral length: 16.1–18.7 mm. Elytral width: 5.6–9 mm. Head length: 3.1–3.6 mm. Pronotal width: 11.5–14.2 mm. Pronotal length: 7.4–8.3 mm. Protibial length: 4.8–5.8 mm.

Geographic distribution. Guyana: unknown. Venezuela: Bolívar (Fig. 35).

Material examined. Type male (ZMNB) labeled: a) “12233”, b) “*bicuspis*/ Erichson/ Brit{ish}. Guyan{a}. Schomb.”, c) “1-30 {1830}, d) “Lectotypus/ *Agaocephala/ bicuspis* Er.”. **Other specimens:** 5 males (CMNC) labeled: a) “Km 125, El Dorado/ Santa Elena BO/ Venezuela/ 1100m, 22.ix.67”, b) “C.J.Rosales/ M. Gelbez/ L. Rodriguez. V”, c) “H. & A. Howden/ Collection/ ex. A. Martinez coll.”, d) “*Agaocephala/ bicuspis* m#/ A. Martinez det. 1975”; 2 males (NHM): a) “Venezuela”, b) “E.Y.Western Coll./ B.M. 1924-176”; 1 male (MNHN): a) “Mt Roraima”, b) “Ex Musaeo H.W. Bates 1892”, c) “*Agaocephala/ bicuspis* Erichson/ F. Dupuis det. 2011”, c) “MNHN/ EC11703”; 1 male (MNHN): a) “*Bicuspis* Erichs{on}./ Guya{na}.”, b) “*Agaocephala/ bicuspis* Erichson / F. Dupuis det. 2011”, c) “MNHN/ EC11702”; 1 male and 1 female (CERPE): a) “Venezuela/ Sierra de Lema/ Edo. Bolivar. 1300m/ IX. 2005/ F. DeLaVilla leg.”

Remarks. *Agaocephala bicuspis* is very distinguishable from all other species in the genus due to its morphology and its distribution, having the northernmost occurrences in *Agaocephala*. Together with *A. duponti* and *A. inermicollis*, *A. bicuspis* forms a group of species with pronotum disarmed. For differences between males of *A. bicuspis* and these two species see the **remarks** section of *A. duponti*. Females of *A. bicuspis* have a strong greenish metallic shine on pronotum (Fig. 26A), lateral posterior margin round (Fig. 16D), protibia with four outer teeth (Fig. 16C), antennal club short (Fig. 23B), mandible with apical tooth distinctly thick and almost 2 times longer than lateral tooth (Fig. 24A), whereas females of *A. duponti* and *A. inermicollis* have less metallic and shiny pronotum (Figs. 11E, 11I), lateral posterior margin straight (Figs. 13D, 15D), protibia with three outer teeth (Figs. 13C, 15C), antennal club elongated (Figs. 8E, 8H), mandibles with apical tooth not thick as in *A. bicuspis* and never more than 1 time longer than lateral tooth (Figs. 9E, 9I).

The distribution of *A. bicuspis* is as far as we know restricted to the ecoregions of the Guiana Shield. The Guiana Shield is one of the oldest geological formation of

South America estimated at 1.7 billion years old and characterized by the *tepui*, distinct highlands with flattened top (Gibbs & Barron 1983). *A. bicuspis* have been collected in areas of altitude over 1000m. This species occurs in Guianan piedmont moist forests, which spreads through the *tepui* formation, and in dry forests of Guianan savannah.

***Agacephala duponti* Laporte, 1832**

(Figs. 2-14, 35)

Agacephala duponti Laporte 1832: 404 (cited); Laporte 1840: 113 (cited); Alvarenga 1958: 47 (cited); Lachaume 1992: 24 (cited)

Agaocephala duponti Burmeister 1847: 284 (cited); Erichson 1848: 560 (cited); Lacordaire 1856: 451 (cited); Thomson 1860: 18 (cited); Prell 1934: 58 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 42 (revision); Endrödi 1985: 210 (catalogue).

Diagnosis. Male: Ocular canthi transverse, tip short and truncate (Fig. 5E). Cephalic horns with dorsal sculpture punctate (Fig. 2G). Surface between cephalic horns slightly flat (Fig. 2G). Distance between eyes equivalent to 2.2 times eye radius (Fig. 2E). Antennal club longer than antennomeres I-VII (Fig. 5E). Clypeus bilobed (Fig. 2F). Pronotum simply convex, no signs of horn or pronotum (Fig. 6D). Protarsomere V with outer edge straight near base (Fig. 5F). Protarsal claws symmetric (Fig. 5F). Elytral spots conspicuous on apical and humeral umbones (Fig. 13A). Parameres, in caudal view, dorsal surface more elevated near inner edge, lateral carinae distinct and convex, base with left side subtriangular and right side semicircular internally concave (Fig. 7E)

Female: Frons with tubercles short, inconspicuous in lateral view (Fig. 8D). Ocular canthi with anterior margin straight and oblique, apex sharp (Fig. 8D). Clypeus with lateral margin broadly converging to apex (Fig. 8D). Labrum with sides obliquely converging to anterior margin, posterior corner protruded, setae only medially on anterior margin (Fig. 9H). Mandibles with outer margin straight and oblique (Fig. 9G). Mandibular teeth elongated (Fig. 9E). Maxilla with galea falciform (Fig. 10D). Mentum elongated, 1.6 times longer than wide, ventral surface scarcely punctate (Fig. 10F). Pronotal disc with punctures moderate and dense, becoming denser towards sides and anterior corners (Fig. 11E). Mesotibia with apical tooth as long as basal tooth (Fig. 11F). Sternite VIII with surface sparsely punctate mesoapically, with setae sparsely distributed on disc (Fig. 11H). Paracoxites wider than long, anterior margin distinctly emarginated (Fig. 12B).

Redescription. Male. **Color:** Surface lustrous; head, pronotum, and venter with metallic red shine, some greenish shine on legs, scutellum and cephalic horns; elytra testaceous (Fig. 13A-B). **Head:** Frons as punctate as vertex; punctures moderate and dense (Fig. 2E). Cephalic horns slightly excavated near outer edge (Fig. 2G); densely punctate, few ocellate punctures near outer edge. Clypeus subtrapezoidal with corners slightly protruded, apex slightly concave; clypeal punctures larger than frontal punctures, more dense laterally than medially (Fig. 2F). Ocular canthi slightly round anteriorly, tip blunt, surface densely punctate, punctures as large as on frons (Fig. 5E). Antennae with 10 segments, lamellae big, almost with same length as the segments I–VII (Fig. 5E). **Mouthparts:** Labrum 2.4 times wider than long, sides oblique and slightly round towards anterior margin, anterior margin truncate (Fig. 3H). Mandibles elongated with two apical teeth and two ventral carinae; in ventral view, outer carina connecting to outer tooth, mandibular outer margin oblique with slight projection basally (Fig. 3E); in lateral view, dorsal socket distinctly large, as wide as molar area (Fig. 3F); in dorsal view, pale thin setae distributed only near socket and near outer tooth, setae near socket denser than setae near tooth (Fig. 3G), mandibular inner margin with mesal brush oblique to molar area and densely hirsute to base of molar area (Fig. 3G). Maxillae with galea almost falciform, base round and apex thin and sharp (Fig. 4D); in ventral view, stipes with posterior inner margin oblique (Fig. 4D), posterior portion of lateral border straight towards cardo (Fig. 4D), palpifer with discrete connection to basal portion of galea; in dorsal view (Fig. 4E). Mentum elongated, ventral surface hirsute, setae curvy like hair, ventral punctuation not visible (Fig. 4I). **Thorax:** Pronotum slightly flat laterally, disc slightly convex with no protuberance. Pronotal punctures moderate and dense on disc, thinner punctures near sides and anterior margin (Fig. 6D). Hypomerum flat near corners. Mesepisternum densely setose, posteriorly less setose than anteriorly. Meso- and metasternum hirsute. Scutellum subtriangular, apex weakly projected; punctures thin and sparse. **Elytra:** Form 2.4 times longer than wide. Surface glabrous, slightly rugose, covered by ocellate punctures; no dark border around punctures (Fig. 13A). Elytral margins darker than disc, slightly upwards near apex in lateral view (Fig. 13A). Humeral umbone finely punctate, with large oval brown spot. Apical umbone finely punctate, with a thin brown patch slightly reaching apical portion of elytral disc (Fig. 13A). **Legs:** Protibia with three external teeth anteriorly increasing in size. Protibial surface finely punctate, punctures thinner

near outer edge, deeper medially. Protarsal claws thin and symmetric, tooth absent (Fig. 5F). Mesotibial apex oblique and straight near apical tooth, outer margin with round moderate punctures basally and C-punctures between teeth (Fig. 5G). Metatibial apex slightly concave near spur; metatibial surface with punctures moderate and sparse (Fig. 5H). Metatarsomere I with projection long almost reaching metatarsomere II medially; metatarsomere V almost two times longer than metatarsomere IV. **Abdomen:** Tergite VIII convex and protruded, 2.6 times wider than long; surface glabrous, covered by thin punctures sparse on disc and agglomerated on corners (Fig. 6E). Sternites glabrous, with thin and sparse punctures. Sternite VII distinctly concave medially on posterior margin. Sternite VIII with short setae on posterior margin (Fig. 6F). **Aedeagus:** Parameres asymmetric basally. In caudal view, dorsal surface more elevated near inner edge, lateral carinae distinct and convex, base with left side subtriangular and right side semicircular internally concave (Fig. 7E). In lateral view, anterior phallobase bigger than posterior phallobase, posterior phallobase corners short and blunt (Fig. 7H), parameres with lateral carinae oblique reaching apex, venter basally slightly prominent (Fig. 7F)). In ventral view, ventral edge wide with sides strongly oblique to inner margins, ventral surface of parameres short and slightly angulated (Fig. 7G).

Male variation. Specimens from Argentina (Fig. 14A-B): Head with punctures on frons and vertex bigger and coalescent, presence of thinner punctures intertwined on vertex. Pronotal punctures on anterior margin and anterior corners large and coalescent, coarse, with thinner punctures among them. Tergite VIII, in lateral view, excavated posteriorly. Mandibles with metallic shine ventrally, apex with two closer teeth, outer edge simply convex, ventral surface with three carinae: one lateral reaching inner edge, and one reaching outer edge, both with origin at mandibular condyle; one medial originated medially, reaching inner tooth. Mentum elongated, apex slightly acuminate, ventral surface with big and dense punctures, densely covered by long thin setae erected, setae only hair-like medially at base.

Measurements. Body length: 26.8–29 mm. Elytral length: 16.4–17.9 mm. Elytral width: 8.6–10.1 mm. Head length: 3.5–3.8 mm. Pronotal width: 11.5–12.6 mm. Pronotal length: 7.7–8.9 mm. Protibial length: 6.9–7.9 mm.

Female. Females are similar to males but hornless (Fig. 13C-D). **Head:** Cephalic horns absent; frons with two carinae oblique and curved, presence of two slightly excavated areas laterally between canthi and clypeus (Fig. 8F). Clypeus subtrapezoidal, densely covered by moderate punctures. Ocular canthi slender, tip sharp,

presence of a thin carina near excavated area on frons (Fig. 8D). **Mouthparts:** Labrum with sides distinctly acute, anterior margin almost truncate, setae absent on disc (Fig. 9H). Mandibles similar to males, but wider; in ventral view, molar area apically projected on inner margin (Fig. 9E), inner carina distinctly angulated towards condyle (Fig. 9E); in lateral view, shape 1.3 time longer than wide, molar area with distinct setae basally (Fig. 9F); in dorsal view, outer margin straight (Fig. 9G). Maxillae similar to males, but with posterior margin of stipes less oblique (Fig. 10D-E). Mentum elongated as in males, apical portion less punctate (Fig. 10F). **Thorax:** Pronotum more flattened than in male, disc as punctate as in male, medial punctures bigger than in male; anterior corners distinctly acute (Fig. 11E). Prosternum with medial portion of anterior margin acuminate and short, with straight connection to adjacent protuberances. Prosternal disc medially thin and keeled. Metasternum densely hirsute, setae wavy like hairs. Metepisternum with same pattern of setae as metasternum. Scutellar apex slightly round. **Legs:** Protibial teeth generally shorter than in male, protarsomere V thin. Protocantheri almost bare, few punctures scattered basally and apically. Mesotibia with basal and apical tooth with same size, medial tooth longer than others; punctures between posterior carina and metatibial apex sparse, punctures from base of mesotibia to posterior carina mixed of C-punctures and round punctures (Fig. 11F). Metafemora thin, surface irregularly punctate, puncture thin and sparse, anterior margin with irregular row of setae, posterior margin with regular row of long thin setae. Metatibial apex crenulated near spur, surface covered by moderate and sparse punctures, presence of two oblique carinae, crenulated and setose, from outer edge (Fig. 11G). **Abdomen:** Tergite VIII convex, straight near apex; longitudinal carina medially on disc; punctures thin and dense on corners and anterior margin, punctures sparse near posterior margin and disc. Sternite IV-VI with disc almost smooth only with few thin punctures sparse and irregularly distributed, presence of long thin setae on sides not reaching middle (Fig. 11H). Sternite VI emarginated medially, surface weakly punctate, short thin setae on posterior margin. Sternite VIII parabolic, punctures thin and sparse, presence of paired row of setae laterally almost reaching apex. Sternite VII two times longer than sternite VI. **Genitalia:** Gonocoxites with not sclerotized connection between distal and proximal portions (Fig. 12B), proximal coxites with basal margin sinuous, disc not setose, inner corner blunt (Fig. 12B), distal coxites distinctly setose, presence of long thin setae (Fig. 12B).

Measurements of females. Body length: 25.4–28.2 mm. Elytral length: 16.8–

17.8 mm. Elytral width: 7.1–7.8 mm. Head length: 3.3–3.4 mm. Pronotal width: 11.7–12.3 mm. Pronotal length: 7.5–7.7 mm. Protibial length: 5.8–5.9 mm.

Geographic distribution. Argentina: Misiones. Brazil: Minas Gerais, Rio de Janeiro (Fig. 35).

Material examined. Neotype male (HNHM) labeled: a) “Theresopolis/ von Brunet, 1887”. **Other specimens:** 1 male (CMNC) labeled: a) “Nov 1951/ Argentina/ Misiones/ Do Frontera/ San Antonio/ Coll. Martinez”, b) “H. & A. Howden/ Collection/ ex. A. Martinez coll.”, d) “*Agaocephala/ duponti* m#/ A. Martinez det. 1962”; 1 male (CMNC): a) “Brazil, MG/ Poços de/ Caldas, x. 1993/ C. Godinho”, b) “*A. duponti*”; 1 male and 1 female (CMNC): a) “Brazil: MG/ Poços de Caldas/ x.1993/ F.Z.Vaz de Mello”, b) “*A. duponti*”; 7 males (RBINS): a) “Brésil”, b) “Thobie”, c) “10147”, d) “*Agaocephala/ duponti/ Casteln./ det.*”; 1 male and 1 female (NHM): a) “Minas”, b) “67.45”, c) “*Duponti/ m# Casteln{au}./ Brazil*”, d) “So named/ in Beiches/ Collection/ C.W.”; 1 female (NHM): a) “Nevinson Coll./ 1918-14”, b) “NHMUK 014560337”; 4 males and 1 female (MNHN): a) “Caldas/ État du Minas Gerais/ Brésil”, b) “*Agaocephala/ duponti* Castelnau/ F. Dupuis det. 2011”, c) “MNHN/ EC11697”; 3 males and 1 female (MNHN): a) “Brésil/ Caraça/ P. Germain/ 2e Semestre 1884”, b) “*Agaocephala/ duponti* Castelnau/ F. Dupuis det. 2011”, c) “MNHN/ EC11696”; 6 males (MNHN): a) “Caraça (Minas Geraez)/ Brésil/ E.Gounelle/ 1-2{I-II}.1885”, b) “*Agaocephala/ duponti* Castelnau/ F. Dupuis det. 2011”, c) “MNHN/ EC11695”; 1 male and 1 female (CERPE): a) “BRASIL, RJ, Nova/ Friburgo, Conquista/ 01-31.XII.2000, 800m/ E. & P. Grossi Legs.”, b) “COLEÇÃO E. & P. GROSSI”; 1 (MZUSP): a) “Brasil. M#/ *Agaocephala/ Duponti* Cast.”, b) “*Agacephala/ Duponti/ Lap./ M. Alvarenga* det. 1958”.

Remarks. *Agacephala duponti* differs from the majority of *Agacephala* species by the absence of a pronotal horn or tubercle, sharing this condition only to *A. inermicollis* and *A. bicuspis*. Of these, *A. duponti* have more similarities to *A. inermicollis* as both species share the pronotum simply convex with anterior margin flat (Figs. 13B, 15B), pronotal sculpture with only punctures (Figs. 6D, 6G), elytra with microsculpture absent (Fig. 13A, 15A) and elongated antennal club (Figs. 5E, 5I) in contrast to *A. bicuspis* that has pronotum distinctly robust on anterior margin (Fig. 16B), pronotal sculpture distinctly wrinkled (Fig. 21A), elytra with microsculpture distinctly shagreened and metallic (Fig. 16A) and short antennal club (Fig. 20A).

Males of *A. duponti* differs from *A. inermicollis* by cephalic horns with dorsal

sculpture punctate (Fig. 2G) [dorsal sculpture wrinkled in *A. inermicollis* (Fig. 2K)], cephalic horns with apex strongly upturned in lateral view (Fig. 2H) [slightly upturned in lateral view in *A. inermicollis* (Fig. 2L)], ocular canthi with apex truncate and shape almost transverse (Fig. 2E) [ocular canthi with apex sharp and shape oblique (Fig. 2I)], maxilla with galea falciform (Fig. 4D) [galea subtriangular in *A. inermicollis* (Fig. 2G)], pronotal punctures moderate and dense on disc (Fig. 6D) [punctures thin and sparse on disc in *A. inermicollis* (Fig. 6G)], parameres narrowing to apex in caudal view (Fig. 7E) [parameres widening to apex in *A. inermicollis* (Fig. 7I)], aedeagus with ventral sclerite flat (Fig. 7G) [ventral sclerite distinctly depressed in *A. inermicollis* (Fig. 7K)]. Females of *A. duponti* can be distinguished by ocular canthi with anterior margin straight and tip sharp (Fig. 8D), clypeal punctures deeply marked (Fig. 8F), mandibles with teeth elongated and with distinct emargination between them (Fig. 9E), mandibular outer margin straight with base protruded (Fig. 9G), maxilla with galea falciform (Fig. 10D), sternite VII with disc not punctate (Fig. 11H) whereas in *A. inermicollis* ocular canthi with anterior margin round and tip blunt (Fig. 8G), clypeal punctures weakly marked (Fig. 8I), mandibles with teeth short and with slight emargination between them (Fig. 9I), mandibular outer margin round (Fig. 9K), maxilla with galea subtriangular (Fig. 10G), sternite VII with disc punctate (Fig. 11L).

The type specimen of *A. duponti* is a mystery. Laporte (1832) only mentioned that it was from “Brésil” with no additional detail. The specimen was supposed to be in Laporte de Castelnau’s collection, but part of his collection had an unfortunate fate and some species were lost, which is the case of *A. duponti* type-specimen (Endrödi, 1970; Evenhuis, 2012). As the whereabouts of *A. duponti* holotype were unknown, Endrödi (1970) designated a specimen from Brazil housed in his collection as the neotype.

Endrödi (1985) mentioned that females of *A. duponti* had four protibial teeth, but we did not find any specimen with that trait even in the former Endrödi collection that is now housed in Budapest.

***Agacephala inermicollis* (Arrow, 1914)**

(Figs. 2-12, 15, 35)

Agacephala inermicollis Alvarenga 1958: 47 (cited); Lachaume 1992: 24 (cited)

Agaocephala inermicollis Arrow 1914: 276 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 42 (revision); Endrödi 1985: 210 (catalogue).

Aegecephala inermicollis Prell 1934: 58 (nomenclatural act)

Diagnosis. Male: Frons with shallow depression near horns, posterior margin of depression inconspicuous (Fig. 2K). Cephalic horns with dorsal sculpture distinctly wrinkled (Fig. 2I). Cephalic horns with dorsal carina straight, abruptly pointing upward on distal third (Fig. 2L). Ocular canthi elongated and oblique, apex sharp (Fig. 5I). Distance between eyes equivalent to 3.8 times eye radius (Fig. 2I). Pronotal disc with punctures thin and sparse (Fig. 6G). Mandibles with outer margin slightly round (Fig. 3K). Mandibular lateral tooth distinctly shorter than apical tooth (Fig. 3I). Aedeagus, in lateral view, with posterior phallobase with distal corners distinctly elongated (Fig. 7L). Aedeagus, in caudal view, with parameres distinctly dilated towards apex, inner margin slightly sinuous, tips round (Fig. 7I). Aedeagus, in ventral view, with ventral sclerite distinctly depressed medially (Fig. 7K).

Female: Frons with tubercles short, discretely visible in dorsolateral view (Fig. 8I). Ocular canthi with anterior margin curved to apex, apex blunt (Fig. 8G). Labrum with anterior corners round, sides not protruded, setae transversely distributed on anterior margin (Fig. 9L). Mandibles with outer margin distinctly convex (Fig. 9K). Mandibular teeth short, blunt (Fig. 9I). Maxilla with galea subtriangular (Fig. 10G). Pronotal disc with punctures moderate and dense, becoming sparser towards posterior margin (Fig. 11I). Mesotibia with apical tooth absent (Fig. 11K). Sternite VIII with surface densely punctate anteriorly with moderate thin setae transversely distributed from sides to middle (Fig. 11L). Paracoxites longer than wide, anterior margin evenly emarginate (Fig. 12C).

Redescription. Male. **Color:** Surface lustrous; head, pronotum, appendages and venter with metallic red shine; elytra testaceous (Fig. 15A-B). **Head:** Frons densely punctate and wrinkled; vertex less punctate than frons (Fig. 2I). Cephalic horns densely wrinkled basally and medially, apex densely punctate; punctures thin (Fig. 2I, K). Dorsal carinae of horns inconspicuous, not joining on vertex (Fig. 2J). Frons with a short elevation between the horns (Fig. 2I). Clypeal area short; clypeus subtrapezoidal, corners pointy, apex medially slightly concave; punctures round near apex, C-punctures near frons (Fig. 2J). Ocular canthi oblique, subtriangular; wrinkled near tip, more punctate basally (Fig. 5I). Antennae with 10 segments, lamellae big, almost with same length as the segments I–VII (Fig. 5I). **Mouthparts:** Labrum densely covered by long setae, sides obliquely converging to curved anterior margin (Fig. 3L). Mandibles subtriangular with two outer

teeth and two ventral carinae; in ventral view, shape elongated lateral tooth distinctly shorter than apical tooth, outer carina curved towards anterior tooth (Fig. 3I), pale thin setae densely distributed mediobasally on surface, long thin setae on outer margin (Fig. 3I); in lateral view, anterior tooth abruptly curved (Fig. 3J), molar area densely covered by mesal brush apically and basally, dorsal socket with margin distinctly elongated (Fig. 3J); in dorsal view, outer margin of mandible oblique with basal portion almost straight (Fig. 3K), mesal brush distinct with apical portion reaching sides of apical tooth, presence of row of pale thin setae on outer margin, setae denser on apex than on base (Fig. 3K). Maxilla with galea subtriangular, in ventral view presence of short tooth near apex on inner margin (Fig. 4G), stipes with posterior margin oblique and posterior outer corner distinctly slender (Fig. 4G), lateral border basally straight on outer margin, palpifer apically truncate (Fig. 4G); in dorsal view, subgalea densely setose on apex and medial portions (Fig. 4H). Mentum with sides round basally and oblique apically, sides densely covered by long thin setae, surface ventrally distinctly punctate (Fig. 4I).

Thorax: Pronotum bordered, disc convex with no protuberance. Pronotal punctures thin and sparse on disc, denser near sides (Fig. 6G). Hypomera excavated laterally.

Mesepisternum densely setose, surface wrinkled. Meso- and metasternum hirsute, with surface visible. Scutellum subtriangular, apex acute; punctures dense basally, absent apically.

Elytra: Form 2.5 times longer than wide. Surface glabrous, slightly rugose, covered by ocellate punctures; presence of dark brown borders around ocellate punctures (Fig. 15A-B). Elytral margins darker than disc. Humeral umbone finely punctate, with a large subquadrangular brown spot (Fig. 15A).

Apical umbone finely punctate, with a distinct brown spot evanescent basally (Fig. 15A). **Legs:** Protibia with three external teeth anteriorly increasing in size. Protibial surface finely punctate. Protarsi simple (Fig. 5J). Mesotibia with basal tooth short, medial tooth long and apical tooth absent, carina present only near medial tooth (Fig. 5K). Metafemora thin 2.7 times longer than wide, with sparse thin punctures near base. Metatibia with three outer teeth, carina only conspicuous near medial tooth (Fig. 5L), metatibial apex emarginated near spur; surface of metatibia evenly punctate. Metatarsomere I with projection long reaching metatarsomere II medially; metatarsomere V more than two times longer than metatarsomere IV.

Abdomen: Tergite VIII convex and protruded, 2.6 times wider than long; surface almost glabrous, presence of short setae on sides near anterior margin, disc covered by thin sparse punctures becoming denser near margins and sides (Fig. 6H). Sternites glabrous. Sternite VII with larger punctures on posterior margin. Sternite VIII

with large punctures on posterior margin, thin punctures on anterior margin reaching disc (Fig. 6I). **Aedeagus:** Parameres asymmetric, basal left portion covering right basal portion. In caudal view, parameres distinctly dilated towards apex, inner margin slightly sinuous, tips round (Fig. 7I); in lateral view, posterior phallobase with distal corners distinctly elongated (Fig. 7L), parameres slender with lateral margin almost touching ventrolateral carina (Fig. 7J), basal portion of parameres with posterior angulation (Fig. 7J); in ventral view, ventral sclerite distinctly depressed medially (Fig. 7K), anterior margin of ventral sclerite slightly V-shaped, parameres with ventral shape subquadrate, with ventrolateral depression round (Fig. 7K), outer margins of parameres round posteriorly (Fig. 7K).

Measurements. Body length: 26.6–35 mm. Elytral length: 17–23.4 mm. Elytral width: 8.6–8.8 mm. Head length: 3.1–3.8 mm. Pronotal width: 11.4–13.6 mm. Pronotal length: 8.5–11.5 mm. Protibial length: 6.8–7.1 mm.

Females. Females as males in general aspect (Fig. 15C-D). **Head:** Cephalic horns absent. Frons with two oblique tubercles, surface slightly rugose near vertex, punctures thin and dense near tubercles, becoming sparser towards vertex (Fig. 8G, I). Clypeus subtrapezoidal, apex truncate, clypeal surface with punctures pattern similar to frons, with thin punctures dense near tubercles and punctures sparser towards margins (Fig. 8G). Ocular canthi with anterior margin curved to apex, apex blunt, surface finely punctate (Fig. 8G). **Mouthparts:** Labrum with anterior corners round, anterior margin straight, sides not protruded (Fig. 9L). Mandibles similar to males; in ventral view, with anterior tooth shorter than in males but still bigger than posterior tooth, pale thin setae from base to apex near tooth (Fig. 9I); in lateral view, tooth abruptly curved, molar area with apical portion blunt, basal portion of inner carina angulated toward condyle (Fig. 9J); in dorsal view, mandibles with outer margin curved, shape elongated, mesal brush not projected towards anterior tooth (Fig. 9K). Maxilla as in males, but galea with tooth absent, stipes more setose with setae reaching posterior portion, lateral border shorter than in males with outer margin slightly projected towards cardo (Fig. 10G-H). Mentum 1.3 times longer than wide, base with sides round obliquely converging to apex, sides densely hirsute (Fig. 10I). **Thorax:** Pronotum flat as in males. Disc with punctures moderate and dense, punctures sparser towards posterior margin (Fig. 11I). Meso- and metasternum densely hirsute, sculpture of tegument barely visible through the setae. Scutellum smooth with few sparse punctures on it. **Elytra:** Shape thin in lateral view, with lateral margins not covering sides of thorax and abdomen (Fig. 15C-D). Humeral

umbones not projecting towards lateral margins, in dorsal view; humeral and apical umbones with soft dark brown patch on them (Fig. 15C). Elytral surface slightly rugose medially from elytral suture to disc. **Legs:** Protibia as in males with three outer teeth, protarsi simple, protarsomere V shorter and rounder than in male. Mesotibia with punctures more excavated than in males, shape as in males (Fig. 11J). Metatibia with outer margin densely covered by C-punctures between teeth (Fig. 11K). **Abdomen:** Tergite VIII slightly concave posteriorly, apex slightly protruded; punctures thin and dense on entire surface. Sternite VIII parabolic, surface densely punctate anteriorly with moderate thin setae transversely distributed from sides to middle, posterior half with no setae and punctures thin and sparse (Fig. 11L). Sternite VII more than 2 times longer than sternite VI, surface with thin punctures sparsely distributed, becoming denser medially and on anterior corners. Sternites V-VI with same pattern of punctures thin and sparse, sternite IV with punctures denser medially than on sternites V-VI. **Genitalia:** Gonocoxites with proximal coxites slightly emarginated, sparse setae on disc and dense setae on inner apical corner, distal coxites projected dorsally with surface densely setose (Fig. 12C).

Measurements of females. Body length: 30.9–34.1 mm. Elytral length: 21.1–21.8 mm. Elytral width: 9.2–9.7 mm. Head length: 2.4–3.1 mm. Pronotal width: 13.9–15.6 mm. Pronotal length: 10.3–10.9 mm. Protibial length: 6.7–7 mm.

Geographic distribution. Brazil: Rio Grande do Sul (Fig. 35).

Material examined. Type male (NHM) labeled: a) “Rio/ Grande”, b) “Fry Coll./ 1905-100”, c) “Type/ H.T.”, d) “*Agaocephala inermicollis*/ type Arrow”, e) “NHMUK 014560298”. **Other specimens:** 1 male and 4 females (University of Kentucky Insect Collection) labeled: a) “Brazil, Rio Grande do Sul, Porto Alegre”, b) “George F Freytag col.”, c) “Light trap”, d) “1978”, e) “*Agaocephala inermicollis* Arrow, 1914”; 1 male (NHM): a) “Rio Grande”, b) “Fry Coll./ 1905-100”; 1 male (MNHN): a) “Canoas/ Rio gr{ande}. Do Sul/ Brésil”, b) “*Agaocephala inermicollis* Arrow/ F. Dupuis det. 2011”, c) “MNHN/ EC11698”; 1 male (MZLU): a) “Sao Leopoldo”, b) “J. W. Stahl”, c) “Collectio Coleopterorum/ Johan Albert Hultgren”, d) “MZLU/ 00161087”, e) “*Agaocephala inermicollis* Arrow/ R. Sobral det. 2021”; 1 male (MZLU): a) “Collectio Coleopterorum/ Johan Albert Hultgren”, b) “*Agaocephala inermicollis*/ Arrow/ det. Dr. Endrödi 1981”, c) “MZLU/ 00161086”, d) “*Agaocephala inermicollis* Arrow/ R. Sobral det. 2021”; 1 male (MSUC): a) “BRAZIL S{outh}. AMER{ICA}./? State {Rio Grande do Sul}/ Porto Alegre/ 15 NOV{XI}.

1967”, b) “*Agaocephala/ inermicollis/ Arrow/ det. G. Parsons 1984*”; 1 female (MZUSP): a) “São Leopoldo”, b) “J. W. Stahl”, c) “*Agacephala/ inermicollis/ det. Dr. Endrödi 1967 Arr{ow}*”; 1 male and 1 female (MZUSP): a) “II. {1}905 M#/ Rio Gr. Do Sul/ *Agaocephala/ Duponti* Cast.”, b) “*Agacephala/ duponti/ Lap./ M. Alvarenga det. 1958*”, c) “*Agacephala iner-/micollis Arrow m#/ P. Grossi det. 2008*”.

Remarks. *Agacephala inermicollis* differs from the majority of *Agacephala* species by the absence of a pronotal horn or tubercle, sharing this condition only to *A. duponti* and *A. bicuspis*. Of those, *A. inermicollis* resembles most *A. duponti*. The differences from both species are mentioned in the **remarks** section of *A. duponti*.

Agacephala inermicollis is the species with the southernmost known distribution in the genus. This species is recorded to areas of low altitude as the Uruguayan savanna (better known in Brazil as “Pampas”) and to areas of higher altitude formed by mosaics of Alto Paraná Atlantic forests and Araucaria moist forests. The habitat of this species is characterized by the cold temperatures and great anthropic fragmentation. The Uruguayan savanna is a complex ecosystem mainly composed by grasslands with distinct native Poaceae such as *Andropogon lateralis*, *Ischaemon minus* and *Paspalum* spp., but with a diversity in phytophysionomies such as wetlands, gallery forests, shrublands and rocky outcrops (Boldrini *et al.* 2010). Over the last decades, native vegetation has been depleted for the use of land as croplands and the plantation of exotic species, such as *Eucalyptus* spp. and *Pinus* spp. (Brazeiro *et al.* 2020). Unfortunately, the same anthropic intervention that affects Uruguayan savanna also affects the other ecoregion where *A. inermicollis* can be found. The Alto Paraná Atlantic forests and Araucaria moist forests are part of the complex of Atlantic forests in eastern Brazil. The vegetation of these areas is characterized by the presence of *Araucaria angustifolia* forming a mosaic of plant associations with other trees from Atlantic forest like species of Lauraceae, Apocynaceae and Fabaceae (Silva 2018).

***Agacephala mannerheimii* Laporte de Castelnau, 1832**

(Figs. 12, 17-26, 28, 35)

Agacephala mannerheimii Castelnau 1832: 404 (original description); Alvarenga 1958: 47 (cited); Lachaume 1992: 23 (cited)

Agaocephala mannerheimi Burmeister 1847: 282 (cited); Erichson 1848: 560 (cited);

Lacordaire 1856: 451 (cited); Thomson 1860: 18 (cited); Prell 1934: 58 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 42 (revision); Endrödi 1985: 210 (catalogue).

Diagnosis. Male: Ocular canthi slightly longitudinal, anterior margin straight only curving to apex, presence of transverse carinae near cephalic horns (Fig. 20I). Cephalic horns elongated with a thick connection between them basally (Fig. 17I). Clypeus subretangular with apex slightly emarginated (Fig. 17J). Mandibles elongated, with teeth subequal (Fig. 18I). Mandibles in ventral view with outer margin slightly round, greenish metallic shine present (Fig. 18I). Maxilla with galea falciform (Fig. 19G). Maxillary lateral border with base sinuous on outer margin (Fig. 19G). Mentum globose, sides equally round, ventral surface distinctly punctate, punctures coalescent (Fig. 19I). Pronotal disc with distinct thoracic horn, thick at base and elongated with apex bifid (Fig. 21G). Pronotal sculpture completely shagrinated (Fig. 21G). Elytra with humeral and apical umbones with same color as disc (Fig. 28A-B). Protibia with three outer teeth (Fig. 28A). Parameres in caudal view with lateral margins projected and flat, apical portion distinctly thin (Fig. 22I). Parameres in lateral view with apex downturned, dorsal surface parabolic, presence of sharp and short projection below lateral margin (Fig. 22J).

Female: Frons with two distinct short tubercles (Fig. 23H, I). Vertex and frons distinctly rugose, area near tubercles less rugose and with thin and sparse punctures (Fig. 23G). Clypeus subtrapezoidal with apex 1.7 times narrower than clypeal base (Fig. 23G). Clypeal base with short round bump towards ocular canthi (Fig. 23H). Labrum with sides slightly curved, anterior margin straight, posterior corners blunt (Fig. 24L). Mandibles in ventral view with outer margin slightly round, greenish metallic shine present (Fig. 24I). Maxilla with galea falciform, apex distinctly oblique (Fig. 25G). Maxillary lateral border with base slightly sinuous on outer margin (Fig. 25G). Mentum with base round and apical portion distinctly elongated, ventral surface with coalescent punctures (Fig. 25I). Mesotibia with short thick setae connected to medial tooth by posterior carina (Fig. 26J). Metatibial base densely punctate by C-punctures near metafemoral apex (Fig. 26K). Gonocoxites with connection sclerotized between proximal and distal coxites (Fig. 12F).

Redescription. Male. **Color:** Elytra lustrous and dark yellow; head, pronotum, appendages and venter with metallic copperish shine, some specimens with metallic greenish shine (Fig. 28A-B). **Head:** Vertex and frons straight and distinctly shagrinated by micropunctures with round thin punctures sparsely distributed (Fig. 17I, K).

Cephalic horns elongated and directed forward, presence of thick connection between horns on frons (Fig. 17L), apex slightly upturned, surface of horns roughly punctate medially and apically on inner and outer margins. Clypeus subtrapezoidal with corners slightly protruded, apex emarginated (Fig. 17J); dorsal surface depressed on sides and densely shagrinated, presence of punctures moderate and thin coalescent on depressions and medially from base to apex. Ocular canthi slightly longitudinal, anterior margin straight only curving to apex, apex blunt, surface totally punctate, punctures thin and moderate dense; presence of almost transverse carinae near cephalic horns (Fig. 20I). Antennae with 10 segments, antennal club short and round, club as long as antennomeres II-VII together, scape elongated and thick, scape and pedicel densely setose (Fig. 20I). **Mouthparts:** Labrum distinctly emarginated medially, sides slightly round with posterior corner blunt, setae densely distributed on anterior and lateral margins reaching medial portion of labrum (Fig. 18L). Mandibles subtriangular with two apical teeth and two ventral carinae; in ventral view, space between carinae subequal with pale thin setae denser on base than on apex, outer margin slightly round with thick setae near margin, greenish metallic shine present (Fig. 18I); in lateral view, molar area short 1.3 times longer than wide, presence of sharp bump near condyle (Fig. 18J); in dorsal view, mesal brush with distinct long setae near apical tooth, setae of mesal brush almost reaching mandibular medial portion (Fig. 18K). Maxillae with galea falciform and densely covered by setae in dorsal view (Fig. 19H); in ventral view, stipes with thin posterior projection, base of lateral border distinctly sinuous on outer margin (Fig. 19G). Mentum globose, sides equally round, ventral surface distinctly punctate, punctures coalescent, presence of greenish metallic shine (Fig. 19I). **Thorax:** Pronotum with lateral margins slightly projected at middle (Fig. 21G); pronotal disc with distinct thoracic horn, thick at base and elongated with apex distinctly bifid (Fig. 21G). Pronotal disc completely shagrinated with thin punctures sparse but barely noticeable (Fig. 21G). Scutellum subtriangular with apex blunt, surface densely punctate, punctures thin with few moderate punctures basally among them. Prosternum with connection to ventral portion of pronotum distinctly depressed (Fig.), prosternal medial portion depressed towards prosternal carina. **Elytra:** Form 2.2 times longer than wide. Surface glabrous and slightly rugose, covered by ocellate punctures with dark borders irregularly distributed on disc. Humeral umbones with brown patches on them (Fig. 28A-B), apical umbones with punctures thinner than on disc. **Legs:** Protibia with three outer teeth, distance between basal and medial teeth longer than between medial and apical teeth,

outer margin with corner distinctly projected, presence of one outer spur; protibial surface shagrinated, punctures thin and moderate densely distributed longitudinally on surface, presence of wrinkles on base at outer margin; protibia in ventral view with sharp and distinct medial projection near base of protarsi. Protarsi asymmetric with superior claw with distinct protuberance basally, outer margin of protarsomere V distinctly curved (Fig. 20J). Mesotibia with two outer teeth, mesotibial apex angulated on outer margin (Fig. 20K). Metafemora completely punctate, punctures thin and sparse on disc, punctures dense on posterior margin towards apex. Metatibia with three outer teeth, surface densely punctate by C-punctures and wrinkles (Fig. 20L). **Abdomen:** Tergite VIII convex and concealed by elytral apex, surface distinctly shagrinated, surface densely covered by short thin setae (Fig. 21H). Sternites IV-VIII distinctly shagrinated. Sternite VIII with V-shaped strong emargination posteriorly, with short thin setae on posterior margins. Sternite VII slightly emarginated medially, presence of distinct row of setae sparsely distributed laterally (Fig. 21I). **Aedeagus:** Parameres asymmetric basally. In caudal view lateral margins projected and flat, apical portion distinctly thin (Fig. 22I). Parameres in lateral view with apex downturned, dorsal surface parabolic, presence of sharp and short projection below lateral margin (Fig. 22J); posterior phallobase depressed near apical corners (Fig. 22L). Parameres in ventral view with ventrolateral projections distinct, anterior margin of ventral sclerite distinctly concave (Fig. 22K).

Measurements. Body length: 26.5–36.2 mm. Elytral length: 16.7–23.5 mm. Elytral width: 6.9–10.9 mm. Head length: 2.8–5.4 mm. Pronotal width: 11.9–17 mm. Pronotal length: 8.3–12.9 mm. Protibial length: 5.8–7.5 mm.

Female. Females as males in general aspect, with elytra wider (Fig. 28C-D). **Head:** Cephalic horns absent. Frons with two short tubercles (Fig. 23I); vertex and frons distinctly rugose, area near tubercles less rugose and with thin and sparse punctures (Fig. 23G). In lateral view, area near eyes slightly prominent (Fig. 23H). Clypeus subtrapezoidal (Fig. 23G), apex slightly upturned and emarginated medially; in lateral view, base of clypeus with short round bump towards ocular canthi (Fig. 23H). Ocular canthi with anterior margin slightly curved, tip blunt, presence of distinct carina at base (Fig. 23G). **Mouthparts:** Labrum with sides slightly curved, anterior margin straight, posterior corners blunt (Fig. 24L). Mandibles as in males, but with outer carina slightly sinuous medially, outer margin round and inner margin slightly emarginated (Fig. 24I); in lateral view as in males (Fig. 24J); in dorsal view, apical portion of mesal

brush distinctly projected, mesobasal portion of mesal brush less setose than apical portion, mandibular outer margin densely covered by row of pale thin setae, basal posterior inner corner slightly elongated (Fig. 24K). Maxilla as in males, but maxillary palpomere IV distinctly round on apex, galea with apex thinner, lateral border with basal outer margin sinuous as in males but thicker (Fig. 25G-H). Mentum with apical portion distinctly more elongated than in male, ventral surface densely setose on lateral and posterior margins, sparser on disc than laterally, presence of coalescent punctures ventrally (Fig. 25I). **Thorax:** Pronotum more flattened than in males, but still convex, disc with copperish metallic shine becoming greenish towards sides and corners (Fig. 26I). Pronotal disc distinctly punctate, punctures large and dense medially, becoming thinner and sparser posteriorly and coalescent towards sides and anterior corners (Fig. 26I). Scutellum not shagrinated, presence of punctures sparse. **Elytra:** Shape 2.2 times longer than wide, punctures shorter and denser than in males (Fig. 28C-D). Apical and humeral umbones with dark brown patches (Fig. 28C-D). **Legs:** Protibia with three outer teeth, area between apical and medial teeth with lateral emargination shorter than area between medial and basal teeth; surface distinctly punctate, punctures moderate and dense from base to apex, thinner punctures near teeth. Meso- and metatibia as in males in general aspect, sculpture with punctures large and coalescent from base to medial tooth (Figs. 26J-K). **Abdomen:** Tergite VIII slightly concave posteriorly, apex slightly protruded; punctures thin and dense on entire surface with microsetae present on corners. Sternite VIII protruded posteriorly, posterior margins with short thin setae, surface wrinkled on anterior margin, with C-punctures medially and thin round punctures towards apex. Sternite VII with medial portion two times longer than sternite VI; pattern of punctures similar from sternite IV to VII with round thin punctures medially with dense C-punctures towards corners, becoming denser laterally (Fig. 26L). **Genitalia:** Gonocoxites with connection sclerotized between proximal and distal coxites (Fig. 12F), proximal coxites with anterior inner corner distinctly sharp, posterior margin slightly convex, few setae sparsely distributed near inner margin (Fig. 12F), distal coxites with apex divergent, surface covered by thin setae longer than on proximal coxites, setae sparse (Fig. 12F).

Measurements of females. Body length: 30.2–35.2 mm. Elytral length: 20–22.8 mm. Elytral width: 8.6–9.3 mm. Head length: 4.3–4.4 mm. Pronotal width: 13.8–15 mm. Pronotal length: 9.1–10.4 mm. Protibial length: 5.1–8.6 mm.

Geographic distribution. Brazil: Bahia, Distrito Federal, Espírito Santo, Mato

Grosso and Minas Gerais (Fig. 35).

Material examined. Non-type specimens: 2 males (NHM) labeled: a) “Cerradao”, b) “BRAZIL: Mato Grosso/ 12°50'S, 51°47'W/ 25-ii-1968/ O.W. Richards”, c) “R.S. & R.G.S./ Expedition/ B.M. 1968-260”; 1 male (NHM): a) “G. B. Rogers/ B.M. 1968-190”, b) “3”, c) “NHMUK 014560290”; 1 male (NHM): a) “Brasilia”, b) “Fry Coll./ 1905-100”, c) “*Agaocephala/ mannerheimi* Casteln./ Brasilia”, d) “NHMUK 014560286”; 1 female (NHM): a) “Cerradao”, b) “BRAZIL: Mato Grosso/ 12°50'S, 51°45'W/ 10-28.iii.1968/ B.E. Freeman”, c) “Roy{al}.Soc{iety}-Roy{al}.Geog{raphical}.Soc{iety}./ Xavantina-Cachimbo/ Exped{ition}. 1967-69”, d) “Brit{ish}.Mus{eum}./ 1973-292”, e) “*Agaocephala/ mannerheimi* Castelnau/ R.-P. Dechambre det. 1976”, f) “NHMUK 014560288”; 1 male (NHM): a) “*Mannerheimi*/ Brésil”, b) “5053.a.”, c) “NHMUK 014560291”; 1 male (NHM): a) “On *Paepalanthus*”, b) “Campo”, c) “BRAZIL: Mato Grosso/ 12°50'S, 51°47'W/ 27-iii-1968/ O.W. Richards”, d) “R.S. & R.G.S./ Expedition/ B.M. 1968-260”, e) “NHMUK 014560282”; 1 male with same data as previous specimen except: e) “NHMUK 014560284”; 1 female (NHM): a) “48/5”, b) “*Agaocephala/ mannerheimi*/ Laporte/ Det. E.J. Grossi 2011”, c) “NHMUK 014560295”; 1 male (NHM): a) “Brazil, Mato Grosso/ Dry Forest Base Camp/ 256km N of Xavantina, ix.1967/ 12°49'S, 51°46'W/ Brian Freeman leg.”, b) “BMNH/ 2009-6”, c) “*Agacephala/ mannerheimi* (Cast.)/ S. Pokorný det. 2011”, d) “NHMUK 011521336”; 2 males (NHM) with same data as previous specimen except: d) “NHMUK 011521338”; d) “NHMUK 011521337”; 1 male (NHM): a) “Nevinson Coll. 1918-14”, b) “*Agacephala/ mannerheimi*/ det. R. Sobral 2019”, c) “NHNMUK 014560297”; 1 female (NHM): a) “Nevinson Coll./ 1918-14”, b) “*Agaocephala/ mannerheimi* Cast.”, c) “NHMUK 014560296”; 1 female (NHM): a) “On *Paepalanthus*”, b) “Campo”, c) “BRAZIL: Mato Grosso/ 12°50'S, 51°47'W/ 13-iii-1968/ O.W. Richards”, d) “R.S. & R.G.S./ Expedition/ B.M. 1968-260”, e) “*Agaocephala/ mannerheimi*/ Laporte/ Det. E.J. Grossi 2011”, f) “NHMUK 014560293”; 1 male (NHM): a) “Nevinson Coll. 1918-14”, b) “*Agaocephala/ mannerheimi*/ Brazil”, c) “NHNMUK 014560292”; 1 male (NHM): a) “Bahia”, b) “Nevinson Coll. 1918-14”, c) “NHNMUK 014560283”; 1 male (CERPE): a) “Grão Mogol-MG-Brasil/ 15-XII-2002/ J. de Nadai Col.”, b) “*Agacephala/ mannerheimi*”; 1 male (MZUSP): a) “Niquelândia/ Goiás/ 20.2{ii}.1990”, b) “*Agacephala/ mannerheimi* Cast./ C. Campaner det. {19}90”, c) “Antrop. Base +/- 20.2.90/ Niquel.”; 1 male (MZUSP): a) “Km 42 Rodov./ Brasilia, Goiania/ xi.{19}78/ C. Coimbra”, b)

“*Agacephala/ mannerheimi/* Cast. 1832/ C. Campaner det. 2003”; 1 male and 1 female (MZUSP): a) “Goyaz/ coll. Pereira/ Magalhães”, b) “*Agacephala/ mannerheimi/* Lap./ M. Alvarenga det. 1958”.

Remarks. *Agacephala mannerheimi* has a wide distribution throughout the Brazilian Cerrado occurring from Mato Grosso to Bahia states. This species occur together with *A. cornigera* in Brasilia, but they can be easily distinguished. For differences between *A. mannerheimi* and *A. cornigera* see the **remarks** section of *A. cornigera*. After studying the holotype of *Agacephala urus* (MNHN) we realized that the shape of parameres are the same as *A. mannerheimi*, therefore what we used to see identified as *A. urus* is in fact a new species that we describe here, and the very small holotype male of *A. urus* is in fact *A. mannerheimi*, that is here considered the senior synonymy of *A. urus*, **new synonymy**. Little is known about the biology of this species (as well as all species of *Agacephala*), but based on information of a specimen label housed in the NHM, we know that this species was seen climbing on *Paepalanthus* sp. but it was not observed if the specimen was feeding on some part of the plant.

The type specimen of *A. mannerheimi* have the same fate as the type of *A. duponti* as they were both lost with the Castelnau collection. Endrödi (1970) then designated a specimen from Misiones, Argentina as the neotype, even though the type locality was “Brazil meridional”. We had access to the former Endrödi collection and we could not find this neotype. Additionally, we examined one specimen from Misiones, Argentina but it was a specimen of *A. duponti* housed in the CMNC. It is hard to imagine that Endrödi could have mistaken a specimen of *A. duponti* with *A. mannerheimi*, but as we did not find the neotype from Misiones we can not be sure if this identification is correct. For that reason, we decided to keep the record of *A. mannerheimi* to Argentina as questionable. The criteria that Endrödi used to designate the neotype was questionable as he should have considered a specimen from Brazil, as it is the country of the type locality. The article 75.2 of The Code states that “A neotype is not to be designated as an end in itself, or as a matter of curatorial routine, and any such neotype designation is invalid”. As there is no doubt about the identity of *Agacephala mannerheimi*, the species can be easily identified based on descriptions and images of previously identified specimens collected from Brazilian Cerrado, and this species is not involved in a complex taxonomic problem, we opt to not designate a new neotype.

Agacephala margaridae Alvarenga, 1958

(Figs. 12, 17-27, 35)

Agacephala margaridae Alvarenga 1958: 47 (original description), 49 (Holotype illustration));
Lachaume 1992: 23 (cited)

Agacephala margaridae Endrödi 1970: 42 (revision); Endrödi 1985: 210 (catalogue).

Diagnosis. Male: Cephalic horns elongated and strongly curved at apex, presence of dorsolateral protuberance strong and sharp (Fig. 17H). Ocular canthi longitudinal with posterior portion thin and projected laterally (Fig. 20E). Protibiae with four external teeth (Fig. 27A). Mesotibiae distinctly curved and wrinkled (Fig. 27A, 20G). Thoracic horn sharp, elongated and directed forward (Fig. 21D). In dorsal view, parameres with mesoapical portion club-like shaped with lateral oblique tooth backwards on both sides (Fig. 22E).

Female: Frons strongly protuberant, tubercles indistinct (Fig. 23E). Head sculpture with wrinkles transversely distributed on clypeal base, coalescent punctures near vertex (Fig. 23D, F). Clypeus round and wide, apex slightly emarginated (Fig. 23D). Ocular canthi with anterior margin slightly protuberant basally, obliquely converging to tip, tip angulated (Fig. 23D). Protibiae with four external teeth (Fig. 27C). Labrum slender, 7 times wider than long, anterior margin medially emarginated (Fig. 18H). Mandibles in ventral view with inner carina distinctly angulated near apical tooth (Fig. 18E). Maxilla with galea falciform (Fig. 19D). Mentum with base broad and apex discretely narrow, ventral surface with large dense punctures (Fig. 19F). Mesotibia with medial tooth paired with other inner tooth (Fig. 20G). Metatibial apex medially projected and sharp (Fig. 20H).

Redescription. Male. **Color:** Surface lustrous; head, pronotum, legs and abdomen dorsally and ventrally with metallic greenish and copperish shine; elytra testaceous (Fig. 27A-B). **Head:** Vertex and frons densely punctate, punctures thin denser on vertex than on frons. Frons bluntly elevated between horns (Fig. 17E). Cephalic horns elongated and strongly curved at apex, presence of dorsolateral protuberance strong and sharp (Fig. 17H), basal portion of horns near clypeus with distinct paired protuberances directed frontward (Fig. 17H); punctures on horns thin and dense dorsally near protuberance, punctures thin and sparse laterally. Clypeus concavely emarginated on apex forming two slightly acuminate corners, clypeal sides smoothly round (Fig. 17F-G); clypeal punctures thin and sparse, becoming thinner on anterior margin (Fig. 17F).

Ocular canthi longitudinal with posterior portion thin and projected laterally (Fig. 20E), presence of long thin setae sparse on posterior portion. Antennae with club short, shorter than antennomeres I-VII, antennomere I and club distinctly hirsute (Fig. 20E).

Mouthparts: Labrum thin, anterior margin widely emarginated medially, sides bilobated (Fig. 18H). Mandibles robust, subtriangular with two apical teeth and two ventral carinae; in ventral view, apical tooth elongated and distant from inner carina, lateral tooth shorter than apical tooth, mandibular outer margin convex, presence of long thin setae from outer side of base to apex near inner carina (Fig. 18E); in lateral view, molar area reniform with basal portion emarginated and apical portion convex, mesal brush densely projecting on molar area (Fig. 18F), presence of small bump near dorsal socket (Fig. 18F); in dorsal view, presence of small bump on outer side of apical tooth near apex of mesal brush, mesal brush evenly convex on outer margin, apical portion with setae longer than at middle, mandibular outer margin with pale thin setae from base to apex near lateral tooth (Fig. 18G). Maxillae with galea falciform, apex of galea thick; in ventral view, palpifer thick and slightly emarginated on outer margin (Fig. 19D), stipes with posterior margin concave, ventral surface with short setae intertwined with long setae denser near outer margin than on inner margin (Fig. 19D); in dorsal view maxilla with subgalea with long thin setae on outer margin and disc bare, stipes densely setose (Fig. 19E). Mentum broad basally, apex discretely narrow (Fig. 19F).

Thorax: Pronotum wider than long; lateral margins sinuous with basal portion prominent near posterior corners, anterior corners distinctly acute, anterior margin projected medially and concave on both sides near anterior corners (Fig. 21D). Pronotal disc with thoracic horn distinctly projected forward, apex sharp (Fig. 21D); pronotal surface densely wrinkles almost on entire surface except a longitudinal medial area near horn with punctures thin and dense posteriorly and thin and sparse towards horn.

Scutellum subtriangular with a greenish/copperish metallic shine, disc with punctures moderate and sparse medially intertwined by thin and sparse punctures not reaching apex nor lateral margins. **Elytra:** Form 2.1 times longer than wide. Surface rugose, elytral punctures ocellate and moderate densely and irregularly distributed on disc, punctures slightly sparser on outer margins (Fig. 27A). Apical umbones discrete, apical and humeral umbones not spotted, both with thin and dense punctures (Fig. 27A). **Legs:** Protibiae with four external teeth, first and second apical teeth connected at base, protibial inner margin curved, inner corner with sharp prominent tooth; protibial surface with moderate punctures sparse distributed mainly near edges, with thinner punctures

densely distributed basally and medially. Protarsi elongated, protarsomere V almost 4 times longer than protarsomere IV, protarsal claws symmetric and simple (Fig. 20F). Mesotibiae distinctly curved and wrinkled (Figs. 27A, 20G). Metatibiae densely wrinkled with a mixed longitudinal zone with thin and moderate punctures intertwined with wrinkles; in lateral view, outer edge with medial and apical pairs of strong teeth obliquely positioned, one lone tooth basally (Fig. 20H). Metatibia with three outer teeth distinctly elongated, medial tooth longer than others, presence of short protuberance near medial tooth (Fig. 20H), metatibial apex distinctly concave near apical tooth (Fig. 20H). **Abdomen:** Tergite VII distinctly elongated and projecting beyond elytral apex, apical portion and sides of tergite VII densely covered by short thin setae (Fig. 21E). Tergite VIII round anteriorly covered by tergite VII, surface shagrinated and with short thin setae on disc and anterior margin. Sternites IV-V with dense agglomeration of large punctures, with thin punctures only medially near posterior margins; sternite VI uniformly slender from sides to middle; sternite VII densely punctate (Fig. 21F). **Aedeagus:** Parameres asymmetric basally. In dorsal view, basal portion with right sclerite blunt and prominent towards left basal sclerite, mesoapical portion club-like shaped with lateral oblique tooth backwards on both sides (Fig. 22E). In lateral view, anterior phallobase almost 3 times longer than posterior phallobase, posterior phallobase ovoid and thick with corners short and blunt (Fig. 22H); parameres with dorsum distinctly round, lateral carina with apex directed forward (Fig. 22F). In ventral view anterior margin of ventral sclerite deeply emarginated, parameres slightly emarginated on inner margin apically, outer sides with short tooth (Fig. 22G).

Measurements. Body length: 30.6–42.1 mm. Elytral length: 20.5–26.2 mm. Elytral width: 9.8–14.1 mm. Head length: 3.1–6.2 mm. Pronotal width: 14.9–21.4 mm. Pronotal length: 8.2–12.8 mm. Protibial length: 7–10.8 mm.

Female. Females as males in general aspect (Fig. 27C-D). **Head:** Cephalic horns absent. Vertex with punctures moderate and coalescent medially, becoming more elongated on sides. Frons distinctly robust and projected (Fig. 23E), surface distinctly wrinkled with some coalescent punctures intertwined among wrinkles (Figs. 23D, F). Clypeus broad and round, apex slightly emarginated, borders slightly deflected, sculpture wrinkled continuous with frons (Fig. 23D). Ocular canthi with anterior margin slightly protuberant basally, obliquely converging to tip, tip angulated; punctures moderate and dense, presence of oblique carinae from canthi base (Fig. 23D).

Mouthparts: Labrum as in males but with anterior margin evenly emarginated, setae

present on medial portion of anterior half (Fig. 24H). Mandibles convex as in males, but less projected, inner carina distinctly angulated apically near apical tooth (Fig. 24E), base with distinct protuberance near lateral margin of molar area (Fig. 24E), ventral surface less setose than in males; in lateral view, molar area small, with mesal brush thick on apical margin (Fig. 24F), dorsal outer margin distinctly projected as well as socket (Fig. 24F); in dorsal view, teeth distinctly projected dorsally (Fig. 24G), presence of pale thin setae on outer margin not reaching lateral tooth (Fig. 24G). Mentum similar to males, base broad and apex discretely narrow, ventral surface with large dense punctures (Fig. 25F). **Thorax:** Pronotum convex. Pronotal disc with punctures large and dense medially and posteriorly, punctures becoming coalescent and denser on sides and corners (Fig. 26E). Prosternum with middle portion of anterior margin parabolic almost with same size as adjacent protuberances, prosternal disc transversely wrinkled. Metasternum hirsute, setae erected and sparse, metasternal surface distinctly punctate, punctures moderate and dense, presence of wrinkles on sides and anterior and posterior corners. Metepisternum with same sculptural pattern as metasternum. Scutellum as in males but with ocellate punctures sparse and scattered. **Elytra:** Surface rugose but less than in males, punctures ocellate, elytral disc moderately punctate, punctures slightly sparser on outer margins, presence of few thinner punctures near elytral suture medially (Fig. 27C). Apical umbones discrete and not spotted, humeral umbones with discrete darker spot anteriorly, apical and humeral umbones with thin and dense punctures (Fig. 27C). **Legs:** Protibiae with four external teeth as in males, first and second apical teeth less connected than in male, distance between second apical tooth and medial tooth shorter than in males; protibial punctures moderate and dense, thin and sparse punctures on teeth, inner apical tooth slightly acuminate. Mesotibia with sharp protuberance medially near medial tooth, mesotibial apex distinctly projected and sharp (Fig. 26F). Metafemora with thin and sparse punctures on disc, posterior margin with rugose area below row of setae. Metatibiae apically and basally with thin and sparse punctures, middle with large and dense punctures; metatibial apical corner projected and acute, in lateral view with 3 pairs of sharp teeth obliquely distributed on outer edge (Fig. 26G). **Abdomen:** Tergite VIII shape convex with apex slightly elongated, surface completely punctate, disc with large and dense punctures, sides covered by wrinkles. Sternite IV densely punctate, punctures moderate and coalescent on sides and anterior half, only separated at middle of posterior margin. Sternites V-VI with coalescent punctures on sides, punctures thin and sparse medially. Sternite VII with punctures sparser than in

sternite VI, sides rugose. Sternite VIII wrinkled on anterior margin and part of disc, presence of C-punctures on apical half, presence of few long thin setae transversely distributed on disc, short thin setae on posterior margin (Fig. 26H). **Genitalia:**

Gonocoxites with proximal coxites with anterior margin concave and outer corners blunt anteriorly, disc distinctly depressed, setae present on inner corners (Fig. 12E), distal coxites subparallel, densely covered by long thin setae (Fig. 12E).

Measurements of females. Body length: 26.3–37 mm. Elytral length: 23.1–24.6 mm. Elytral width: 9.9–18.6 mm. Head length: 3.3–3.9 mm. Pronotal width: 14.2–18.4 mm. Pronotal length: 9.9–12.4 mm. Protibial length: 7.3–8 mm.

Geographic distribution. Brazil: Mato Grosso, Pará (Fig. 35).

Material examined. Holotype male examined (MNRJ – destroyed by the 2018 fire) labeled: a) “Coleção/ M. Alvarenga”, b) “HOLOTIPO”, c) “Cachimbo (E{stado do}. Pará)/ Travassos Oliveira/ & Adão, 25/9.10.{1}956”, d) “Agacephala/ *margaridae*/ m./ M. Alvarenga det. 1958”. **Paratypes** 1 male (MNHN) labeled: a) “Cachimbo (E{stado do}. Pará)/ Travassos Oliveira/ & Adão, 25/9.10.{1}956”, b) “Coleção/ M. Alvarenga”, c) “Paratipo”, d) “Agacephala/ *margaridae*/m./ M. Alvarenga det. 1958”, e) “Muséum Paris/ coll. Générale”, f) “PARATYPE”, g) “MNHN/ EC2456”; 1 male (MNHN) labeled as the previous specimen except by: b) “Coleção/ M. Alvarenga/ N. 2296” and g) “MNHN/ EC2457”; 1 female (MNHN): a) “Pará/ Cachimbo/ x-{1}955/ Pe. Pereira”, b) “Coleção/ M. Alvarenga/ N. 2384”, c) “PARATYPUS”, d) “AGACEPHALA/ MARGARIDAE/ ALVARENGA/ M. Alvarenga det. 1958”, e) “Muséum Paris/ coll. Générale”, f) “PARATYPE”, g) “MNHN/ EC2459”; 1 female (MNHN) with same labels except: b) “Coleção/ M. Alvarenga/ N. 2407” and g) “MNHN/ EC2458”; 2 males (NHM): a) “Coleção/ M. Alvarenga”, b) “Paratipo”, c) “Cachimbo (E{stado do}. Pará)/ Travassos Oliveira/ & Adão, 25/9.10.{1}956”, d) “Agacephala/ *margaridae*/m./ M. Alvarenga det. 1958”; 1 female (NHM): a) “Coleção/ M. Alvarenga”, b) “Paratipo”, c) “Pará/ Cachimbo/ x-{1}955/ Pe. Pereira”, d) “Agacephala/ *margaridae*/m./ M. Alvarenga det. 1958”, e) “NHMUK 014560303”; 2 females (NHM) with same data as previous specimen except: e) “NHMUK 014560302”; e) “NHMUK 014560301”; 7 males and 6 females (EPGC) with same data as holotype; 6 males and 18 females from MNRJ were also destroyed by the fire in 2018 and were examined by PCG. **Other specimens:** 1 male (UFMT) with following data: a) “BRA, MT, Juína/ IFMT, campus Juína/ 11° 26' 54.5"S, 58° 43' 21.3"W/ 18.IV.2019/ VC. Manochio col.”; 1 male (UFMT): a) “BRASIL: Mato Grosso/ Novo

Mundo/ Manual/ 27-X-2013/ A. P. S. Oliveira”.

Remarks. *Agacephala margaridae* is unique among species of the genus. It is the biggest species in the genus and it is the only *Agacephala* with sharp dorsolateral protuberance on cephalic horns (17H) and mesotibia strongly curved (Fig. 27A). Small females of *A. margaridae* can be slightly similar to *A. bicuspis* due to the distinct greenish metallic shine of pronotum and the protibiae with four outer teeth, but they can be easily distinguished by: *A. margaridae* with frons strongly protuberant, tubercles indistinct (Fig. 23E), ocular canthi with anterior margin slightly protuberant basally (Fig. 23D), mandibles in ventral view with inner carina distinctly angulated near apical tooth (Fig. 18E), mesotibia with medial tooth paired with other inner tooth (Fig. 20G) and metatibial apex medially projected and sharp (Fig. 20H) whereas in *A. bicuspis* frons slightly protuberant (Fig. 23B), ocular canthi with anterior margin slightly round (Fig. 23A), mandibles in ventral view with inner carina smoothly round to apical tooth (Fig. 24A), mesotibia with medial tooth paired with short protuberance with thick setae on tip (Fig. 26B), metatibial apex medially projected but not sharp (Fig. 26C).

A. margaridae is also the only Brazilian species occurring in the Amazon biome, specifically in the southernmost portion, covering the ecoregions of Madeira-Tapajós moist forests and Mato Grosso tropical dry forests. The type locality of *A. margaridae* is the Serra do Cachimbo, a Brazilian orographic region with high altitude of 743m (Zamadei *et al.* 2019). The phytophysionomy recurrent in Serra do Cachimbo is a mosaic of Amazon forest such as the Campina, characterized by the woody vegetation of 4-6m tall and presence of shrubs like *Pagamea guianensis* and *Palicourea nitidella*, Campinarana and phytophysionomies of Cerrado such as Campo sujo and Cerrado fields (Lleras & Kirkbride Jr. 1978).

***Agacephala melolonthida* (Thomson, 1860)**

Agacephala melolonthida Lachaume 1992: 24 (cited)

Agaocephala melolonthida Thomson 1860: 19 (original combination); Endrödi 1970: 45 (cited); Endrödi 1985: 210 (catalogue).

Diagnosis can be seen in the original description (Thomson 1860).

Remarks. *Agacephala melolonthida* is almost an urban legend among those who study the Agaocephalini. Since the original description, no one is known to have seen this specimen. The majority of Thomson collection is housed in the Natural History

Museum in London, but not an even trait of *A. melolonthida* could be found. The main diagnostic trait of this species is the body metallic blue with elytra reddish brown, and the type locality is Brasilia, the same locality where *A. mannerheimi* and *A. cornigera* occur. Based on certain characters in the description, such as antennal club longer than other segments together and presence of eight weak wrinkles on elytra, Endrödi (1970) thought that if this specimen still exists, it fits best in Rutelinae than in Dynastinae. However, since there is no specimen to confirm the hypothesis we keep considering *A. melolonthida* as a valid species in the genus.

***Agacephala mineira* Grossi & Sobral, new species**

(Figs. 29, 31-32, 35)

Holotype description, male. Body length: 26.3 mm; maximum width of elytra: 11.8 mm (Fig. 29A). **Body:** Form elongate convex, head, pronotum, scutellum, legs and venter metallic cooper; elytral disc pale brown, suture brownish dark. **Head:** Surface completely and irregularly punctate, punctures smaller and more regular on clypeus; clypeus trapezoid, lateral edges thinner, rounded, disc concave. Frontal horns very slender, parallel and slightly upturned; ventral surface with a longitudinal carina on each horn joining clypeal lateral margin, just above antennal insertion, and with external margin straight near canthus. Canthi rugose, weakly concave externally, apically obtuse (Fig. 31A). **Thorax:** Border complete, surface distinct punctate, tegument smooth. Border in anterior middle thicker, turned up in a smooth line that joins to pronotal ventral margin; punctures denser at sides, on anterior angles and on horns edges, sometimes coalescent; disc with sparse and irregular punctures, anteriorly at middle with a forwarded, emarginated short horn, ending before frons, and with a carina on each side (Fig. 31C); anterior and posterior angles distinctly obtuse. Scutellum with surface strongly and irregularly punctate anteriorly, punctures weak and sparse posteriorly. Prosternal process thin and elevated. Metasternum wrinkled and densely setose. **Elytra:** Disc regularly punctate, wrinkled; punctures anteriorly bigger, concave. Humeri brownish dark. Lateral margin slightly emarginated anteriorly. **Legs:** Protibiae distinctly with three external, strong teeth in anterior third, increasing in size distally; distance between apical and medial teeth shorter than distance between medial and basal ones. Internal margin distally with an acute downturned tooth, ventrally with other less acute tooth; spur acute and downcurved. Base of inner claw weakly lobed (Fig. 31E). Mesotibiae setose with 2

medial spines, distal one bigger, and one apical with a convex external edge. Spine between spurs with a half of the length of distal spur; external edge with 3 spines increasing in size distally, distal spine larger at base, distinctly visible in ventral view. Metatibiae with spurs almost with the same size, with a small spine between them; external edge with 3 spines, distal spine robust. **Abdomen:** Tergite VIII with shape convex, weakly and regularly reticulated, with sparse setae. **Aedeagus:** Parameres longer than wider with metallic lustre. Shape asymmetric, anteriorly turned down, truncate; laterally expanded, expansion 2 times wider than dorsal elevation; expansion with an acute process turned back on anterior third; right paramera with an obtuse internal downturned process. (Fig. 32A).

Measurements of males. Body length: 27.5–31.1 mm. Elytral length: 18.3–21.7 mm. Elytral width: 9.3–10 mm. Head length: 2.6–3.9 mm. Pronotal width: 15–16.4 mm. Pronotal length: 8.8–10.2 mm. Protibial length: 6.3–7.1 mm.

Paratype females description. General aspects as male, differing in the following characters. Body length: 26.4–27.7 mm; maximum width of elytra: 12.8–13.1 mm (Fig. 29B). **Head:** Clypeus upturned and completely concave; frons strongly wrinkled, disarmed. **Thorax:** Surface strongly punctate, with coalescent punctures on disc; anterior middle simply convex, anterior angles acute. Scutellum with surface more punctate, apex more acute. **Elytra:** Apical umbones brownish dark, sutural macula wider, punctures bigger. **Legs:** Anterior tibiae shorter, incurved, with flatten teeth; inner claw simple. Mesotibiae with internal spurs smaller, and metatibiae with proximal spine bigger. **Abdomen:** Tergite VIII laterally less convex.

Measurements of females. Body length: 28.3–29.7 mm. Elytral length: 18.2–20.5 mm. Elytral width: 9.6–9.9 mm. Head length: 2.6–3.3 mm. Pronotal width: 12.9–14.2 mm. Pronotal length: 7.6–9.2 mm. Protibial length: 5.5–6.7 mm.

Geographical distribution. Brazil: Espírito Santo, Minas Gerais (Fig. 35).

Material examined. Holotype male (CERPE) labeled: a) "BRASIL, Minas Gerais, Ipatinga,/ 28.XII.1995, 220 m,/ P. C. Grossi leg.". **Paratypes** 21 specimens labeled as follows: 1 male (EPGC) labeled as holotype except "26.xii.1988, G. Turrer leg."; 3 males (CERPE): a) "Viçosa, UFV, xii.1993, R. G. Sá leg."; 1 male (CEMT): a) "Viçosa, UFV, 15.viii.1998, R. Proque leg.". 18 females labeled with same data as holotype except: 1 female (CERPE): a) "25.xii.1989, E. & P. Grossi legs."; 3 females (CERPE, EPGC, CEMT): "18.xii.1989, E. & P. Grossi legs."; 3 females (EPGC): "i.1989, E. & P. Grossi legs."; 1 female (CERPE): a) "09.xii.1989, E. & P. Grossi legs."; 1 female

(CERPE): a) "16.xii.1989, E. & P. Grossi legs."; 2 females (CERPE, CEMT): a) "Viçosa, UFV, 20.xii.1995, F. Z. Vaz-de-Mello leg."; 1 female (EPGC): a) "Viçosa, UFV, xii.1993, R.G. Sá leg."; 1 female (EPGC): a) "Viçosa, UFV, 05.v.1999, A. E. Moreira leg."; 1 female (CEMT): a) "Viçosa, UFV, viii.1997, E. Cartor leg."; 1 female (CERPE): a) "Viçosa, UFV, 20.xii.1995, F. Z. Vaz-de-Mello leg."; 1 female (CEMT): a) "Viçosa, UFV, xi.1997, S. A. Falqueto leg." 2 females (CERPE, EPGC): a) "Marliéria, xii. 1997, E. & P. Grossi legs.".

Remarks. *Agacephala mineira* was found in regions of Dense Atlantic Forest (Ipatinga and Marliéria) and in Semideciduous Atlantic Forest (Viçosa), both in Minas Gerais State. Since these collects presented here, no additional specimen was found, and recently efforts have been made with no success and we consider this species to be threatened as there is a strong pressure of human occupation near the areas where the specimens were collected, as well as the recent catastrophic break-up of a mining dam in Mariana municipality that destroyed the most important river of the region, Doce River, that crosses the municipality of Ipatinga.

Agacephala mineira can be easily distinguished from all other species within the genus by its pronotum surface that is smooth and punctate, and with a medial anterior horn (Fig. 29A). The other species with a medial horn have the pronotal surface opaque by the microgranulose aspect, never shining (Fig. 30A). The anterior tarsi with inner claw weakly lobed basally is also diagnostic, being distinctly toothed in the remaining species, except in *A. margaridae*. Another feature can be found on pronotal horn base, which has a carina in each side (Fig. 31C). Females could be confused with the other new species described here, but distinct by the more rounded pronotum, with surface more strongly punctate and on disc with some punctures coalescing.

Etymology. The specific epithet refers to the State where the first specimens were collected, Minas Gerais, and "mineira" is how a person who was born in Minas Gerais is called. The name is in apposition.

Agacephala alvarengai Grossi & Sobral, new species

(Figs. 30– 32, 35)

Holotype description. Male. Body length: 28.3 mm; maximum width of elytra: 13.4 mm (Fig. 30A). **Body:** Shape elongate convex, metallic cooper on head, pronotum, scutellum, legs and ventrally, more shining on pronotum with green shimmering; elytral

disc pale brown with darkish brown suture, epipleura and humeri. **Head:** Surface completely punctate; punctures bigger and distinct on clypeus, smaller and coarse on frons. Clypeus trapezoidal, dorsally concave, with apex strongly emarginate and slightly upturned with lateral edges thicker and rounded. Frontal horns thin, slightly upturned, with a discrete apical carina on the tip. Ventrally with a longitudinal continuous carina. Clypeal lateral margin reaching the ventral carina near antennal insertion. Clypeal external margin more rounded near canthus. Canthus short, with large punctures, outer side strongly convex and apex rounded (Fig. 31B). **Thorax:** Bordered, completely wrinkled and with small punctures, mainly on superior surface of pronotal horn. Anterior margin bordered and narrower medially, punctures sparse. Surface wrinkled, wrinkles denser laterally; punctures more distinct around the edges of pronotal horn (Fig. 31D). Disc slightly elevated with prothoracic horn directed forward, apex incised, ending before frons, and with a smooth line ending just below the apex. Scutellum with surface punctate; punctures strong, denser medially. Color metallic cooper; metasternum wrinkled, glabrous, with dense rows of setae at middle around longitudinal furrow. **Elytra:** Disc regularly punctate, punctures anteriorly bigger and concave. Depression between disc and sides shallow. Wrinkles strong, distributed along the sides of elytral suture and above the epipleuron. Humeral calli darkish brown with small punctures. **Legs:** Protibiae tridentate, with teeth increasing in size distally. Distance of medial and basal teeth almost 1.5 times longer than the distance of apical and medial teeth; internal margin with an acute downturned spine at the side of tibial spur, and with a wider spine on ventral side; spur acute and downturned; base of inner claw toothed; tooth obtuse (Fig. 31F). Mesotibiae setose, wrinkled, with distal spur bigger than apical spur; external edge with three spines, medial longer than others, distal acute, obsolete in ventral view. Metatibiae with 2 spurs, proximal longer than distal, with a small spine between them; external edge with 3 spines, distal spine acute. **Abdomen:** Tergite VIII with shape convex, finely punctate, and with sparse setae; punctures small. **Aedeagus:** Paramera longer than wider with metallic luster; in dorsal view, lateral carina expanded, almost one time wider than dorsal elevation; paramera apex parallel, not incurving; basal process in right paramera incurved (Fig. 32B).

Measurements of males. Body length: 22.4–30.2 mm. Elytral length: 14.9–19.5 mm. Elytral width: 6.4–8.1 mm. Head length: 2.3–3.1 mm. Pronotal width: 9.7–12.9 mm. Pronotal length: 6.4–9.4 mm. Protibial length: 4.9–6.6 mm

Female paratype description. In general aspect as holotype except as follows: Body length: 25.4–27.5 mm; maximum width of elytra: 12.3–14.1 mm. **Head:** Clypeus strongly upturned, concave. Frons strongly wrinkled, disarmed. Canthus densely setose on tip. **Thorax:** Shape simply convex, tegument smooth, surface densely punctate; punctures big; wrinkled near anterior margin. Scutellum with surface less punctate; punctures denser basally; apex more acute. Metasternum with shallower furrow. Abdominal sternites more densely setose. **Elytra:** Surface covered by bigger punctures, humeri darker and less wrinkled. **Legs:** Anterior tibiae shorter, external teeth wider, almost equidistant one from each other; anterior claws simple, not toothed. Mesotibiae shorter. Mesocoxae and metacoxae with bigger punctures. **Abdomen:** Tergite VIII with sides concave with bigger basal punctures than in male.

Measurements of females. Body length: 22.4–34.2 mm. Elytral length: 13.8–19.2 mm. Elytral width: 6.4–9.6 mm. Head length: 2.6–3.4 mm. Pronotal width: 7.4–12.8 mm. Pronotal length: 5.2–7.4 mm. Protibial length: 4.4–6.4 mm

Geographic distribution. Brazil: Bahia, Minas Gerais (Fig. 35).

Material examined. **Holotype** male labeled: Brasil, Minas Gerais, Águas Vermelhas, XI, E. & P. Grossi legs. **Paratypes** 50 males and 50 females labeled as holotype, except by: one paratype male labeled: a) “Bahia, Camacã,/ 02-xii-1976, J. Becker (MNRJ)”; 1 male (NHM) labeled: a) “Espírito Santo”, b) “Fry Coll./ 1905-100”, c) “*Agaocephala/ urus/ Thomson/ Det E.J. Grossi 2011*”, d) “NHMUK 014560304”.

Remarks. *A. alvarengai* is known from some particular Brazilian savanna areas from northeastern Minas Gerais state and southeastern Bahia state, with a confluence of two more Brazilian biomes, Atlantic Forest and Caatinga, characterized by several endemic species, as *Hypocephalus armatus* Desmarest [Coleoptera, Vesperidae] (Araújo 1954). As other species of the genus it is commonly attracted to artificial lights, but adults were also collect over bushes in open areas. Curiously, this new species was misidentified since Lachaume (1992) based on several specimens collected in the type locality and dispersed among all collections we know, including some of those listed in the materials and methods. Curiously *A. alvarengai* is very similar to *A. mineira*, with some characters, especially on males, that facilitate their identifications, as the surface of the pronotum, shiny in *A. mineira* and opaque in *A. alvarengai*. Both species with *A. mannerheimi* can be considered an isolated species group within *Agacephala*, possessing an elongate pronotal horn, distinct from *A. cornigera*, that is not elongated, and protarsal inner claws basally dentate in males.

A. alvarengai is very close related to *A. mineira* sp. n. and differs in males from *A. mineira* and *A. mannerheimi* by the shape of ocular canthus that is more developed, and compact with outer side convex (Fig. 31B) and in the two other related species is more elongated, and with outer side straight or almost straight. Also, it differs from *A. mannerheimi* by the body shape more convex and elongated, the punctures of elytra smaller, and the discrete bifurcation of pronotal horn, while in the related species the body shape is flattened and rounded, punctures of elytra bigger and pronotal horn distinctly bifurcated. Can be easily distinguished from *A. mineira* by its pronotum surface that is finely wrinkled (Fig. 31D), the depression on elytra, and the characters of paramera that have lateral carina expanded almost one time wider than dorsal elevation and apex almost straight.

Females of *A. alvarengai* can be distinguished by the elytral depression and by the pygidium more rounded, while in *A. mineira* the elytra is smooth and the pygidium more acute. In *A. mannerheimi* the apical calli has a strong, dark brown spot, and bigger punctures on elytra, whereas in the new species the apical calli has no macula and the elytral punctures are smaller. Tergite VIII medially less concave in *A. alvarengai* than in *A. mannerheimi*.

Etymology. This species is named in honor to the past kind friend Cel. Moacyr Alvarenga, one of the greatest Coleoptera collector in Brazil, and who presented the type locality to the father of PCG about thirty years ago.

Key for *Agacephala* Saint-Fargeau & Audinet-Serville, 1825 species (modified from Endrödi 1985)

1 Male specimens; head with a pair of frontal horns; pronotum with or with no tubercle or horn. **2**

- Female specimens; head simply concave or convex with no horns, usually double tubercled; pronotum convex. **9**

2 At least elytra shining, only in *A. mannerheimi* Castelnau and *A. margaridae* Alvarenga somewhat opaque, but in these species pronotum with a horn shaped tubercle, and bronze lustre. **2**

- Pronotum and elytra nearly pale very finely wrinkled with dense and unequal annular punctures (Fig. 16A). Metallic green (Fig. 21A-C). Elytra brown with greenish metallic lustre (Fig. 16B). Guiana and East of Venezuela. ***A. bicuspis* Erichson, 1848)**

3 Pronotum disarmed, simply convex. **4**

- Pronotum with a horn shape elevation, or tubercle in very small males. **5**

4 Pronotum along middle very finely and sparsely punctate (Fig. 6G); punctures denser on sides. Brazil (Rio Grande do Sul, São Paulo, Minas Gerais). *A. inermicollis* Arrow, **1914**

- Pronotum along the disc strongly punctated (Fig. 6D) (Minas Gerais, Rio de Janeiro, São Paulo, Paraná). *A. duponti* Laporte, **1832**

5 Frontal horns very long, above (Fig. 27A), toothed near middle, apex acute (Fig. 17H). Brazil (Pará, Mato Grosso). *A. margaridae* Alvarenga, **1958**

- Frontal horns simple, not toothed, apex acute. **6**

6 Pronotum with a strong, forward directed horn, on apex more or less strongly emarginated, in big males reaching apex of frontal horns (Fig. 28A). Brazil (Bahia, Espírito Santo, Mato Grosso, Goiás, Minas Gerais, Paraná), Argentina (Misiones). *A. mannerheimi* Laporte, **1832**

- Pronotal horn short. Pronotum and elytra shining. **7**

7 Head between horns deeply hollowed, basis of horns connected by a high carina (Fig. 2B). Knob of pronotum short and furrowed above (Fig. 2C). Brazil (Rio de Janeiro, Minas Gerais, Goiás and Distrito Federal). *A. cornigera* Saint-Fargeau & Audinet-Serville, **1825**

- Head between horns only declivous, no carina present. Pronotum with small and thin forward directed horn. **8**

8 Pronotum with very small coalescent punctures, with a reticular uniform surface (Fig. 30A); inner claw of anterior tarsi indented (Fig. 31F). Brazil (Bahia, Espírito Santo and Minas Gerais). *A. alvarengai* Grossi & Sobral n. sp.

- Pronotum with sparse and distinct punctures, never coalescent at disc and smooth surface (Fig. 29A). Anterior tarsi with inner claw weakly lobed (Fig. 31E) (Minas Gerais). *A. mineira* Grossi & Sobral n. sp.

9 Head and pronotum metallic blue (Brasilia). *A. melolonthida* Thomson, **1860**

- Head and pronotum without metallic blue. **10**

10 Anterior tibiae with four external teeth. **11**

- Anterior tibiae with three external teeth. **12**

11 Ocular canthus protruded basally (Fig. 23D), clypeus small (Fig. 23D), head on disc distinctly convex (Fig. 23E). *A. margaridae* Alvarenga, **1958**

- Ocular canthus rounded (Fig. 23A), clypeus large and not bifurcated (Fig. 23A), head

on disc not convex (Fig. 23B). *A. bicuspis* Erichson, 1848

12 Pronotal disc with moderately dense punctures, shinier than sides, with punctures clearly bigger (Fig. 11I); head on disc with two weak tubercles (Fig. 8I). *A. inermicollis* Arrow, 1914

- Pronotal disc also with big and round punctures. 13

13 Clypeus anteriorly concave, anterior and lateral margins nearly upturned. 14

- Clypeus not concave anteriorly. 15

14 Pronotum strongly and densely punctured, anteriorly on disc punctures frequently coalescent (Fig. 30B). *A. alvarengai* Grossi & Sobral n. sp.

- Pronotal punctures smaller, less dense, and rarely coalescent on anterior discal middle (Fig. 29B). *A. mineira* Grossi & Sobral n. sp.

15 Clypeus trapezoidal with apex narrow (Fig. 8A). Width between lateral angles less than a third of the width of frons inter eyes (Fig. 8A). *A. cornigera* Saint-Fargeau & Audinet-Serville, 1825

- Clypeus trapezoidal with apex wide. Width between lateral angles at least a half of width of frons in eyes. 16

8 Elytral disc strongly punctured with big and round punctures, sometimes coalescent (Fig. 28C). Sternite VII densely punctate (Fig. 26L) *A. mannerheimi* Laporte, 1832

- Elytral disc weakly punctured, and with simple punctures (Fig. 13C). Sternite VII sparsely punctate (Fig. 11H) *A. duponti* Laporte, 1832

Notes on *Agacephala* (*Lycocephala*) *brasiliانا* (Martínez & Alvarenga, 1987)

Antonio Martínez and Moacyr Alvarenga described *Agacephala* (*Lycocephala*) *brasiliانا* as a subgenus of “*Agaocephala*” and up until now only one species is known from southwestern Bahia State, in Encruzilhada municipality (Martínez & Alvarenga 1985). Examining one male Paratype (MNRJ) and one female (Campos Seabra Collection, with no data) it is clearly that this is a genus distinct from *Agacephala* and from any other *Agaocephalini* genera. Based on some distinctive characters we here raise it to the generic status *Lycocephala* Martínez & Alvarenga **new status**. *Lycocephala* can be readily distinguished from *Agacephala* based on many morphological characters that are followed described:

Genus *Lycocephala* Martínez & Alvarenga, stat. nov.

Agaocephala (*Lycocephala*) Martínez & Alvarenga 1987: 21 (original combination); Krajcik 2005: 4 (catalogue); Abadie, Grossi & Wagner 2008: plate 09, (list and pictures)
Agacephala brasiliiana Martínez & Alvarenga. Lachaume 1992: 24 (citation and comments).

***Lycocephala brasiliiana* (Martínez & Alvarenga, 1987) new comb.**

(Figs. 33–35)

Diagnosis. Male (Fig. 33A-B). **Head:** Frontal horns strongly excavated externally at base. Frons with disc and vertex with long setae, more concentrated on vertex (Fig. 34A). Ocular canthi expanded externally and sharply pointed forward (Fig. 34B). **Thorax:** Disarmed with no horns or tubercles; surface densely and strongly punctured; punctures moderate, large, many coalescent, and with scattered yellowish short setae (Fig. 34D); lateral borders crenulated (Fig. 34E). **Elytra:** Surface opaque, covered by minute gray scales, tomentose; posteriorly near above and after apical calli setose; apical calli distinctly carinate. **Legs:** Protibiae with three small external teeth, surface strongly punctured; punctures deeply impressed. Anterior tarsi with third and fourth tarsomeres expanded forward and ventrally; inner claws trapezoidal, toothed (Fig. 34C). Mesotibiae with no spines; internal apical half with long, scattered setae; setae two times longer than mesotibiae width. Metatibiae as metatibiae, but internally with a brush-like yellowish red long setae (Fig. 34F). Arolium with more than six bristles. **Abdomen:** Tergite VIII round in lateral view and densely setose. Sternites completely covered by short thin setae, presence of thin punctures densely distributed on surface. **Aedeagus:** Parameres asymmetric with right paramere posteriorly projected, in an acute, long apophysis; left paramere with apophysis smaller. Apical portion of parameres subquadrate, narrowing medially and widening basally, inner margin distinctly sinuous, medial portion convex (Fig. 34G). In lateral view, posterior phallobase distinctly excavated medially, straighten to base, with distal corners elongated, surface flat (Fig. 34I), parameres with lateral margin restricted to apical portion, presence of short bump near apex (Fig. 34H).

Female: As male except in the following aspects. **Body** more flattened specially elytra (Fig. 33C-D). **Head:** with no horns, cathi less developed. **Legs:** Anterior tarsi simple. Posterior tibiae with one tooth at middle, apex sharply pointed; inner margin with thinner and shorter setae. **Abdomen:** Abdominal sternum more setose with longer setae.

Material examined. Paratype male (MNRJ – destroyed by a fire occurred in 2018) labeled as: a) “Brasil, Estado da Bahia, Município da Divisa, Encruzilhada, Km.

965 de la BR-16, XII-1980 (Moacir y Margarida Alvarenga, Juana P.R. de y Antonio Martínez-coll), luz artificial?”. **Other specimens.** 1 female (MNRJ – destroyed by the fire) with no data.

Table 1. Mainly differential diagnostic characters between *Agacephala* and *Lycocephala*.

	<i>Agacephala</i> Saint-Fargeau & Audnet-Serville	<i>Lycocephala</i> Martínez & Alvarenga
Ocular canthi	Simply rounded, never projected.	Distinctly projected forward.
Pronotum	With or with no horn, borders smooth.	Hornless, with borders crenate.
Elytra	Smooth, glabrous, shiny.	Tomentose, opaque.
Anterior tibiae	Teeth wide, big, giving an appearance of a dilated tibiae.	Teeth small, tibiae not dilated.
Posterior tibiae	Internal margin simple, glabrous.	Inner margin densely setose, setae more than twice longer than tibial width.
Abdominal sternites	Glabrous, at most with scattered setae.	Distinctly setose.

Acknowledgments

We thank all the curators from the cited collections for their contributions of material for this study. We thank Max Barclay, Michael Geiser and Keita Matsumoto for all the support to RS during his time in the Natural History Museum (London, United Kingdom). We thank Dr. José Wellington de Moraes for all the support to RS during his time at INPA (Manaus, Brazil). Miguel A. Monné (MNRJ) is thanked to loan the unique specimens housed at a Brazilian collection of *Lycocephala* to PCG. Everardo J. Grossi is thanked for the opportunity to study almost all the known Agaocephalini species housed in his collection. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. RS acknowledge the Instituto Nacional de Pesquisas da Amazônia for research support; the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for the PhD scholarship to RS and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Sandwich Doctorate scholarship to RS. PCG acknowledges the Universal Project, 449366/2014-6.

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Figures

FIGURE 1. Male and female of *Agacephala cornigera*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.

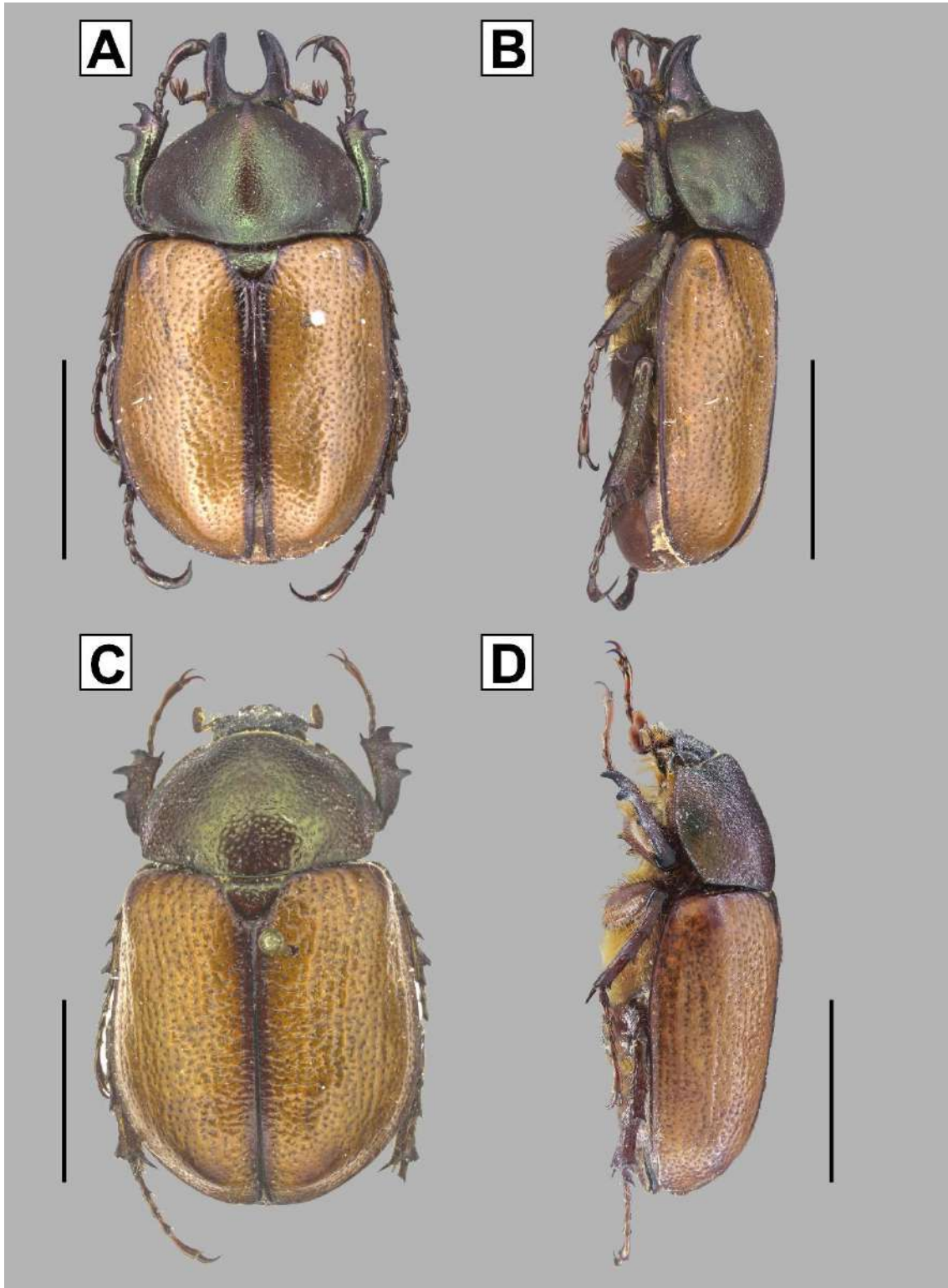


FIGURE 2. Male head of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Head of *A. cornigera* in dorsal view. Superior white arrow pointing to lateral margin of horn; inferior white arrow pointing to connection between horns. **B**, Head of *A. cornigera* in frontal view. Superior white arrow pointing to frontal depression; inferior white arrow pointing to clypeal protuberances. **C**, Head of *A. cornigera* in dorsolateral view. White arrow pointing to connection between horns. **D**, Head of *A. cornigera* in lateral view. **E**, Head of *A. duponti* in dorsal view. **F**, Head of *A. duponti* in frontal view. Black arrows pointing to clypeal apical corners. **G**, Head of *A. duponti* in dorsolateral view. Black arrow pointing to frontal depression; white arrow pointing to punctures on cephalic horn base. **H**, Head of *A. duponti* in lateral view. White arrow showing the elevation of apex of horns. **I**, Head of *A. inermicollis* in dorsal view. Black arrow pointing to ocular canthi anterior margin. **J**, Head of *A. inermicollis* in frontal view. **K**, Head of *A. inermicollis* in dorsolateral view. Black arrow pointing to frontal depression; white arrow pointing to sculpture of cephalic horn base. **L**, Head of *A. inermicollis* in lateral view. White arrow showing the elevation of apex of horns. Scale bars: 1 mm.

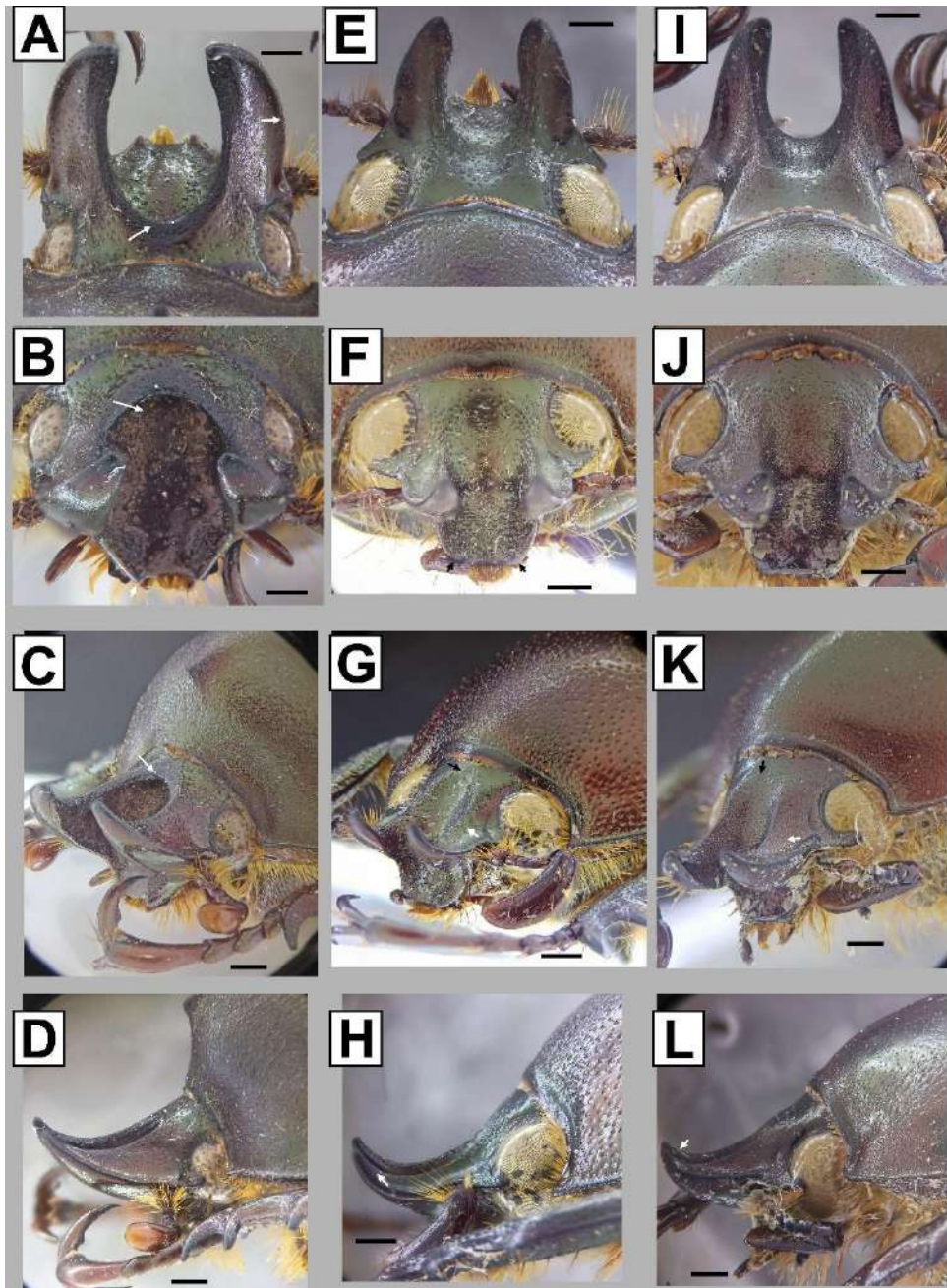


FIGURE 3. Male mandible and labrum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Mandible of *A. cornigera* in ventral view. Left black arrow pointing to middle of mesal brush; right black arrow pointing to outer margin of mandible. **B**, Mandible of *A. cornigera* in lateral view. Left black arrow pointing to dorsal socket; white arrow pointing to mesal brush covering molar area; right black arrow pointing to bump anterior to condyle. **C**, Mandible of *A. cornigera* in dorsal view. White arrow pointing to apex of mesal brush. **D**, Labrum of *A. cornigera* in dorsal view. **E**, Mandible of *A. duponti* in ventral view. White arrow pointing to outer margin of mandible. **F**, Mandible of *A. duponti* in lateral view. **G**, Mandible of *A. duponti* in dorsal view. White arrows pointing to setae on outer margin of mandible. **H**, Labrum of *A. duponti* in dorsal view. Double-headed arrow comparing the length to width. **I**, Mandible of *A. inermicollis* in ventral view. White arrow pointing to the point of curvature of outer carina. **J**, Mandible of *A. inermicollis* in lateral view. White arrow pointing to outer carina reaching tooth. **K**, Mandible of *A. inermicollis* in dorsal view. Inferior white arrow pointing to outer margin of mandible. Superior white arrow pointing to mesal brush. **L**, Labrum of *A. inermicollis* in dorsal view. Scale bars: 1 mm.

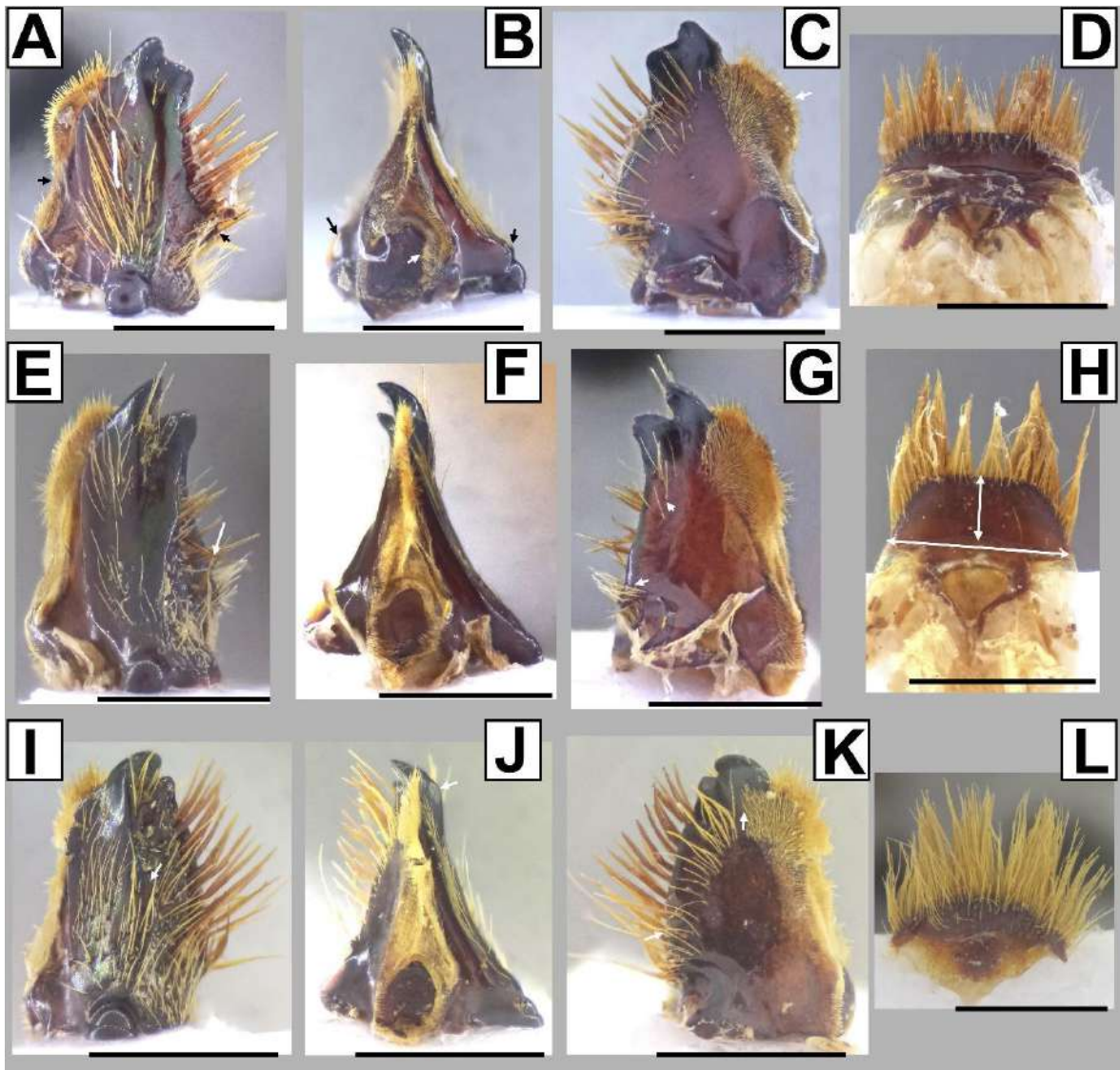


FIGURE 4. Male maxilla and mentum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Maxilla of *A. cornigera* in ventral view. Left black arrow pointing to posterior margin of stipes; right black arrow pointing to setae on base of lateral border. **B**, Maxilla of *A. cornigera* in dorsal view. **C**, Mentum of *A. cornigera* in ventral view. **D**, Maxilla of *A. duponti* in ventral view. **E**, Maxilla of *A. duponti* in dorsal view. **F**, Mentum of *A. duponti* in ventral view. **G**, Maxilla of *A. inermicollis* in ventral view. **H**, Maxilla of *A. inermicollis* in dorsal view. **I**, Mentum of *A. inermicollis* in ventral view. Scale bars: 1 mm.

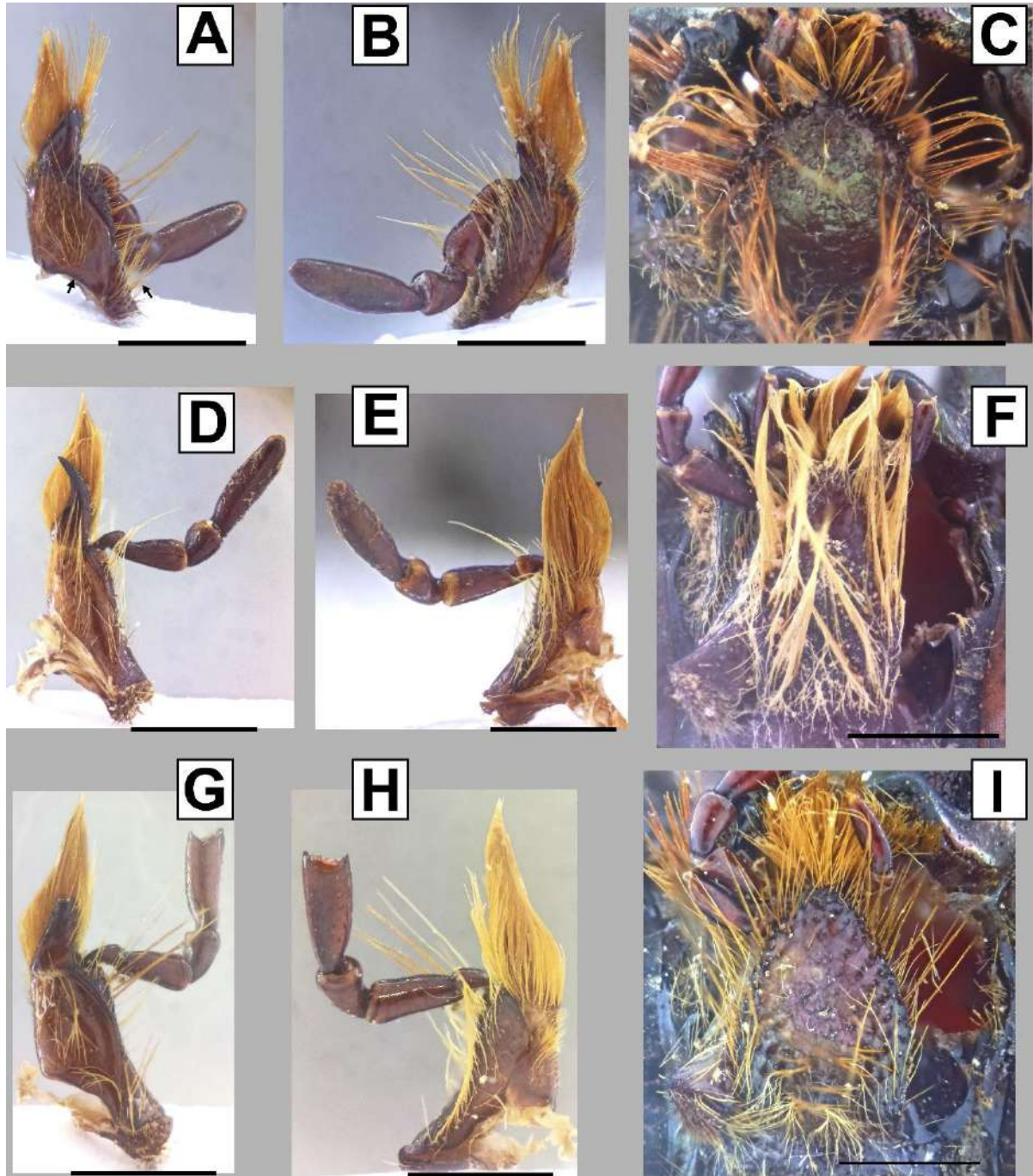


FIGURE 5. Male head and legs of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Ocular canthus and antennae of *A. cornigera* in dorsal view. Black arrow pointing to ocular canthus. **B**, Protarsus of *A. cornigera* in dorsal view. Superior black arrow pointing to claw tooth; inferior black arrow pointing to outer margin of protarsomere V. **C**, Mesotibia of *A. cornigera* in lateral view. Black arrow pointing to connection between metatibial apex and apical tooth. **D**, Metatibia of *A. cornigera* in lateral view. White arrows pointing to punctuation. **E**, Ocular canthus and antennae of *A. duponti* in dorsal view. Black arrow pointing to ocular canthus. **F**, Protarsus of *A. duponti* in dorsal view. Black arrow pointing to outer margin of protarsomere V. **G**, Mesotibia of *A. duponti* in lateral view. **H**, Metatibia of *A. duponti* in lateral view. **I**, Ocular canthus and antennae of *A. inermicollis* in dorsal view. **J**, Protarsus of *A. inermicollis* in dorsal view. **K**, Mesotibia of *A. inermicollis* in lateral view. **L**, Metatibia of *A. inermicollis* in lateral view. Scale bars: 1 mm.

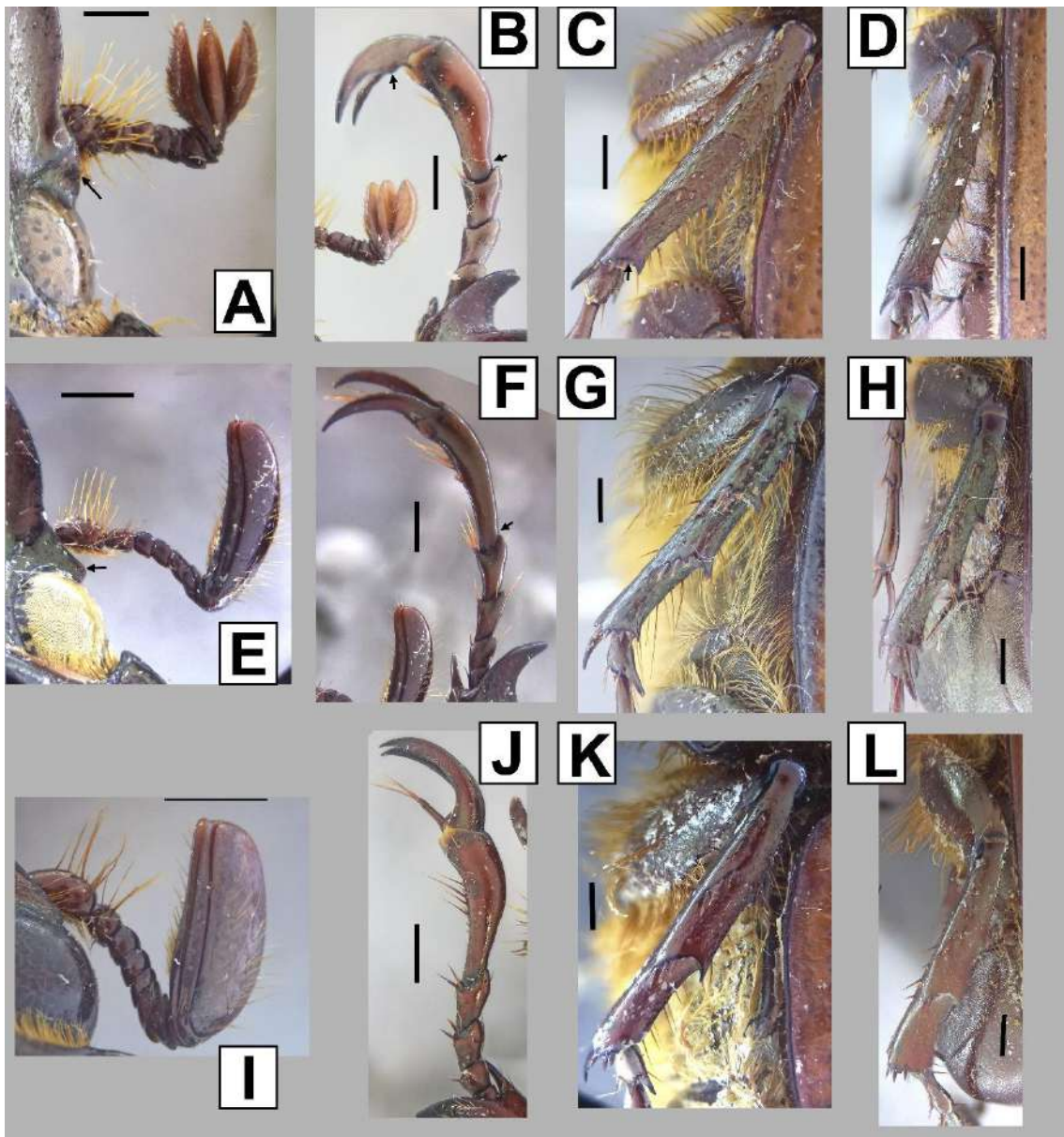


FIGURE 6. Male thorax and abdomen of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Pronotum of *A. cornigera* in dorsal view. White arrow pointing to pronotal tubercle. **B**, Tergite VIII of *A. cornigera* in posterior view. **C**, Abdomen of *A. cornigera* in ventral view. **D**, Pronotum of *A. duponti* in dorsal view. Black square showing shape of punctures. **E**, Tergite VIII of *A. duponti* in posterior view. **F**, Abdomen of *A. duponti* in ventral view. **G**, Pronotum of *A. inermicollis* in dorsal view. Black square showing shape of punctures. **H**, Tergite VIII of *A. inermicollis* in posterior view. **I**, Abdomen of *A. inermicollis* in ventral view. Scale bars: 5 mm.

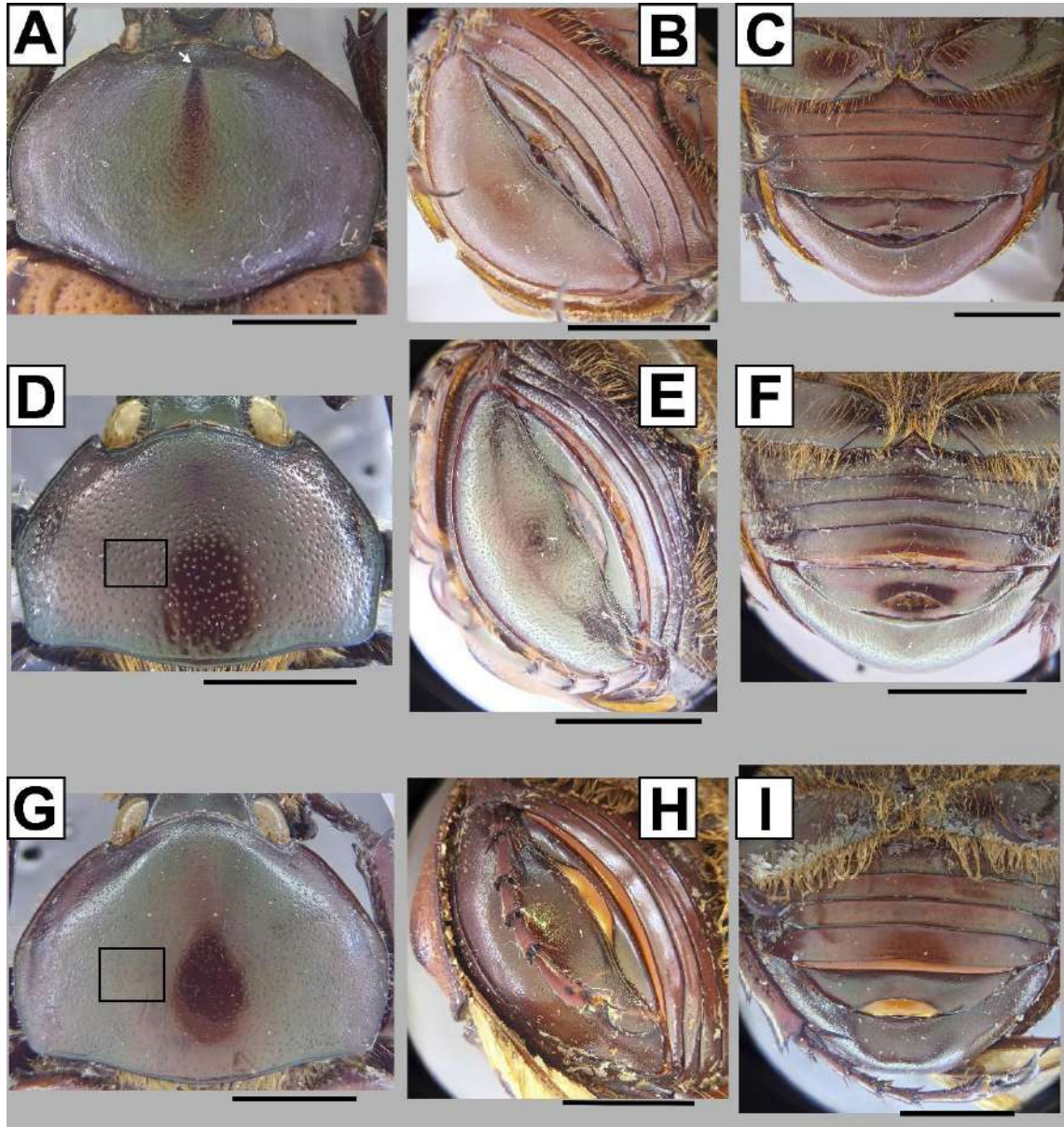


FIGURE 7. Male genitalia of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Parameres of *A. cornigera* in caudal view. White arrow pointing to basal portion of parameres. **B**, Parameres of *A. cornigera* in lateral view. White arrow pointing to ventrolateral carina reaching lateral carina. **C**, Parameres of *A. cornigera* in ventral view. White arrow pointing to margin of ventral sclerite. **D**, Aedeagus of *A. cornigera* in lateral view. **E**, Parameres of *A. duponti* in caudal view. White arrow pointing to elevation of inner caudal portion of parameres; black arrows pointing to inner margin of parameres. **F**, Parameres of *A. duponti* in lateral view. White arrow pointing to lateral carina. **G**, Parameres of *A. duponti* in ventral view. Black arrow pointing to basal connection of parameres with ventral sclerite. **H**, Aedeagus of *A. duponti* in lateral view. White arrow pointing to apical corner of posterior phallobase. **I**, Parameres of *A. inermicollis* in caudal view. **J**, Parameres of *A. inermicollis* in lateral view. Left white arrow pointing to ventrolateral carina; right white arrow pointing to lateral carina. **K**, Parameres of *A. inermicollis* in ventral view. Black arrows pointing to lateral depression of parameres; white arrow pointing to depression. **L**, Aedeagus of *A. inermicollis* in lateral view. White arrow pointing to apical corners of posterior phallobase. Scale bars: 1 mm.

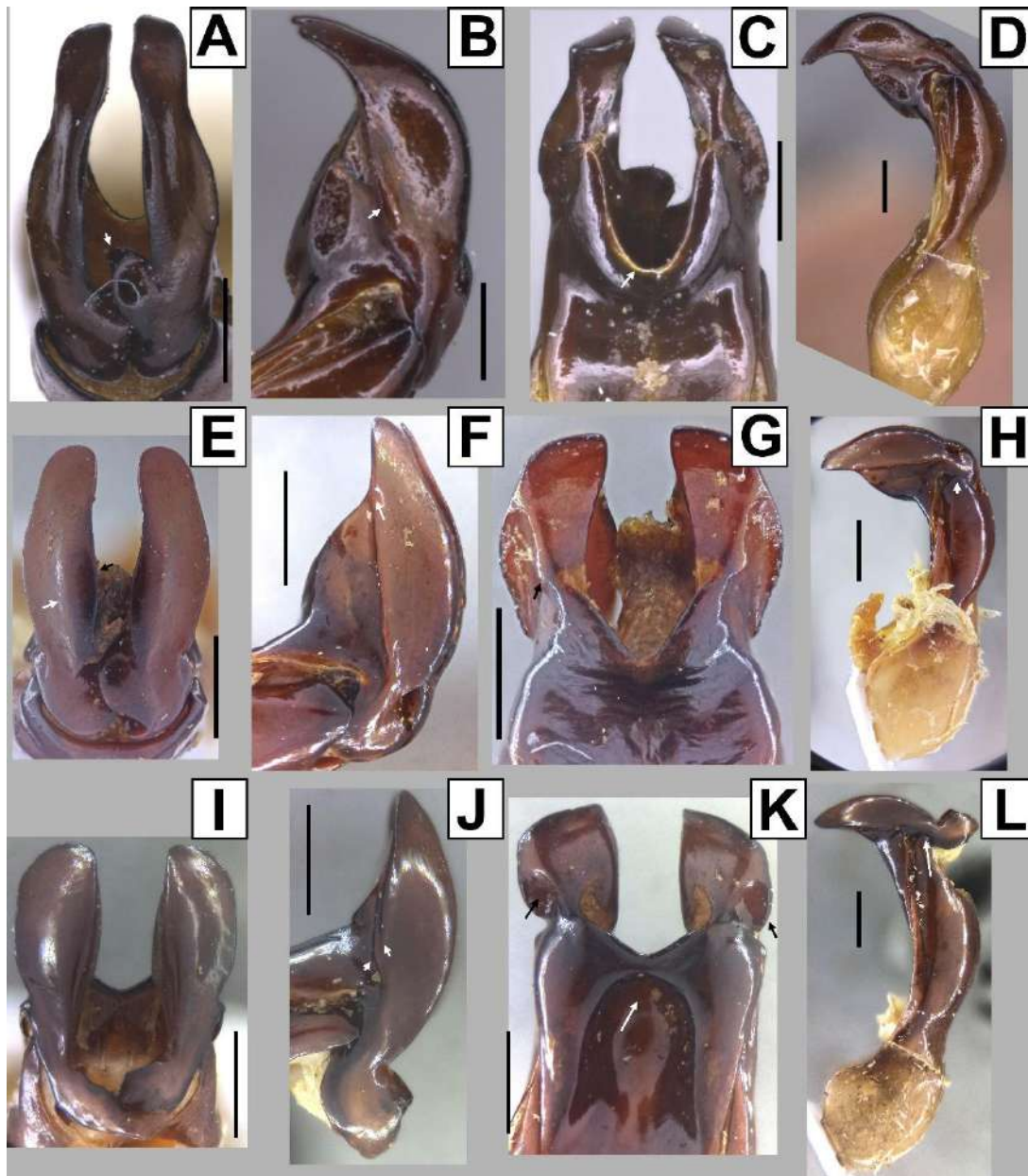


FIGURE 8. Female head of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Head of *A. cornigera* in dorsal view. **B**, Head of *A. cornigera* in lateral view. **C**, Head of *A. cornigera* in dorsolateral view. **D**, Head of *A. duponti* in dorsal view. White arrows pointing to tubercles; black arrow pointing to apex of ocular canthus. **E**, Head of *A. duponti* in lateral view. **F**, Head of *A. duponti* in dorsolateral view. White arrows pointing to lateral depressions on frons; black square showing the shape of punctures. **G**, Head of *A. inermicollis* in dorsal view. Black arrow pointing to apex of ocular canthus. **H**, Head of *A. inermicollis* in lateral view. **I**, Head of *A. inermicollis* in dorsolateral view. White arrows pointing to lateral depressions on frons; black square showing the shape of punctures. Scale bars: 1 mm.

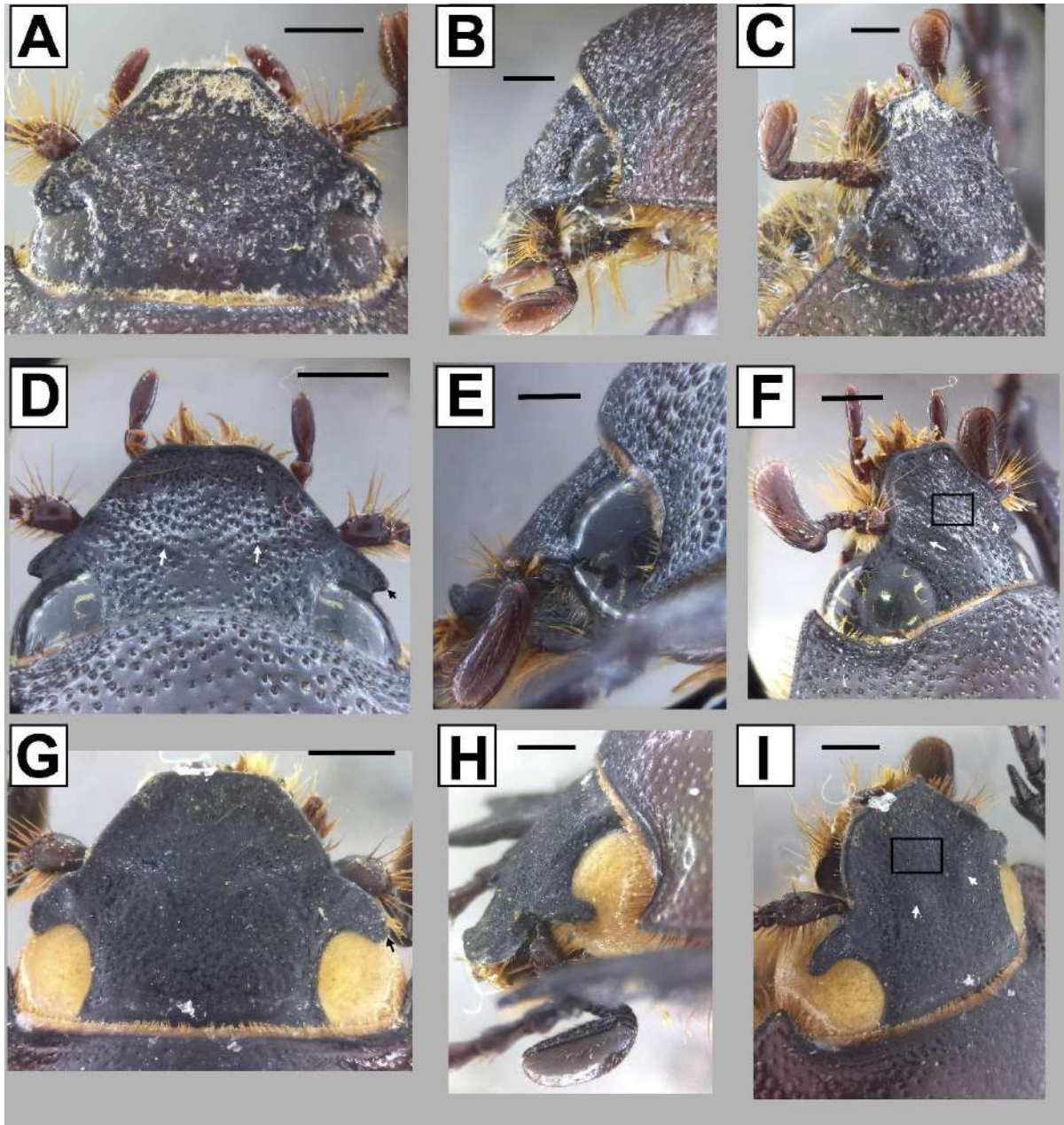


FIGURE 9. Female mandible and labrum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Mandible of *A. cornigera* in ventral view. Left white arrow pointing to middle of mesal brush; right white arrow pointing to outer carina. **B**, Mandible of *A. cornigera* in lateral view. **C**, Mandible of *A. cornigera* in dorsal view. Black arrow pointing to outer margin of mandibles. **D**, Labrum of *A. cornigera* in dorsal view. **E**, Mandible of *A. duponti* in ventral view. Black arrow pointing to base of inner carina. **F**, Mandible of *A. duponti* in lateral view. Black arrows pointing to mesal brush expanding to molar area. **G**, Mandible of *A. duponti* in dorsal view. Black arrows pointing to outer margin. **H**, Labrum of *A. duponti* in dorsal view. White arrow pointing to setae. **I**, Mandible of *A. inermicollis* in ventral view. Black arrow pointing to emargination between teeth. **J**, Mandible of *A. inermicollis* in lateral view. **K**, Mandible of *A. inermicollis* in dorsal view. White arrow pointing to outer margin of mandible. **L**, Labrum of *A. inermicollis* in dorsal view. Scale bars: 1 mm.

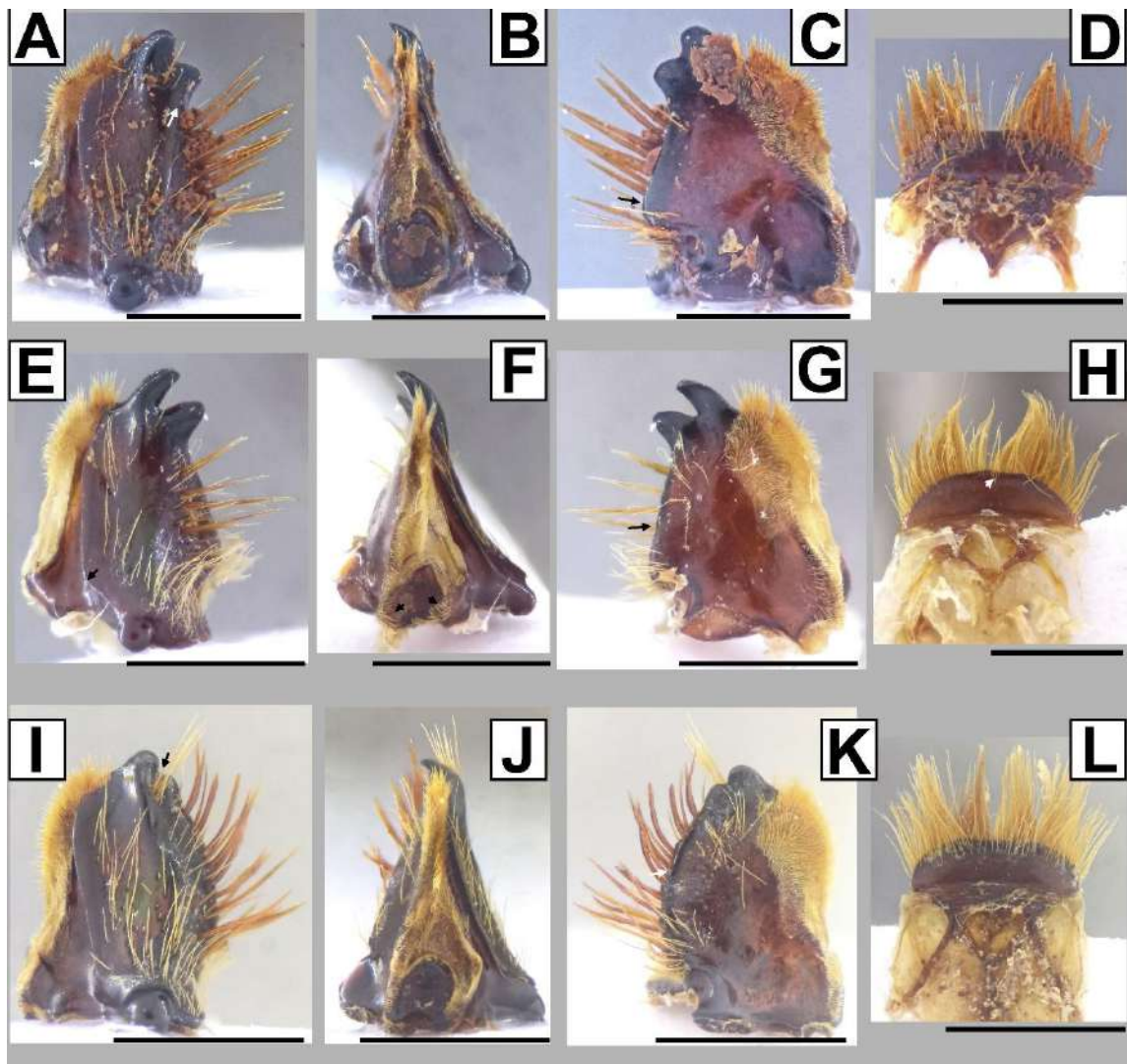


FIGURE 10. Female maxilla and mentum of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Maxilla of *A. cornigera* in ventral view. Black arrows pointing to setae. **B**, Maxilla of *A. cornigera* in dorsal view. **C**, Mentum of *A. cornigera* in ventral view. **D**, Maxilla of *A. duponti* in ventral view. **E**, Maxilla of *A. duponti* in dorsal view. **F**, Mentum of *A. duponti* in ventral view. Double-headed arrows comparing maximum length to maximum width. **G**, Maxilla of *A. inermicollis* in ventral view. **H**, Maxilla of *A. inermicollis* in dorsal view. **I**, Mentum of *A. inermicollis* in ventral view. Scale bars: 1 mm.

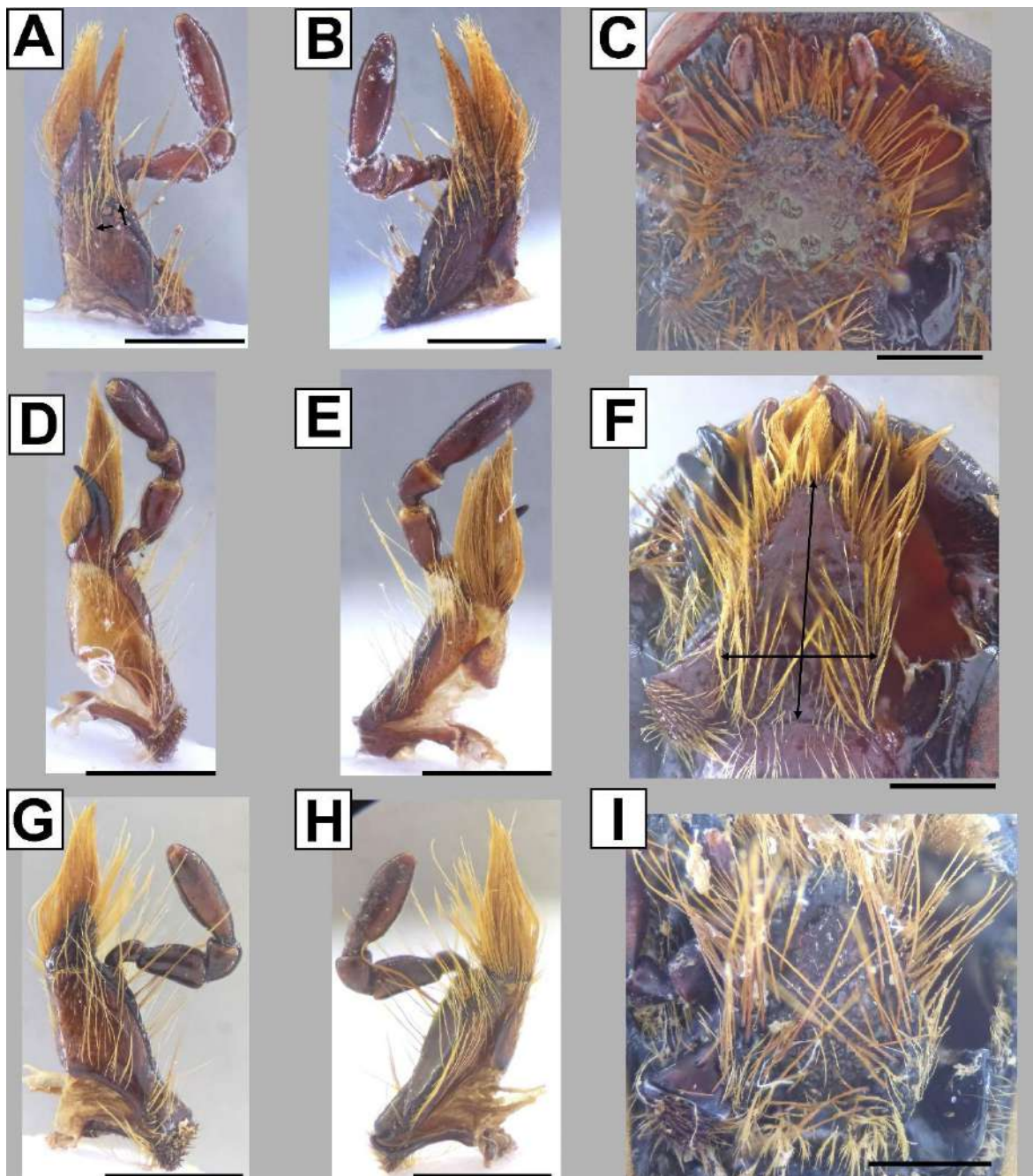


FIGURE 11. Female thorax, legs and abdomen of *Agacephala cornigera*, *Agacephala duponti* and *Agacephala inermicollis*. **A**, Pronotum of *A. cornigera* in dorsal view. **B**, Mesotibia of *A. cornigera* in lateral view. White arrow pointing to anterior carina. **C**, Metatibia of *A. cornigera* in lateral view. Black arrows pointing to anterior and posterior carina respectively. **D**, Abdomen of *A. cornigera* in ventral view. **E**, Pronotum of *A. duponti* in dorsal view. **F**, Mesotibia of *A. duponti* in lateral view. White arrows pointing to basal and apical tooth respectively. **G**, Metatibia of *A. duponti* in lateral view. White arrows pointing to setae parallel to teeth. **H**, Abdomen of *A. duponti* in ventral view. White square showing punctuation of sternite VII. **I**, Pronotum of *A. inermicollis* in dorsal view. **J**, Mesotibia of *A. inermicollis* in lateral view. **K**, Metatibia of *A. inermicollis* in lateral view. **L**, Abdomen of *A. inermicollis* in ventral view. White square showing punctuation of sternite VII. Scale bars: A,D, E,H, I,L, 5 mm; B-C, F-G, J-K, 1 mm.

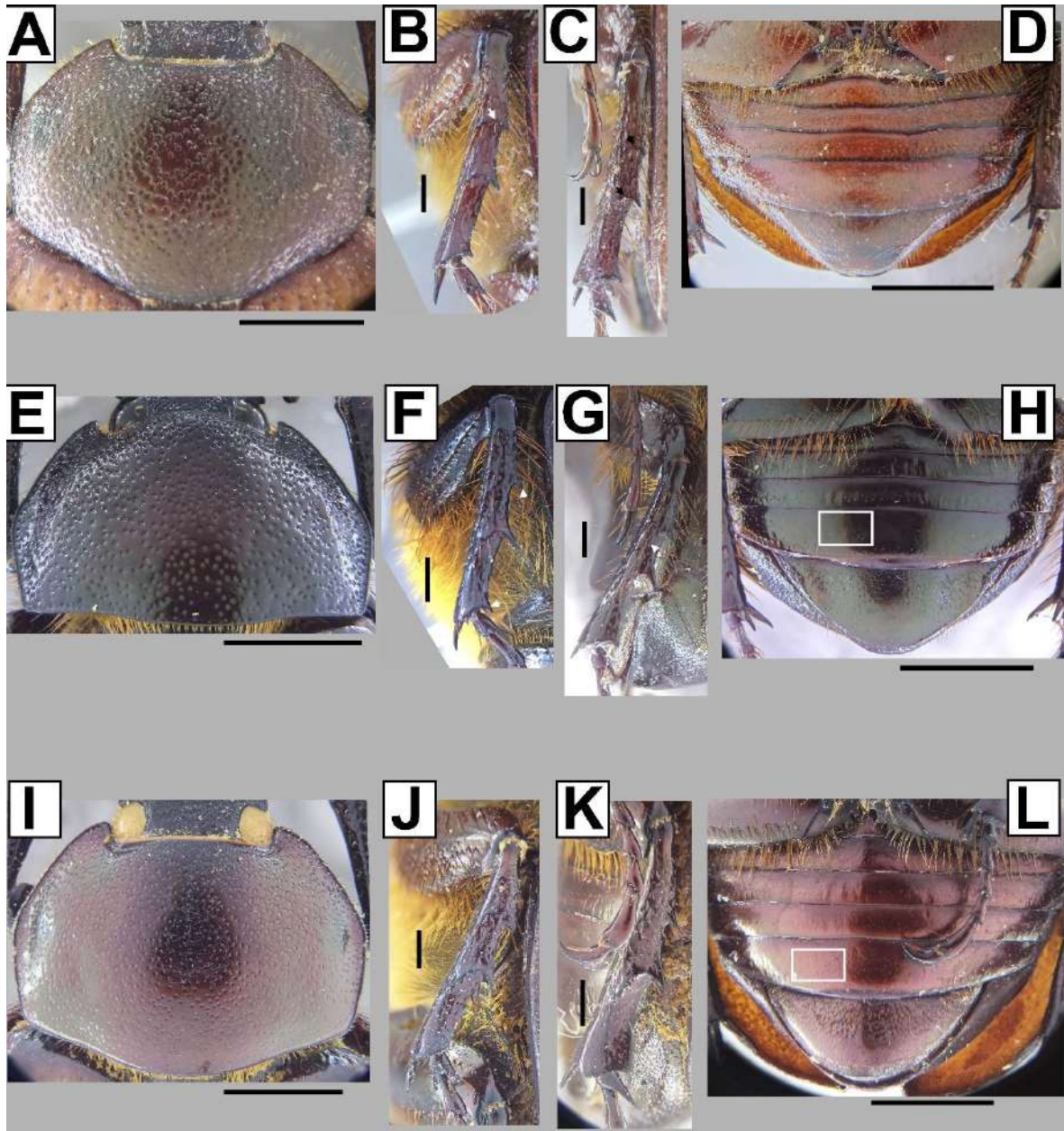


FIGURE 12. Female genitalia of *Agacephala cornigera*, *Agacephala duponti*, *Agacephala inermicollis*, *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Gonocoxites of *A. cornigera* in ventral view. Left black arrow pointing to posterior corners; superior black arrow pointing to distal coxites; white arrows pointing to setae on inner margin. **B**, Gonocoxites of *A. duponti* in ventral view. Black double-headed arrows comparing length to width. **C**, Gonocoxites of *A. inermicollis* in ventral view. Left regular arrows pointing to setae on inner apical corner; black double-headed arrows comparing length to width. **D**, Gonocoxites of *A. bicuspis* in ventral view. Black arrows pointing to setae. **E**, Gonocoxites of *A. margaridae* in ventral view. Black arrows downward pointing to distal coxites; black arrows pointing upward to apical margin; white arrows showing ventral depression. **F**, Gonocoxites of *A. mannerheimi* in ventral view. White arrows showing the divergent position of distal coxites; left black arrow pointing to connection between distal and proximal coxites; right arrows pointing to setae. Scale bars: 1 mm.

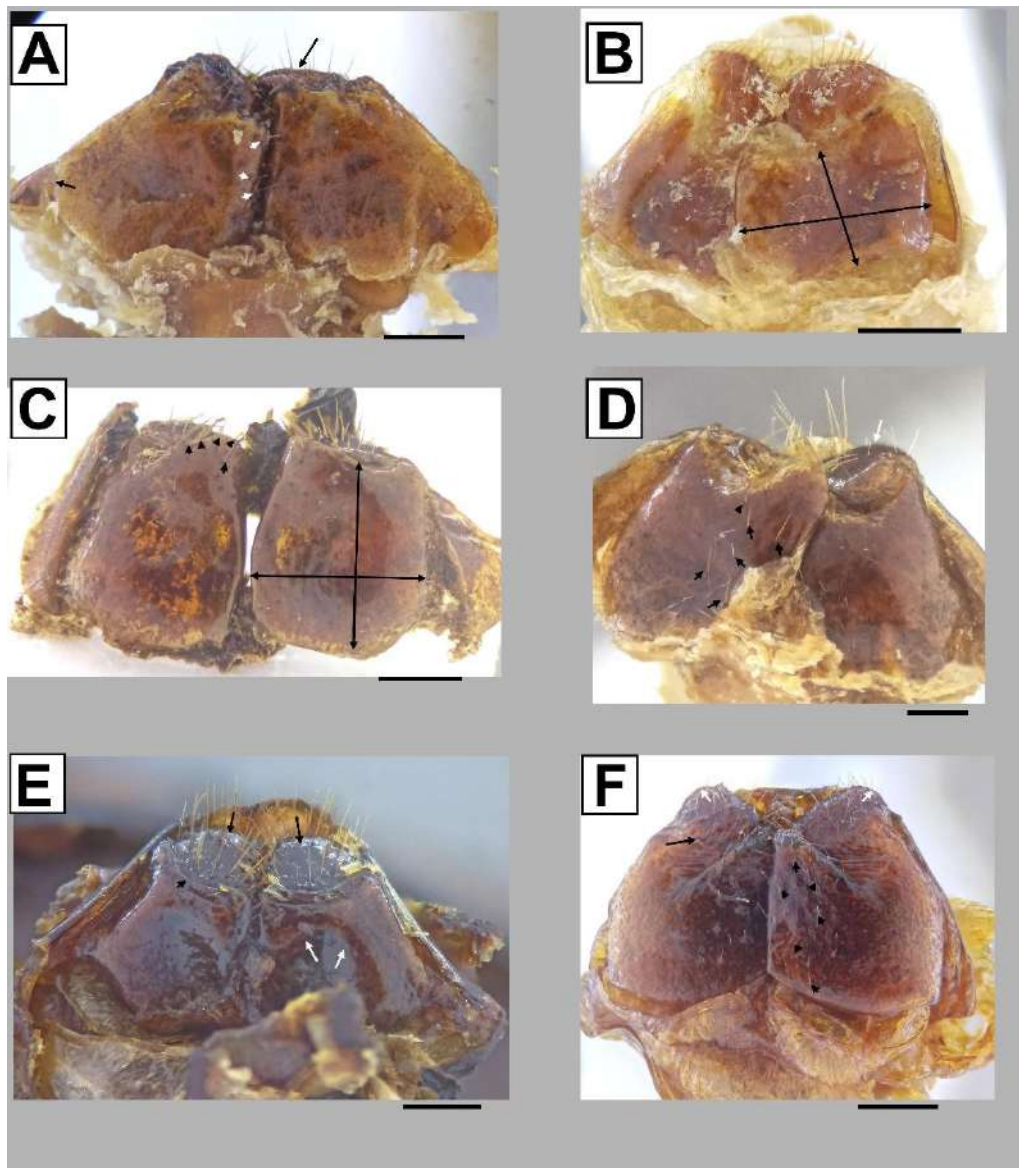


FIGURE 13. Male and female of *Agacephala duponti*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Black arrow pointing to lateral posterior margin. Scale bars: 10 mm.

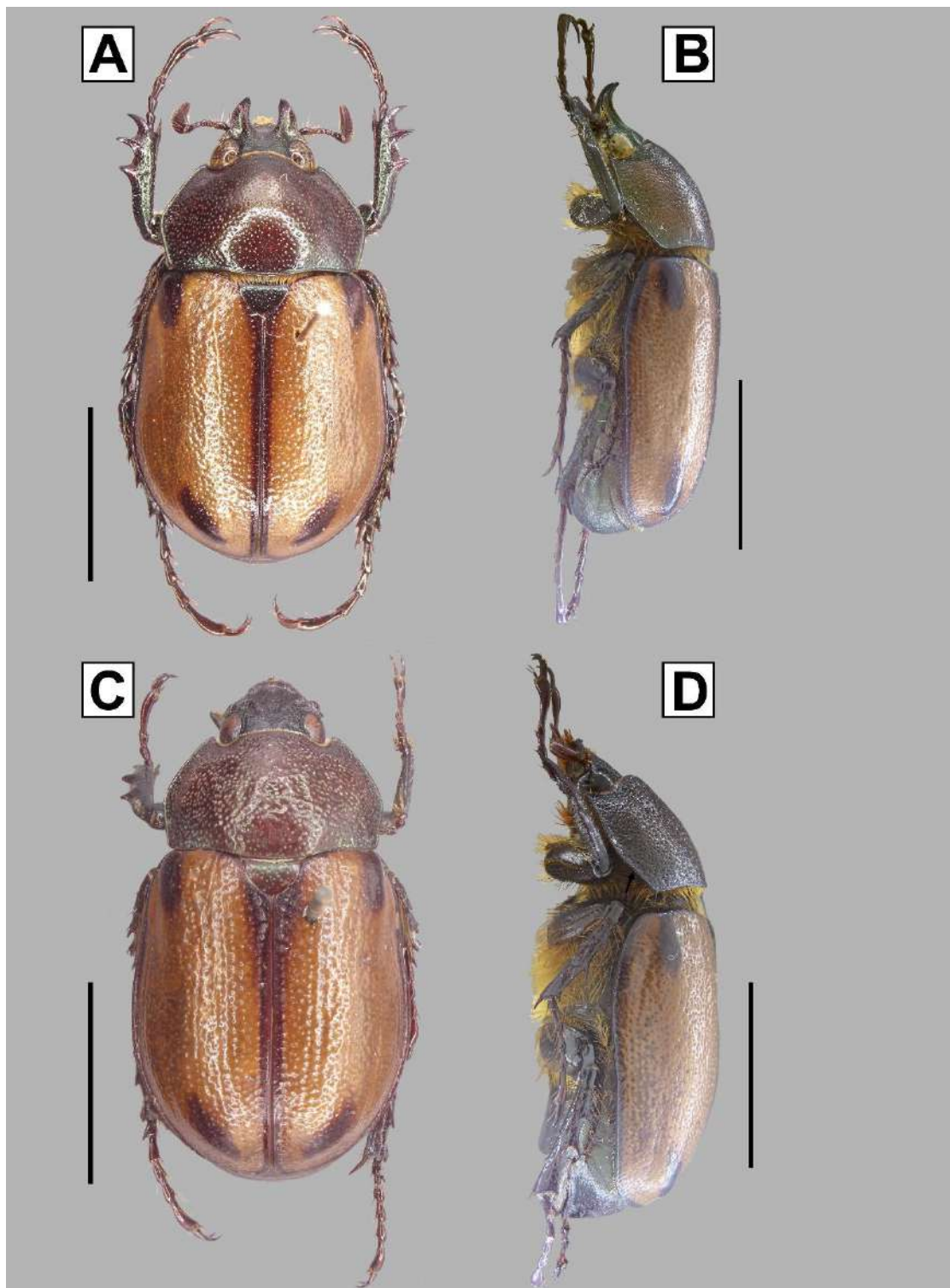


FIGURE 14. Male of *Agacephala duponti* from Argentina. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. Scale bars: 10 mm.

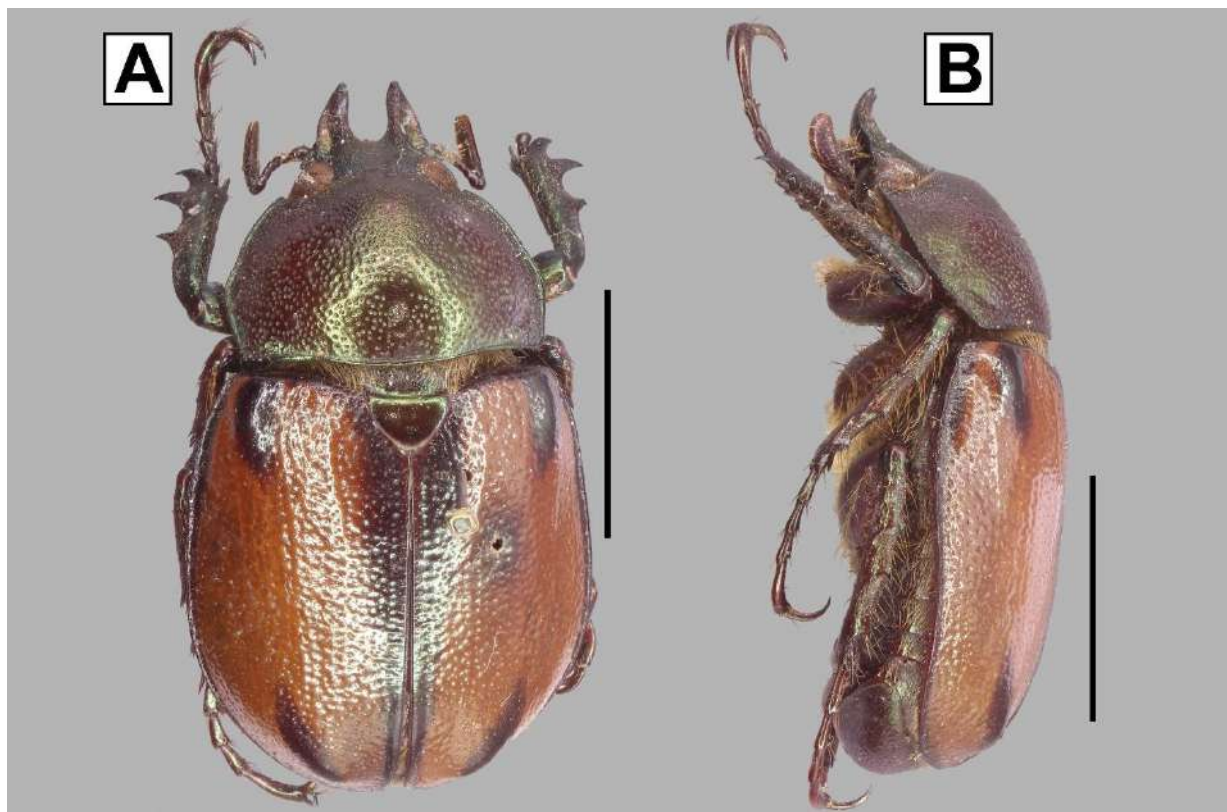


FIGURE 15. Male and female of *Agacephala inermicollis*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Black arrow pointing to lateral posterior margin. Scale bars: 10 mm.

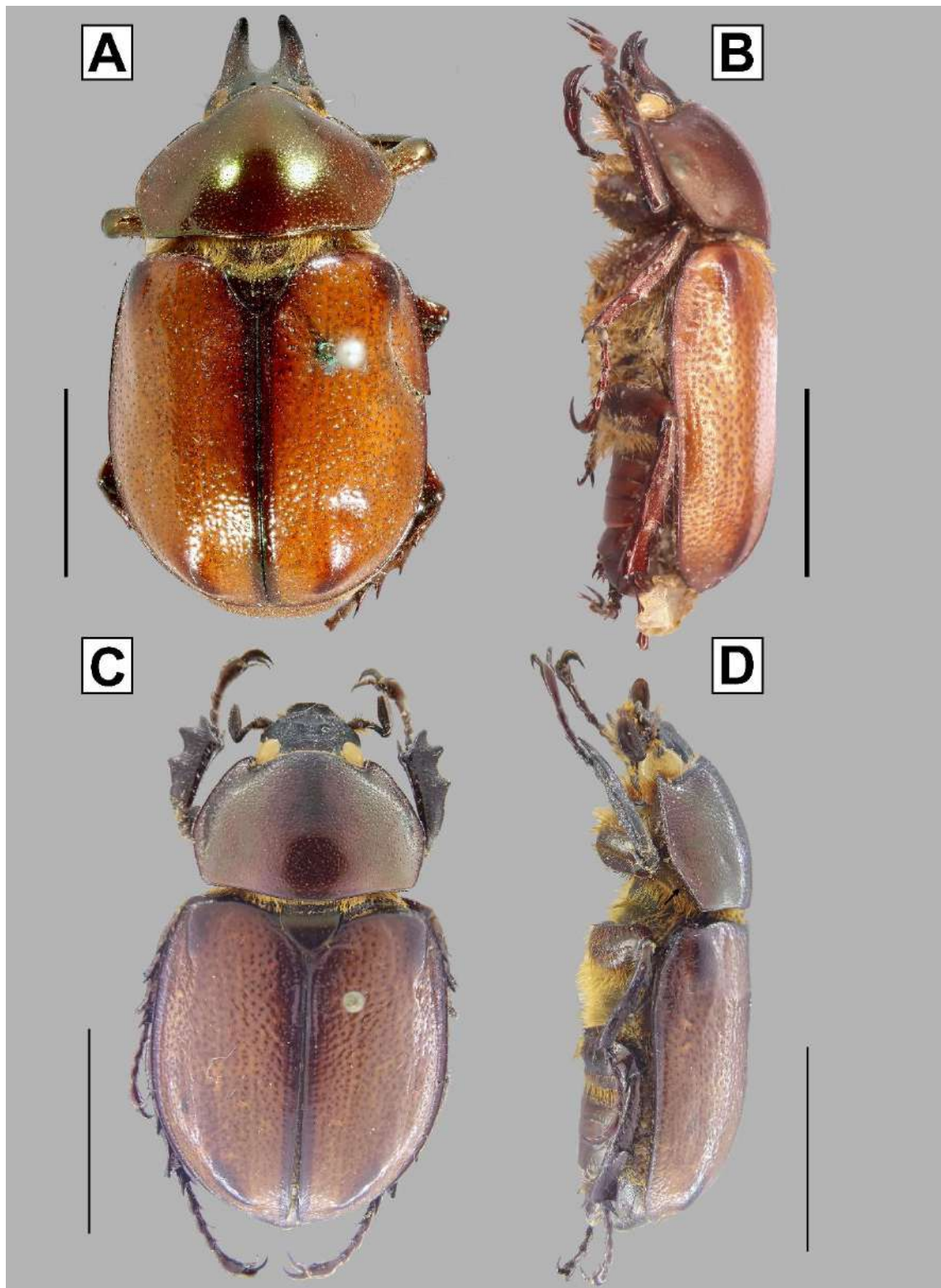


FIGURE 16. Male and female of *Agacephala bicuspis*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. White arrow pointing to lateral posterior margin. Scale bars: 10 mm.

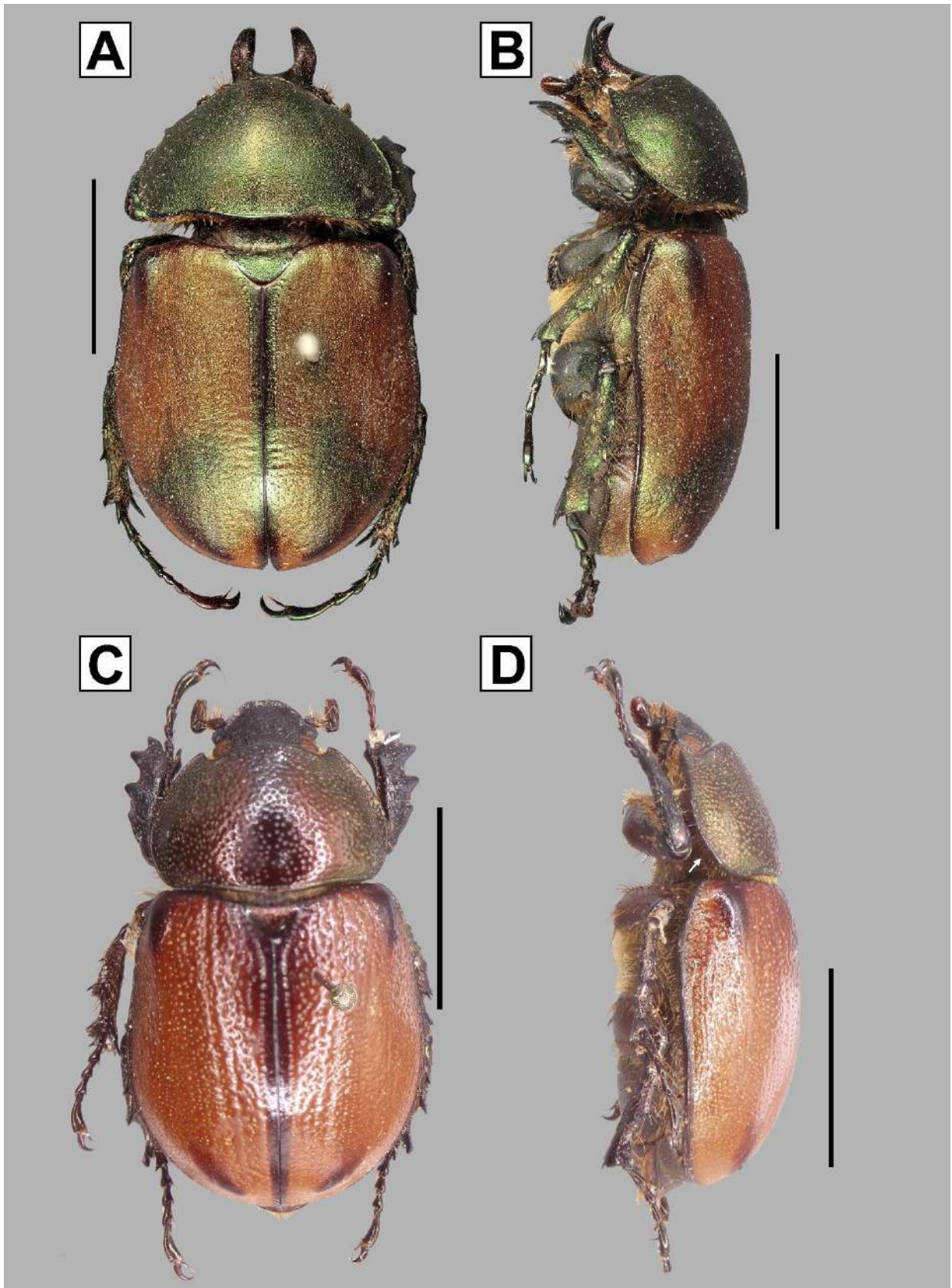


FIGURE 17. Male head of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Head of *A. bicuspis* in dorsal view. Black arrow pointing to connection between horns. **B**, Head of *A. bicuspis* in frontal view. **C**, Head of *A. bicuspis* in dorsolateral view. **D**, Head of *A. bicuspis* in lateral view. Black arrow pointing to anterior margin of pronotum. **E**, Head of *A. margaridae* in dorsal view. **F**, Head of *A. margaridae* in frontal view. **G**, Head of *A. margaridae* in dorsolateral view. **H**, Head of *A. margaridae* in lateral view. Black arrows pointing to dorsal protuberances on horns. **I**, Head of *A. mannerheimi* in dorsal view. White arrow pointing to lateral margin of horn. **J**, Head of *A. mannerheimi* in frontal view. White arrow pointing to connection between horns; black arrow pointing to clypeal apical corner. **K**, Head of *A. mannerheimi* in dorsolateral view. **L**, Head of *A. mannerheimi* in lateral view. Scale bars: 1 mm.

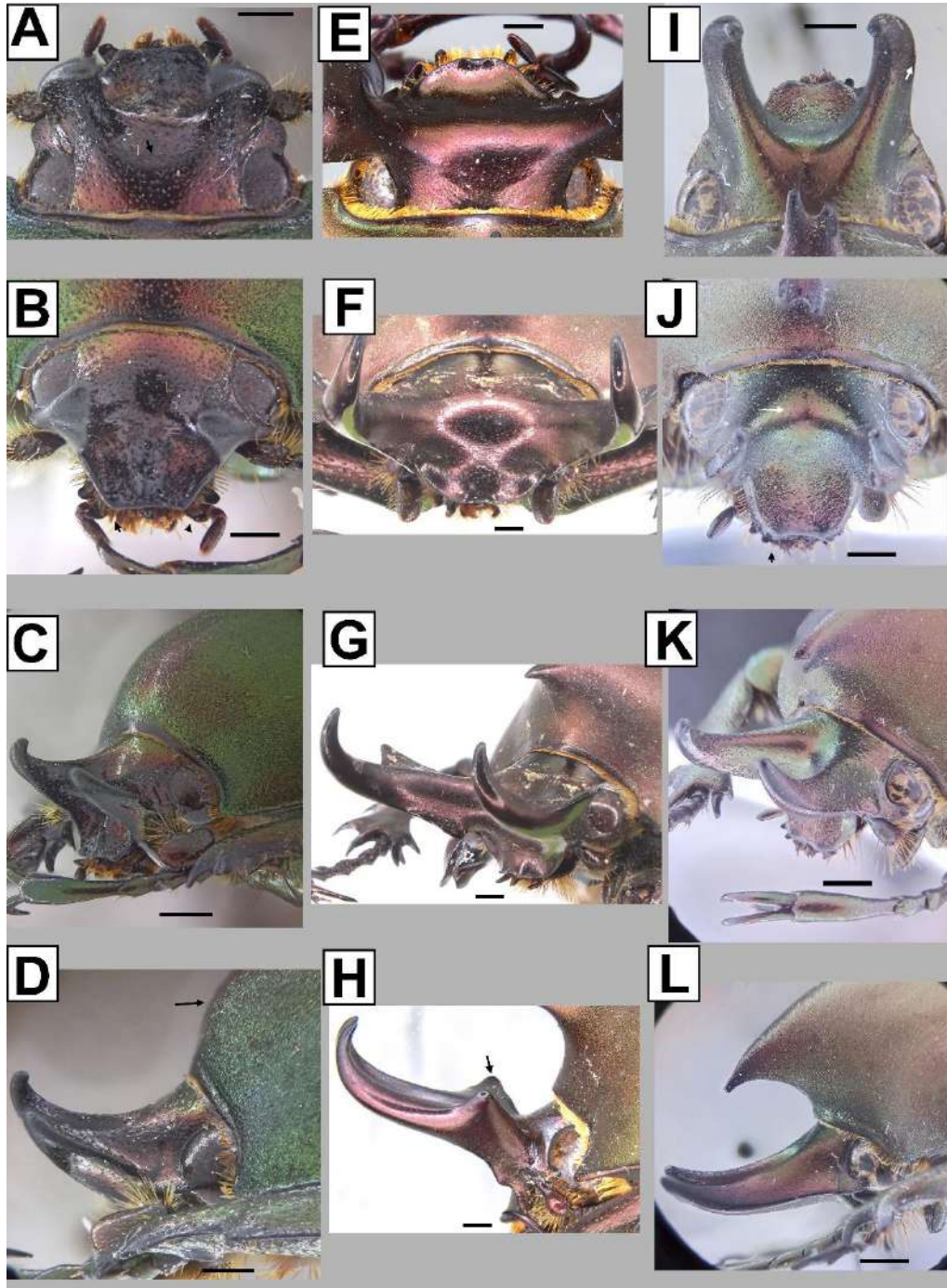


FIGURE 18. Male mandible and labrum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Mandible of *A. bicuspis* in ventral view. White arrow pointing to outer carina; black arrow pointing to outer margin. **B**, Mandible of *A. bicuspis* in lateral view. **C**, Mandible of *A. bicuspis* in dorsal view. Black arrows pointing to carinae. **D**, Labrum of *A. bicuspis* in dorsal view. Black arrow pointing to emargination of anterior margin. **E**, Mandible of *A. margaridae* in ventral view. White arrow pointing to inner carina; black arrow pointing to outer margin. **F**, Mandible of *A. margaridae* in lateral view. Black arrow pointing to bump near socket; white arrow pointing to concavity on basal portion of molar area. **G**, Mandible of *A. margaridae* in dorsal view. Black arrow pointing to protuberance near tooth. **H**, Labrum of *A. margaridae* in dorsal view. **I**, Mandible of *A. mannerheimi* in ventral view. Black arrow pointing to outer margin. **J**, Mandible of *A. mannerheimi* in lateral view. Black arrow pointing to bump near condyle. **K**, Mandible of *A. mannerheimi* in dorsal view. Black arrow pointing to apex of mesal brush. **L**, Labrum of *A. mannerheimi* in dorsal view. Scale bars: 1 mm.

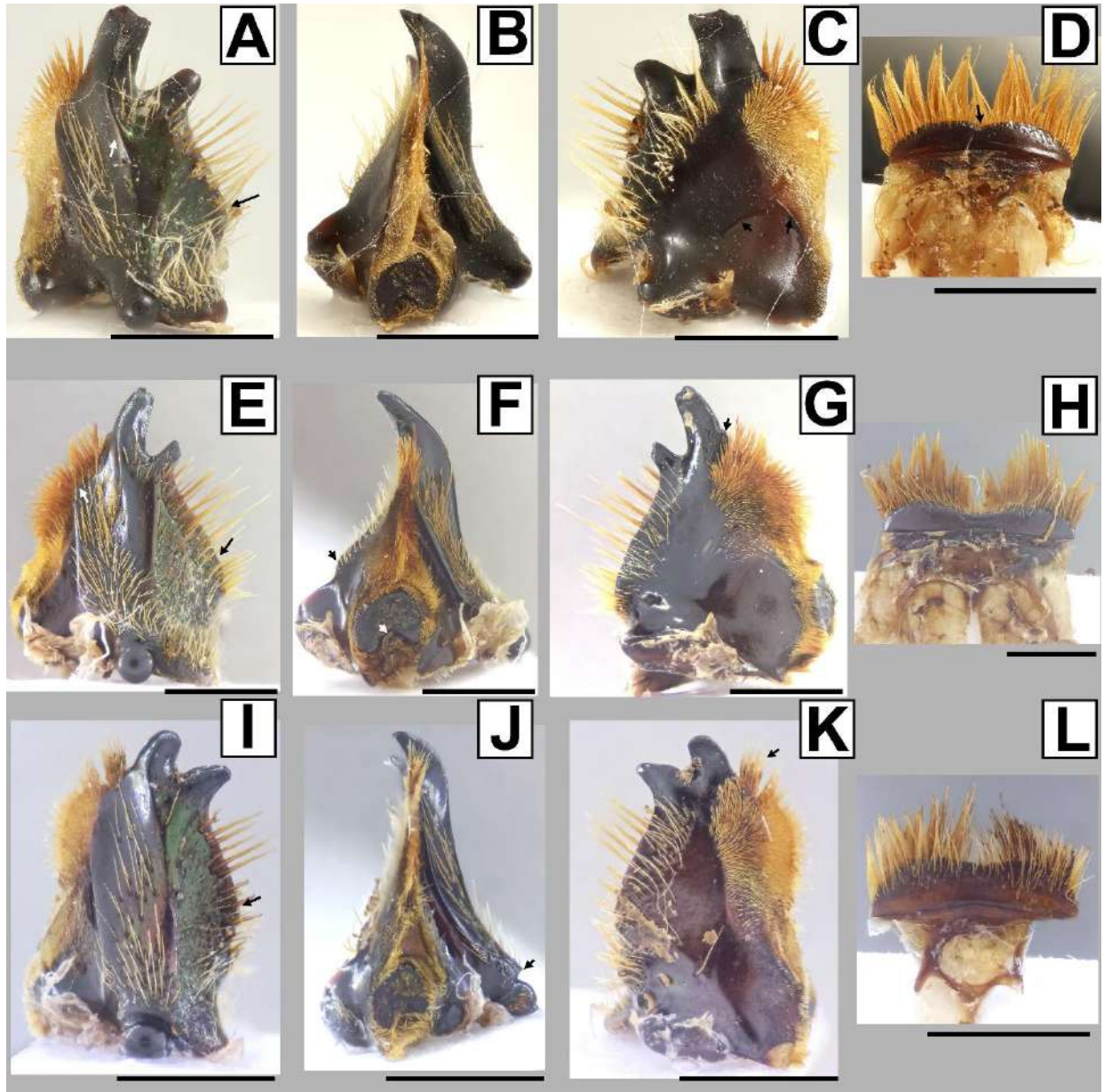


FIGURE 19. Male maxilla and mentum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Maxilla of *A. bicuspis* in ventral view. White arrows pointing to short teeth. **B**, Maxilla of *A. bicuspis* in dorsal view. **C**, Mentum of *A. bicuspis* in ventral view. **D**, Maxilla of *A. margaridae* in ventral view. White arrow pointing to emargination of palpifer; black arrow pointing to posterior margin of stipes. **E**, Maxilla of *A. margaridae* in dorsal view. **F**, Mentum of *A. margaridae* in ventral view. **G**, Maxilla of *A. mannerheimi* in ventral view. Black arrow pointing to outer margin of lateral border of stipes. **H**, Maxilla of *A. mannerheimi* in dorsal view. **I**, Mentum of *A. mannerheimi* in ventral view. Scale bars: 1 mm.

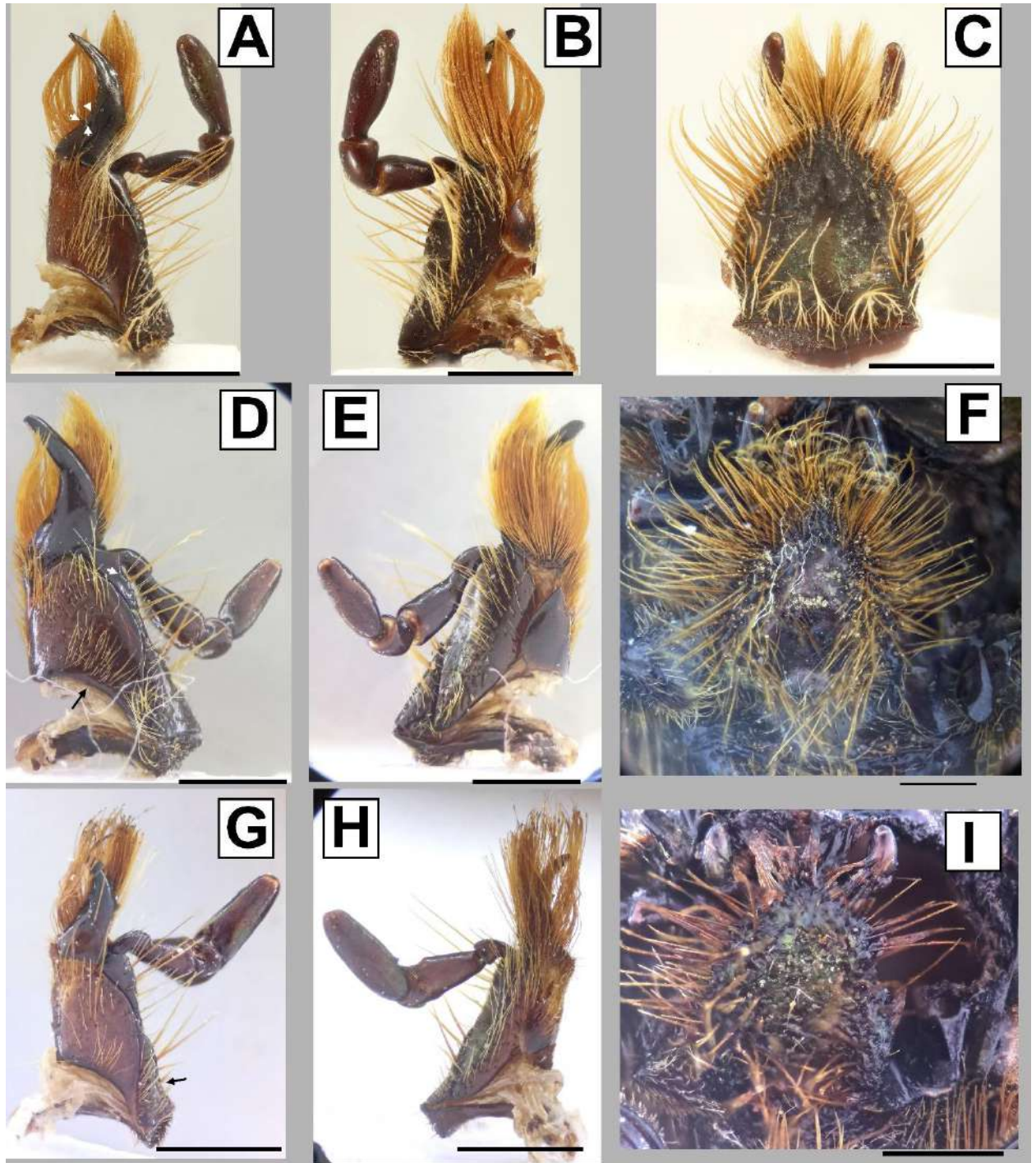


FIGURE 20. Male head and legs of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Ocular canthus and antennae of *A. bicuspis* in dorsal view. Black arrow pointing to ocular canthus. **B**, Protarsus of *A. bicuspis* in dorsal view. **C**, Mesotibia of *A. bicuspis* in lateral view. **D**, Metatibia of *A. bicuspis* in lateral view. **E**, Ocular canthus and antennae of *A. margaridae* in dorsal view. **F**, Protarsus of *A. margaridae* in dorsal view. **G**, Mesotibia of *A. margaridae* in lateral view. White arrow pointing to inner tooth. **H**, Metatibia of *A. margaridae* in lateral view. Black arrow pointing to metatibial apex. **I**, Ocular canthus and antennae of *A. mannerheimi* in dorsal view. **J**, Protarsus of *A. mannerheimi* in dorsal view. Left black arrow pointing to basal tooth of claw; right black arrow pointing to outer margin of protarsomere V. **K**, Mesotibia of *A. mannerheimi* in lateral view. Black arrow pointing to apical outer corner. **L**, Metatibia of *A. mannerheimi* in lateral view. Scale bars: 1 mm.

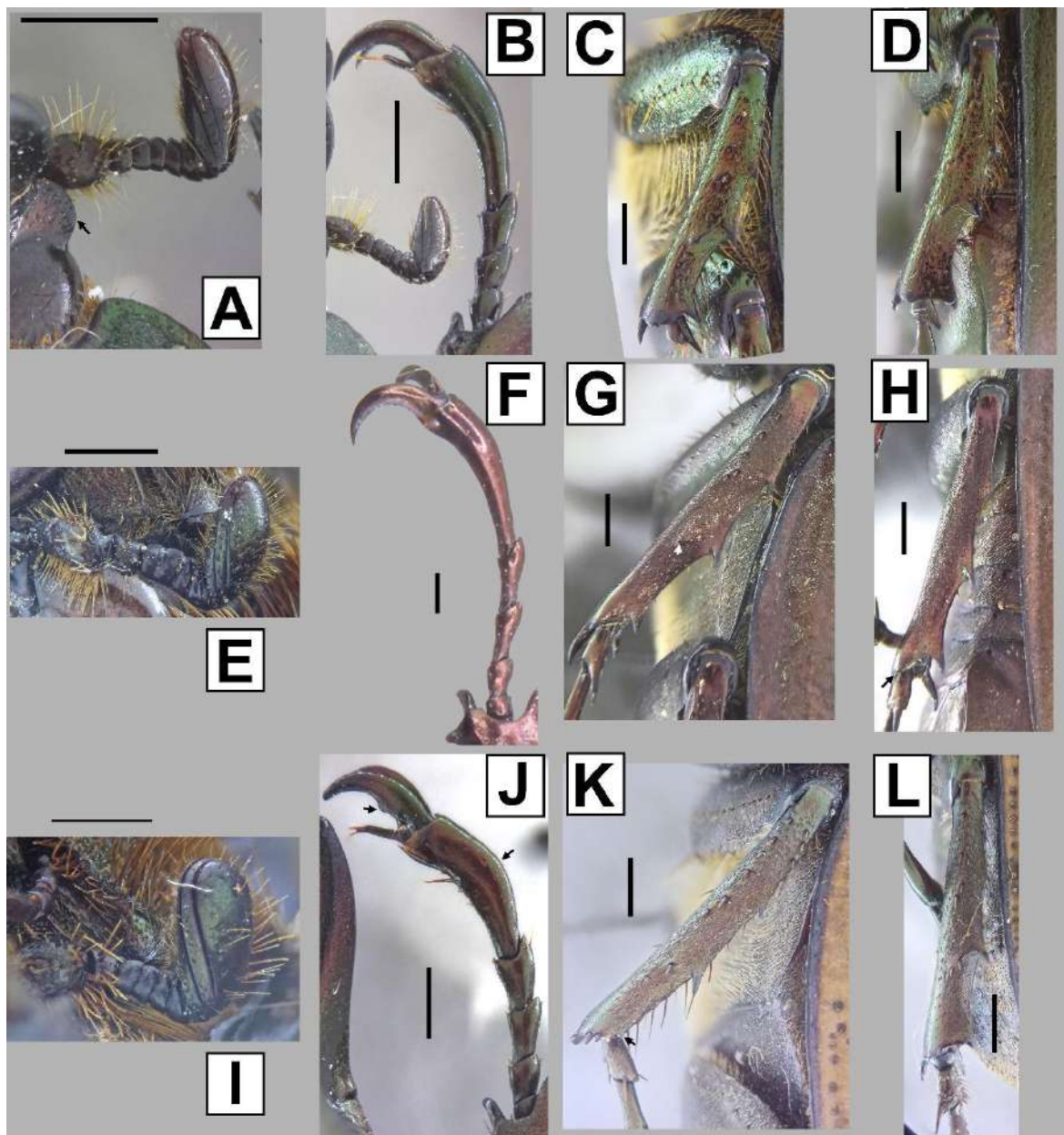


FIGURE 21. Male thorax and abdomen of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Pronotum of *A. bicuspis* in dorsal view. **B**, Tergite VIII of *A. bicuspis* in posterior view. **C**, Abdomen of *A. bicuspis* in ventral view. **D**, Pronotum of *A. margaridae* in dorsal view. **E**, Tergite VIII of *A. margaridae* in posterior view. **F**, Abdomen of *A. margaridae* in ventral view. **G**, Pronotum of *A. mannerheimi* in dorsal view. White arrow showing apex of thoracic horn. **H**, Tergite VIII of *A. mannerheimi* in posterior view. White arrows pointing to setae on tergite VIII. **I**, Abdomen of *A. mannerheimi* in ventral view. Scale bars: 5 mm.

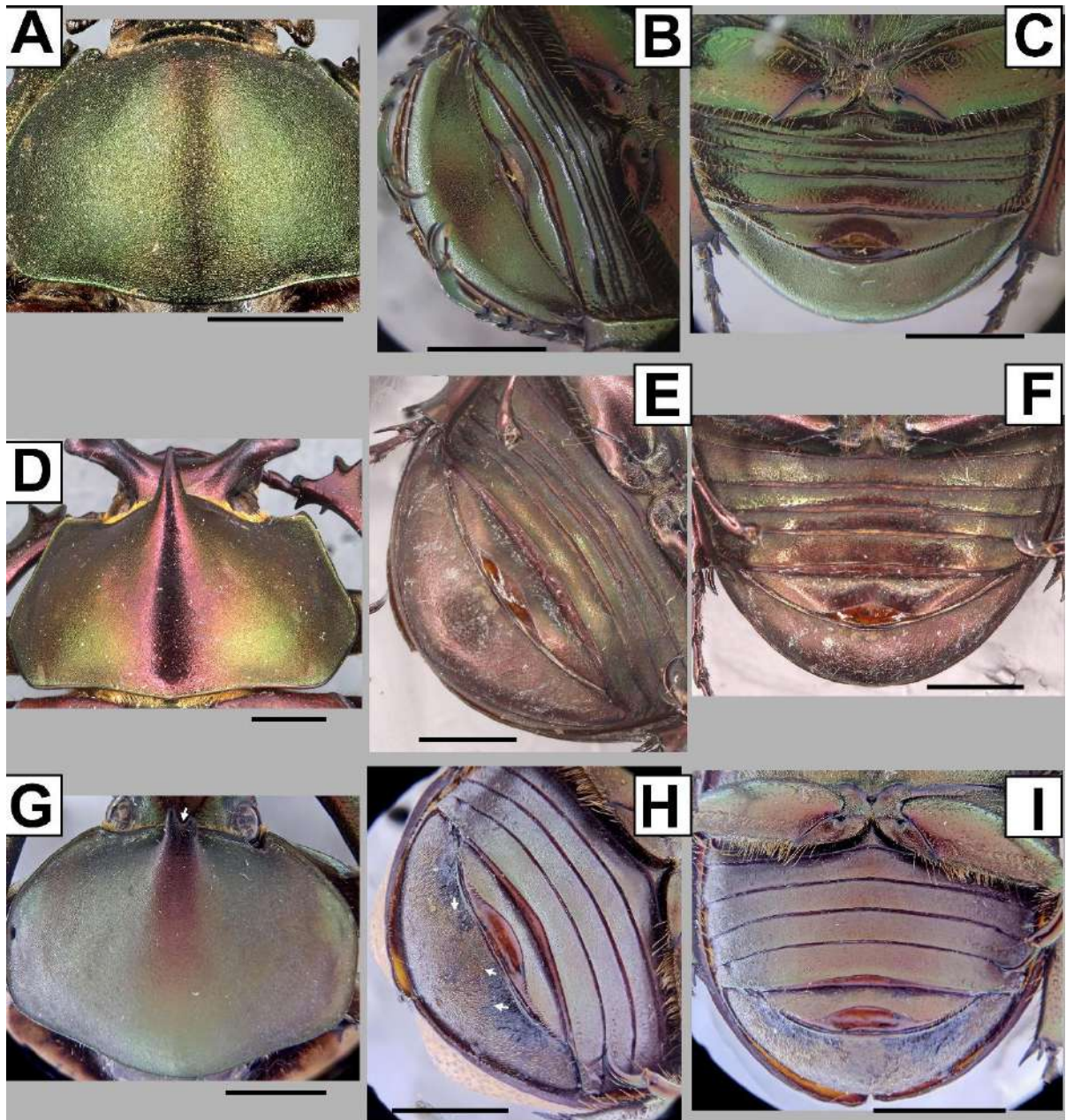


FIGURE 22. Male genitalia of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Parameres of *A. bicuspis* in caudal view. Left black arrow pointing to basal angulation of lateral margin; white arrow pointing to lateral margin on apex; right black arrow pointing to inner margin. **B**, Parameres of *A. bicuspis* in lateral view. White arrow pointing to ventrolateral carina. **C**, Parameres of *A. bicuspis* in ventral view. **D**, Aedeagus of *A. bicuspis* in lateral view. **E**, Parameres of *A. margaridae* in caudal view. Black arrow pointing to tooth. **F**, Parameres of *A. margaridae* in lateral view. Black arrow pointing to apex of parameres. **G**, Parameres of *A. margaridae* in ventral view. White arrow pointing to tooth; black arrow pointing to inner margin of parameres. **H**, Aedeagus of *A. margaridae* in lateral view. **I**, Parameres of *A. mannerheimi* in caudal view. Black arrow pointing to apex of parameres; white arrow pointing to lateral margin. **J**, Parameres of *A. mannerheimi* in lateral view. Left white arrow pointing to ventrolateral tooth; right white arrow pointing to dorsal margin of parameres. **K**, Parameres of *A. mannerheimi* in ventral view. White arrows pointing to ventrolateral teeth. **L**, Aedeagus of *A. mannerheimi* in lateral view. Scale bars: 1 mm.

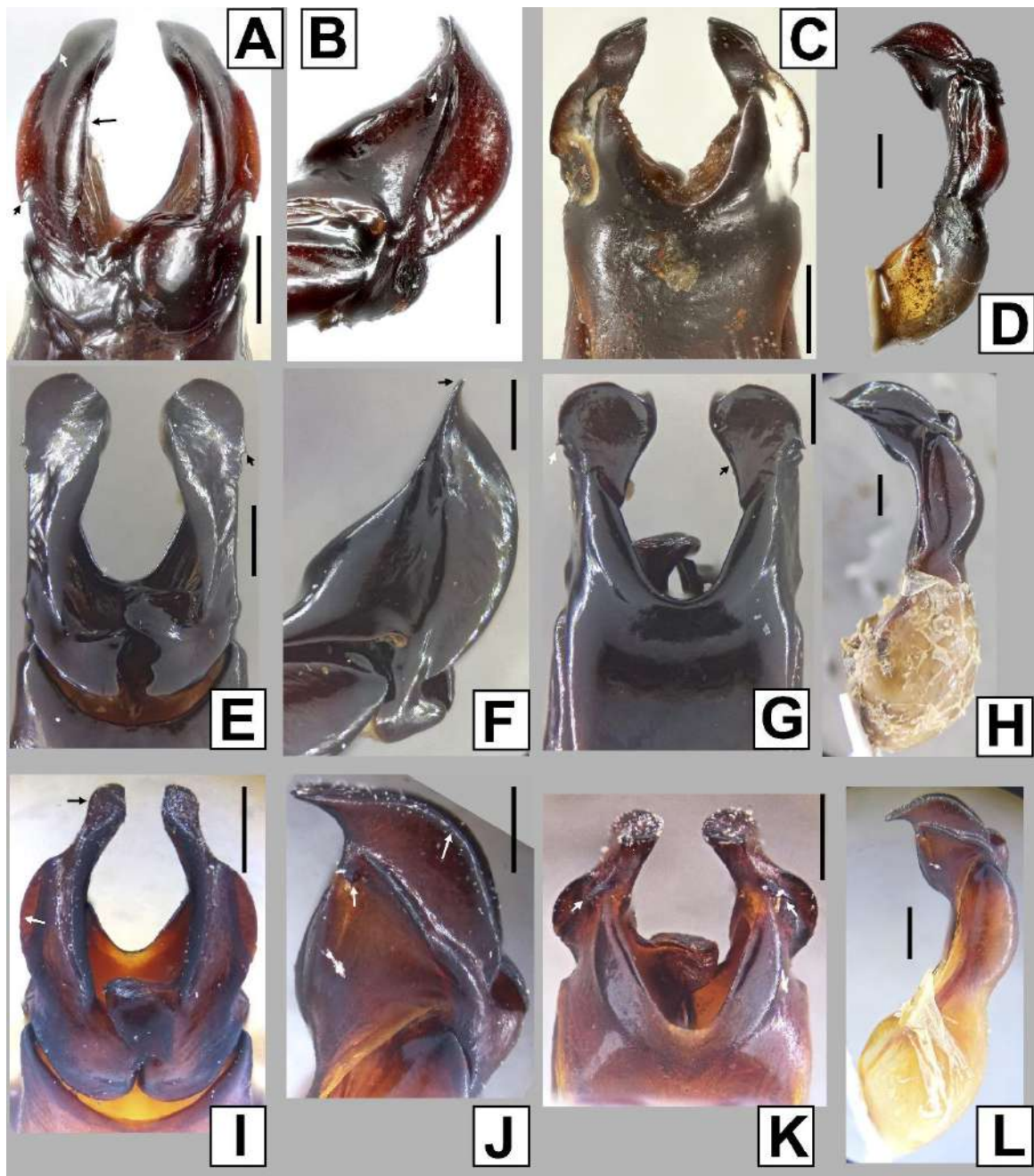


FIGURE 23. Female head of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Head of *A. bicuspis* in dorsal view. White arrows pointing to tubercles; left black arrow pointing to clypeal depression; right black arrow pointing to canthus. **B**, Head of *A. bicuspis* in lateral view. Black arrow pointing to tubercles. **C**, Head of *A. bicuspis* in dorsolateral view. **D**, Head of *A. margaridae* in dorsal view. Left black arrow pointing to ocular canthus base; right black arrow pointing to clypeal apex. **E**, Head of *A. margaridae* in lateral view. Black arrow pointing to protuberance on frons. **F**, Head of *A. margaridae* in dorsolateral view. **G**, Head of *A. mannerheimi* in dorsal view. **H**, Head of *A. mannerheimi* in lateral view. Black arrow pointing to tubercles; left white arrow pointing to clypeal base; right white arrow pointing to carina near eye. **I**, Head of *A. mannerheimi* in dorsolateral view. White arrows pointing to tubercles. Scale bars: 1 mm.

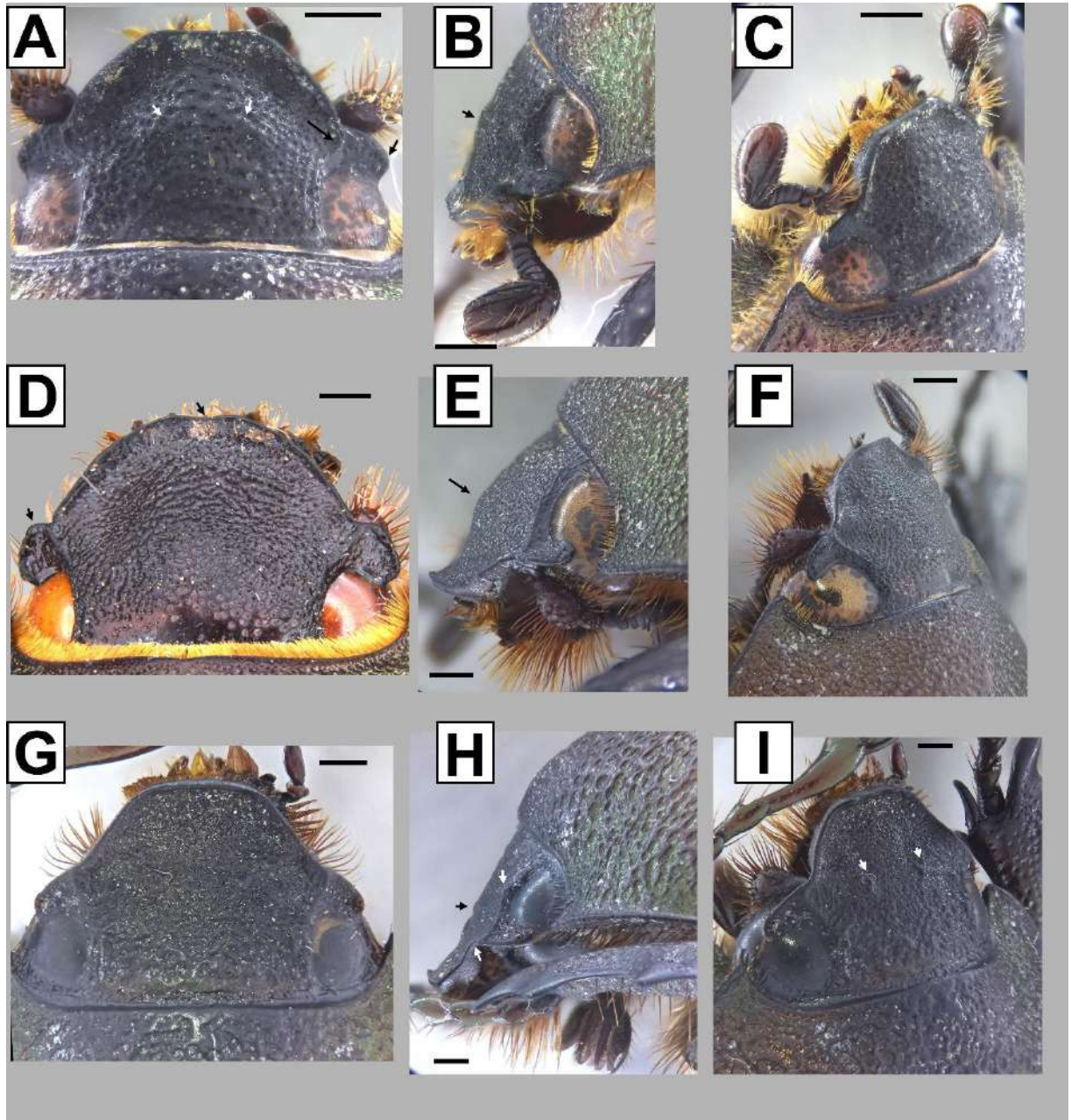


FIGURE 24. Female mandible and labrum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Mandible of *A. bicuspis* in ventral view. White arrow pointing to outer carina. **B**, Mandible of *A. bicuspis* in lateral view. Black arrow pointing to outer carina. **C**, Mandible of *A. bicuspis* in dorsal view. Black arrow pointing to outer margin; white arrow pointing to setae. **D**, Labrum of *A. bicuspis* in dorsal view. Black arrow pointing to emargination on anterior margin. **E**, Mandible of *A. margaridae* in ventral view. Superior white arrow pointing to inner carina; inferior white arrow pointing to basal protuberance. **F**, Mandible of *A. margaridae* in lateral view. **G**, Mandible of *A. margaridae* in dorsal view. Left white arrow pointing to setae; right white arrow pointing to apical tooth. **H**, Labrum of *A. margaridae* in dorsal view. **I**, Mandible of *A. mannerheimi* in ventral view. Left white arrow pointing to outer carina; right white arrow pointing to outer margin. **J**, Mandible of *A. mannerheimi* in lateral view. **K**, Mandible of *A. mannerheimi* in dorsal view. Left black arrow pointing to outer margin; right black arrow pointing to mesal brush. **L**, Labrum of *A. mannerheimi* in dorsal view. Scale bars: 1 mm.

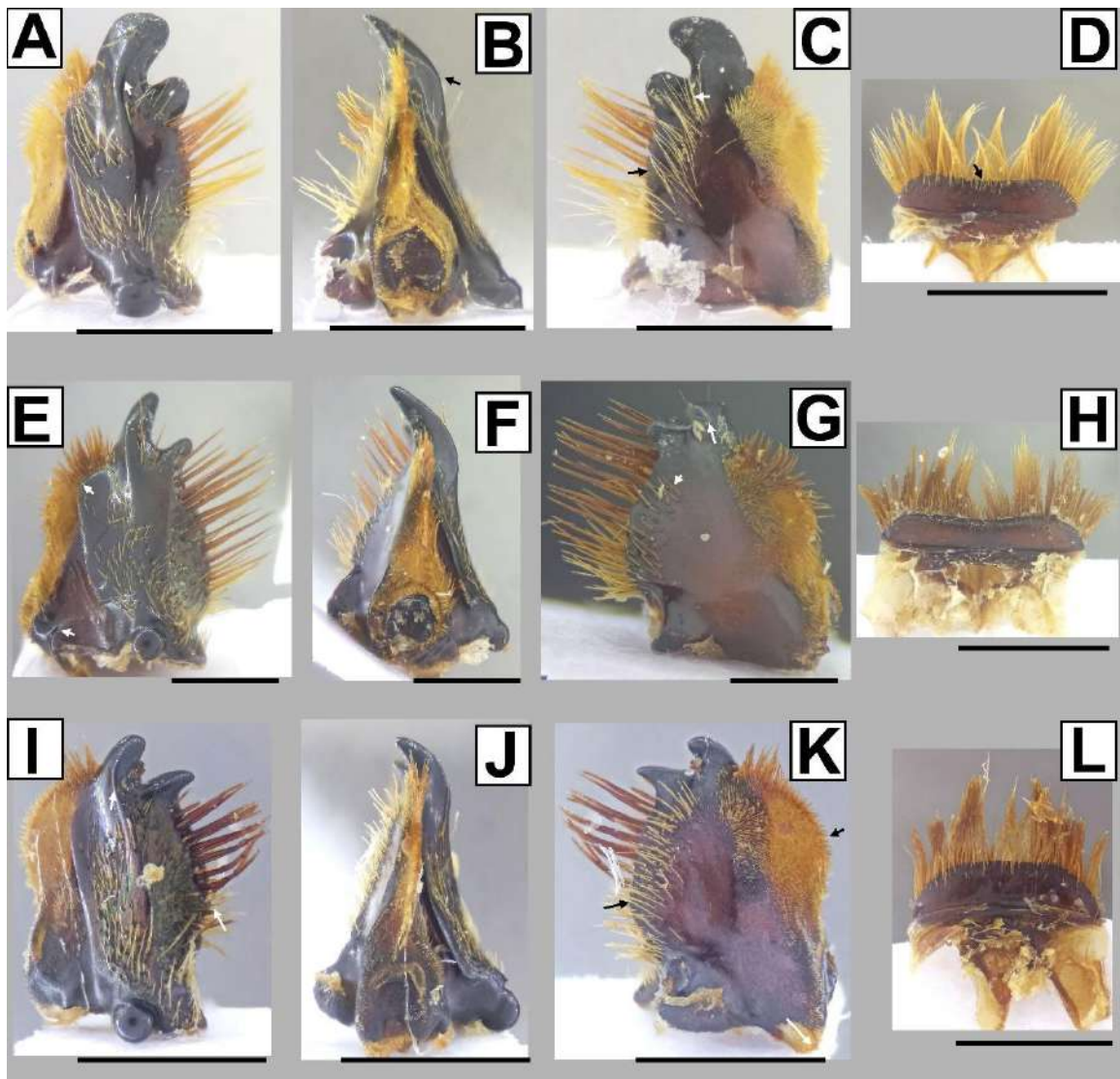


FIGURE 25. Female maxilla and mentum of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Maxilla of *A. bicuspis* in ventral view. Black arrow pointing to outer margin of lateral border base. **B**, Maxilla of *A. bicuspis* in dorsal view. **C**, Mentum of *A. bicuspis* in ventral view. **D**, Maxilla of *A. margaridae* in ventral view. **E**, Maxilla of *A. margaridae* in dorsal view. **F**, Mentum of *A. margaridae* in ventral view. **G**, Maxilla of *A. mannerheimi* in ventral view. Superior black arrow pointing to apex of galea; inferior black arrow pointing to outer margin of lateral border base. **H**, Maxilla of *A. mannerheimi* in dorsal view. **I**, Mentum of *A. mannerheimi* in ventral view. Scale bars: 1 mm.

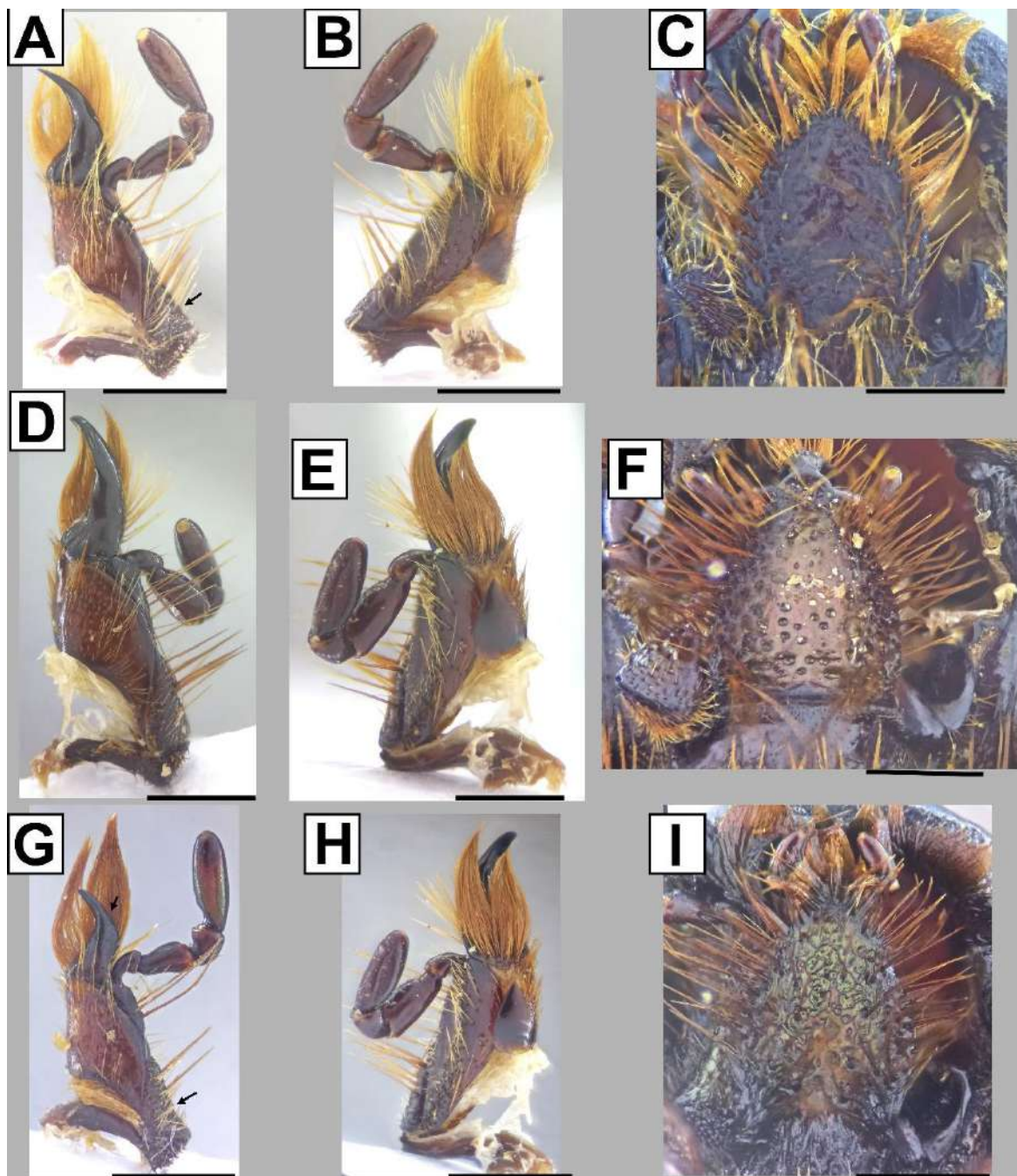


FIGURE 26. Female thorax, legs and abdomen of *Agacephala bicuspis*, *Agacephala margaridae* and *Agacephala mannerheimi*. **A**, Pronotum of *A. bicuspis* in dorsal view. **B**, Mesotibia of *A. bicuspis* in lateral view. White arrow pointing to round thick setae. **C**, Metatibia of *A. bicuspis* in lateral view. **D**, Abdomen of *A. bicuspis* in ventral view. Black arrows pointing to transverse row of setae; white arrows pointing to setae on posterior margin. **E**, Pronotum of *A. margaridae* in dorsal view. **F**, Mesotibia of *A. margaridae* in lateral view. White arrow pointing to inner tooth. **G**, Metatibia of *A. margaridae* in lateral view. **H**, Abdomen of *A. margaridae* in ventral view. **I**, Pronotum of *A. mannerheimi* in dorsal view. **J**, Mesotibia of *A. mannerheimi* in lateral view. Superior white arrow showing absence of anterior carina; inferior white arrow pointing to thick setae. **K**, Metatibia of *A. mannerheimi* in lateral view. White arrow pointing to sculpture. **L**, Abdomen of *A. mannerheimi* in ventral view. Scale bars: A,D, E,H, I,L, 5 mm; B-C, F-G, J-K, 1 mm.

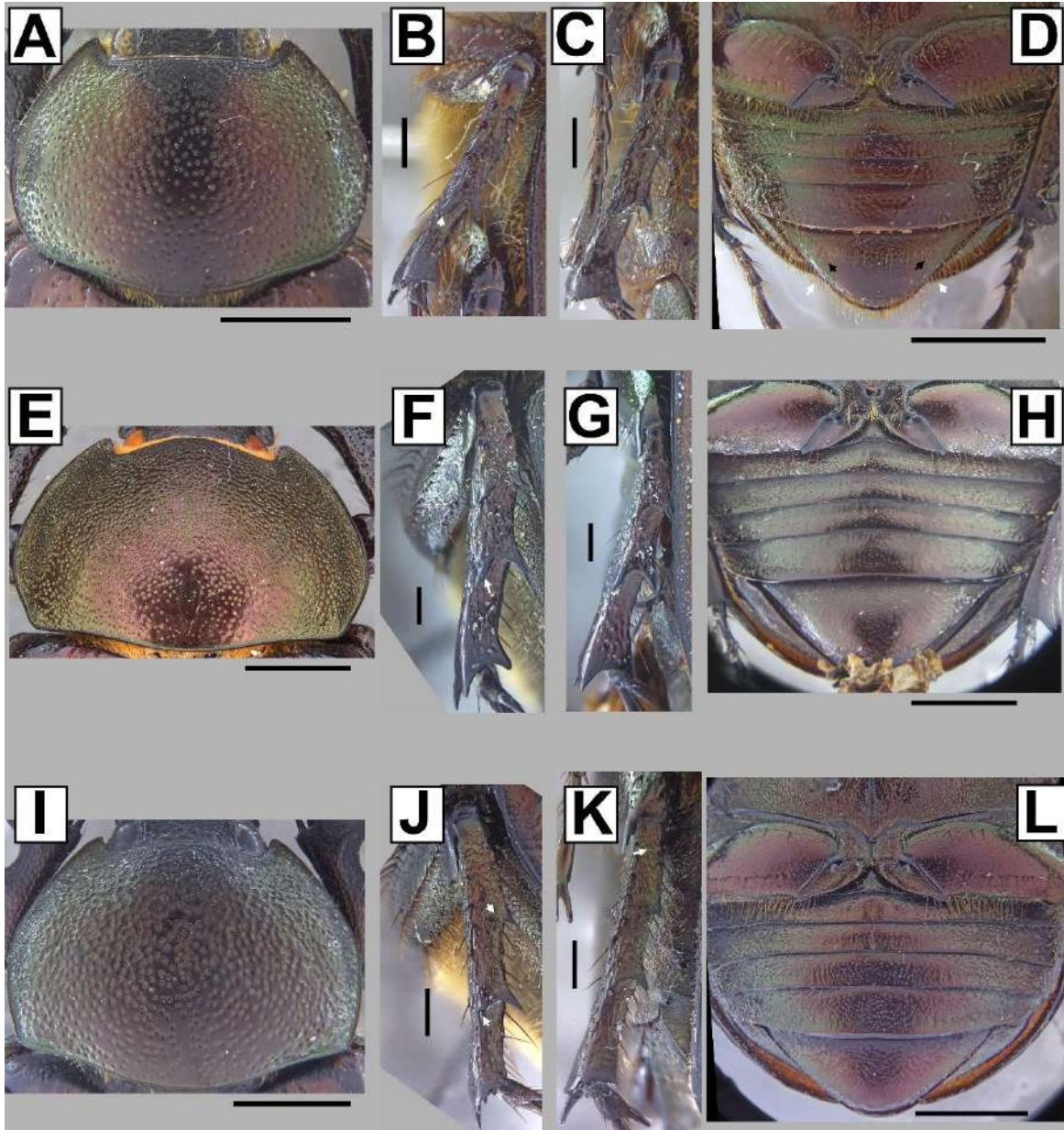


FIGURE 27. Male and female of *Agacephala margaridae*. **A**, Habitus of male in dorsal view. Black arrow pointing to mesotibia. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.

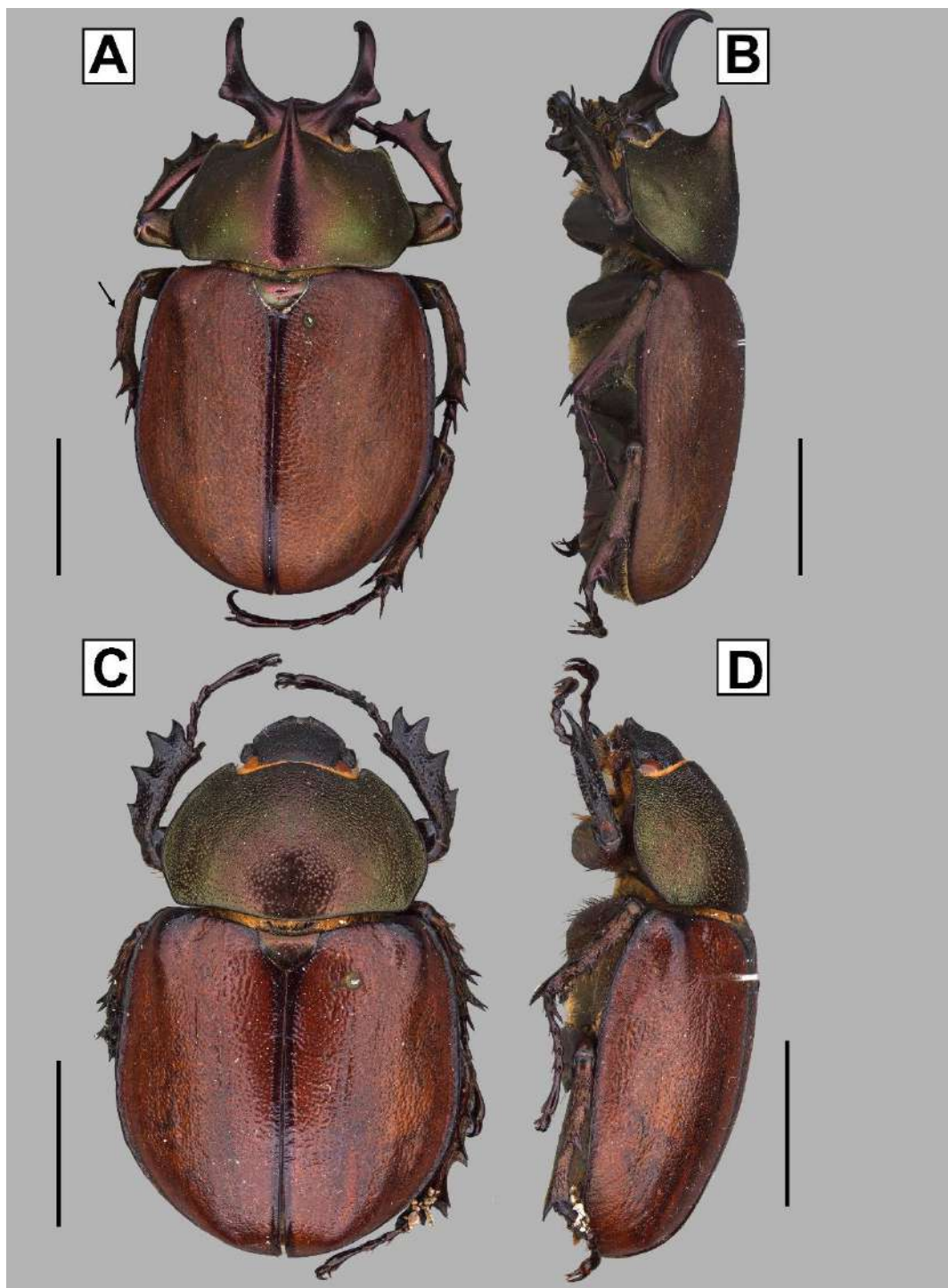


FIGURE 28. Male and female of *Agacephala mannerheimi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.

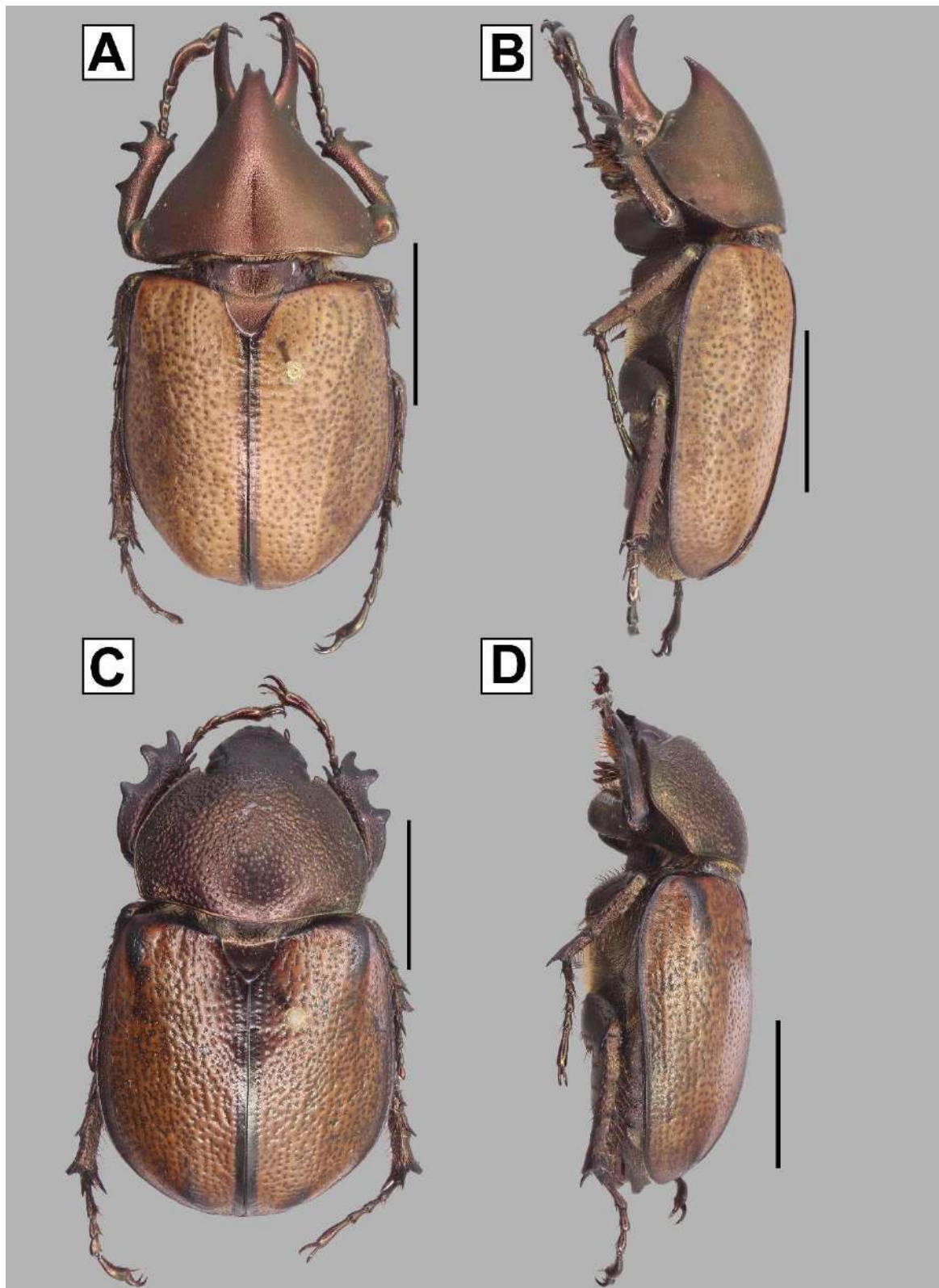


FIGURE 29. Male and female of *Agacephala mineira*. **A**, Habitus of male in dorsal view; **B**, habitus of female in dorsal view. Scale bars: 10 mm.

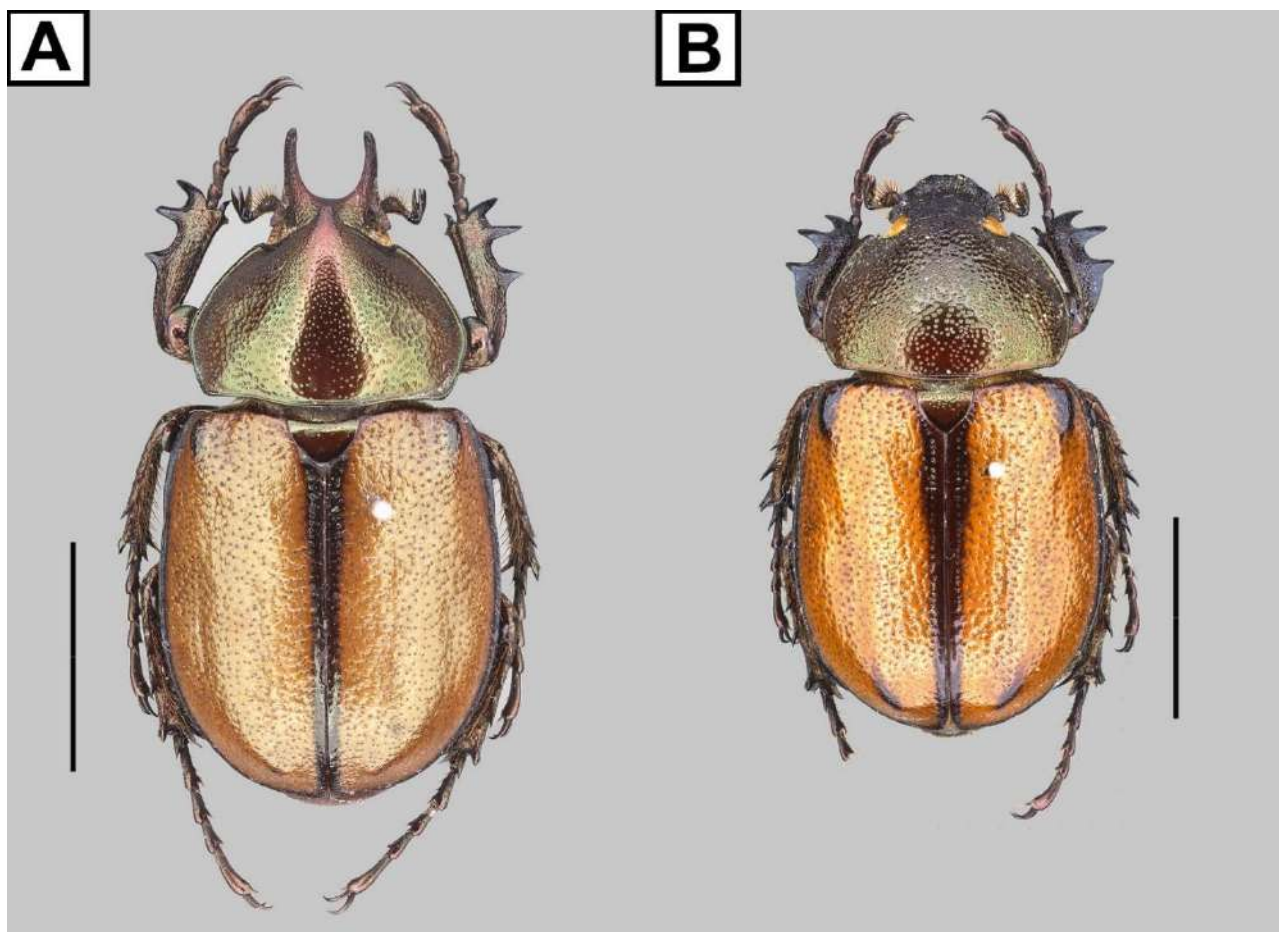


FIGURE 30. Male and female of *Agacephala alvarengai*. **A**, Habitus of male in dorsal view; **B**, habitus of female in dorsal view. Scale bars: 10 mm.

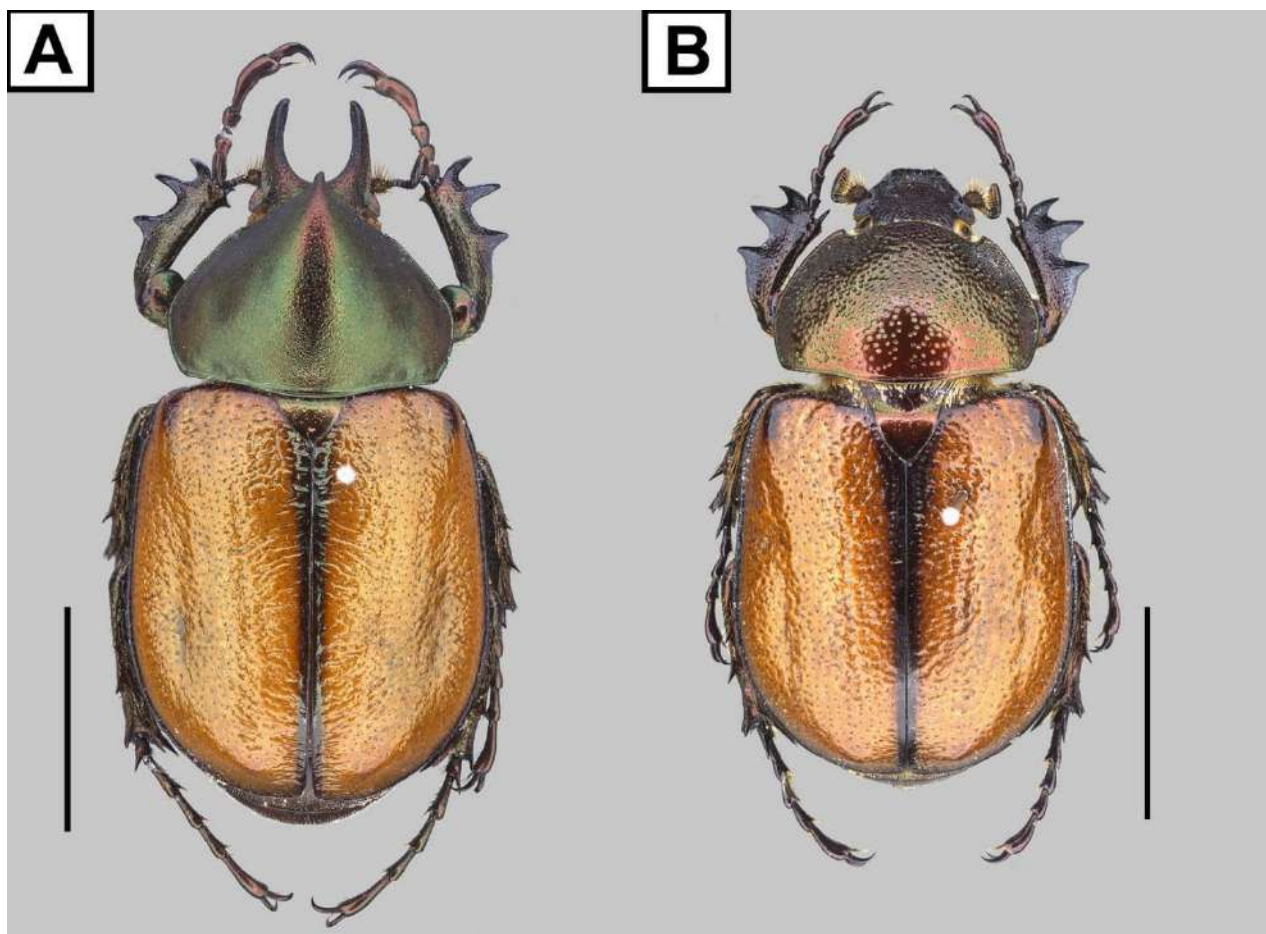


FIGURE 31. Male head, thorax and proleg of *Agacephala mineira* and *Agacephala alvarengai*. **A**, Ocular canthus of *A. mineira* in dorsal view. **B**, Ocular canthus of *A. alvarengai* in dorsal view. **C**, Pronotum of *A. mineira* in frontolateral view. **D**, Pronotum of *A. alvarengai* in frontolateral view. **E**, Protarsus of *A. mineira* in dorsal view. **F**, Protarsus of *A. alvarengai* in dorsal view. Scale bars: 1 mm.

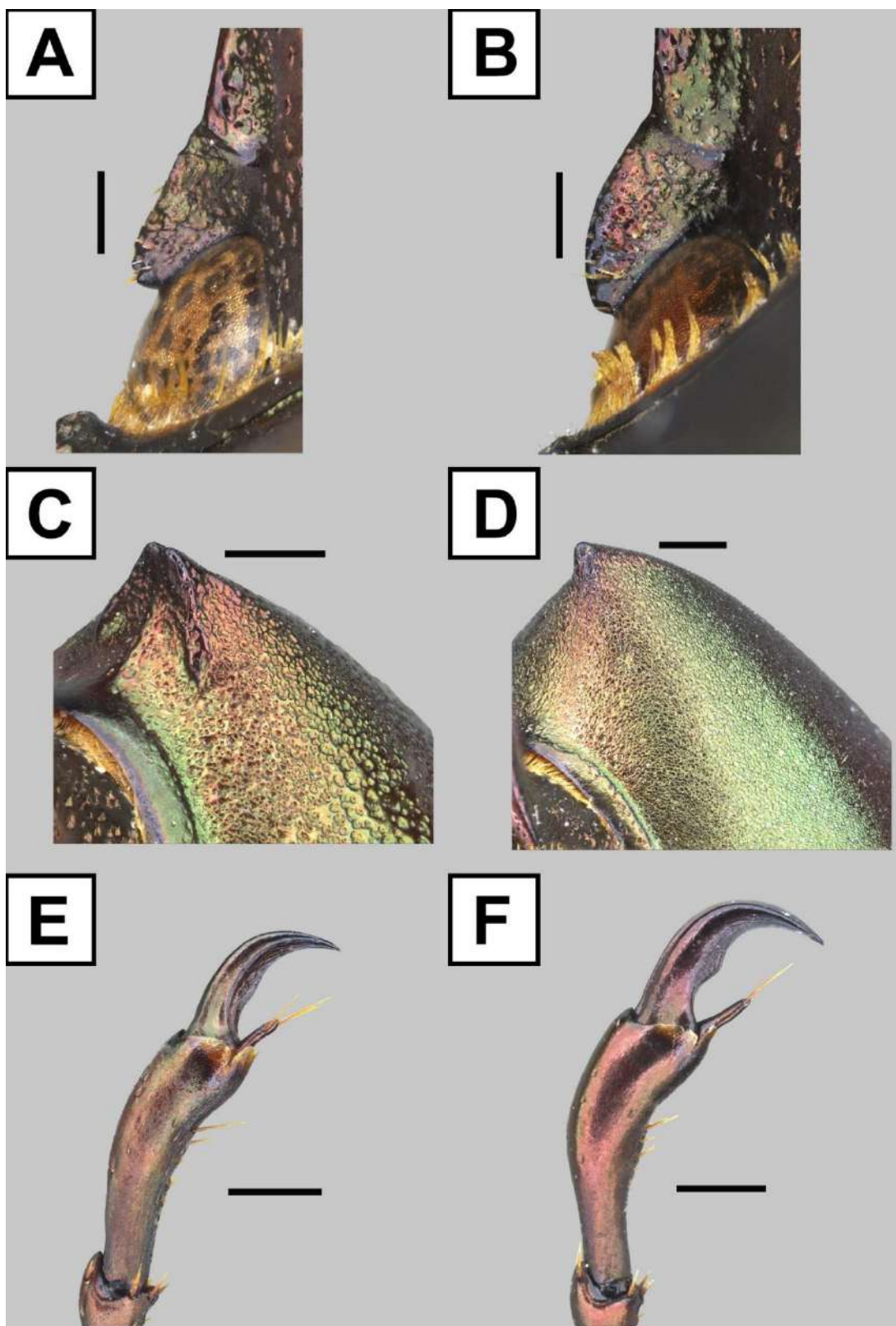


FIGURE 32. Genitalia of *Agacephala mineira* and *Agacephala alvarengai*. **A**, Parameres of *A. mineira* in caudal view. **B**, Parameres of *A. alvarengai* in caudal view. Scale bars: 1 mm.

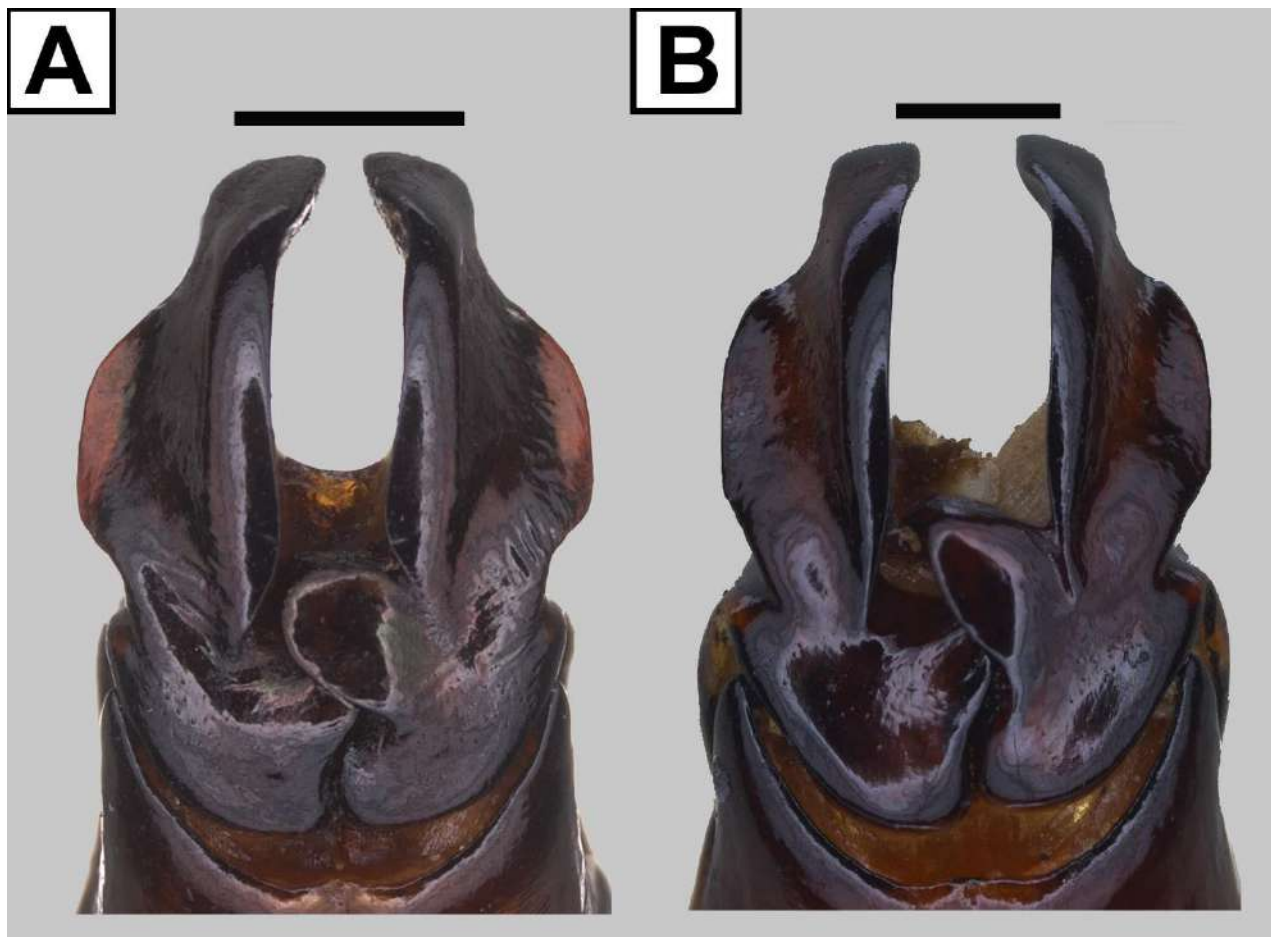


FIGURE 33. Male and female of *Lycocephala brasiliiana*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.

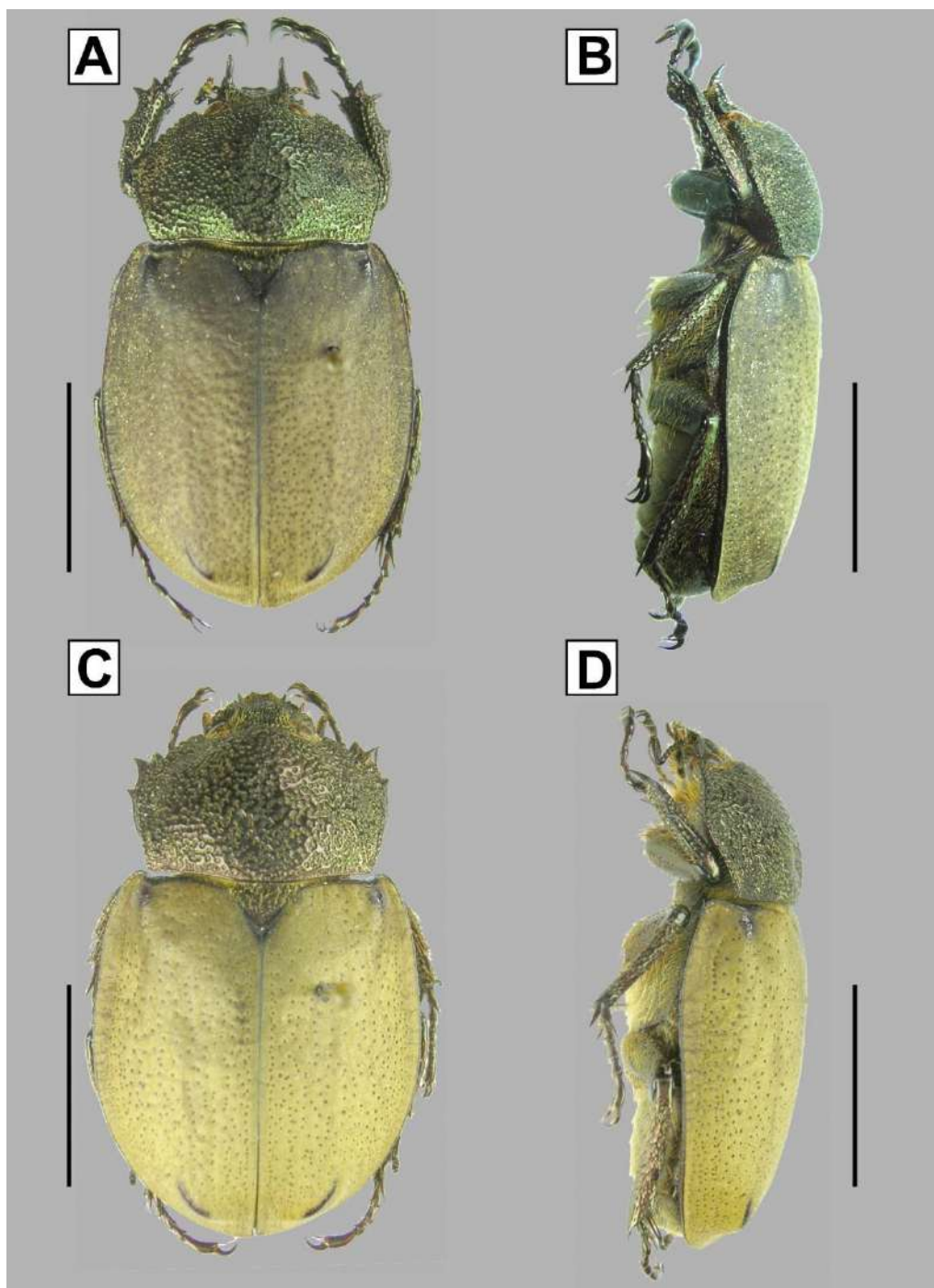


FIGURE 34. Male head, thorax, legs and genitalia of *Lycocephala brasiliiana*. **A**, Head of *L. brasiliiana* in dorsal view. **B**, Ocular canthus of *L. brasiliiana* in dorsal view. **C**, Protarsus of *L. brasiliiana* in dorsal view. **D**, Pronotum of *L. brasiliiana* in dorsal view. **E**, Pronotal lateral margin of *L. brasiliiana* in dorsal view. **F**, Metatibia of *L. brasiliiana* in ventral view. **G**, Parameres of *L. brasiliiana* in caudal view. **H**, Parameres of *L. brasiliiana* in lateral view. **I**, Aedeagus of *L. brasiliiana* in lateral view. Scale bars: A-C, G-E, I, 1 mm; D, F, 5 mm.

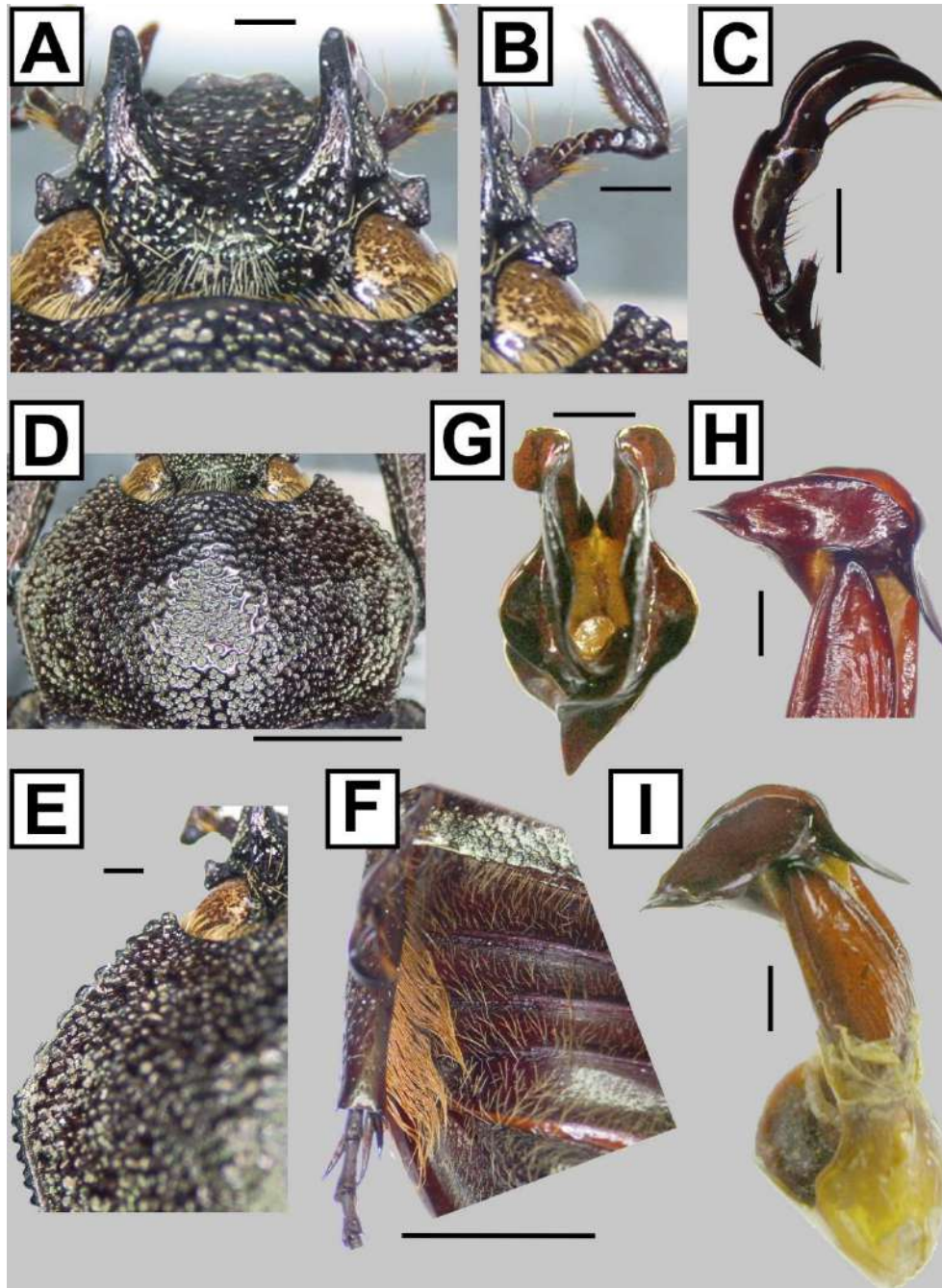


FIGURE 35. Distribution map of *Agacephala* and *Lycocephala*.

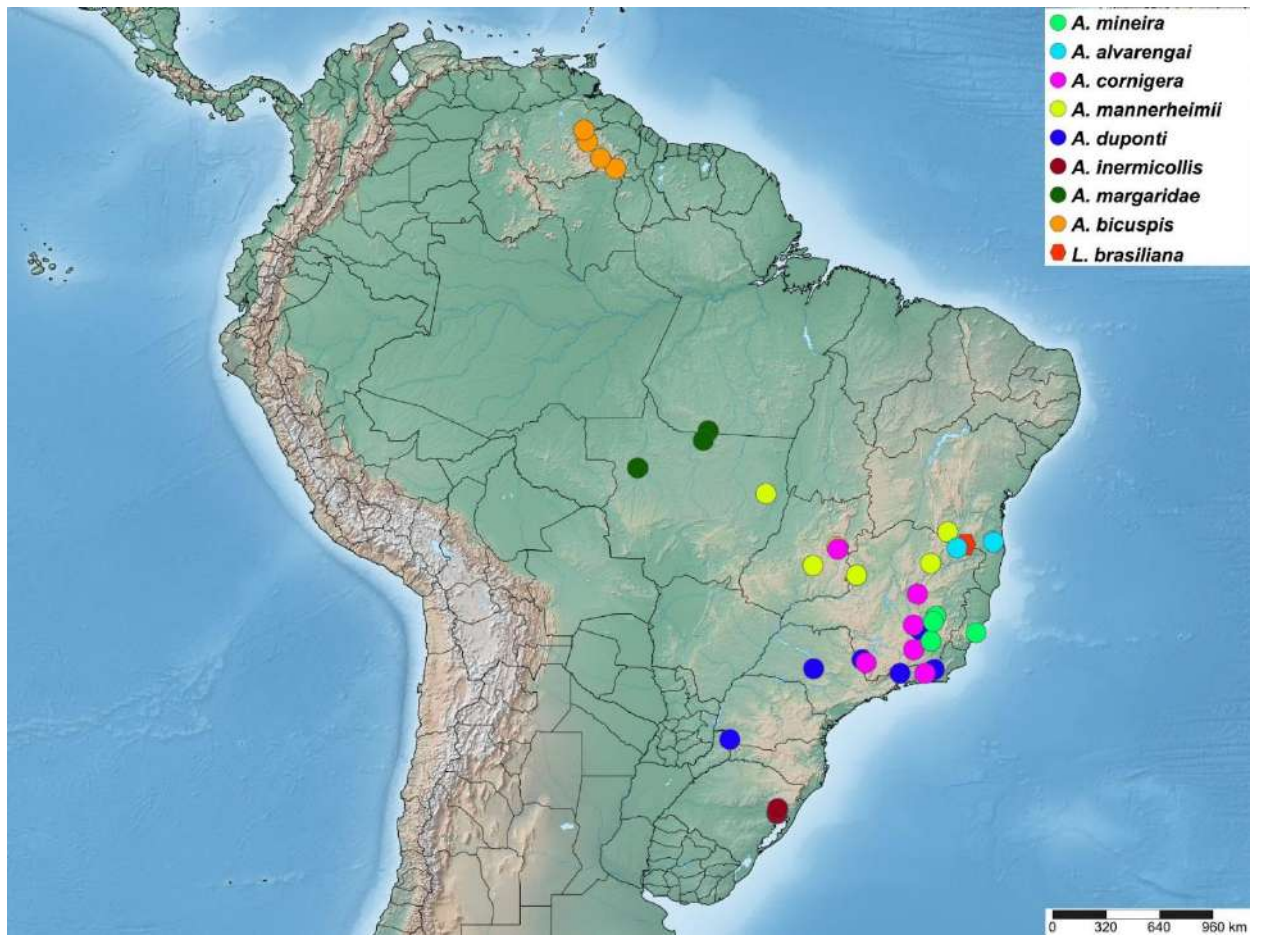


FIGURE 36. Male and female of *Aegopsis*. **A**, Habitus of *Aegopsis curvicornis* in dorsal view. **B**, Habitus of *Aegopsis curvicornis* in lateral view. Black arrow pointing to thoracic horn. **C**, Head of *Aegopsis curvicornis* in dorsolateral view. Black arrow pointing to clypeal apex. **D**, Head of *Aegopsis curvicornis* in frontal view. Black arrow pointing to clypeal sides. **E**, Habitus of female *Aegopsis bolboceridus* in dorsal view. **F**, Habitus of female *Aegopsis bolboceridus* in lateral view. Black arrow pointing to tergite VII. **G**, Head of female *Aegopsis bolboceridus* in dorsal view. **H**, Head of female *Aegopsis curvicornis* in dorsal view. Black arrow pointing to clypeal base. Scale bars: 1 mm.

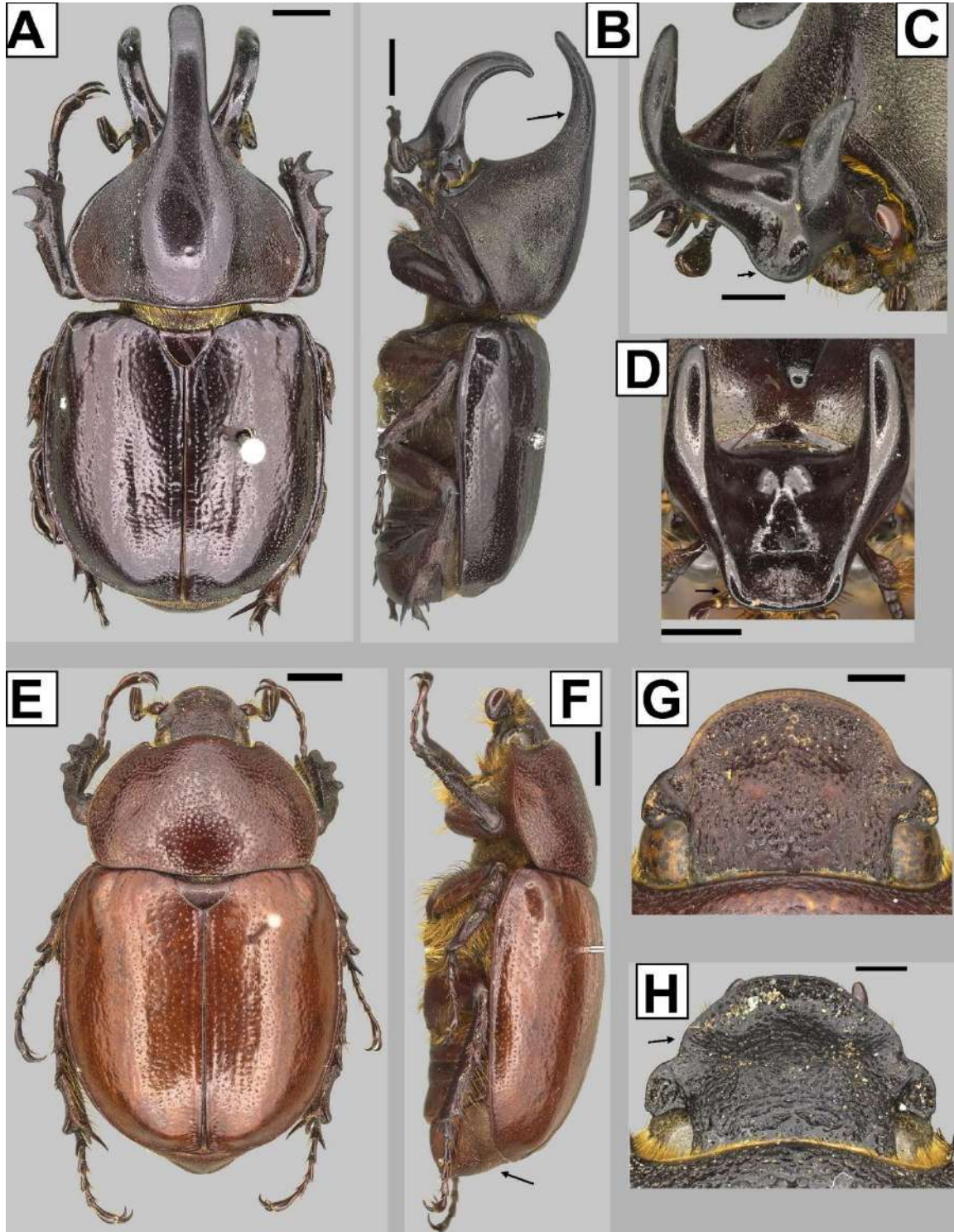


FIGURE 37. Diagnostic traits of head and thorax of Agaocephalini. **A**, Head and pronotum of *Agacephala* sp. **B**, Head and pronotum of *Spodistes* sp. **C**, Head and pronotum of *Minisiderus* sp. **D**, Head and pronotum of *Brachysiderus* sp.

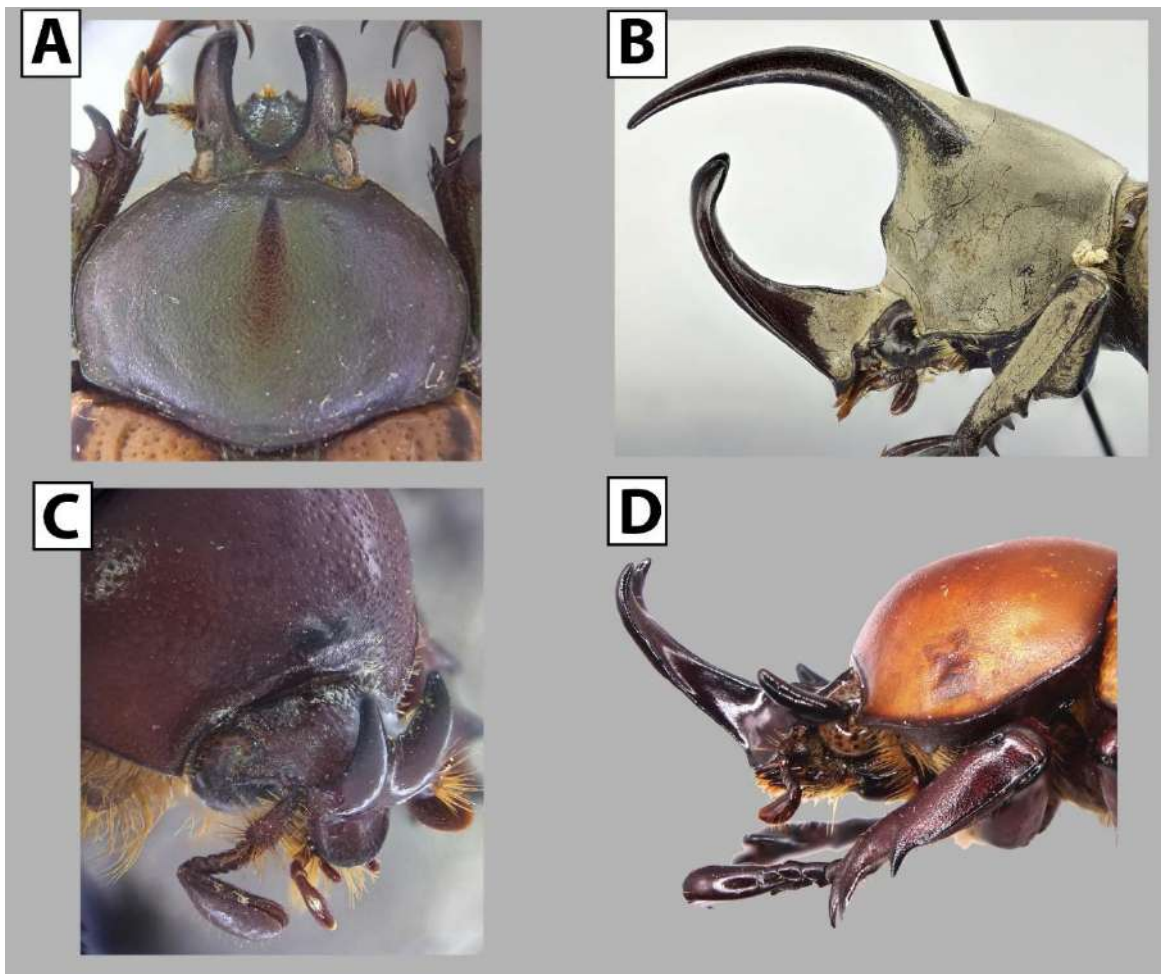


FIGURE 38. Diagnostic traits of appendages, head, thorax and mouthparts of Agocephalini. **A**, Protarsus of male *Agacephala* sp. in dorsal view. **B**, Protarsus of female *Agacephala* sp. in dorsal view. **C**, Head of *Agacephala* sp. in dorsolateral view. White arrows pointing to tubercles. **D**, Head and pronotum of *Minisiderus* sp. in dorsolateral view. **E**, Elytra of male *Agacephala* sp. in dorsal view. **F**, Mandible of *Agacephala* sp. in dorsal view. **G**, Mandible of *Agacephala* sp. in lateral view. White arrow pointing to molar area. **H**, Metatarsomere I of *Agacephala* sp. in ventral view. **I**, Prosternum of *Lycomedes* sp. in ventral view. White arrow pointing to prosternal process. **J**, Prosternum of *Aegopsis* sp. in ventral view.

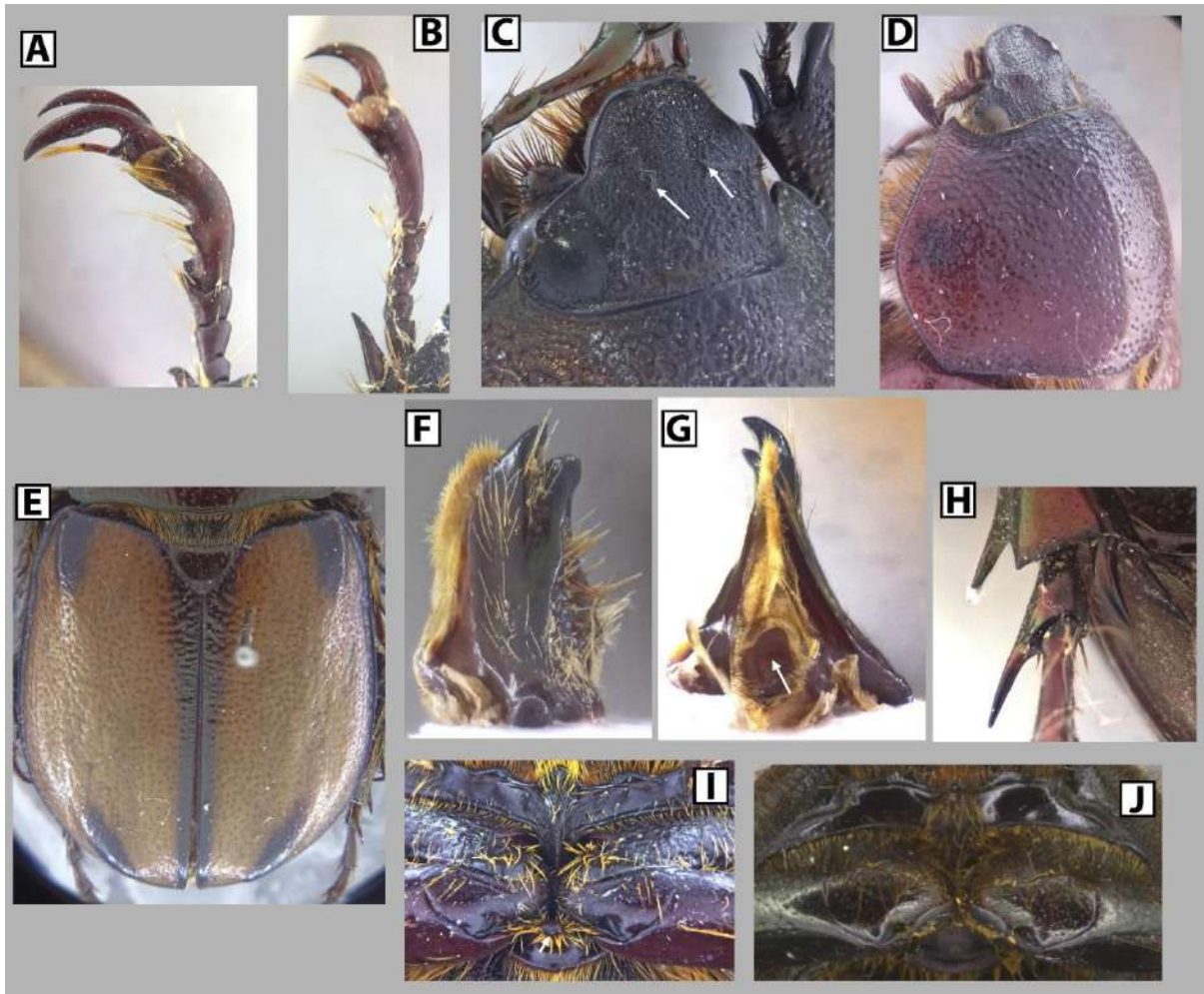


FIGURE 39. Comparison between Agaocephalini and *Colacus*, *Democrates* and *Gnathogolofa*. **A**, Mandible of *Colacus* sp. in dorsal view. **B**, Protibia of *Democrates* sp. in ventral view. White arrow pointing to base of protarsomere I; black arrow pointing to inner corner of protibia. **C**, Metatarsomere I of *Gnathogolofa* sp. in lateral view. **D**, Head and pronotum of *Gnathogolofa* sp. in lateral view. **E**, Mandible of *Agacephala* sp. in dorsal view. **F**, Protibia of *Agacephala* sp. in ventral view. White arrow pointing to base of protarsomere I; black arrow pointing to inner corner of protibia. **G**, Metatarsomere I of *Agacephala* sp. in ventrolateral view. **H**, Head and pronotum of *Minisiderus* sp. in lateral view.

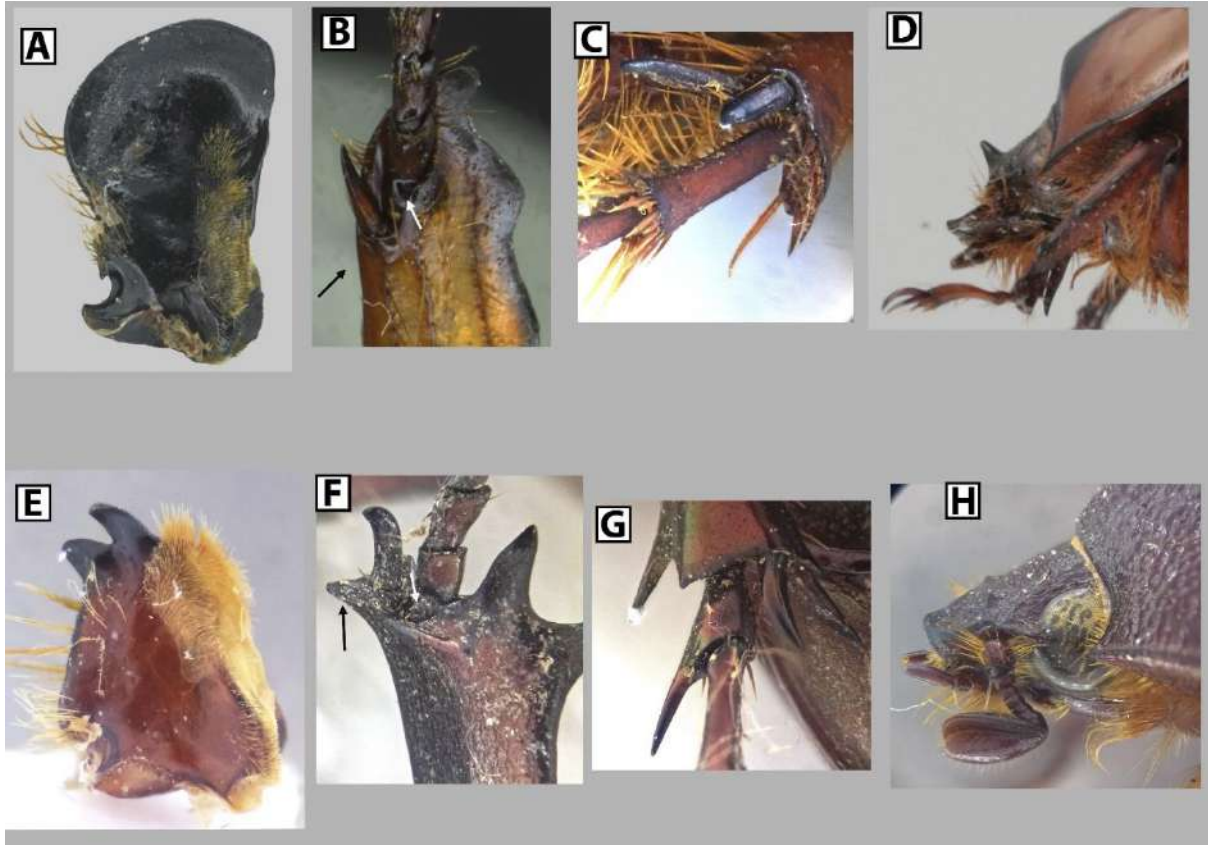


FIGURE 40. Diagnostic traits of *Agaocephalina subtrib. nov.* **A**, Protarsus of *Agacephala duponti* in dorsal view. **B**, Protarsus of *Agacephala mannerheimi* in dorsal view; **C**, Protarsomere IV of *Agacephala mannerheimi* in dorsal view. **D**, Ocular canthus of *Agacephala* sp. in dorsal view. **E**, Head of *Minisiderus* sp. in dorsal view. **F**, Head of female *Minisiderus* sp. in dorsal view. **G**, Head and pronotum of female *Minisiderus* sp. in dorsal view. **H**, Head of *Agacephala* sp. in dorsal view.

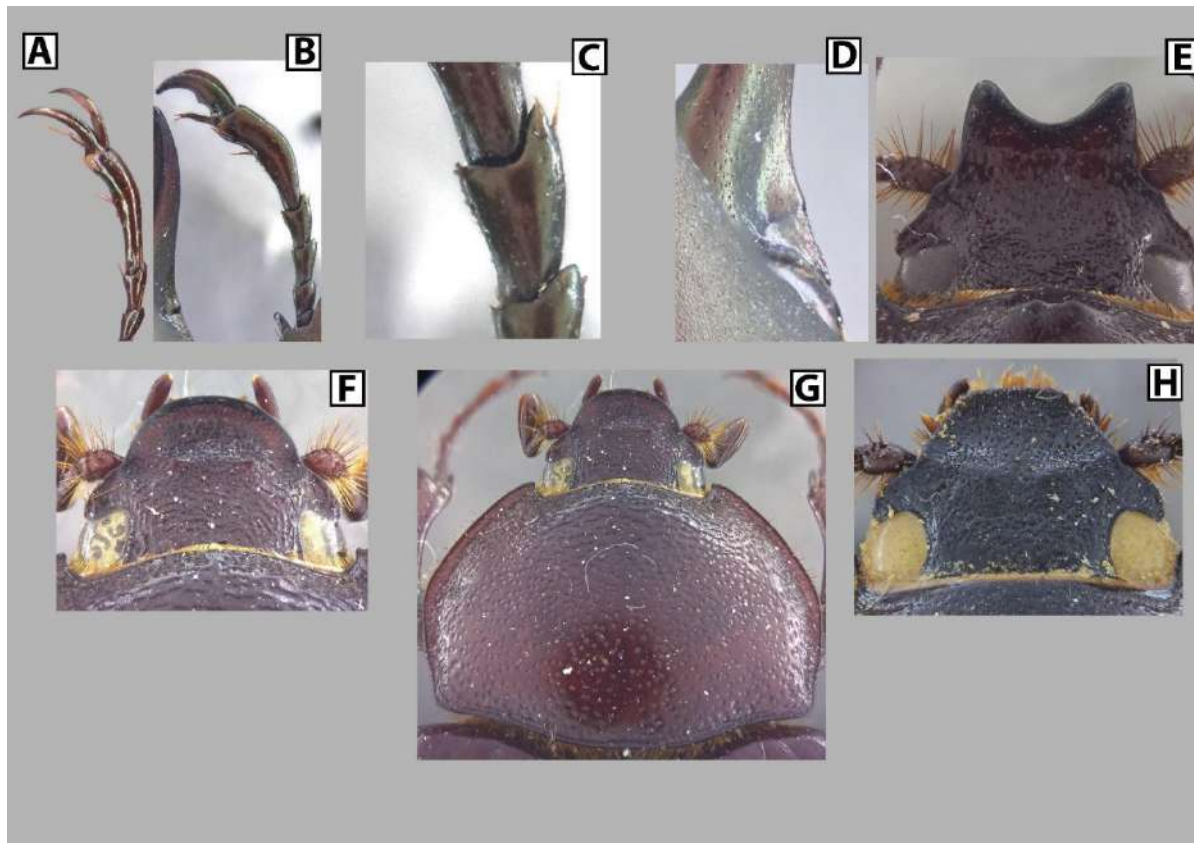


FIGURE 41. Diagnostic traits of *Lycomedina subtrib. nov.* **A**, Protarsus of *Brachysiderus* sp. in dorsal view. **B**, Protarsomere IV of *Brachysiderus* sp. in dorsal view; **C**, Head of *Brachysiderus* sp. in dorsal view. **D**, Head of *Lycomedes* sp. in dorsal view. **E**, Head of female *Lycomedes* sp. in dorsal view. **F**, Pronotum of female *Lycomedes* sp. in dorsal view. **G**, Head of female *Brachysiderus* sp. in dorsal view.

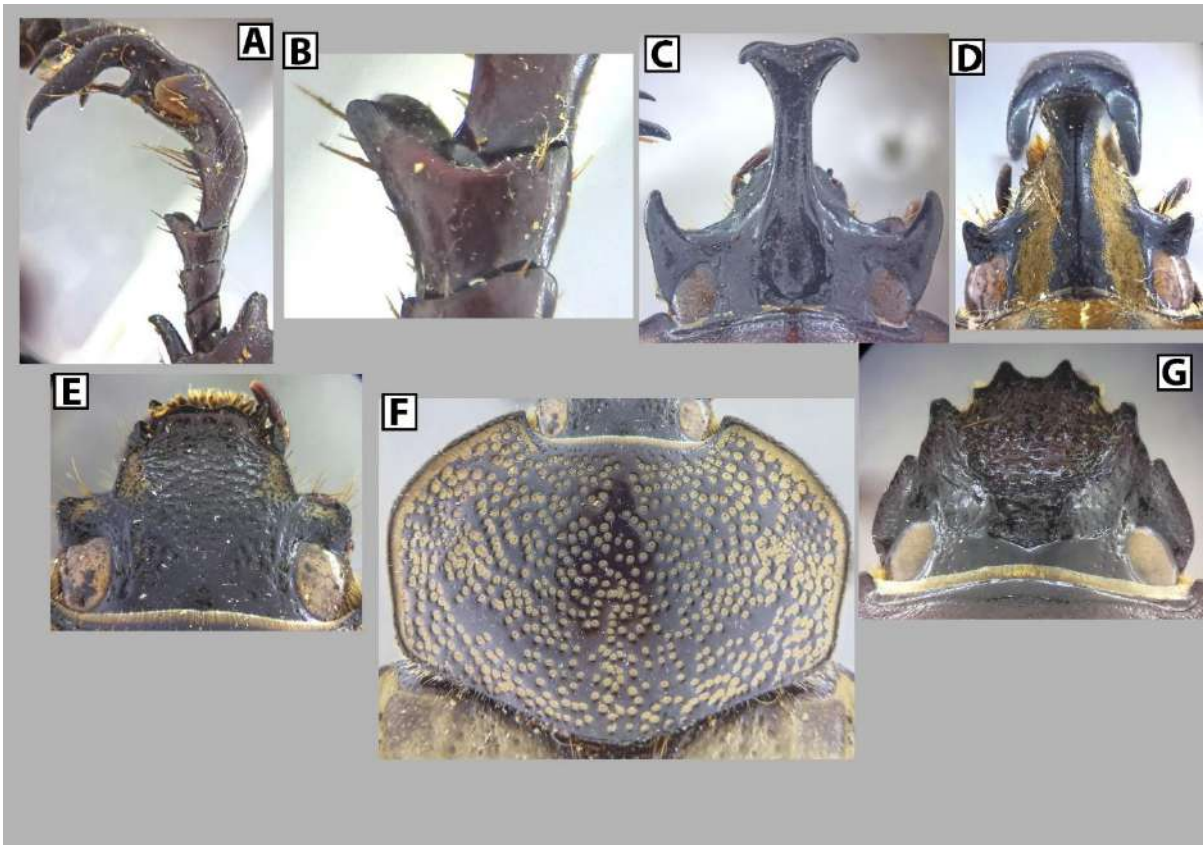


FIGURE 42. Habitus of *Antodon goryi*. **A**, Male of *Antodon goryi* in dorsal view. **B**, Female of *Antodon goryi* in dorsal view. Scale bars: 10 mm.

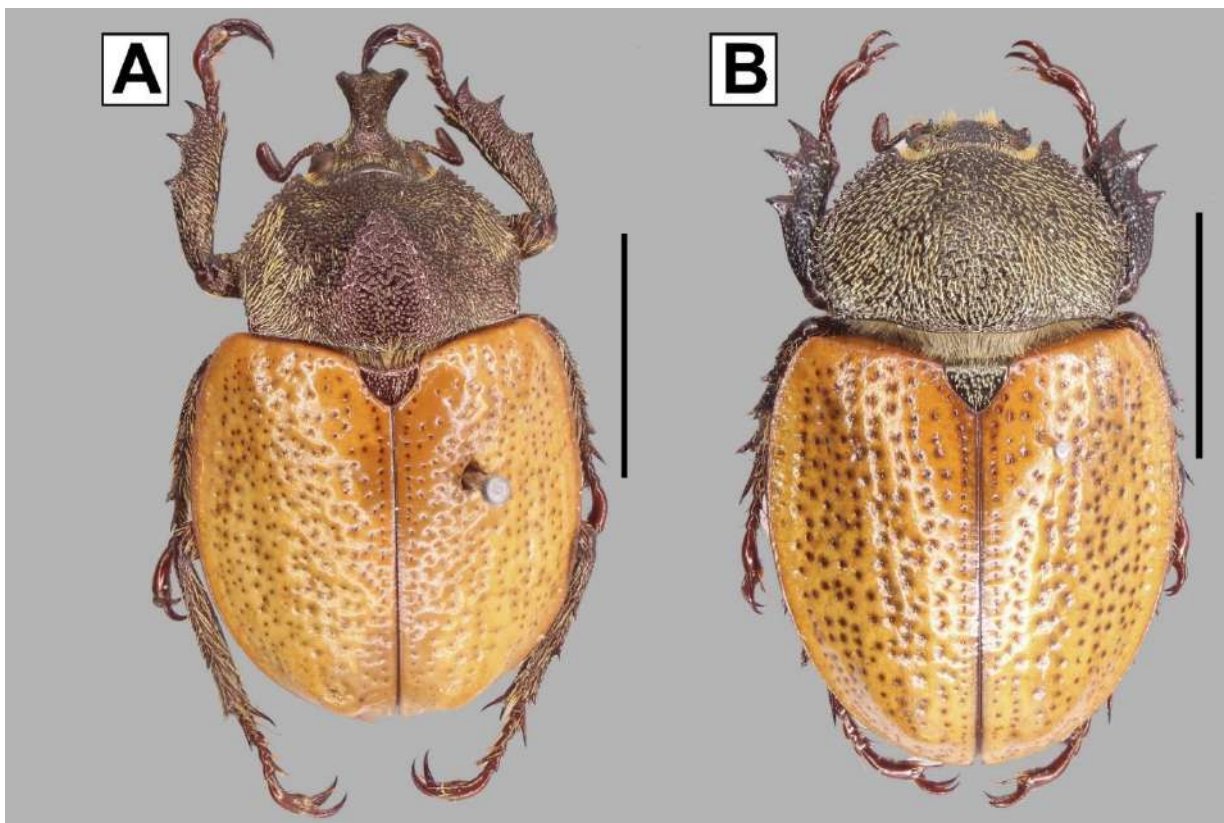
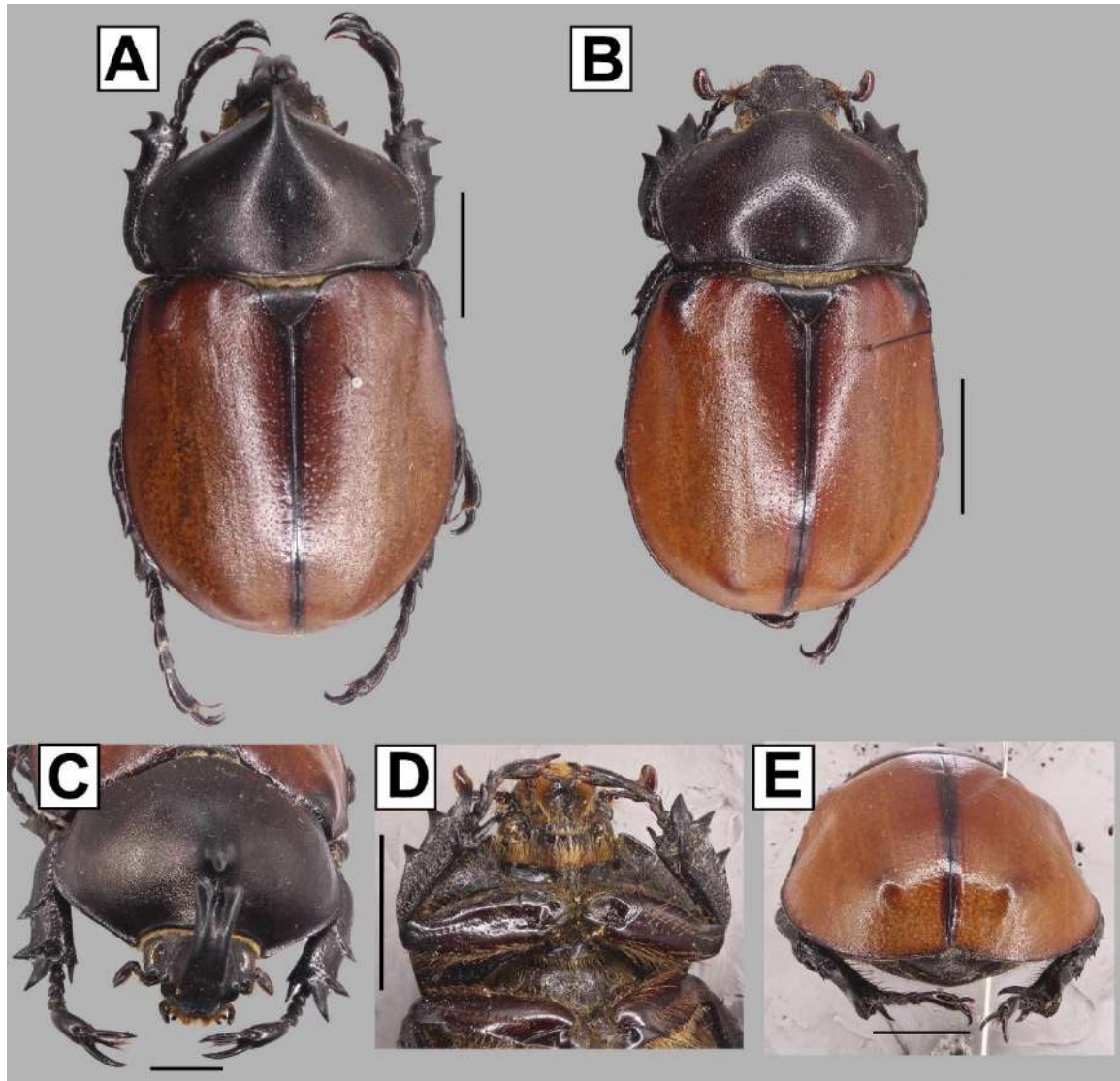


FIGURE 43. Habitus of *Mitracephala humboldti*. **A**, Male of *Mitracephala humboldti* in dorsal view. **B**, Female of *Mitracephala humboldti* in dorsal view. **C**, Head of male *Mitracephala humboldti* in frontal view. **D**, Legs and part of thorax of female *Mitracephala humboldti* in ventral view. **E**, Elytra and tergite VIII of female *Mitracephala humboldti* in posterior view. Scale bars: A-B, D-E, 10 mm; C, 5 mm.



CAPÍTULO II

Sobral, R. & Grossi, P.C. Revision of *Minisiderus* Endrödi (Coleoptera, Scarabaeoidea, Dynastinae), with five new species described from Brazil. Manuscrito em preparação para submeter à revista Zootaxa.

Revision of the genus *Minisiderus* Endrödi (Coleoptera, Scarabaeoidea, Dynastinae), with description of the female of three known species and five new species described from Brazil

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Abstract

The genus *Minisiderus* (Endrödi, 1970) is revised, redescribed and illustrated. Five new species are described to western Cerrado in Mato Grosso to eastern Cerrado in Minas Gerais. After comparison with the holotype of *Minisiderus paranensis* (Arrow, 1902), *Minisiderus lenorae* (Grossi, Dechambre & Grossi, 2012) **new status** is erected to the species status. A new diagnosis is proposed to the genus, and remarks regarding the taxonomy and geographic distribution of each species are discussed. The female of *M. martinae*, *M. benjamini* and *M. mielkeorum* are here described for the first time. Morphological teratologies are reported for the first time to a species of *Minisiderus*. A new distribution map and a key to male and female species are provided with new records to the species, including the first record of *Minisiderus martinae* (Abadie, 2010) to Brazil, new country record.

Key words: Agaocephalini, *Brachysiderus*, rhinoceros beetles, Melolonthidae, Neotropical region

Resumo

O gênero *Minisiderus* (Endrödi, 1970) é revisado, redescrito e ilustrado. Cinco novas espécies são descritas para o oeste do Cerrado no Mato Grosso e a porção leste do Cerrado em Minas Gerais. Após comparações com o holótipo de *Minisiderus paranensis* (Arrow, 1902), *Minisiderus lenorae* (Grossi, Dechambre & Grossi, 2012) **status novo** é elevada a nível de espécie. Novas diagnoses são propostas para machos e fêmeas, e detalhes

acerca da taxonomia e distribuição geográfica de cada espécie são discutidos. As fêmeas de *M. martinae*, *M. benjamini* and *M. mielkeorum* são aqui descritas pela primeira vez. Anomalias morfológicas são aqui reportadas pela primeira vez para uma espécie de *Minisiderus*. Um novo mapa de distribuição e uma chave dicotômica para machos e fêmeas de *Minisiderus* são fornecidos, com novos registros para as espécies, incluindo o primeiro registro de *Minisiderus martinae* (Abadie, 2010) para o Brasil, **novo registro para o país**.

Introduction

Minisiderus Endrödi, 1970 is a South American genus of rhinoceros beetles characteristic of tropical dry-forested areas from Brazilian Cerrado and Bolivian Chaco (Milani 2018). The taxon *Minisiderus* was originally proposed as a subgenus of *Brachysiderus* Waterhouse, 1881 by Endrödi (1970), that realized that the morphology of the smaller species from Brazil described by Ohaus (1930) were too different from the Andean *Brachysiderus* that they should belong to a different group. However, it was not until recently when *Minisiderus* had its status raised by Milani (2018), which considered that the diagnostic characteristics of *Minisiderus* were sufficient to support it as a distinct genus apart from *Brachysiderus*.

Minisiderus can be recognized by the brownish to reddish brown color, size ranging from 20 to 30 mm, cephalic horns of males short and bifurcated, male pronotum with two anterior tubercles, and the protarsomere V thin and simple as in female (Milani 2018). Currently, the genus has 9 species: *Minisiderus paranensis* (Arrow, 1902), *M. minicola* (Ohaus, 1930), *M. matogrossensis* (Ohaus, 1930), *M. goyanus* (Ohaus, 1930), *M. mielkeorum* (Grossi & Grossi, 2005), *M. elyanae* (Dechambre, 2009), *M. martinae* (Abadie, 2010), *M. benjamini* (Abadie, 2014) and *M. bertolossiorum* (Abadie, Godinho & Koike, 2016). Of those species, only *M. martinae* is not found in Brazil, occurring in dry forests of Bolivia. The other species have a wide distribution within Brazilian Cerrado, occurring in Northeastern, Central-Western and Southeastern Regions. (Abadie 2010; Milani, 2018).

Considering the taxonomic history of *Minisiderus*, we can divide it into two temporal events. The first consists in the description of the type species *M. paranensis* by Arrow (1902) and the description of the three species by Ohaus (1930). There was, then, a huge gap of 75 years until the description of another new species of *Minisiderus*.

This gap ended when Grossi & Grossi (2005) described *M. mielkeorum*, the first species of this genus found in the Northeastern region of Brazil. After that, four new species were added to *Minisiderus* and more species were described in the 2000's and 2010's (*M. elyanae*, *M. martinae*, *M. benjamini* and *M. bertolossiorum*) as well as a new subspecies: *Minisiderus paranensis lenorae* Grossi, Dechambre & Grossi, 2012. However, all those new taxa of last event were described based only on male specimens, but *M. p. lenorae*. The females of this genus are really scarce in the collections and even in field collecting it is difficult to gather female specimens. Recently, Milani (2018) described the female of *M. elyanae* based on one specimen from the state of Maranhão, Brazil, given to him by the French entomologist Thierry Porion. Up until now, *M. martinae*, *M. benjamini* and *M. mielkeorum* still have females unknown.

After years of gathering material from field excursions and some Brazilian and foreign entomological collections, we observed that some specimens that have been treated in collections as *M. minicola* and *M. goyanus* are actually new species. Also, some female specimens were found in localities sympatric to *M. martinae*, *M. mielkeorum*, *M. benjamini*. Therefore, herein we propose a revision of *Minisiderus* with the description of five new species from Brazil, the first description of the females of the three species previously mentioned and the elevation of *Minisiderus paranensis lenorae* to the species status. An identification key is provided for males and females of *Minisiderus* and the distribution map of the species in the genus is updated.

Materials and methods

More than a hundred specimens were studied from the following collections (acronyms according Evenhuis (2009) when available).

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

CEMT Seção de Entomologia da Coleção Zoológica da Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso, Brazil (Fernando Z. Vaz-de-Mello)

CMNC Canadian Museum of Nature, Ottawa, Canada (François Génier)

DZUP Coleção Entomológica Padre Jesús Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (Lúcia Massutti de Almeida)

EPGC Everardo and Paschoal Grossi Collection, Nova Friburgo, Rio de Janeiro, Brazil (Everarado J. Grossi)

MNRJ Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (Marcela L. Monné)

MNHN Muséum National d'Histoire Naturelle, Paris, France (Antoine Mantillieri)
MSUC Michigan State University Albert J. Cook Arthropod Research Collection
(Anthony Cognato, Gary Parsons)
MZLU Lund Museum of Zoology, Lund, Sweden (Christoffer Fägerström)
MZUSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Sônia Casari)
NHM Natural History Museum, London, United Kingdom (Max Barclay)

Terminology follows in part Endrödi (1985) for the general traits of the body, Nel & Scholtz (1990) for mouthparts, Cristóvão & Vaz-de-Mello (2020) for abdomen and genitalia and Führmann (2010) for punctuation. The aedeagi were dissected after boiling specimens for 10 to 20 minutes in warm water with neutral soap, and then glued in card mount, and pinned just below each specimen. Images were obtained with a smartphone Xiaomi Redmi Note8 Pro attached at a stereoscopic microscope Digilab DI 106-T with stacked images made on software Helicon Focus 7, and edited using Adobe Photoshop CS6.

The map was made using SimpleMappr (<http://www.simplemappr.net>) (Shorthouse, 2010). For specimens whose latitude and longitude data were missing from the tags, a point was established using *GoogleMaps* within the limits of the most restricted location information available on the tag (reserve, park, district, municipality, etc.). For distribution records in the literature whose specimens were not found or could be examined, the original information was considered.

Results

Taxonomy

Minisiderus Endrödi, 1970

(Figs. 1-50)

Minisiderus Milani 2018: 79 (proposed new status).

Brachysiderus (*Minisiderus*) Endrödi 1970: 57 (original description); Endrödi 1985: 217 (cited);

Grossi & Grossi 2005: 79 (description of new species); Dechambre 2009: 100 (description of

new species); Abadie 2010: 201 (description of new species); Grossi, Dechambre & Grossi

2012: 10 (description of new subspecies); Abadie 2014: 127 (description of new species);

Abadie, Godinho Jr. & Koike 2016: 234 (description of new species).

Type species: *Minisiderus paranensis* (Arrow, 1902): 261. By monotypy.

Diagnosis. *Minisiderus* differs from other genera of Agaocephalini by the combination of the following characters. **Males:** body elongated and convex, surface lustrous, color of body and appendages varying from brown to dark reddish brown (Figs. 8A, 15A, 16A, 22A, 23A, 26A, 27A, 30A, 32A, 38A, 39A, 44A, 46A, 48A), elytra yellowish in some species (Figs. 1A, 2A, 7A). Head with a pair of cephalic horns connected basally (Figs. 3D, 9C). Ocular canthi short, not crossing the outer margin of eye, anterior margin straight at apex with basal margin without protuberance (Figs. 3I, 9A) or with protuberance (Figs. 9D). Mandibles with two ventral carinae, some species with a third short carina near apical tooth (Fig. 10A), mandibular apex with one thick tooth, tooth emarginated (Fig. 10F), elongated (Fig. 18A) or short (Fig. 10A). Pronotum bordered and convex with a pair of tubercles present near pronotal anterior margin (Fig. 1A-B, 8A-B). Protarsal claws simple, curved (Fig. 15A). **Females:** body elongated and convex, as in males (Figs. 15C, 16C, 22C, 30A, 44C, 46C). Clypeus round (Fig. 14D, 37A). Tergite VIII generally hidden by elytral apex in dorsal view (Fig. 15C, 16C). Head hornless, but with a pair of short or inconspicuous tubercles (Fig. 14E, 21G). Ocular canthi elongated, shape slender or thick, anterior margin slightly curved or straight with no protuberance (Fig. 14F, 21A). Pronotum bordered and convex, tubercles absent (Fig. 15C-D).

Male description. Color: Body lustrous, head, thorax, abdomen, appendages, elytra and venter with color ranging from brown to dark reddish brown (Fig. 8A, 15A, 16A, 22A, 23A, 26A, 27A, 30A, 32A, 38A, 39A, 44A, 46A, 48A), elytra yellowish in some species (Figs. 1A, 2A, 7A). **Head:** Frons with a pair of cephalic horns connected basally, basal connection deep (Fig. 17F) or shallow (Fig. 17A). Frontal surface mainly straight (Fig. 3K), but it can be depressed (Fig. 40I) or with presence of protuberance (Fig. 17B, 17G). Ocular canthi short, not crossing the outer margin of eye, anterior margin straight (Figs. 3I, 9A) or with basal protuberance (Figs. 40C). Clypeus almost perpendicular in relation to frons (Fig. 3H, 9C), sides either oblique or suparallel with apex round, emarginated or truncate (Figs. 3D, 9A, 33B). Antennae 10-segmented, scape distally dilated and completely covered by long thin setae, pedicel caliciform with crown of long thin setae surrounding it, antennomeres III-V similar with shape slightly wider than long, antennomeres VI-VII flattened, antennomeres VIII-X lamellate, presence of short thin setae either on outer and inner face of lamellae. **Mouthparts:**

Mandibles, in ventral view, subtriangular with two subparallel carinae from apex to base, some species with a third carina short on apex (Fig. 10A); mandibular apex with one distinct tooth, tooth emarginated (Fig. 10F), elongated (Fig. 18A) or short (Fig. 10A). In lateral view, mandibles with molar area short almost as long as wide, distinctly depressed medially (Fig. 4C); in dorsal view, socket big as long as molar area, inner margin covered by mesal brush, mesal brush distinctly setose apically and membranous mesobasally (Fig. 4B). Maxillae with galea subtriangular and short, circa same length of maxillary palpomere III, teeth absent, dorsal surface densely hirsute, stipes with lateral border constricted medially (covered or not by the basistipes) and basal portion distinctly triangular, palpifer not covered by basistipes (Fig. 5A-B). Mentum with sides curved, base 3 times wider than apex, apex sharp or emarginated, shape elongated (Fig. 5C) or robust (Fig. 16F). **Thorax:** Pronotum convex, slightly bordered, with a pair of tubercles present near pronotal anterior margin (Fig. 1A-B, 8 A-B) or pronotum with a distinct fovea near anterior margin with moderate horn emerging from anterior margin (Figs. 32A, 38A). Pronotal disc punctate, presence of wrinkles on anterior margin or near tubercles (Fig. 1A, 33A). Tubercles short and conspicuous (Fig. 8B, 16B) or short and almost inconspicuous (Figs. 1B, 2B). Prosternal process absent, posterior margin of prosternum projected or not in ventral view (Fig. 41E, 41H). Meso- and metasternum hirsute, surface densely punctate or with some wrinkles. **Elytra:** Form elongated, ranging from 2 to 2.5 times longer than wide, disc densely punctate, punctures irregular only with traits of regular rows near elytral suture, apical and humeral umbones round, not projected (Fig. 8B) or slightly projected (Fig. 1B, 2B). **Legs:** Protarsi simples, protarsal claws simple and thin, with subequal length; protarsomere V slightly curved, more than 2 times longer than protarsomere IV; protarsomeres IV and III subequal in length, longer than II and I; protarsomere I longer than II, with base narrowing to the insertion on protibia (Fig.). Protibia slightly arcuate with three (Fig. 2A) or four (Fig. 32A) outer teeth and one outer spur; in ventral view, outer corner slightly sharp, protarsal insertion posterior to insertion of spur. Meso- and metatibia with three outer teeth and two outer carinae, posterior carina connected to medial tooth, anterior carina connected (Fig. 8B) or not with basal tooth (Fig. 1B). Meso- and metatibia with two spurs on inner portion of apex, meso- and metatarsomere basal with distinct acute projection to tarsomere IV. **Abdomen:** Tergite VIII round with slight constrictions on corners of posterior margin. Surface with variant patterns of wrinkles and moderate punctures. Sternite VIII with posterior margin notched medially, presence of long thin

setae on lateral portions of posterior margin. Sternite VII almost 2 times longer than sternite VI. Sternites IV-VI with almost same size, sternite IV sometimes longer than V or VI, surface with distinct patterns of thin punctures and with rows of setae laterally. **Aedeagus:** Parameres symmetric, in dorsal view, with basal portion folded to middle (Fig. 12A) or asymmetric with laminar projection on basal portion, posterior phallobase deeply emarginated (Fig. 6A).

Female description. Body: Shape oblong, similar to males but more convex, color pattern as in males (Figs. 15C, 16C, 22C, 30A, 44C, 46C). **Head:** Cephalic horns absent, frons with a pair of short or inconspicuous tubercles (Figs. 14E, 21G). Clypeus round, with basal portion slightly elevated near ocular canthi (Fig. 21C) or not (Fig. 14E). Ocular canthi elongated, anterior margin slightly curved with no protuberance (Fig. 14F, 21A). Antennae as in males, but shorter. **Thorax:** Pronotum bordered and convex, slightly flattened than in males, tubercles absent, pronotal disc distinctly punctate (Fig. 15C). Prosternal process absent. Meso- and metasternum as in males, but less hirsute. **Elytra:** Shape more than 2 times longer than pronotum, elytral disc with ocellate punctures bigger than in males, first third on elytra near elytral suture with three to four regular rows of punctures. Apical umbones not projected in lateral view. **Legs:** Protarsi simple, protarsal claws subequal and thin (Fig. 15C). Pro-, meso- and metatibiae as in males, except by basal meso- and metatarsomeres thicker than in males and more excavated between medial and apical teeth, length of tarsi shorter than in males (Fig. 15D). **Abdomen:** Tergite VIII convex but with posterior margin slightly sharp, hidden by elytral apex in dorsal view (Fig. 15C, 16C). Sternite VIII longer than in males with posterior margin projected, sternite VII with same length as sternites V-VI together, punctures more robust, denser on sides than medially.

Geographical distribution. Restricted to South America until now, recorded to the following countries: Bolivia and Brazil (Fig. 50). Regarding biogeographical regions (Morrone 2014), the distribution of *Minisiderus* range from the Pará province in northern Brazil to the Chacoan and Parana Forest provinces in eastern Bolivia and southern Brazil respectively. In Brazil, species of *Minisiderus* are recorded to the following states: Bahia (new record), Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná and Rondônia (Fig. 50).

Remarks. In spite of being considered a subgenus of *Brachysiderus* for many years, *Minisiderus* is not similar to its former genus. While males of *Minisiderus* are small and have a pair of horns connected on base (Fig. 51A, 51C), males of

Brachysiderus are big and have a single frontal horn projected and bifid on apex (Fig. 51B). Also, males of these two genus can be distinguished by: in *Minisiderus*, shape of ocular canthi thin, not crossing outer margin of eye, apical protuberance absent (Fig. 51A, 51C), protarsal claws symmetric and thin, protarsomere V slender with inner margin curved (Fig. 51H), whereas in *Brachysiderus* shape of ocular canthi long and thick, crossing the outer margin of eye, with apical portion distinctly projected as a sharp protuberance (Fig. 51B), protarsal claws asymmetric, protarsomere V thick and distinctly arcuated with notch on inner margin (Fig. 51I). Female *Minisiderus* has clypeus round with margins simple (Fig. 51D), base of clypeus curved to ocular canthi (Fig. 51D), ocular canthi elongated, but with no sharp protuberances basally (Fig. 51D), pronotal sculpture formed mainly by moderate punctures on disc (Fig. 51D), elytra completely brown with darker spots absent on apical and humeral umbones (Fig. 51F), whereas female *Brachysiderus* has clypeus elongated with sharp protuberances on apical corners (Fig. 51E), base of clypeus sharp and projected (Fig. 51E), ocular canthi long and thick with basal sharp protuberance (Fig. 51E), pronotal sculpture formed mainly by thin punctures (Fig. 51E), elytra dark yellow with dark brown spots on both apical and humeral umbones (Fig. 51G).

The only other genus that bear resemblances to *Minisiderus* (except those in *M. paranensis* group) is *Aegopsis*, especially minor males of *Aegopsis* that have pronotal horn very short as well as cephalic horns and females. These two genera are also sympatric through the Brazilian Cerrado, but they can be distinguished by the following characters: males of *Minisiderus* with pair of horns connected basally (Fig. 51A-C, 52A), pronotum with a pair of tubercles near anterior margin (Fig. 52A), pronotal sculpture mainly punctate, wrinkles only near tubercles when present (Fig. 52A), parameres in ventral view with ventral sclerite not continuous to ventral carinae (Fig. 52C), ventral area of parameres short and subrectangular (Fig. 52C), whereas males of *Aegopsis* with a pair of horns distinct, not connected basally (Fig. 52B), pronotum with a distinct horn emerging from disc in major males (Fig. 52B), minor males with anterior half of pronotum distinctly wrinkled from middle to corners, wrinkles entangled, parameres, in ventral view, with ventral sclerite continuous to ventral carinae (Fig. 52D), ventral area of parameres elongated (Fig. 52D). Females of *Minisiderus* have generally tergite VIII hidden by elytral apex in dorsal view (Fig. 52I), ocular canthi elongated with base not elevated (Fig. 52E), clypeus in frontal view distinctly thickened (Fig. 52G), whereas females of *Aegopsis* have tergite VIII crossing the apex of elytra in

dorsal view (Fig. 52J), ocular canthi short and slightly protruded basally (Fig. 52F), clypeus in frontal view distinctly narrow (Fig. 52H).

It is interesting how it took more than a hundred years until the *Minisiderus* were separated from *Brachysiderus*. Arrow (1902), in the description of *M. paranensis*, recognized the characteristic differences between that new species and *Brachysiderus quadrimaculatus* (the only species of the genus at that time), but decided to include it in the genus based on the general form and color. The placement of the species that we know today as *Minisiderus* within *Brachysiderus* had been questioned even when Ohaus (1930) described *M. minicola*, *M. matogrossensis* and *M. goyanus*. Ohaus (1930) had doubts about the genus in which those species should be described, considering their description in *Brachysiderus* as a provisional placement, only certain about the relation of those new species to *Agacephala* and *Antodon*. Endrödi (1970) took the first step to the separation with the creation of subgenus *Minisiderus*, but it was Milani (2018) who decided to review this status and to elevate *Minisiderus* to generic status based on the morphological differences and geographical distribution. We here are using the Milani's generic concept of *Minisiderus*.

***Minisiderus paranensis* (Arrow, 1902)**

(Figs. 1, 3-6, 50)

Brachysiderus paranensis Arrow 1902: 146 (original description, original combination);
Brachysiderus (Minisiderus) paranensis Endrödi 1970: 61 (review); Endrödi 1985: 217 (cited);
Grossi & Grossi 2005: 28 (cited); Abadie 2010: 201 (cited); Grossi, Dechambre & Grossi 2012:
12 (cited); Abadie 2014: 127 (cited); Abadie, Godinho Jr. & Koike 2016: 234 (cited);
Brachysiderus (Minisiderus) paranensis paranensis Grossi, Dechambre & Grossi 2012: 12 (new
status);
Minisiderus paranensis paranensis Milani 2018: 79 (new status, new combination).

Diagnosis. Male: Body with head, thorax, abdomen and legs testaceous, elytra yellowish with margins testaceous and testaceous patches on humeral and apical umbones (Fig. 1A-B). Cephalic horns distinctly elongated, with base connected (Fig. 3E). Horns in lateral view with apex smoothly upturned (Fig. 3G). Ocular canthi elongated, anterior margins concave, apex slightly emarginated (Fig. 3E). Antennae with club elongated, almost 3 times longer than high, club longer than antennomeres I-VII together (Fig. 3G). Pronotum with pair of tubercles distinctly emarginated medially,

in dorsal view (Fig. 1A). Pronotal anterior margin, in lateral view, straightly connected with base of tubercles (Fig. 1B). Protibia with three outer teeth. Parameres asymmetric basally with laminar projection projected internally, in caudal view apical medial portion not carinated at inner margin (Fig. 6E). Basal portion of parameres with five inner ridges decreasing in size anteriorly (Fig. 6E,H).

Redescription. Male. **Color:** Surface slightly lustrous; head and pronotum reddish brown; appendages and venter brown, elytra dark yellow on disc with margins dark brown (Fig. 1A-B). **Head:** Cephalic horns projected and elongated, connected basally, presence of two dorsal carinae smooth from horns to frons; lateral margins of horns with shallow depression on connection with ocular canthi (Fig. 3E). Vertex and frons with surface smooth and densely punctate; punctures near vertex larger than frontal punctures near base of horns, C-punctures laterally near eyes and thin small punctures medially. Clypeus rectangular, dorsal surface with lateral borders depressed, middle slightly elevated (Fig. 3F); punctures densely agglomerated near borders, C-punctures densely distributed on medial elevation. Ocular canthi with anterior margin smoothly connected with lateral margin of horns, canthi base slightly round, apex near tip slightly deflected (Fig. 3H); punctures bigger near anterior margin of canthi than medially, setae absent, presence of strongly curved carina basally (Fig. 3E).

Mouthparts: Labrum bilobated, lateral margins slightly elongated (Fig. 4H). Mandibles subtriangular, in ventral view with two apical teeth, outer margin distinctly projected with a slight depression (Fig. 4E), inner margin of molar area slightly round (Fig. 4E); in dorsal view, basal portion near molar area as long as wide (Fig. 4F), mesal brush on inner margin not expanded beyond the line of inner tooth (Fig. 4F), in lateral view, with molar area excavated and mesal brush reaching base of molar area (Fig. 4G). Maxillae with galea with one tooth acute, ventral portion of stipes almost covering lateral border at outer margin, lateral border with base of setae visible in ventral view, maxillary palpomere II 2.5 times longer than wide, palpomere IV short and round (Fig. 5D); in dorsal view, galea densely hirsute, maxillary palpomere IV with sensorial area ellipsoid and thin, distance from sensorial area to apex of 1.5 times the sensorial area length (Fig. 5E). Mentum with shape elongate, surface hirsute on margins and with moderate punctate sparsely distributed in ventral view, base slightly depressed (Fig. 5F). **Thorax:** Pronotum convex, anterior margin not excavated, presence of two short tubercles oblique; anterior margin thick medially (Fig. 3F). Pronotal tubercles directed upward,

pronotal anterior margin oblique towards tubercles (Fig. 3G). Pronotal punctures moderate and sparse medially, presence of C-punctures near lateral margins, punctures denser and thinner surrounding tubercles, pronotal posterior margin with punctures not agglomerated (Fig. 1A). Metasternum hirsute, setae laterally more thick and dense than medially, presence of medial depression posteriorly. Scutellum subtriangular, lateral margins smooth, surface with dense thin punctures with few ocellate punctures near base. **Elytra:** Form 2.3 times longer than wide. Elytral disc covered by ocellate punctures strongly marked, few coalescent punctures near elytral suture and lateral margins, punctures thinner on apical and humeral umbones, presence of short orange spot on both umbones (Fig. 1A). **Legs:** Protibia with three outer teeth increasing in size distally, dorsal surface covered by C-punctures near inner margin and thin punctures sparse near outer margin; in ventral view, apical outer corner with slender and slightly elongated spine near spur. Protarsi slender and simple, claws symmetric and thin. Mesotibiae with two outer teeth, presence of longitudinal carina near inner margin, carina not crossing line of basal tooth (Fig. 1B); thick setae absent near oblique carina of apical tooth. Metatibial apex convex, punctures thin and sparse near apex. Metacoxae with smooth agglomeration of punctures near posterior margin. **Abdomen:** Tergite VIII round and distinctly projected in lateral view (Fig. 1B), surface densely covered by thin punctures, disc medially with punctures dense. Sternites IV–VI with few thin punctures on disc, more punctate on sides, presence of thin and sparse setae on sides not reaching middle. Sternite VII more punctate on sides than sternite VI and with posterior row of setae more spread than sternites V–VI. Sternite VIII distinctly bilobated, posterior margin V-shaped, surface densely punctate, punctures thin, presence of setae from lateral margins to apex of lobes. **Aedeagus:** Parameres asymmetric basally, in caudal view apical medial portion not carinated at inner margin (Fig. 6E), basal portion with left posterior margin round (Fig. 6E), right posterior margin with laminar projection projected internally, basal portion with five inner ridges decreasing in size anteriorly (Fig. 6E,H), posterior phallobase with corners distinctly depressed (Fig. 6E). In lateral view, parameres with ventral portion 2.3 times longer than wide (Fig. 6F), ventral portion with depression short, distant from margin (Fig. 6F). In ventral view, ventral sclerites connected with parameres by ventral carinae, shape thick, sides round, anterior margin deeply emarginated, parameres with ventral carina short, apex blunt (Fig. 6G).

Measurements of holotype. Body length: 31.5 mm. Cephalic horns length: Elytral length: 19 mm. Elytral width: 10.1 mm. Pronotal length: 10.3 mm. Pronotal

width: 18.4 mm. Protibial length: 5.3 mm.

Male variation. Few males with tergite VIII distinctly elongated, ocular canthi with anterior margin straight and apex round, cephalic horns in lateral view with apex abruptly upturned. Body length: 23.3–28.4 mm. Elytral length: 14.8–16.7 mm. Elytral width: 7.7–8.9 mm. Head length: 3.3–3.8 mm. Pronotal width: 10.5–12.3 mm. Pronotal length: 6.5–8.3 mm. Protibial length: 6.2–6.9 mm.

Female. Not examined.

Geographic distribution. Brazil: Minas Gerais, Paraná, São Paulo (Fig. 50).

Material examined. Holotype 1 male (NHM): a) “Castro,/ Parana/ E.D. Jones/ 99.105”, b) “Type”, c) “Brachysiderus/ paranensis/ type M# Arrow”, d) “NHMUK 014560408”. **Other specimens:** 1 male (NHM): a) “Brachysiderus/ paranensis. Arrow.”, b) “Nevinson Coll./ 1918-14”, c) “NHMUK 014560407”; 1 male (CERPE): a) “Brasil, Minas Gerais, São/ Gonçalo do Rio Preto, P. E./ Rio Preto, 22.xii.2011. Luz/ Negra, Oliveira & Ferreira {leg.}”; 1 male (CERPE) with same data as holotype. 1 male (CERPE) labeled: a) “MG, São Roque de Minas/ PN Serra da Canastra/ Entrada do Parque, Campo Limpo/ 20°15'39”S, 46°24'37”W/ 27.XII.07. M.F. Souza”; 1 male (MZUSP): a) “Minas Geraes/ V.d. Hoven leg./ Anno 1922”; 1 male (MZUSP): a) “São Paulo/ Ypiranga I/ 12551”; 1 male (MZUSP): a) “Parq. Estado./ S. Paulo/ 1936”, b) “Coll. J. Guerin/ S. Paulo, Brasil/ 10882”; 1 male (MZUSP): a) “São Paulo/ Ypiranga/ 20620”; 1 male (MZUSP): a) “S. Paulo cidade/ 1914”.

Remarks. *Minisiderus paranensis* is only similar to *M. lenorae*, differing from it by: males with clypeus subrectangular elongated, lateral margins round (Fig. 3F), cephalic horns narrower than clypeal apex (Fig. 3F), frons not wrinkled (Fig. 3E), parameres in caudal view with apical portion medially not carinated at inner margin (Fig. 6E) and basal portion with left posterior margin round (Fig. 6E), whereas in *M. lenorae* clypeus subtrapezoidal short, lateral borders oblique (Fig. 3B), cephalic horns wider than clypeal apex (Fig. 3B), frons with distinct wrinkles diagonally connected with base of horns (Fig. 3A), parameres in caudal view with apical portion medially carinated at inner margin (Fig. 6A), basal portion with left posterior margin angulated (Fig. 6A).

Although this species was first described from Paraná state, it was never collected again in South Brazil, and all the other records are from São Paulo and Minas Gerais states, in southeastern Brazil, even with efforts during more than ten years at the type locality. Recent collections demonstrated that this species is related to rupestrian

Cerrado, and as most of the Cerrado fields of South Brazil have become crop fields, it is very probable that *M. paranensis* is extinct in that region.

***Minisiderus lenorae* (Grossi, Dechambre & Grossi, 2012) stat. nov.**

(Figs. 2–6, 50)

Brachysiderus (Minisiderus) paranensis lenorae Grossi, Dechambre & Grossi 2012: 10 (original description);

Minisiderus paranensis lenorae Milani 2018: 79 (new status, new combination).

Diagnosis. Males: clypeus subtrapezoidal short, lateral borders oblique, middle slightly emarginated (Fig. 3E). Cephalic horns wider than clypeal apex (Fig. 3E). Ocular canthi with anterior margin slightly oblique and apex truncate (Fig. 3A). Frons with distinct wrinkles diagonally connected with base of horns (Fig. 3A). Pronotal anterior margin distinctly concave on corners (Fig. 3G). Pronotal tubercles distinctly marked in frontolateral view (Fig.). Parameres asymmetric basally with laminar projection projected internally, in caudal view apical medial portion carinated at inner margin (Fig. 6A), basal portion with left posterior margin angulated (Fig. 6A), basal portion with six inner ridges decreasing in size anteriorly (Fig. 6A,D), posterior phallobase with corners slightly depressed (Fig. 6A).

Redescription. Male. **Color:** Surface slightly lustrous; head and pronotum reddish brown; appendages and venter brown, elytra dark yellow on disc with margins dark brown; greenish metallic shine on head and pronotal borders (Fig. 2A-B). **Head:** Cephalic horns parallel and connected at basal inner margins, triangular in cross-section with dorsal carina on both horns, horns directed forward and tip upward, presence of depression medially on base between horns (Fig. 3B). Vertex not excavated, frons with depressions lateral depressions near horns and ocular canthi; punctures moderate and sparse on vertex, becoming smaller and denser towards frons (Fig. 3A). Clypeus subtrapezoidal broad, lateral margins slightly emarginated, apex bilobate, surface excavated on sides and apex, flat medially (Fig. 3B); punctures large and dense laterally, becoming thinner medially. Ocular canthi with anterior margin basally acute, becoming concave towards lateral margins of horns, tip round, surface with thin and sparse punctures abundant, presence of short curved carina barely reaching frons (Fig. 3D). **Mouthparts:** Labrum bilobated, lateral margins slightly angulated (Fig. 4D).

Mandibles subtriangular with two apical teeth, in ventral view with strong basal depression on outer portion near condyle (Fig. 4A), inner margin of molar area angulated; in dorsal view, mesal brush not reaching basal portion, surface of mandibles mostly flat, apex slightly concave, base distinctly depressed near basal sclerite (Fig. 4B). Maxillae with galea with one tooth acute and oblique directed to inner side, in ventral view with a short basal carina and a short round protuberance near apex, palpomere II almost 3 times longer than palpomere I (Fig. 5A-B). Mentum with shape elongate, surface hirsute and densely punctate in ventral view; in dorsal view, presence of lateral carina near apical corners, apex at middle parabolic (Fig. 5C). **Thorax:** Pronotum convex, anterior margins and posterior corners slightly excavated, presence of two short tubercles oblique and divergent with apex slightly emarginated; anterior margin distinctly bordered (Fig. 3B). Pronotal punctures moderate and sparse medially, C-punctures laterally on disc, marginal punctures dense and mixed, punctures thin near tubercles, posterior margin of pronotum with oblique row of agglomerated punctures (Fig. 2A). Metasternum hirsute, setae laterally more thick and dense than medially, presence of medial depression posteriorly. Scutellum subtriangular, base wide, slightly angulate, surface with ocellate punctures moderate and dense becoming sparser towards apex. **Elytra:** Form 2.4 times longer than wide, in dorsal view apical portion distinctly oblique (Fig. 2A). Surface covered by ocellate punctures irregularly distributed, punctures of different sizes on disc, few punctures coalescent near elytral suture, punctures smaller and ocellate on apical and humeral umbones, apical umbones with slightly elongate orange spot (Fig. 2A). **Legs:** Protibia with three external teeth increasing in size distally, dorsal surface with thin and sparse punctures basally, punctures near teeth and apex thinner than on base, presence of large punctures on setae rows. Protarsi slender and simple, claws symmetric and thin. Meso- and metafemora with two distinct rows of setae near anterior and posterior margins, presence of dense coalescent punctures between both rows and the respective margins. Mesotibiae with two outer teeth, thick setae present near oblique carina of apical tooth (Fig. 2B). Metatibial apex convex and slightly projected, apical margin distinctly crenulated, thick setae of distal carinae and dorsal surface ending in same position, punctures thin and sparse near apex. Metacoxae with distinct agglomeration of punctures near posterior margin. **Abdomen:** Tergite VIII round and slightly projected in lateral view; surface densely wrinkles on sides, disc with thin and sparse punctures medially, more dense towards posterior margin. Sternites IV–VI with few thin punctures on disc, more

punctate on sides, presence of thin and sparse setae on sides not reaching middle. Sternite VII less hirsute on sides than sternite VI but more punctate, presence of few bigger punctures on disc, punctures dense and coalescent near posterior margin medially. Sternite VIII distinctly bilobated, posterior margin V-shaped, surface with thin punctures denser on disc medially, presence of long thin setae on lateral margins. **Aedeagus:** Parameres asymmetric basally, in dorsal view basal projection originated at right side expanding towards posterior phallobase, shape laminar; presence of 6 ridges on base, apex parallel as wide as base (Fig. 6A,D). In lateral view, anterior phallobase more than two times shorter than posterior phallobase, posterior phallobase distinctly excavated medially forming two elongate lateral projections with apex slightly depressed, ventral portion of parameres with depression elongated, almost reaching margin (Fig. 6B); parameres with ventral sclerite oblique, fovea absent, dorsal sclerite distinctly angulate towards ventral sclerite (Fig. 6C). In ventral view, ventral sclerite not flat, distinctly detached from phallobase, apical portion with short ventral carina hook-shaped (Fig. 6C).

Measurements. Body length: 26.5 mm. Elytral length: 18.1 mm. Elytral width: 10 mm. Head length: 3.7 mm. Pronotal width: 12.6 mm. Pronotal length: 8.4 mm. Protibial length: 7.2 mm.

Females. Not examined.

Geographic distribution. Brazil: Distrito Federal, Goiás (Fig. 50).

Material examined. Holotype male (DZUP): “Brasília, Fazenda Água Limpa, DF, Brésil, 28.I.1986”. **Paratypes.** 3 males with same data as holotype (CERPE); 4 males (EPGC) with same data as holotype, except “13.I.1986”; 2 males (CERPE) with same locality as holotype, but “28.I.1986”; 1 male (CERPE) with same locality as holotype, but “13.II.1986”; 2 males (EPGC) labeled: “Brasília, DF, Brésil, XI. 1992”; 2 males: “Brasília, Parque Olhos D’Água, DF, Brésil, 04.II.2003”; 1 male (R.P. Dechambre collection) with same locality as holotype, but “13.I.1986”; 1 male (F. Dupuis collection) with same locality as holotype, but “13.I.1986”. **Other specimens.** (CMNC): a) “LEOPOLDO BULHOES/ Est. {State of} Goyaz, Dez. {19}37/ Dr. Nick.”, b) “H. & A. HOWDEN/ COLLECTION/ ex. A. Martinez coll.”.

Remarks. *Minisiderus lenorae* was erected to the status of species due to its diagnostic characters and geographic distribution considered distinct enough from *M. paranensis* to be maintained as the same species. Differences between *M. lenorae* and *M. paranensis* can be seen in the **diagnosis** section of *M. paranensis*.

***Minisiderus benjamini* (Abadie, 2014)**

(Figs. 9-12, 14-15, 50)

Brachysiderus (*Minisiderus*) *benjamini* Abadie 2014: 126 (original description); Abadie,

Godinho Jr. & Koike 2016: 234 (cited);

Minisiderus benjamini Milani 2018: 79 (new combination).

Diagnosis. *Minisiderus benjamini* differs from other *Minisiderus* (except *M. minicola*, *M. mielkeorum* and *M. elyanae*) by the protibiae with three outer teeth (Fig. 15A). For differences between *M. benjamini* and *M. minicola* see the Diagnosis section of *M. minicola*. Male of *M. benjamini* can be distinguished from *M. mielkeorum* and *M. elyanae* by frons depressed (Fig. 9F) [frons with protuberances in *M. mielkeorum* (Fig. 17B) and *M. elyanae* (Fig. 17G)], in lateral view, posterior phallobase concave near corners (Fig. 12E) [posterior phallobase straight near corners in *M. mielkeorum* (Fig. 20B) and *M. elyanae* (Fig. 20E)], in caudal view, parameres with outer margin round with distinct notch towards apex (Fig. 12D) [parameres with outer margin not round with (Fig. 20D) and without notch (Fig. 20A) in *M. elyanae* and *M. mielkeorum* respectively].

Females of *M. benjamini* differs from other species by the following characters: Clypeus round and 2.5 times wider than long (Fig. 14D). Ocular canthi thick, with anterior margin round (Fig. 14D). Frons with a pair of sharp and short tubercles (Fig. 14E). Elytra, in lateral view, with margins round and apex thick (Fig. 15D). Tergite VIII with posterior margin almost straight laterally (Fig. 15D).

Redescription. Male. **Color:** Surface slightly lustrous; head and pronotum dark reddish brown; appendages, elytra and venter brown (Fig. 15A-B). **Head:** Cephalic horns transverse projected forward and slightly upward, dorsal surface flat, frontal surface slightly thick (Figs. 9E-F). Frons and vertex flat; punctures coalescent and large, transverse on vertex, ellipsoid on frons. Clypeus subtrapezoidal, apex slightly truncate, surface covered by large and sparse punctures, punctures coalescent near horn (Fig. 9E). Ocular canthi oblique, tip round, anterior margin protruded basally at connection with horn base, presence of a thin carinae perpendicular to protuberance (Fig. 9D); surface with short coalescent punctures, few setae on tip. **Mouthparts:** Labrum in dorsal view with anterior margin round, sides slightly sharp (Fig. 10H). Mandibles subtriangular

with two subparallel carinae, mandibular apex distinctly elevated with a distinct tooth on outer corner, mesal brush slightly protrude on inner corner (Fig. 10E); in dorsal view, tooth distinctly emarginated, outer margins crenulated near base (Fig. 10F); in lateral view, molar area with anterior portion slender (Fig. 10K). Maxilla with galea subtriangular, inner margin straight (Fig. 11D), ventral stripes with basal portion short near base of lateral border (Fig. 11D); in dorsal view, cardum distinctly crossing margin of stipes (Fig. 11E). Mentum 1.5 times longer than wide, apical corners distinctly narrowing to apex (Fig. 11F). **Thorax:** Pronotum slightly bordered, disc convex with two short protuberances near anterior margin (Fig. 9E); presence of shallow fovea posterior to protuberances, only conspicuous in lateral view (Fig. 15B). Pronotal disc mainly covered by thin and sparse punctures on sides and posteriorly intertwined by few micropunctures, punctures bigger and dense near anterior corners, area near protuberances with some wrinkles and coalescent punctures. Prosternum with some wrinkles laterally, presence of foveae on prosternal corners anteriorly. Metepisternum and metasternum densely hirsute, presence of wrinkles laterally on metasternum. Scutellum subtriangular with wide base, surface covered by short and large ocellate punctures basally, apex barely punctate. **Elytra:** Form 2.3 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed (Fig. 15A). Apical and humeral umbones with thin sparse punctures, not ocellate. **Legs:** Protibia with three distinct external teeth increasing in size distally, protibia longer than protarsus; in dorsal view, protibia narrowing on inner edge between basal and medial teeth (Fig. 15A). Protibial surface punctate, punctures moderate and sparse in dorsal view; in ventral view, inner apical margin with short tooth near spur. Metatibia with surface punctate, thinner punctures near junction with metafemur; in ventral view, presence of short thick setae on surface near inner margin reaching apex of carina of middle metafemoral tooth. Metatibial apex slightly concave near ventral spur, apical margin edgy towards apical metafemoral external tooth. **Abdomen:** Tergite VIII round with a smooth constriction towards corners; surface with microsetae, densely covered by C-punctures on disc and wrinkles on corners and posterior margin, posterior margin with thick microsetae at middle. Sternite VIII with rows of dense setae laterally towards corners, presence of flat punctures near anterior margin, disc barely punctate. Sternite VII almost 2 times longer than sternite VI. Sternites IV–VII with disc finely punctate, posterior margins with punctures bigger and sparser than disc, presence of setae on corners not reaching middle. **Aedeagus:** Parameres symmetric, in dorsal view, with

basal portion folded to middle, outer margin oblique basally ending in small protuberances, slightly round medially, narrowing to apex, tips divergent (Fig. 12D). In lateral view, anterior phallobase longer than parameres, posterior phallobase with corners extended reaching parameres basally (Fig. 12E); parameres with lateral carina not covering ventrolateral fovea (Fig. 12E). In ventral view, ventral sclerite of parameres flat, ventrolateral depression fusiform with medial portion distinctly wider than apical and basal portions, apical sclerite as long as wide (Fig. 12F).

Measurements. Body length: 18.3–27.2 mm. Elytral length: 11.6–16.9 mm. Elytral width: 6.9–9.4 mm. Head length: 2.9–4.2 mm. Pronotal width: 9–13.9 mm. Pronotal length: 6.2–8.5 mm. Protibial length: 5.5–6.3 mm.

Females. Females oblong, general shape similar to males but hornless (Fig. 15C-D). **Head:** Frons with two separated distinct tubercles near clypeal base (Fig. 14D), tubercles short and sharp (Fig. 14E). Frons and vertex distinctly rugose with few thin punctures intertwined among them near tubercles. Clypeus round and 2.5 times wider than long (Fig. 14D), clypeal base slightly elevated and round toward ocular canthi (Fig. 14E); clypeal punctures moderate and sparse apically, becoming denser and thinner basally, base with few wrinkles anteriorly. Ocular canthi thick, with anterior margin round, apex sharp, surface rugose (Fig. 14D). **Thorax:** Pronotum convex, pronotal tubercles absent, punctures moderate and dense on disc, bigger punctures on posterior corners, anterior half with coalescent punctures transversely distributed (Fig. 15A). Lateral margins of pronotum flattened (Fig. 15A). Elytra in dorsal view with basal surface longitudinally rugose (Fig. 15A); in lateral view, elytra with margins round and apex thick (Fig. 15D). **Legs:** Metatibia with medial tooth distinctly elongated, posterior carinae crenulated, surface with C-punctures longitudinally distributed from base to almost reaching apex (Fig. 14G). Tergite VIII with posterior margin almost straight laterally (Fig. 15D).

Measurements of females. Body length: 23.3 mm. Elytral length: 14.7 mm. Elytral width: 8.2 mm. Head length: 3 mm. Pronotal width: 10.1 mm. Pronotal length: 7.3 mm. Protibial length: 5.7 mm.

Geographic distribution. Brazil: Mato Grosso (Fig. 50).

Material examined. **Holotype** male (CEMT): a) “Tangara da serra/ Mato Grosso, Brazil,/ 11-VIII-2006/ Ricardo Silva leg.”. **Other specimens:** 1 male (NHM): a) “Rosario Oeste/ M{ato} Grosso, Brés {Brazil}, {1}969”, b) “ex coll./ R.-P. Dechambre”, c) “Brit{ish}. Mus{eum}./ 1978 525”; d) “Brachysiderus/ minicola

Ohaus/ R.-P. Dechambre det. 1974”; 1 male (NHM): a) “Brazil, Mato Grosso/ Dry Forest Base Camp/ 256km N of Xavantina, xi. 1967/ 12°49'S, 51°46'W/ Brian Freeman leg.”; b) “BMNH/ 2009-6”, c) “*Brachysiderus/ minicola* Ohaus/ S. Pokorný det. 2011”; 1 male (CERPE): a) “BRASIL, MT,/ Alto Rio Arinos/ Diamantino X. {19}98/ E. Furtado leg.”; 1 male (CERPE): a) “BRASIL, MT,/ Alto Rio Arinos/ Diamantino X. {19}98/ E. Furtado leg.”; 1 male (UFMT): a) “UFMT {diagonal}/ MT, Cuiabá/ 13-XI-1993/ Mirian A. Serranto”; 1 female (UFMT): a) “BRASIL, MT,/ Diamantino, Faz. Vale/ da Solidao,/ luz, E. Furtado leg.”; 1 male (UFMT): a) “BRASIL: Mato Grosso, Po-rto Estrela. EES das Arar/ as. Sede. 15°39'09"S, 57°/12'53"W, 217m, 8-12-X-/2011, light. Vaz-de-Mello”.

Remarks. *Minisiderus benjamini* occurs in the western part of Brazilian Cerrado from the transitional areas between Cerrado and the Chiquitano dry forests to areas of mixed shrubland and arboreal Cerrado phytophysiognomies in Cuiaba lowlands at the foothills of the Chapada dos Guimarães. The distribution of this species apparently is not limited by the diverse areas of Chapadas and lowlands along the Cerrado formations in Mato Grosso, with its northernmost record in the Mato Grosso Tropical dry forests, a transitional area between Cerrado and the Amazonian southern moist forests.

Due to the morphological similarity between species of *Minisiderus*, some specimens of *M. benjamini* were deposited in collections labeled as *M. minicola*. In the original description, Abadie (2014) had access only to a single male specimen that he used as the holotype. Herein we describe for the first time a female of *M. benjamini* based on a specimen from Diamantino, Mato Grosso.

***Minisiderus bertolossiorum* (Abadie, Godinho Jr & Koike, 2016)**

(Figs. 9-12, 26, 50)

Brachysiderus (*Minisiderus*) *bertolossiorum* Abadie, Godinho Jr. & Koike 2016: 232 (original description);

Minisiderus bertolossiorum Milani 2018: 79 (new combination).

Diagnosis. Males of *M. bertolossiorum* can be distinguished from other species by: Clypeal base with two distinct lateral protuberances with apex divergent (Fig. 9G). Distance between tips of cephalic horns 2.1 times narrower than clypeal base, sides of horns not touching sides of clypeus (Fig. 9H). Antennae with club long and large, bigger than other segments together (Fig. 9I). Pronotum with two short tubercles near

anterior margin, tubercles transverse and flat, emarginated on apex (Fig. 9H). Mandibles in lateral view with ventral condyle big, almost of same size as molar area (Fig. 10K), lateral portion of mesal brush with dorsal side straight to molar area (Fig. 10J).

Metatibial anterior carina oblique and slightly curved to basal tooth, in lateral view (Fig. 26B). Mesotibial apex with slight concavity towards apical tooth (Fig. 26B). Parameres, in caudal view, with outer margin on basal portion evenly round and on apical almost straight to apex, inner margin with distinct deep notch medially and slightly concave near folding (Fig. 12G). Parameres, in lateral view, with lateral carina almost touching margin of ventral sclerite, carina on basal portion of parameres straight, (Fig. 12H). In ventral view, ventral sclerite covering part of ventral carinae of parameres, apical margin of ventral sclerite distinctly acute on corners (Fig. 12I).

Redescription. Male. **Color:** Surface slightly lustrous; head, pronotum, appendages, elytra and venter reddish brown (Fig. 26A-B). **Head:** Cephalic horns transverse and projected forward, united basally, distance between tips of horns 2.1 times narrower than clypeal base, sides of horns not touching sides of clypeus (Fig. 9H). Frons and vertex not protuberant, vertex sparsely punctate with moderate punctures, frons densely punctate with moderate punctures, frontal punctures becoming sparser near horns base, presence of few wrinkles only on frontal sides (Fig. 9G). Clypeus subparabolic with sides oblique and slightly sinuous, corners and apex round, surface distinctly excavated with elliptical shape; clypeal punctures thin and sparse (Fig. 9H). Frontal base of horns reaching mesoapical region of clypeus, clypeal apex with excavated area 2.2 times wider than long (Fig. 9H). Clypeal base with two distinct lateral protuberances with apex divergent (Fig. 9G). Ocular canthi with anterior margin slightly convex, tip truncate, surface densely punctate, punctures coalescent and deeper on apex than basally (Fig. 9G); presence of inconspicuous semicircular carinae basally. Antennae with club long and large, bigger than other segments together (Fig. 9I). **Mouthparts:** Labrum with anterior margin distinctly round, sides blunt (Fig. 10L). Mandibles subtriangular with two subparallel carinae, mandibular apex with tooth short and inconspicuous, outer carina forming a distal angulation of circa 100° in ventral view (Fig. 10I); in lateral view, ventral condyle big, almost of same size as molar area (Fig. 10K), lateral portion of mesal brush with dorsal side straight to molar area (Fig. 10J); in dorsal view, tooth slightly protruded to outer corner, outer margin slightly sinuous, inner corner with mesal brush (Fig. 10J). Maxillae with galea subtriangular, inner margin straight, outer

margin distinctly convex (Fig. 11G); stipes, in ventral view with main sclerite almost losangular (Fig. 11G); in dorsal view not setose on inner margin; subgalea crossing part of stipes in dorsal view (Fig. 11H). Mentum 1.3 times longer than wide, densely setose on margins and base, sides slightly round, ventral surface with moderate and sparse punctures (Fig. 11I). **Thorax:** Pronotum slightly bordered, pronotal disc convex with two short tubercles near anterior margin; tubercles transverse and flat, emarginated on apex (Fig.). Pronotal disc completely covered by punctures, punctures moderate and sparse, becoming denser near anterior portions of lateral margins and anterior corners, punctures thinner and denser on anterior margin than on disc. Prosternum densely hirsute on corners and on medial protuberance. Scutellum subtriangular, densely punctate, punctures thinner on sides than on disc. **Elytra:** Form 2.1 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed (Fig. 26A). Apical umbones sparsely punctate by thin punctures, humeral umbones surrounded by thin punctures and densely punctate. **Legs:** Protibia with three outer teeth increasing in size distally, teeth with apex directed laterally, surface distinctly punctate, punctures thin and sparse, denser on teeth. Meso- and metatibiae with two oblique carinae at outer margin, presence of three outer teeth with basal and medial teeth connected to anterior and posterior carinae respectively; in lateral view, anterior carina oblique and slightly curved to basal tooth; basal tooth short, medial tooth longer than other teeth (Fig. 26B); mesotibial apex with slight concavity towards apical tooth (Fig. 26B). **Abdomen:** Tergite VIII round, wrinkles on corners and on anterior margin, disc and posterior margin densely punctate, punctures coalescent on disc, microsetae on entire surface, posterior margin with transverse row of short thin setae medially. Sternite VIII with posterior margin covered by long and short setae not reaching middle, surface finely punctate. Sternites VI longer than sternites IV-V laterally, surface finely punctate, presence of sparse row of short setae near posterior margin almost reaching middle. **Aedeagus:** Parameres symmetric, in caudal view, with basal portion folded to middle, outer margin on basal portion evenly round and on apical almost straight to apex, inner margin with distinct deep notch medially and slightly concave near folding (Fig. 12G). In lateral view, lateral carina almost touching margin of ventral sclerite, carina on basal portion of parameres straight, posterior phallobase with no distinct depression on corners (Fig. 12H). In ventral view, ventral sclerite covering part of ventral carinae of parameres, apical margin of ventral sclerite distinctly acute on corners (Fig. 12I).

Measurements. Body length: 22.3 mm. Elytral length: 13.6 mm. Elytral width:

7.4 mm. Head length: 3.8 mm. Pronotal width: 11.3 mm. Pronotal length: 6.8 mm.
Protibial length: 5.2 mm.

Female. Unknown.

Geographic distribution. Brazil: Goiás (Fig. 50).

Material examined. Holotype male (MNRJ): a) “Raizama, Goias, Brasil,/ 30-X to 40X-2015,/ Celso Godinho Jr coll.2”. **Paratypes:** 23 males (CGC) with same data as Holotype; 1 male (MNRJ) with same data as Holotype; 2 males (CERPE) with same data as Holotype.

Remarks. *Minisiderus bertolossiorum* is a unique species in the genus due to the distinct lateral protuberances at clypeal base, so it is difficult to mistake it with another species in the genus. This species occurs in areas of Cerrado in the complex of the Chapada dos Veadeiros as well as *M. veadeirensis* sp. nov. However, these two species differ by: clypeal base with two distinct lateral protuberances with apex divergent (Fig. 9G), pronotal tubercles transverse and flat (Fig. 9H-I), antennal club long and large, bigger than other segments together (Fig. 9I), parameres in caudal view with inner margin with distinct deep notch medially and slightly concave near folding (Fig. 12G), whereas in *M. veadeirensis* clypeal base directly connected to lateral margins of horns, with no protuberances (Fig. 24A), pronotal tubercles thick and not elongated transversely (Fig. 12B-C), antennal club short, not longer than other segments together (Fig. 12C), parameres in caudal view with inner margin of apical portion oblique with short notch medially, basal portion with inner margin oblique (Fig. 25A).

***Minisiderus elyanae* (Dechambre, 2009)**

(Figs. 17-22, 50)

Brachysiderus (Minisiderus) elyanae Dechambre 2009: 99 (original description); Abadie 2010: 201 (cited); Abadie 2014: 127 (cited); Abadie, Godinho Jr. & Koike 2016: 234 (cited); *Minisiderus elyanae* Milani 2018: 88 (new combination).

Diagnosis. Males of *M. elyanae* can be distinguished by the following characters: clypeus subrectangular, 2.1 times wider than long, sides parallel with round corners and apex (Fig. 17F). Ocular canthi with apex round, anterior margin straight (Fig. 17H). Area between cephalic horns narrow, in frontal view, 1.7 times narrower than clypeal base (Fig. 17F). Frons with two parallel short protuberances (Fig. 17G). In dorsolateral view, cephalic horns with inner margin not projected (Fig. 17G). Pronotal tubercle flat

and short, apex slightly emarginated (Fig. 17A). Mesotibia with anterior and posterior carinae equally oblique (Fig. 17I). Parameres, in caudal view, with outer margin distinctly notched near apex, basal portion with inner margin round after medial notch (Fig. 20D). In lateral view, ventrolateral carina reaching posterior angulation of lateral carina (Fig. 20E). Outer margin of parameres round posteriorly, apical margin of ventral sclerite emarginated and narrow with sides convex (Fig. 20F).

Females: Clypeus round and 2.1 times wider than long (Fig. 14E). Clypeal punctures sparsely distributed near tubercles, punctures on apex inconspicuous (Fig. 21E). Clypeal tubercles inconspicuous (Fig. 21G). Vertex and frons with wrinkles distinctly marked (Fig. 21E). Ocular canthi slender and almost transverse, apex round (Fig. 21E). Proximal coxites with shallow notch on apical margins (Fig. 21F). Elytra with apex round, exposing part of tergite VIII dorsally (Fig. 22C). Tergite VIII with posterior margin slightly emarginated laterally (Fig. 22D).

Redescription. Male. **Color:** Surface slightly lustrous; head and pronotum dark reddish brown; appendages, elytra and venter reddish brown (Fig. 22A-B). **Head:** Cephalic horns transverse projected forward, dorsal surface of horns slightly depressed, carinae present on inner margins but not projected (Fig. 17G), distance between horns short 1.7 times narrower than clypeal base (Fig. 17F). Frons with two short protuberances paired near vertex; frontal surface densely wrinkled on sides, densely punctate with large and dense punctures medially near protuberances (Fig. 17G). Clypeus subrectangular, sides subparallel with anterior corners round and tip truncate, dorsal surface straight except by two short slightly depressed areas laterally, clypeal apex not deflected (Fig. 17F); clypeal punctures dense, moderate punctures abundant with thin punctures among them. Ocular canthi elongated, anterior margin straight and oblique, tip round, surface wrinkled with few setae on tip (Fig. 17H); carinae round on canthi base. **Mouthparts:** Labrum with sclerotized portion thin, 4.7 times wider than long, sides slightly projected and blunt, anterior margin almost completely straight except by medial short bump (Fig. 18H). Mandibles subtriangular with two subparallel carinae, mandibular apex with distinct large tooth slightly emarginated, apex continuously curved between inner carina and tooth base, lateral side of molar area forming an angle of 90° with base of mesal brush (Fig. 18E); in lateral view, presence of short bump anteriorly to ventral condyle (Fig. 18G), molar area with basal portion distinctly excavated, mesal brush reaching base of molar area; in dorsal view, apical outer corner convex and densely covered by

mesal brush, inner margin crenulated (Fig. 18F). Maxillae with galea subtriangular, inner margin slightly concave, tip blunt; stipes, in ventral view, 1.3 times longer than wide, outer margin covering lateral border medially (Fig. 19D); in dorsal view, ventrobasal margin of stipes oblique and straight (Fig. 19E). Mentum 1.4 times longer than wide, densely setose on margins, sides slightly round, apex slightly notched, ventral surface with moderate and sparse punctures (Fig. 19F). **Thorax:** Pronotum slightly bordered, posterior margin straight medially, lateral margins distinctly downturned, pronotal disc convex with two distinct tubercles near anterior margin; tubercles connected basally, space between apex notched, tubercular shape short and flat (Fig. 17G). Pronotal disc densely covered by moderate and thin punctures, punctures sparse on disc, becoming bigger and denser on sides and corners; punctures near pronotal tubercles thinner and denser, wrinkles densely distributed on anterior margin. Prosternum with medial protuberance of anterior margin with same size as lateral protuberances, prosternal surface smooth with inconspicuous transverse carinae posteriorly to lateral protuberances. Scutellum subtriangular, apex blunt, surface densely punctate, punctures moderate. **Elytra:** Form 2.2 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed (Fig. 22A). Apical umbones sparsely punctate by thin punctures, humeral umbones with similar pattern as apical umbones. Sides of elytra slightly widened at apical third. **Legs:** Protibia with three outer teeth increasing in size distally, distance between basal and medial teeth longer than distance between basal and apical teeth, teeth distinctly downturned. Surface finely punctate, punctures denser on medial and apical teeth, sparser on basal tooth. Metafemora smooth with long and transverse row of setae near posterior margin, presence of punctures dense posteriorly to row of setae. Metatibia with two oblique carinae at outer margin, anterior and posterior carinae equally oblique (Fig. 17I); presence of three distinct teeth on outer margin, medial tooth more than 3 times longer than basal tooth (Fig. 17I); metatibial apex slightly round in ventral view, margin slightly crenulated; metatibial surface similarly punctate, punctures thin and sparse. **Abdomen:** Tergite VIII round with surface densely wrinkled, disc with some large punctures surrounded by wrinkles, lateral corners densely wrinkled. Sternite VIII with setae densely distributed on lateral portions of posterior margin, surface rugose on corners and near anterior margin. Sternites IV-VI equally long and punctate, punctures moderate and dense on sides, evenly marked medially. Sternite VII longer than previous sternites, presence of short row of setae near corners. **Aedeagus:** Parameres symmetric,

in caudal view, with outer margin distinctly notched near apex, basal portion with inner margin round after medial notch (Fig. 20D). In lateral view (Fig. 17J), ventrolateral carina reaching posterior angulation of lateral carina (Fig. 20E). Outer margin of parameres round posteriorly, apical margin of ventral sclerite emarginated and narrow with sides convex (Fig. 20F).

Measurements. Body length: 26.2 mm. Elytral length: 16.1 mm. Elytral width: 8.6 mm. Head length: 3.9 mm. Pronotal width: 12.9 mm. Pronotal length: 8.3 mm. Protibial length: 6.4 mm.

Female. Females are oblong, general shape similar to males but hornless (Fig. 22C-D). **Head:** Cephalic horns absent, frons with two inconspicuous tubercles near clypeal base (Fig. 21G); frontal surface with punctures thin and sparse between wrinkles (Fig. 21E). Clypeus round, clypeal base not elevated near canthus, clypeal apex discretely deflected (Fig. 21G); surface slightly excavated, with punctures thin and sparse, punctures on apex inconspicuous. Ocular canthi similar to male but thicker, presence of slightly oblique carina on base (Fig. 21E). **Mouthparts:** Mentum with base rounder than in males, apex narrow. Maxillae with stipes densely hirsute on base. **Thorax:** Pronotum convex, flatter than in males, pronotal tubercles absent, pronotal length 2.4 times longer than head (Fig. 22C); punctures bigger than in males, punctures on posterior half of disc thin and sparse, anterior half with punctures moderate and dense (Fig. 22C); pronotal posterior margins slightly sinuous on sides, anterior corners not crossing the line of canthi apex (Fig. 21G). Prosternum with anterior margin with middle portion distinctly longer than lateral protuberances, presence of circular depressions on anterior corners. **Legs:** Mesofemora shorter and thicker than in males; mesofemoral surface near posterior margin not as punctate as in males. Mesotibiae as in males, surface with punctures moderate and sparse. Metatibia with space between medial and apical teeth slightly excavated, surface with moderate punctures distinctly marked and sparse (Fig. 21H). **Abdomen:** Tergite VIII convex, densely punctate on disc with wrinkles surrounding margins. Sternite VIII longer than in males, surface densely wrinkled on anterior half with short setae sparsely distributed transversely near anterior margin. Sternite VII as long as sternite V-VI together, punctures densely distributed on corners near anterior margin. Sternites IV-VI with same pattern of punctures, punctures thin and sparse medially, becoming denser on corners. **Genitalia:** Proximal coxites with shallow notch on apical margins, long thin setae sparse on inner corners, bigger setae on distal coxites (Fig. 21F).

Measurements of females. Body length: 21.8 mm. Elytral length: 12.6 mm. Elytral width: 7.6 mm. Head length: 2.6 mm. Pronotal width: 9.3 mm. Pronotal length: 6.2 mm. Protibial length: 5.3 mm.

Geographic distribution. Brazil: Maranhão (Fig. 50).

Material examined. Holotype male (UFPR): a “Serra do Penitente,/ 480 m., Balsas Co,/ Maranhão, Brasil”. **Paratypes:** 10 males with same data as Holotype.

Other specimens: 1 male (CERPE): a “Brasil, MA, Caxia,/ Reserva Ecol{ógica}. Inhamum/ Povoado Coités/ 04°54'43"S, 43°25'30"W”, 1 female (CERPE): a “Brasil, MA, Urbano Santos/ Faz{enda}. Sol Nascente/ 19.I.2006 Luz {collected on}/ C.M. Maia”.

Remarks. *Minisiderus elyanae* is distributed through the northernmost part of Brazilian Cerrado and the Maranhão babaçu forests. The distribution in the Cerrado is almost the same as *M. mielkeorum*, occurring in areas of Chapadas and in urbanized areas. The northernmost distribution of this species occurs in areas of Maranhão babaçu forests, an area of transition between the Amazonian moist forests and the shrub-like vegetation of Cerrado, mainly characterized by the presence of the Babaçu palm (*Attalea speciosa*). This ecoregion is threatened by criminal burning and deforestation which has been causing such degradation that almost 50% of that is made of secondary forest or pasture (Sears, 2018).

M. elyanae only can be mistaken with *M. mielkeorum* due to the locality similarities and as those are the only species in *Minisiderus minicola* species group with frontal tubercles. For the differences between *M. elyanae* and *M. mielekorum* see the **Remarks** of *M. mielkeorum*. Milani (2018) provided the first description of a female *M. elyanae* from Feira Nova do Maranhão, a municipality localized 100km from Balsas, where the type specimen was collected. This area is composed by the phytophysiology of Cerrado characterized by open trees and scrub woodlands (Correia-Filho *et al.* 2011). Therefore, the female specimen described in this work is the first female of *M. elyanae* from an area of Babaçu Maranhão forests and corresponds to the northernmost distribution to the genus.

***Minisiderus goyanus* (Ohaus, 1930)**

(Figs. 39-43, 50)

Brachysiderus goyanus Ohaus 1930: 263 (original description or original combination);

Brachysiderus (Minisiderus) goyanus Endrödi 1970: 63 (review); Endrödi 1985: 218 (cited);

Grossi & Grossi 2005: 29 (cited); Abadie 2010: 201 (cited); Abadie 2014: 127 (cited); Abadie, Godinho Jr. & Koike 2016: 234 (cited);
Minisiderus goyanus Milani 2018: 79 (new combination).

Diagnosis. Male: frons not depressed (Fig. 40A). Ocular canthi slender with base protruded and apex round (Fig. 40B). Pronotum with lateral margins slightly curved towards anterior corners (Fig. 40A). Pronotal disc with posterior half sparsely punctate, punctures moderate, becoming shagrinated towards posterior corners (Fig. 39A, 40A). Pronotal tubercles short and thick (Fig. 40A). Area between anterior margin and tubercles straight in lateral view (Fig. 40A). Procoxae and protrocantheri densely hirsute, surface of procoxae completely rugose (Fig. 41B). Protibia with four outer teeth (Fig. 39B). Parameres in lateral view elongated with outer margin notched at apex (Fig. 43B). Inner margin of parameres with deep notch medially (Fig. 43A). Basal portion of parameres asymmetric, inner margin distinctly oblique (Fig. 43A). Posterior phallobase with apical corners distinctly fit into depression formed by ventral sclerite of parameres (Fig. 43C).

Redescription. Male. **Color:** Surface slightly lustrous; head, pronotum and appendages dark reddish brown; elytra brown (Fig. 39A-B). **Head:** Cephalic horns transverse and flat, connected basally, apex distinctly divergent (Fig. 40C). Frons not depressed (Fig. 40A); surface of frons and vertex with C-punctures dense medially and sparser laterally, regular punctures towards cephalic horns. Ocular canthi slender with base protruded and apex round (Fig. 40B); surface rugose, presence of curved carinae on base.

Mouthparts: Mentum with lateral margins basally parallel, curved towards apex, base 1.5 times wider than apical corners, ventral surface densely hirsute (Fig. 42C). Mandibles subtriangular, apex with round tooth slightly projected, tooth slightly notched mesolaterally, mesal brush on inner apical corner, outer margin with two separated rows of thin setae (Fig. 42A). Maxilla with galea slightly emarginated on apex, maxillary palpomere III elongated (Fig. 42B). **Thorax:** Pronotum slightly bordered, disc convex, fovea absent, presence of two short tubercles near anterior margin (Fig. 41A). Pronotal disc with posterior half sparsely punctate, punctures moderate, becoming shagrinated towards posterior corners (Fig. 39A, 40A). Pronotum with lateral margins slightly curved towards anterior corners (Fig. 40A). Pronotal tubercles short and thick (Fig. 40A). Area between anterior margin and tubercles

straight in lateral view (Fig. 40A). Prosternum with anterior margin with medial projection slightly longer than lateral projections, medial carina thick, prosternal corners distinctly hirsute from anterior to posterior margin (Fig. 41B). **Elytra:** Form 2.3 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed. Apical and humeral umbones with regular and thin punctures. Elytral apex slightly narrower than base (Fig. 39A). **Legs:** Protibia with four outer teeth, basal tooth almost inconspicuous (Fig. 39B); surface densely punctate, punctures thin and dense on outer margin, longitudinal row of thinner punctures medially. Procoxae and protrocantheri densely hirsute, surface of procoxae completely rugose (Fig. 41B). Mesotibiae with basal and medial teeth distinct, basal shorter than medial, apical tooth inconspicuous, anterior and posterior carina connected with basal and medial tooth respectively, carinae surface distinctly carinated. Metatibiae with basal tooth inconspicuous, medial and apical tooth distinct, metatibial surface with C-punctures on outer side between teeth (Fig. 41C). **Abdomen:** Tergite VII densely hirsute, posterior margin not crossing anterior margin of tergite VIII. Tergite VIII completely wrinkled, presence of short thin setae aggregated on medial portion of posterior margin (Fig. 41C). **Aedeagus:** Parameres, in caudal view, with apex distinctly notched, inner margin of parameres with deep notch medially, basal portion of parameres asymmetric, inner margin distinctly oblique (Fig. 43A). Parameres in lateral view elongated with outer margin notched at apex, lateral margins distinctly directed ventrally, not covering ventral carina (Fig. 43B). In dorsal view, posterior phallobase with apical corners distinctly fit into depression formed by ventral sclerite of parameres (Fig. 43C).

Measurements. Body length: 27.2 mm. Elytral length: 16.9 mm. Elytral width: 9.4 mm. Head length: 4.2 mm. Pronotal width: 13.9 mm. Pronotal length: 8.5 mm. Protibial length: 6.3 mm.

Material examined. Holotype male (ZMNB): a) “Lectotypus/ *Brachysiderus/ goyanus* Oh{au}s.”, b) “Goyaz/ Rio Verde/ (G.A. Baer S).”.

Remarks. For almost 80 years, specimens of *Minisiderus* with four protibial teeth and no pronotal fovea from Brazilian Cerrado were considered in the collections as *M. goyanus*. The description of *Minisiderus martinae* by Abadie (2010), a morphologically close specimen from Bolivia in an area relatively near Brazilian Cerrado, indicated that the diversity of species with similar traits throughout the Cerrado could be underrated. *M. goyanus* has a unique aedeagus with shape elongated, inner margin with deep notch and asymmetry on basal portion of parameres (Fig. 43A)

and no other specimen investigated by us had similar traits. *M. goyanus* was found in an area of Cerrado with patches of Alto Paraná Atlantic forests. However, the majority of native vegetation was turned into agricultural crops. The species previously identified in the collections as *M. goyanus* from areas of Cerrado in Mato Grosso were considered by us as new and their description was given after the topic of *M. martinae*.

***Minisiderus martinae* (Abadie, 2010)**

(Figs. 40-41, 43-45)

Brachysiderus (Minisiderus) martinae Endrödi 1970: 63 (original description); Abadie 2014: 127 (cited); Abadie, Godinho Jr. & Koike 2016: 234 (cited); *Minisiderus martinae* Milani 2018: 79 (new combination).

Diagnosis. Males: cephalic horns with space between them distinctly deep, 2.7 times wider apically than basally, apex of horns divergent (Fig. 40F). Clypeus broad and subtrapezoidal, 2.1 times wider than long, sides slightly oblique, corners round (Fig. 40F). Ocular canthi oblique with anterior margin almost straight, tip truncate, presence of a short carina semicircular from canthi base to base of horns (Fig. 40E). Protibiae with four outer teeth (Fig. 44A). Pronotum convex with two short tubercles flat and distinct; in lateral view, space between anterior margin and tubercles concave (Fig. 40D). Parameres, in caudal view, with basal posterior projection blunt and short, outer margin of apical portion almost straight, inner margin of apical portion distinctly angulated (Fig. 43D). Parameres in lateral view with lateral margin distinctly projected ventrally, covering most part of ventral carina (Fig. 43E). Parameres in ventral view with apex subrectangular and slender, ventral depression constricted between lateral and ventral carinae, ventral sclerite with anterior margin parabolic and convex at corners and parabolic and concave medially (Fig. 43F).

Female: Vertex smooth near anterior margin (Fig. 45A). Frons rugose, but border of rugosities not distinctly marked (Fig. 45A). Frontal tubercles short and transverse (Fig. 45B). Clypeal base slightly deflected (Fig. 45B). Connection between clypeal base and ocular canthi laterally angulated (Fig. 45A). Ocular canthi oblique, anterior margin straight, apex blunt (Fig. 45C). Ocular canthi carina inconspicuous (Fig. 45C). Protibia with four outer teeth (Fig. 44C). Metatibial apex with connection to apical tooth with angulated emargination (Fig. 44D). Distance between medial and apical teeth more than 2 times longer than distance between basal and medial teeth (Fig.

44D). Elytral base distinctly rugose near scutellum and humeral umbones (Fig. 44C). Coxites with V-shaped emargination (Fig. 45D).

Redescription. Male. **Color:** Surface slightly lustrous; head and pronotum dark reddish brown; appendages, elytra and venter brown (Fig. 44A-B). **Head:** Cephalic horns transverse and apex directed forward, concavity between horns distinctly deep reaching horns base, apex of horns divergent (Fig. 40F). Posterior portion of frons and vertex flat, anterior portion of frons slightly depressed near horns; vertex with large punctures, punctures coalescent on frons medially, sides of both vertex and frons with punctures coalescent and bigger than medial punctures (Fig. 41D). Clypeus broad and subtrapezoidal, margins thick, surface depressed near apex, punctures large and dense (Fig. 40F). Ocular canthi oblique with anterior margin almost straight, tip truncate, surface with moderate and dense punctures, presence of a short carina semicircular from canthi base to base of horns (Fig. 40E). **Mouthparts:** Labrum with anterior margin elevated medially, sides blunt (Fig. 34L). Mandibles subtriangular, ventral surface with two longitudinal carinae, apex with one thick tooth slightly emarginated and with presence of outer projection round (Fig. 34I); in dorsal view, mesal brush with setae distinctly erected crossing apical tooth, outer margin angulated basally, mesal brush only reaching molar area apically (Fig. 34J); in lateral view, molar area with outer margin thickened, covering part of ventral carina, ventral projection elongated with no bump anterior to condyle (Fig. 34K). Maxilla subtriangular, apex blunt, stipes densely setose, maxillary palpomere II distinctly narrow basally (Fig. 35A); in dorsal view subgalea projecting over margin of stipes (Fig. 35H). Mentum with base wide, sides oblique, apex distinctly narrow; surface covered by long thin setae on lateral margins and basal ventral portion, presence of shorter setae on entire surface except apex (Fig. 35I). **Thorax:** Pronotum slightly bordered, disc convex, fovea absent, presence of two short tubercles slightly oblique near pronotal anterior margin, presence of concavity between tubercles (Fig. 40F). Pronotal punctures moderate and dense on disc, becoming sparser near posterior margin and posterior corners, punctures progressively changing to coalescent surrounding tubercles, punctures on tubercles thin and sparse (Fig. 41D). Metepisternum densely hirsute, metasternum hirsute with medial setae denser than lateral setae, presence of wrinkles on metasternum. Scutellum triangular, acute, surface with punctures of same size as pronotal punctures. **Elytra:** Form 2.3 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed, punctures

cohesive, never more than one puncture of distance from another, few punctures coalescent near elytral suture, surface with longitudinal grooves (Fig. 44A). Apical and humeral umbones with thin sparse punctures, not ocellate. **Legs:** Protibia with four external teeth increasing in size distally (Fig. 44A), dorsal surface with moderate and sparse punctures near teeth, few coalescent punctures, micropunctures near irregular row of punctures of inner edge. Protarsi slender and simple, protarsomeres II–IV as thick as basal portion of protarsomere V, claws symmetric and thin. Prosternum with anterior margin with lateral sides round, profemur with basolateral connection with protrocanter with no punctures (Fig. 41E). Connection between mesocoxae and mesotrochanter thick. Metatibia with three sharp and elongated outer teeth (Fig. 41F). Metatibial apical margin distinctly crenulated with more than 5 thick setae. Posterior row of setae on metafemora not reaching base. **Abdomen:** Tergite VIII round in lateral view; surface densely covered by wrinkles on sides, anterior and posterior margins, presence of few sparse punctures on disc; short thin setae on disc, setae longer and denser near posterior margin medially. Sternite IV densely punctate except medially with punctures sparser than on sides. Sternites V–VII with same punctuation pattern, punctures sparser on disc and dense on sides and lateral portion of anterior margins. Sternite VIII with posterior margin evenly concave, presence of long and short setae intertwined on posterior margin, punctures on disc thin and sparse, presence of wrinkles near anterior margin. **Aedeagus:** Parameres, in caudal view, with basal posterior projection blunt and short, outer margin of apical portion almost straight, inner margin of apical portion distinctly angulated (Fig. 43D). Parameres in lateral view with lateral margin distinctly projected ventrally, covering most part of ventral carina (Fig. 43E). Parameres in ventral view with apex subrectangular and slender, ventral depression constricted between lateral and ventral carinae, ventral sclerite with anterior margin parabolic and convex at corners and parabolic and concave medially (Fig. 43F).

Measurements. Body length: 20.8–23.3 mm. Elytral length: 12.6–14.8 mm. Elytral width: 7.4–8.2 mm. Head length: 3.2–3.9 mm. Pronotal width: 10.3–11.9 mm. Pronotal length: 6.5–7.3 mm. Protibial length: 5.4–6.7 mm.

Female. Females are similar to males but hornless (Fig. 44C-D). **Head:** Cephalic horns absent, frons with two short transverse tubercles slightly separated dorsally (Fig. 45B); surface of frons densely punctate, punctures large and coalescent, presence of few wrinkles laterally near eyes (Fig. 45A). Clypeus slightly elongated and subtrapezoidal, apex slightly round, densely punctate (Fig. 45A). Ocular canthi with

anterior margin straight, apical corner angulated, tip truncated, surface densely punctate, presence of short thick carinae curved (Fig. 45C). **Thorax:** Pronotal shape entirely convex, but more flat than in males; pronotal margins distinctly round, surface broad. Pronotum, in dorsal view, completely flat on anterior margin (Fig. 44C); pronotal punctures large and dense laterally, becoming sparser medially, anterior margin with wrinkles (Fig. 44C). **Legs:** Mesotibiae evenly depressed between medial and apical teeth, medial tooth short and thin but still bigger than basal and apical teeth; brush of setae present between mesotibial and mesofemoral joint. Metatibial apex with margin distinctly crenulated with six short crenulations; surface covered by thin and sparse punctures, denser punctures only near junction to metafemora. **Abdomen:** Tergite VIII convex, surface completely wrinkled intertwined by thin punctures barely conspicuous; corners with microsetae, but no conspicuous setae present. Abdomen not covering apex of elytra in ventral view. Sternite VIII long and wide, apex truncate, surface wrinkled with few thin punctures near posterior margin, presence of long setae on lateral margins, middle with short setae. **Genitalia:** Coxites with V-shaped emargination anteriorly, few setae distributed medially (Fig. 45D).

Measurements of females. Body length: 20.1 mm. Elytral length: 13.1 mm. Elytral width: 7 mm. Head length: 3.2 mm. Pronotal width: 9.4 mm. Pronotal length: 6.2 mm. Protibial length: 4.3 mm.

Geographic distribution. Brazil: Mato Grosso do Sul. Bolivia: Santa Cruz (Fig. 50).

Material examined. 1 male (CERPE): a) “R. Verde, MT{MS}/ BR, x.1966/ A. Maller leg.”, b) “*Minisiderus/ martinae* Abadie M#/ P. Grossi det. 2013”; 1 male and 1 female (EPGC): a) “BRASIL. Mato Grosso do Sul./ Três Lagoas. Horto Rio Verde/ Três Lagoas Agroflorestal./ 19-X-/ 1993. Black light trap. Cerrado/ stand. C Flechtmann”, b) “C665/19-10-93/ VLC”; 1 male (CERPE): a) “D113, var. M#/ *Agaocephala/ duponti* Cast./ Rio Verde, M{ato}. Grosso/ 10.63”, b) “BRASIL, MT/ Rio Verde/ X.1963”, c) “D113/ MUSEU NACIONAL/ UFRJ – Empréstimo/ em III.2004”.

Remarks. Despite the labels of the specimens referenced to the locality as “Rio Verde, MT (an abbreviation to the state of Mato Grosso)”, nowadays this local belongs to the state of Mato Grosso do Sul. These two Brazilian states were separated in 1977. As the specimens were collected in 1966 the locality was still under domain of Mato Grosso, which explain the information in the labels. As the type-locality of *M. goyanus*

is in an homonymous city (Rio Verde, in Goiás), perhaps for that reason specimens in collections labeled from “Rio Verde, Mato Grosso” has been identified as *Minisiderus goyanus*. However, these two species differ by the following characters: in *M. martinae* males with pronotal tubercles flattened (Fig. 40D), space between anterior margin and tubercles concave in lateral view (Fig. 40D), ocular canthi not protruded basally and with tip truncate (Fig. 40E), parameres short with lateral margin almost straight (Fig. 43E), inner margin of parameres with short notch medially (Fig. 43D), whereas in *M. goyanus* males have pronotal tubercles thick (Fig. 40A), space between anterior margin and tubercles straight in lateral view (Fig. 40A), ocular canthi protruded basally and with tip round (Fig. 40B), parameres elongated with outer margin notched at apex (Fig. 43B), inner margin of parameres with deep notch medially (Fig. 43A).

The type locality of *M. martinae* is an area of Chiquitano dry forests with great influence of the Bolivian Dry Chaco. Herein we are providing the first record of *M. martinae* to Brazil in an area of Cerrado particularly close to Pantanal. The vegetation of this area is a mosaic of Cerradão, characterized more by trees than shrubs, and semideciduous seasonal alluvial forests intertwined by pastures. This new record to Brazil lead us to two hypothesis: one that indicates that Pantanal, that is right in between the two localities, is not acting as a barrier to *M. martinae* distribution or that *M. martinae* spreads through the dry habitats, with the Dry Chaco acting as a bridge between the Chiquitano dry forests and Cerrado.

***Minisiderus matogrossensis* (Ohaus, 1930)**

(Figs. 32-37, 50)

Brachysiderus matogrossensis Ohaus 1930: 264 (original description);

Brachysiderus (Minisiderus) matogrossensis Endrödi 1970: 64 (review); Endrödi 1985: 218 (cited); Grossi & Grossi 2005: 79 (cited); Abadie 2010: 201 (cited); Abadie 2014: 127 (cited); Abadie, Godinho Jr. & Koike 2016: 234 (cited);

Minisiderus matogrossensis Milani 2018: 79 (new combination).

Diagnosis. *Minisiderus matogrossensis* differs from the species on *M. minicola* group by the protibia with four outer teeth (Fig. 32A), instead of three. Males of *M. matogrossensis* also differ from the *M. goyanus* species group by the presence of fovea on anterior portion of pronotum (Fig. 32A) and a projected horn on pronotal anterior margin (Fig. 32B). *M. matogrossensis* can also be distinguished from other species by

the following characters of males: clypeus subtrapezoidal with apex truncate (Fig. 33B). Connection between canthi base and horns angulated (Fig. 33C). Frons densely setose (Fig. 33B). Fovea ellipsoid and big, 2 times wider than long, lateral sides evenly marked (Fig. 33A). Pronotal horn medial on apical margin, shape elongated and slightly flat laterally (Fig. 32B). Posterior phallobase with apical corners round (Fig. 36E). Parameres, in caudal view, with distinct medial notch on inner edge, outer edge round and narrowing to apex (Fig. 36A). Parameres, in lateral view, with lateral margin distinctly projected ventrally, presence of slightly elongated carina ventrally below lateral margin (Fig. 36C). Parameres, in ventral view, with continuous deep concavity between lateral and ventral margins (Fig. 36D).

Females: Clypeus parabolic and short, 3 times wider than long (Fig. 37A). Frontal tubercles inconspicuous in dorsal view (Fig. 37A), only detectable in lateral view (Fig. 37C). Ocular canthi almost transverse, apex truncate and densely setose, anterior corner angulated (Fig. 37C). Pronotum 3.6 times wider than distance between lateral margins of frons near eyes (Fig. 32C). Protibia with four outer teeth (Fig. 32D). Metatibia with posterior carina straight and oblique, not crenulated (Fig. 37E). Metatibial apex with connection to apical tooth straight (Fig. 32D). Distance between medial and apical teeth less than 2 times longer than distance between basal and medial teeth (Fig. 32D).

Redescription. Male. **Color:** Surface slightly lustrous; head and pronotum reddish brown; appendages, elytra and venter brown (Fig. 32 A-B). **Head:** Cephalic horns transverse and directed forward, apex slightly upward, concavity between horns almost reaching base, space between horns 2.1 times wider than eye (Fig. 33B). Frons and vertex slightly concave; surface of vertex and frons with wrinkles sparse but forming cells, punctures moderate and sparse within each wrinkled cell, wrinkles diminishing near horns; presence of setae on vertex, denser medially than laterally (Fig. 33B). Clypeus subtrapezoidal, apex truncate, surface punctate, punctures with same size as on vertex, denser near clypeal apex and sparser towards base (Fig. 33B). Ocular canthi smoothly curved from anterior margin to tip, anterior margin slightly deflected upward, tip slightly turned posteriorly, presence of punctures smaller than on vertex but denser, few wrinkles on base, carina absent (Fig. 33C). **Mouthparts:** Labrum with anterior margin round, sides blunt (Fig. 34D). Mandibles subtriangular, ventral surface with two longitudinal carinae, apex with one thick tooth, mesal brush distinctly posterior to tooth

base at inner margin, lateral sclerite near molar area distinctly angulated at inner margin (Fig. 34A); in dorsal view, tooth emarginated, outer margin distinctly sharp basally, densely covered by long thick setae, mesal brush not reaching molar area basally (Fig. 34B); in lateral view, presence of short bump anterior to condyle (Fig. 34C). Maxilla subtriangular, apex blunt, stipes densely setose, maxillary palpomere II distinctly narrow basally (Fig. 35A); in dorsal view subgalea reaching stipes but not projecting over it (Fig. 35B). Mentum slightly wider on base than on apical corner, surface with long thin setae on margins (Fig. 35C). **Thorax:** Pronotum slightly bordered, disc convex on posterior half, anterior half with a deep fovea medially reaching pronotal horn; pronotal fovea wider than distance between foveal edge and pronotal lateral margin (Fig. 33A); presence of pronotal horn on anterior margin medially, shape prolonged as a slightly oblique small stem, apex emarginated (Fig. 32B). Pronotal punctures ocellate, short and sparse on posterior half medially, becoming larger and denser near lateral margins and anterior corners; fovea wrinkled (Fig. 33A). Prosternum with distinct diagonal fissures from anterior corners to posterior margin, anterior margin more protruded laterally than medially. Metepisternum and metasternum densely hirsute, punctures covered by setae. Scutellum subtriangular, base wide, surface with small punctures sparser on apex than on base, few setae apically. **Elytra:** Form 1.9 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed, elytral punctures shorter than pronotal lateral punctures (Fig. 32A). Apical and humeral umbones with thin sparse punctures, not ocellate. Presence of microsetae on elytral apex. **Legs:** Protibia with four external teeth increasing in size distally, surface punctate, punctures thin and sparse; protibial inner apical corner almost straight. Protarsi slender and simple, claws symmetric and thin. Procoxae, protochanteri and profemora densely hirsute. Mesotibia with three outer teeth, middle tooth much bigger than others, outer surface between middle and apical teeth deeply excavated (Fig. 33D). Mesotibia with short crenulation between thick setae on posterior carina, anterior carina not connected to basal tooth (Fig. 33D). Metatibial apex distinctly emarginated externally. **Abdomen:** Tergite VIII round in lateral view (Fig.); surface covered by long thin setae more dense laterally than medially. Sternites IV–VII distinctly constricted medially, surface covered by reticulated microsculpture, punctures thin and sparse near posterior margins. Sternite VII X times longer than sternite VI. Sternite VIII with posterior margin distinctly V-shaped, presence of setae on sides and on posterior margin, punctures thin and sparse on anterior margin. **Aedeagus:** Parameres symmetric,

basal portion folded only at a small portion medially, inner margin basally convex and divergent, inner margin medially with distinct indentation, outer margin basally wrinkled (Fig. 36A). In lateral view, lateral margin with shape truncate (Fig. 36C), posterior phallobase with shape thick, apical corners short and blunt (Fig. 36E); in dorsolateral view parameres with short carina basally, not crossing the division between apical and basal portions (Fig. 36B). In ventral view, ventral sclerite of parameres flat, ventrolateral fovea distinctly not limited posteriorly, apex slightly oblique (Fig. 36D).

Measurements. Body length: 21.2–27.2 mm. Elytral length: 11.6–16.9 mm. Elytral width: 6.9–9.4 mm. Head length: 2.9–4.2 mm. Pronotal width: 9–13.9 mm. Pronotal length: 6.2–8.5 mm. Protibial length: 5.5–6.3 mm.

Female. Females are similar to males but hornless (Fig. 32C-D). **Head:** Cephalic horns absent, frons with no tubercles (Fig. 37B); surface of frons densely wrinkled, wrinkles ending before clypeus, presence of thin punctures intertwined with wrinkles on frons and vertex (Fig. 37A). Clypeus short and round, densely punctate, punctures bigger than on frons (Fig. 37A). Ocular canthi with anterior margin straight, apical corner thick and round, tip slightly emarginated, punctures on surface dense as in males (Fig. 37C); presence of oblique thick carina basally towards frons. **Mouthparts:** Distal labial palpi slightly thin. **Thorax:** Pronotal shape entirely convex, but more flat than in males; pronotal margins evenly round. Pronotum, in dorsal view, with anterior portion slightly thickened; pronotal punctures densely distributed on entire surface, posterior punctures regular, medial and anterior punctures coalescent, wrinkles present on anterior half (Fig. 32C). **Legs:** Mesotibiae as in males, deeply excavated between medial and apical teeth; brush of setae absent on mesotibial and metafemoral joint. Metatibial apex with posterior carina smooth (Fig. 37E). **Abdomen:** Tergite VIII convex, densely punctate on disc, densely wrinkled on sides; short but distinct setae on corners. Sternite VIII long and wide, surface with short setae transversely distributed on anterior half of disc and on posterior margins (Fig. 37D). Abdomen concealing apex of elytra in ventral view (Fig. 37D).

Measurements of females. Body length: 20.9 mm. Elytral length: 12.6 mm. Elytral width: 7.4 mm. Head length: 2.4 mm. Pronotal width: 9.9 mm. Pronotal length: 6.7 mm. Protibial length: 4.4 mm.

Geographic distribution. Brazil: Mato Grosso and Mato Grosso do Sul (Fig.).

Material examined. Holotype male (ZMNB): a) “Matogrosso/ Corumba/ (J. Richter S.)”, b) “Lectotypus/ *Brachysiderus/ matogrossensis* Ohs.”, c) “*B. Ohaus/*

matogrossensis/ Det. Dr. Endrödi 1968". **Other specimens:** 1 male (NMPC): a) "Sesc Pantanal/ 01.X.2003/ Armadilha Malaise col.", b) "ex coll. S. Pokorný/ National Museum/ Prague, Czech Republic", c) "*Brachysiderus/ matogrossensis*/ Ohaus"; 2 males (CERPE): a) "UFMT perpendicular to label/ Santonio}. Leverger, MT, BRA/ 05-VII-2009/ FERREIRA, P. P. col."; 1 male and 1 female (UFMT): a) "BRASIL: Mato Grosso, Rosário/ Oeste, Fazenda/ Cocal. 19-XI-2012. MANUAL/ SE Silva".

Remarks. *Minisiderus matogrossensis* shares only with *M. cyclofoveatus* sp. nov. the presence of distinct pronotal fovea and elongate horn on anterior margin of pronotum. However, these two species differ by the following characters: *M. matogrossensis* have clypeus subtrapezoidal with apex truncate (Fig. 33B), fovea ellipsoid and big, 2 times wider than long, lateral sides evenly marked (Fig. 33A), parameres in lateral view with lateral margin distinctly projected ventrally (Fig. 36C), posterior phallobase with apical corners short and round (Fig. 36E), whereas *M. cyclofoveatus* have clypeus distinctly elongated with sides oblique and apex slightly round (Fig. 33F), fovea round and short, 1.5 times wider than long, lateral sides marked (Fig. 33E), parameres in lateral view with lateral margin not strongly projected and round (Fig. 36H), posterior phallobase with apical corners long and acute (Fig. 36J). *M. matogrossensis* is recorded to Pantanal and Cerrado.

***Minisiderus mielkeorum* (Grossi & Grossi, 2005)**

(Figs. 16-21, 50)

Brachysiderus (Minisiderus) mielkeorum Grossi & Grossi 2005: 25 (original description); Dechambre 2009: 100 (cited); Abadie 2010: 201 (cited); Abadie 2014: 127 (cited); Abadie, Godinho Jr. & Koike 2016: 234 (cited);

Minisiderus mielkeorum Milani 2018: 79 (new combination).

Diagnosis. Males of *M. mielkeorum* differ from other species by: clypeus subtrapezoidal, 2.3 times wider than long, sides oblique with truncate apex (Fig. 17A). Ocular canthi with apex acute, anterior margin slightly round (Fig. 17C). Area between cephalic horns wide, in frontal view, as wide as clypeal base (Fig. 17A). Frons with protuberance transverse and distinct with apex angulated (Fig. 17B). In dorsolateral view, cephalic horns with inner margin distinctly projected to frons (Fig. 17B). Pronotal tubercle thick and moderately long, distinctly separated medially (Fig. 17B). Metatibia

with anterior carina slightly perpendicular to posterior carina (Fig. 17D). Parameres, in caudal view, with outer margin straight near apex, basal portion with inner margin slightly angulated after medial notch (Fig. 20A). In lateral view, ventrolateral carina not reaching posterior angulation of lateral carina (Fig. 20B). Outer margin of parameres distinctly angulated posteriorly, apical margin of ventral sclerite emarginated and wide with sides oblique (Fig. 20C)

Females: Clypeus slightly elongated, 2.1 times wider than long (Fig. 21A). Clypeal punctures densely distributed near tubercles, punctures on apex dense and distinct (Fig. 21A). Ocular canthi slender, with anterior margin straight (Fig. 21A). Elytra in lateral view with apex distinctly slender than base (Fig. 16D). Tergite VIII with posterior margin distinctly emarginated laterally (Fig. 15D). Proximal coxites with deep notch on apical margins (Fig. 21B).

Redescription. Male. **Color:** Surface slightly lustrous; appendages, elytra and venter reddish brown, head and pronotum darker than elytra (Fig. 16A-B). **Head:** Cephalic horns transverse projected forward, dorsal surface of horns with distinct carinae (Fig. 17B, distance between horns as wide as clypeal base (Fig. 17A). Frons with distinct transversal protuberance medially, connected with horn carinae; surface of frons and vertex distinctly wrinkled, wrinkles vertical and oblique (Fig. 17C). Clypeus subtrapezoidal, sides oblique with anterior corners slightly round and tip emarginated medially (Fig. 17A), dorsal surface slightly depressed and clypeal apex slightly deflected in lateral view (Fig. 17B); clypeal punctures moderate and sparse near base, punctures thinner and denser near apex. Ocular canthi elongated, anterior margin oblique and slightly convex medially, tip blunt, surface with punctures thin and sparse on margins, bigger and denser on dorsum; carinae transverse and angulated on canthi base (Fig. 17C). **Mouthparts:** Labrum with sclerotized portion subrectangular, sides slightly round, tip slightly protruded medially (Fig. 18D). Mandibles subtriangular with two subparallel carinae, mandibular apex with distinct tooth large and blunt, outer carina almost reaching tip of tooth in ventral view (Fig. 18A); in lateral view, presence of thick bump anteriorly to ventral condyle, molar area 1.3 times wider than long (Fig. 18C) with central surface distinctly depressed, mesal brush reaching base of molar area; in dorsal view, apical inner corner convex and densely covered by mesal brush, outer margin straight (Fig. 18B). Maxillae with galea subtriangular, inner margin slightly concave; stipes, in ventral view 1.1 times wider than long, outer margin not covering

completely lateral border (Fig. 19A); in dorsal view, ventrobasal margin of stipes sinuous (Fig. 19B). Mentum 1.4 times longer than wide, densely setose on margins, sides slightly round, apex truncate, ventral surface with moderate and sparse punctures (Fig. 19C). **Thorax:** Pronotum slightly bordered, posterior margin slightly emarginated medially, pronotal disc convex with two distinct tubercles near anterior margin (Fig. 16A); tubercles with distinct emargination between them (Fig. 17A), tubercular shape moderately long (Fig. 17B). Pronotal disc densely covered by moderate punctures, becoming bigger and denser on sides; punctures near pronotal tubercles thinner and denser, wrinkles densely distributed transversally from anterior corners to tubercles. Prosternum with medial protuberance of anterior margin longer than lateral protuberances, prosternal surface smooth with long thin setae on anterior corners. Scutellum subtriangular, surface sparsely punctate, punctures thin and sparse on disc. **Elytra:** Form 2.1 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed (Fig. 16A). Apical umbones densely punctate by thin punctures, humeral umbones sparsely punctate by thin punctures. **Legs:** Protibia with three outer teeth increasing in size distally, distance between basal and medial teeth longer than distance between basal and apical teeth. Metafemora smooth with long and transverse row of setae near posterior margin, row not reaching apex. Metatibia with two oblique carinae at outer margin, anterior carina slightly perpendicular to posterior carina (Fig. 17D); metatibial apex slightly round in ventral view, margin slightly crenulated; metatibial surface more punctate medially and basally than apically, punctures on apex thin and sparse (17D). **Abdomen:** Tergite VIII round with surface densely wrinkled, disc with some large punctures surrounded by wrinkles, lateral corners densely wrinkled; presence of sparse thin setae on corners near anterior margin. Sternite VIII with posterior margin densely covered by long setae, surface wrinkled anteriorly. Sternites IV-VI almost with same length, surface equally covered by C-punctures densely distributed near corners, presence of transverse row of setae laterally not reaching middle. **Aedeagus:** Parameres symmetric, in caudal view, with basal portion folded to middle, inner margin of parameres with deep notch medially forming obtuse angulation towards base, outer margin straight towards apex (Fig. 20A). In lateral view, ventrolateral carina not reaching posterior angulation of lateral carina; basal surface distinctly parabolic (Fig. 20B). In ventral view, outer margin of parameres distinctly angulated posteriorly, apical margin of ventral sclerite emarginated and wide with sides oblique (Fig. 20C)

Measurements. Body length: 23.8 mm. Elytral length: 14.3 mm. Elytral width: 8 mm. Head length: 3.2 mm. Pronotal width: 11.9 mm. Pronotal length: 7.6 mm. Protibial length: 5.7 mm.

Female. Females are oblong, general shape similar to males but hornless (Fig. 16C-D). **Head:** Cephalic horns absent, frons with distinct transverse tubercle near clypeal base (Fig. 21C); frontal surface with punctures thin and sparse between wrinkles, wrinkles not reaching tubercle (Fig. 21A). Clypeus round, clypeal base slightly elevated basally near canthus, clypeal apex slightly deflected (Fig. 21C); surface slightly excavated, with punctures thin and sparse medially and apically, becoming denser near base. Ocular canthi similar to male but with discrete bump near clypeus, tip blunt, presence of slightly oblique carina on base (Fig. 21A). **Mouthparts:** Mentum with base rounder than in males, apex narrow. Maxillae with stipes glabrous on base. **Thorax:** Pronotum convex, flatter than in males, pronotal tubercles absent, punctures bigger than in males (Fig. 16C); pronotal length 3 times longer than head (Fig. 16C); pronotal anterior and posterior margins almost straight, anterior corners distinctly projected, crossing the line of canthi apex (Fig. 21C). Prosternum similar to males, but with long thin setae sparsely distributed on anterior and posterior margins laterally, almost reaching lateral protuberances medially. **Legs:** Mesofemora as in males but shorter and thicker; posterior row of setae shorter than in males, surface of posterior margin distinctly punctate with coalescent punctures. Mesotibiae as in males, but more excavated between medial and apical tooth; anterior carina almost inconspicuous, posterior carina not as crenulated as in males, medial tooth distinctly big; surface finely punctate (Fig. 21D). **Abdomen:** Tergite VIII convex, wrinkled on corners and densely punctate on disc. Sternite VIII longer than in males, surface densely wrinkled on anterior half, posterior half with thin punctures. Sternite VII as long as sternite V-VI together, surface densely punctate by C-punctures. **Genitalia:** Proximal coxites with deep notch on apical margins, long thin setae sparse on inner corners (Fig. 21B).

Measurements of females. Body length: 23.9 mm. Elytral length: 15.4 mm. Elytral width: 8.2 mm. Head length: 2.9 mm. Pronotal width: 11.4 mm. Pronotal length: 7.7 mm. Protibial length: 5.6 mm.

Geographic distribution. Brazil: Maranhão (Fig. 50).

Material examined. Holotype male (MZUSP): a) “BRASIL, MA, Balsas/ Serra do Penitente/ Alt. 480m 5-6.XI.2004/ C. Mielke Leg.”, b) “COLEÇÃO/ E & P. Grossi”, c) “*Brachysiderus mielkeorum* n. sp./ Holotype/ Grossi & Grossi det. 2005”. **Paratypes:**

2 males (CERPE) with same data as Holotype; 1 male (CERPE) with same data as Holotype except “a) “13-XI-2004, 500m/ ex col. E. Furtado”. **Other specimens:** 1 female (CERPE): a) “BRASIL (MA), Mirador/ Parque Est{adual}. Mirador/ Base da Geraldina”, b) “Armadilha Luminosa/ 20-24.xii.2006, F./ Limeira-de-Olivera”, c) “*Brachysiderus mielkeorum*/ Grossi & Grossi, 2005/ P.C.Grossi det. 2016”; 1 male (CERPE): a) “BRASIL, MA, Balsas/ Serra do Penitente/ Alt. 480m 30.XI.2005/ C.G.C. Mielke Leg.”, b) “COLEÇÃO/ E & P. Grossi”, c) “*Brachysiderus mielkeorum*/ Grossi & Grossi, 2005/ P.C.Grossi det. 2016”; 4 males (MZUSP): a) “BRASIL: MA/ Balsas Gerais/ Nov. 1999”, b) “*Brachysiderus/ mielkeorum*/ Grossi y Grossi/ C. Campaner det. 2010”.

Remarks. *Minisiderus mielkeorum* is distributed through the northernmost part of Brazilian Cerrado. The distribution in the Cerrado is to areas of Chapadas with range between 350 to 600 meter of altitude practically as high islands surrounded by plantations of sorghum and corn near their foothills (Dantas *et al.* 2013). *M. mielkeorum* shares this distribution with *Minisiderus elyanae*, but these two species can be distinguished by: males with transverse strong protuberance on frons (Fig. 17B), area between cephalic horns wide, in frontal view, as wide as clypeal base (Fig. 17A), parameres in caudal view with outer margin straight near apex, basal portion with inner margin slightly angulated after medial notch (Fig. 20A) in *M. mielkeorum* and males with two parallel short protuberances on frons (Fig. 17G), area between cephalic horns narrow, in frontal view, 1.7 times narrower than clypeal base (Fig. 17F), parameres in caudal view with outer margin distinctly notched near apex, basal portion with inner margin round after medial notch (Fig. 20D) in *M. elyanae*. Females of *M. mielkeorum* have clypeal punctures densely distributed near tubercles, puncturers on apex dense and distinct (Fig. 21A) and proximal coxites with deep notch on apical margins (Fig. 21B) whereas in *M. elyanae* clypeal punctures sparsely distributed near tubercles, puncturers on apex inconspicuous (Fig. 21E) and proximal coxites with shallow notch on apical margins (Fig. 21F).

***Minisiderus minicola* (Ohaus, 1930)**

(Figs. 8-14, 50)

Brachysiderus minicola Ohaus 1930: 261 (original description);

Brachysiderus (Minisiderus) minicola Endrödi 1970: 62 (review); Endrödi 1985: 217 (cited);

Grossi & Grossi 2005: 79 (cited); Dechambre 2009: 100 (cited); Abadie 2010: 201 (cited);

Abadie 2014: 127 (cited); Abadie, Godinho Jr. & Koike 2016: 234 (cited);
Minisiderus minicola Milani 2018: 79 (new combination).

Diagnosis. *Minisiderus minicola* can be distinguished from the majority of other species of *Minisiderus* by males having protibiae with three outer teeth, cephalic horns flattened (Fig. 9A) with basal junction narrow almost 6 times narrower than distance between horn tips (Fig. 9B). Compared with the other *Minisiderus* species with three protibial outer teeth, male of *M. minicola* differs from *M. mielkeorum* and *M. elyanae* by pronotal tubercle short (Fig. 8B), presence of medial carina near pronotal anterior margin (Fig. 9B) and frons with protuberance absent (Fig. 9C) whereas in *M. mielkeorum* and *M. elyanae* pronotal tubercle slightly elongated (Figs. 17B,G), carina absent near pronotal anterior margin (Figs. 17A,F), frons with distinct transverse protuberance in *M. mielkeorum* (Fig. 17B) and frons with discrete protuberance in *M. elyanae* (Fig. 17G). Male of *M. minicola* also differs from *M. benjamini* by the clypeal apex round (Fig. 9B), basal junction of cephalic horns strait, almost 6 times narrower than distance between horn tips (Fig. 9B) and in caudal view, parameres with outer margins truncate and oblique (Fig. 12A), whereas in *M. benjamini* clypeal apex truncate (Fig. 9E), basal junction of cephalic horns wide, almost 3 times narrower than distance between horn tips (Fig. 9E) and in caudal view, parameres with outer margins round (Fig. 12D).

Redescription. Male. **Color:** Surface slightly lustrous; head and pronotum dark reddish brown; appendages, elytra and venter brown (Fig. 8A-B). **Head:** Cephalic horns transverse and erected, united basally, lateral margins slightly round, horns base flat medially; basal junction between horns narrow, almost 6 times narrower than distance between horn apices (Fig. 9B). Frons and vertex densely punctate; punctures bigger on vertex than on frons near basal junction of horns, lateral punctures thin near eyes (Fig. 9A). Clypeus elongated with corners round, lateral margins slightly round, surface depressed on sides and slightly elevated longitudinally at middle; dorsal surface of clypeus with no erected setae (Fig. 9B). Ocular canthi slender and elongated, tip sharp, base with short protuberance; base of canthi with conspicuous oblique carina (Fig. 9A). **Mouthparts:** Mentum elongated, ventral surface distinctly depressed basally, lateral margins slightly sinuous, apex sharp (Fig. 11C); ventral surface densely covered by long setae, presence of punctures large and dense. Maxillar cardo with outer edge blunt and short (Fig. 11B). **Thorax:** Pronotum slightly bordered, disc convex, presence of

distinct short tubercle near anterior margin. Pronotal tubercles short with shallow concavity (Fig. 9B); in frontal view, lateral margins of tubercle oblique and turned to pronotal disc posteriorly (Fig. 9C). Pronotal disc densely punctate, punctures thin and sparse medially and posteriorly, punctures large and dense near pronotal tubercle (Fig. 8A). Pronotal depression posterior to pronotal tubercle, shape longitudinal and shallow. Scutellum subtriangular with wide base, punctures moderately dense basally, scarce near apex. Prosternum with longitudinal fissure medially near procoxae.

Mesoepisternum completely hirsute. Metepisternum densely hirsute laterally, setae scarce medially near metepisternal suture, punctures thin and dense. **Elytra:** Form 2.1 times longer than wide. Elytral surface glabrous, irregularly punctate, punctures ocellate and dense on disc, punctures thin and sparse on apical and humeral umbones (Fig. 8A).

Legs: Protibia with three distinct external teeth, medial tooth slightly longer than apical and basal teeth, base slightly dilated posteriorly to basal tooth. Protibial surface dorsally with thin and moderately dense punctures, protibial inner corner slightly projected.

Protarsal claw with empodium almost with same length as apical setae. Metatibia with three distinct outer teeth, medial tooth distinctly slender and longer than other teeth (Fig. 8B). Metatibial apex continuous to outer edge, outer edge sharp (Fig. 8B).

Abdomen: Tergite VIII smoothly round, surface with microsetae scarcely distributed along disc, distinct groups of microsetae on posterior margin at middle and on corners. Sternite VIII with rows of setae along posterior margin. Sternites IV-VI with punctures thin and sparse, presence of short setae on lateral margins. Sternite VII densely punctate, punctures thin. **Aedeagus:** Parameres symmetric and elongated. In dorsal view, outer margins of parameres straight, inner margins of parameres straight to apex after medial notch (Fig. 12A). In lateral view, parameres with medial notch shallow, lateral margins distinctly projecting ventrally (Fig. 12B).

Measurements. Body length: 21.5–28.4 mm. Elytral length: 13.3–16.6 mm. Elytral width: 7.6 – 9.2 mm. Head length: 4.1–4.4 mm. Pronotal width: 10.1–13.8 mm. Pronotal length: 7.2–8.8 mm. Protibial length: 5.3–6.5 mm.

Female. Not examined.

Geographic distribution. Brazil: Minas Gerais (Fig. 50).

Material examined. Holotype male (ZMNB): a) “Minas geraes:/ Agua Suja/ Naschod S.”, b) “Lectotypus/ *Brachysiderus/ minicola* Ohs.”, c) “*B. Ohaus/ minicola*/ Det. Dr. Endrödi 1968”. **Other specimens:** 1 male (CEMT): a) “Três Marias MG/ BRASIL – XI. {19}92”, b) “Coleção/ F.Z. Vaz de Mello”; 1 male (CEMT): a) “Três

Marias MG/ BRASIL – XI.1991”; 1 male (CEMT): a) “Montes Claros/ MG BRASIL I.1989”; 1 male (CERPE): a) “IPEACO – Sete Lagoas/ Minas Gerais – Brasil/ 20/x/1969/ V.O. Becker leg.”, b) “Dpto. Zool./ UF – Paraná”, c) “*Minisiderus M# minicola* (Ohaus)/ P.Grossi det. 2013”.

Remarks. *Minisiderus minicola* is distributed throughout the southeastern portion of Brazilian Cerrado. *M. minicola* can be found in distinct areas within the Cerrado as in transitional areas between Cerrado and Caatinga characterized by the dry climate, semideciduous shrub-like forests and the range of plateaus and depressions near the basin of São Francisco river (Caminhas & Fonseca, 2020), and in areas of Campo Limpo, with predominance of herbaceous vegetation.

In one specimen of *M. minicola* it was found an anomaly in the antennae (Figs. 13A-B). Left antennae has a short club, 2.6 times longer than wide (Fig. 13D), whereas right antennae has a regular club, 4 times longer than wide (Fig. 13C). Antennomeres I-VII do not have differences. At first sight, we thought that it could be just another specimen’s antennae glued in this specimen’s head. However, after examining the antennal insertion it is possible to see that antennomere It is clearly articulated in antennal socket (Fig. 13 C-D).

***Minisiderus* sp.**

(Figs. 30-31, 50)

Description. Head: Cephalic horns absent, frons with a pair of short transverse tubercles (Fig. 31B). Frons and vertex rugose; in dorsal view, moderate dense punctures on anterior portion of frons near clypeus (Fig. 31A). Clypeus round, with basal portion distinctly elevated basally near ocular canthi (Fig. 31A); in lateral view, these basal margins distinctly sharp and elevated (Fig. 31B). Clypeal punctures moderate and sparse medially, becoming thinner towards margins. Ocular canthi with anterior margin curved, tip distinctly sharp, surface rugose with few long thin setae on apex (Fig. 31C).

Thorax: Pronotum convex, lateral margins distinctly blunt with surface flap-like (Fig. 30A), anterior margin slightly convex medially (Fig. 30A). Pronotal disc distinctly punctate, punctures large and moderate medially and posteriorly, becoming coalescent laterally and anteriorly, anterior third with surface rugose and wrinkles near anterior corners (Fig. 30A). Prosternum with anterior margin distinctly projected medially with a pair of lateral projection with border thick, shorter than medial projection. **Elytra:** Shape 2.2 times longer than wide, surface slightly smooth near scutellum, disc with 5

rows of regular punctures, punctures irregular between the rows (Fig. 30A). **Legs:** Protarsi simple, protarsal claws subequal and thin. Protibiae with three outer teeth (Fig. 30A-B). Meso- and metatibiae with three outer teeth and two outer carinae connected to basal and medial teeth. Mesotibia with medial and basal teeth short, apical tooth more than two times longer than them (Fig. 31E). Metatibia with basal tooth inconspicuous, medial and apical tooth long and subequal, surface rugose anteriorly to basal and medial teeth (Fig. 30B). **Abdomen:** Tergite VIII convex, with posterior margin slightly sharp, hidden by elytral apex in dorsal view (Fig. 30A). Sternite VIII elongated with tip truncate, lateral margins densely covered by long thin setae, surface with C-punctures denser on disc than on posterior margin, base transversely wrinkled on anterior margin (Fig. 31D). Sternite VII bigger than sternite VI, sternite VI bigger than sternite V; surface of sternites V-VII completely punctate, punctures thin and sparse, becoming denser laterally, presence of rows of thin setae on sides. **Genitalia:** Proximal coxites with shallow notch on apical margins near outer side, surface with long and short thin setae densely distributed on medial and inner surface, distance between setae equivalent to 2 to 4 setae (Fig. 31F).

Measurement of female. Body length: 21.9 mm. Elytral length: 13.9 mm. Elytral width: 7.7 mm. Head length: 2.8 mm. Pronotal width: 10.3 mm. Pronotal length: 6.7 mm. Protibial length: 6.1 mm.

Geographic distribution. Brazil: Bahia (Fig. 50).

Material examined. 1 female (CERPE) labeled as: a) “Barreiras/ XI.1991”.

Remarks. *Minisiderus* sp. is very distinct from other females in the genus due to the frons distinctly rugose (Fig. 31A) and the sides of clypeal base distinctly sharp and elevated (Fig. 31B). Since there is no male specimen collected nearby the locality of Barreiras where this female was collected, it is difficult to determine if it is a new species or a female of a known species. The species located closest to Barreiras are *M. minicola* in northern Minas Gerais, *M. bertolossiorum* and *M. veadeirensis* in northeastern Goiás. However, in this study, we did not examine females of *M. minicola* and we could not find any female of *M. bertolossiorum* or *M. veadeirensis*. For that reason, we decided to describe the female but not include it in any known species. *Minisiderus* sp. was found in an area of the western Chapadas do Rio São Francisco, a highland area surrounded by lowlands where the tributaries of São Francisco River flow. The vegetation of this area is composed by Veredas at the foothills, a phytophysiology of Cerrado characterized by the moist soils with herb-shrub

vegetation, in which one species predominant is the Buriti, *Mauritia flexuosa* (Passo *et al.* 2010, da Silva *et al.* 2018).

***Minisiderus cyclofoveatus* Sobral & Grossi sp. nov.**

(Figs. 33-36, 38, 50)

Diagnosis. Males: fovea round and short, 1.5 times wider than long, lateral sides marked (Fig. 33E). Clypeus distinctly elongated with sides oblique and apex slightly round (Fig. 33F). Pronotal horn distinct with shape broad (Fig. 38B). Connection between canthi base and horns with a short convex protuberance (Fig. 33G). Frons sparsely setose (Fig. 33F). Protibia with four outer teeth (Fig. 38A). Posterior phallobase with apical projections slightly angulated towards corners (Fig. 36J). Parameres, in dorsolateral view, with carina reaching basal portion of parameres (Fig. 36G). Parameres, in lateral view, with short ventrolateral carina, lateral margins round (Fig. 36H). Parameres, in ventral view, with basally interrupted deep concavity between lateral and ventral margins (Fig. 36I).

Description. Holotype. Male. **Color:** Surface slightly lustrous; head and pronotum reddish brown, appendages, elytra and venter brown (Fig. 38A-B). **Head:** Cephalic horns transverse and flat, apex sharp and directed upward, base of horns connected (Fig. 33F). Frons and vertex depressed; surface densely punctate, punctures large basally, coalescent laterally and frontally near horns. Clypeus distinctly elongated with sides oblique and apex truncate; dorsal surface completely concave, punctures large and sparse, only near apex with thin punctures (Fig. 33F). Ocular canthi with anterior margin straight, tip truncate, surface densely punctate, punctures coalescent, presence of thin oblique carina (Fig. 33G); connection between canthi base and horns with a short convex protuberance (Fig. 33G). **Thorax:** Pronotum in general convex with presence of deep fovea on anterior half medially (Fig. 33E); presence of pronotal tubercle distinct on anterior margin medially, shape short with apex broad (Fig. 38B). Pronotal fovea round and short, almost as wide as long, lateral borders of fovea marked (Fig. 33E). Pronotal punctures almost with same size on entire disc, punctures densely distributed; pronotal fovea with wrinkles (Fig. 33E). Prosternum with medial carina almost with no setae on it. Scutellum subtriangular, surface finely punctate, punctures sparse reaching apex. **Elytra:** Form 2 times longer than wide. Surface glabrous with ocellate punctures

covering disc irregularly distributed, some punctures coalescent near elytral suture (Fig. 38A). Apical and humeral umbones inconspicuous, with thin sparse punctures, not ocellate. **Legs:** Protibia with four external teeth increasing in size distally, distance from fourth tooth to third tooth shorter than distance from third to second tooth apically. Protibial surface with two rows of setae longitudinally distributed near inner margin; punctures thinner and sparser on teeth. Protarsi simple and thin, protarsal claws symmetric, empodium with two divergent setae on apex. Mesotibia with three outer teeth, space between middle and apical teeth slightly excavated (Fig. 33H); presence of longitudinal carina near inner margin, not crossing the line of basal tooth (Fig. 33H). **Abdomen:** Tergite VIII round in lateral view; surface hirsute on sides and with agglomeration of shorter setae medially on posterior margin. Sternite IV with medial portion almost concealed by metafemora, surface with thin punctures. Sternites V-VI densely punctate by thin punctures, sides densely setose. Sternite VII almost with same length of sternites V-VI combined, punctures mostly thin with some wrinkles near posterior margin. Sternite VIII distinctly notched medially, setae present on entire posterior margin. **Aedeagus:** Parameres slightly asymmetric. Parameres in caudal view, with outer margin slightly emarginated apically, inner margin with shallow notch medially (Fig. 36F). In frontolateral view, with carina reaching basal portion of parameres (Fig. 36G); posterior phallobase with apical projections slightly angulated towards corners (Fig. 36J). Parameres, in lateral view, with short and almost inconspicuous carina ventrolaterally (Fig. 36H). In ventral view, parameres with ventral sclerite with apical lobes short (Fig. 36I).

Measurements of holotype. Body length: 22.6 mm. Elytral length: 14.5 mm. Elytral width: 8.4 mm. Head length: 3.7 mm. Pronotal width: 12.3 mm. Pronotal length: 7.8 mm. Protibial length: 6.1 mm.

Female. Unknown.

Material examined. Holotype male (CERPE): a) "BRASIL, Mato Grosso, 20km/ S. Vila Bela da Santíssima/ Trindade, 15°11'38"S, 59°59' 32"W, 200m, at light, 22-/ 23.x.2016, Y.V.B.S., Marques".

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

Etymology. From the Latin, "*Cyclus*" meaning "circular", "*fovea*" meaning "pit" and "*atus*" meaning "bearer", in reference to the circular small fovea on anterior margin of pronotum.

Remarks. *Minisiderus cyclofoveatus* shares only with *M. matogrossensis* the presence

of distinct pronotal fovea and elongate horn on anterior margin of pronotum. To see the differences between these two species, see **Remarks** of *Minisiderus matogrossensis*. The only specimen of *M. cyclofoveatus* was found in an area of Chiquitano dry forests. The Chiquitano dry forests are an ecoregion characteristic to eastern Bolivia, but it extends to the southwest of Mato Grosso in Brazil. In this ecoregion, occurs a complex of forests with characteristics of humid and semi-arid habitats, lair of endemic plants like *Acosmium cardenasii* and *Cereus tacuaralensis* (Killeen *et al.* 2005).

***Minisiderus furtadoi* Sobral & Grossi sp. nov.**

(Figs. 40-41, 43-46)

Diagnosis. Males of *M. furtadoi* sp. nov. differs from other species by: ocular canthi with protuberance inconspicuous on anterior margin (Fig. 40H). Clypeus semicircular deeply excavated, connection with cephalic horns distinct, not excavated (Fig. 40I). In frontal view base of pronotal tubercle large, 3 times wider than diameter of eye (Fig. 40I). In frontal view, cephalic horns with apex oblique and divergent, presence of a slight emargination near apex (Fig. 40I). Parameres, in caudal view, with shallow mesobasal notch on inner margin (Fig. 43G), basal region of parameres with inner portion oblique (Fig. 43G). Parameres, in lateral view, with base smoothly convex dorsally and with posterior portion slightly elongated (Fig. 43H). Parameres, in ventral view, with ventral depression oblique, lateral margin not projecting to depression (Fig. 43I).

Females: Vertex and frons completely rugose (Fig. 45E). Borders of rugosities distinctly marked with microsetae among them (Fig. 45E). Frontal tubercles short and transverse (Fig. 45F). Clypeal base slightly deflected (Fig. 45F). Connection between clypeal base and ocular canthi laterally angulated (Fig. 45F). Ocular canthi thick, anterior margin round, apex truncate (Fig. 45G). Ocular canthi with conspicuous carina slightly curved (Fig. 45G). Pronotum 3.2 times wider than distance between lateral margins of frons near eyes (Fig. 46C). Elytra smooth near humeral umbones (Fig. 46C). Protibia with four outer teeth (Fig. 46D).

Description. HOLOTYPE Male. **Color:** Surface slightly lustrous; head and pronotum dark reddish brown; appendages, elytra and venter brown (Fig. 46A-B). **Head:** Cephalic horns transverse and united basally, apex divergent, inner margin of horns slightly

emarginated (Fig. 40I). Frons and vertex distinctly depressed medially (Fig. 40I); frontal depression with sparser punctures than sides, C-punctures intertwined with regular punctures on depression, sides mainly covered by C-punctures. Clypeus short and round, surface dorsally excavated, clypeal punctures thin and sparse (Fig. 40I). Ocular canthi oblique with anterior margin distinctly angulated towards tip, tip blunt, surface densely punctate, presence of short transverse carina near canthi base (Fig. 40H). **Mouthparts:** Labrum with dorsal side with anterior corners round, middle truncate (Fig. 34H). Mandible subtriangular, ventral surface with two longitudinal carinae, apex with one short tooth distinctly emarginated medially (Fig. 34E); in dorsal view inner margin with mesal brush apically almost at same level as tooth, margin distinctly round, mesal brush reaching sides of molar area (Fig. 34F); in lateral view, ventral margin with distinct bump anterior to condyle, mesal brush completely setose on dorsal margin (Fig. 34G). **Thorax:** Pronotum convex, presence of two short tubercles near anterior margin, tubercular sides distinctly marked in frontal (Fig. 40I) and lateral view (Fig. 40G); pronotal punctures large and dense, punctures denser near corners, presence of few wrinkles near sides of tubercles (Fig. 41G). Prosternum with posterior margin flat and short, surface smooth (Fig. 41H). Scutellum subtriangular, apex acute, punctures large and dense on sides, middle with no punctures longitudinally. **Legs:** Profemur in ventral view with basolateral projection with C-punctures large and thin densely distributed (Fig. 41H). Mesotibiae with three distinct outer teeth, basal carina near basal tooth short, presence of short carina on inner margin near joint to mesofemora. Metatibia with basal tooth inconspicuous, apical tooth slightly curved, presence of thin punctures sparsely distributed between teeth (Fig. 41I). **Abdomen:** Tergite VIII round, surface only with microsetae present, posterior margin smooth, punctures thin and dense on anterior margin and corners with few sparser areas medially. Sternites IV-VII with large and setose punctures on sides, middle with thin punctures, setae absent. Sternite VIII evenly concave medially, posterior margin completely setose, long setae laterally and short setae medially. **Aedeagus:** Parameres symmetric. In caudal view, basal posterior projection sharp and slightly elongated, presence of longitudinal depression dorsally from base to middle (Fig. 43G). Parameres, in lateral view, with base smoothly convex dorsally and with posterior portion slightly elongated (Fig. 43H). In ventral view, ventral sclerite with apical lobes sinuous at inner margins (Fig. 43I).

Measurement of holotypes. Body length: 22.6 mm. Elytral length: 13.8 mm.

Elytral width: 8.1 mm. Head length: 3.8 mm. Pronotal width: 10.9 mm. Pronotal length: 6.9 mm. Protibial length: 6.6 mm.

Paratypes variation, males. Males with body length: 23.9–25.4 mm, elytral length: 15.1–15.6 mm, elytral width: 8.1–9 mm, head length: 3.9–4.1 mm, pronotal width 12.1–12.6 mm, pronotal length: 7.7–8 mm, protibial length: 5.9–6.6 mm. Head with vertex and frons basally densely covered by C-punctures, frontal surface near horns with thin and sparse punctures. Clypeus slightly elongated, subtrapezoidal with apex slightly round, dorsal surface excavated with punctures large and dense (Fig.). Ocular canthi oblique with anterior margin straight, tip sharp, surface densely covered by short C-punctures. Pronotum with wrinkles connecting sides of tubercles with anterior margin, pronotal punctures large, denser laterally and posteriorly with sparse sections on disc, punctures large and dense near tubercles with some punctures coalescent. Mesotibiae with basal carina near basal tooth long, presence of longitudinal carina crossing line of basal tooth on inner margin near joint to mesofemora. Abdomen with tergite VIII with punctures thinner and denser on posterior margin than on anterior margin, disc with zones not punctate. Sternite IV with large and setose punctures laterally, punctures thin and dense medially; sternites V-VI with few large punctures laterally and few setae, presence of thin and sparse punctures medially; sternite VII as sternites V-VII but with longer setae laterally and denser punctures medially. Aedeagus with lateral margins of parameres more projected ventrally in lateral view; in caudal view apical outer margin with notch more distinct, basal portion with microsetae on posterior projection.

Paratype description, females. Females are similar to males but hornless (Fig. 46C-D). **Head:** Frons with pair of short and transverse tubercles (Fig. 45F), sculpture of vertex and frons completely rugose, borders of rugosities distinctly marked with microsetae among them (Fig. 45E). Clypeus round, 2.6 times wider than long, clypeal base slightly deflected (Fig. 45F). Connection between clypeal base and ocular canthi laterally angulated (Fig. 45F). Ocular canthi thick, anterior margin round, apex truncate (Fig. 45G). Ocular canthi with conspicuous carina slightly curved (Fig. 45G). **Thorax:** Pronotum 3.2 times wider than distance between lateral margins of frons near eyes (Fig. 46C). Pronotal disc with punctures moderate and dense on anterior half, posterior half with punctures slightly sparser, punctures on sides and corners shagrinated. Elytra smooth near humeral umbones (Fig. 46C). **Legs:** Protibia with four outer teeth (Fig. 46D). Mesotibiae with three outer teeth distinctly sharp, medial tooth bigger than basal

and apical teeth. Mesotibial apex with short concave connection to apical tooth.

Metatibial apex with connection to apical tooth distinctly concave (Fig. 46D).

Abdomen: Tergite VIII convex, with posterior margins depressed, apex elongated; surface densely wrinkled, wrinkles on corners, anterior and posterior margins; disc with less wrinkles than sides. Sternites VIII with surface wrinkled on anterior margin, posterior margin with thin punctures sparse. Sternite VII almost 2 times longer than sternite VI; surface with thin and sparse punctures reaching middle. Sternite V-VI with same length and same pattern of punctuation, thin punctures in a transverse row medially.

Measurements of females. Body length: 21.3 mm. Elytral length: 13.8 mm. Elytral width: 7.6 mm. Head length: 3.3 mm. Pronotal width: 9.9 mm. Pronotal length: 6.7 mm. Protibial length: 5.1 mm.

Geographic distribution. Brazil: Mato Grosso (Fig. 50).

Material examined. Holotype male (CERPE): a) “BRASIL, MT,/ Diamantino,/ Rio Arinos/ 12.X.1998/ E. Furtado leg.”, b) “*Brachysiderus/ goyanus/* Ohaus, 1830/ E.J. Grossi/ Det. 2009”, c) “HOLOTYPE/ *Minisiderus furtadoi/* Sobral & Grossi/ det. R. Sobral & P. Grossi 2022”; **Paratypes:** 1 male (CEMT): a) “MT, Chapada dos/ Guimarães. xi./ 2013. P. Wagner {det}”, b) “PARATYPE/ *Minisiderus furtadoi/* Sobral & Grossi/ det. R. Sobral & P. Grossi 2022”; 1 male (CERPE): a) “BRASIL, MT, Chapada/ dos Guimarães, PNCG/ 24.X-06.XI.2008/ S. P. Rosa Leg./ Ex-Coleção UFMT”, b) “PARATYPE/ *Minisiderus furtadoi/* Sobral & Grossi/ det. R. Sobral & P. Grossi 2022”; 1 male (CEMT): a) “BRASIL, Mato Grosso,/ Cuiabá, 15°16'45"S, 56°00' 06"W, 07.xii.2015, A. Frolov/ & L. Akhmetova”, b) “PARATYPE/ *Minisiderus furtadoi/* Sobral & Grossi/ det. R. Sobral & P. Grossi 2022”; 2 males (CERPE): a) “BRASIL, MT,/ Diamantino,/ Rio Arinos/ 12.X.1998/ E. Furtado leg.”, b) “*Brachysiderus/ goyanus/* Ohaus, 1830/ E.J. Grossi/ Det. 2009”, c) “PARATYPE/ *Minisiderus/ Minisiderus furtadoi/* Sobral & Grossi/ det. R. Sobral & P. Grossi 2022”.

Etymology. The name is a homage to Eurides Furtado, a Brazilian entomologist who collected part of the type series. Eurides was a collaborator at the Zoological Collection of the Federal University of Mato Grosso (CEMT) and responsible for collecting numerous specimens of insects that are housed nowadays in the CEMT.

Remarks. *Minisiderus furtadoi* is similar to *M. martinae* but these two species can be distinguished by: males with ocular canthi anterior margin slightly curved, with inconspicuous basal protuberance, apex round (Fig. 40H), clypeus round and deeply

excavated (Fig. 40I), cephalic horns in frontal view with emargination near apex (Fig. 40I), parameres in caudal view with inner margin not angulated apically, basal portion distinctly depressed externally, posterior margin elongated (Fig. 40G) in *M. furtadoi*, and males with ocular canthi anterior margin straight, with apex truncate (Fig. 40E), clypeus subtrapezoidal and shallow (Fig. 40F), cephalic horns in frontal view simply curved to apex (Fig. 40F), parameres in caudal view with inner margin angulated apically, basal portion not depressed externally, posterior margin short and blunt (Fig. 40D) in *M. martinae*.

Minisiderus furtadoi is part of a complex of species that includes *M. martinae* and one other new species that we are describing in the next topic. These species have been considered as *M. goyanus* in the collections due to their similarities on external morphology and occurrence to Brazilian Cerrado. However, the Cerrado is a heterogenic habitat with a diverse variation of phytophysiognomies, from dense forests to open formations, and a relief diversity of Chapadas, inselbergs, ridges and lowlands (Ribeiro & Walter, 1998). The diversity in relief, vegetation and climate may act as geographical limitations to the species throughout Cerrado, as seen in anurans, birds and reptiles (Valdujo *et al.* 2012, Laranjeiras *et al.* 2012, Domingos *et al.* 2014). Therefore, that may explain the species diversity of *Minisiderus* in the Cerrado, where species in the easternmost patches with Amazonian influences are not found in westernmost patches with Caatinga and Atlantic Forest influences nor in southern patches with Pantanal and Chacoan influences. *M. furtadoi* can be found along the highlands of Diamantino plateau and Chapada dos Guimarães and the lowlands of Cuiabana and Paranatinga depressions in areas with vegetal coverage by phytophysiognomies of Cerrado, whereas the occurrence of *M. martinae* in Brazilian Cerrado is up until now restricted to a transitional area with traits of Pantanal.

Within the specimens of *M. furtadoi* it is a small male with an anomaly on the base of right antennae. The specimen has an elongate structure emerging from ventral portion of pedicellum. The structure is as long as II-VI together, base thin with an elliptical structure at apex, ventral surface of apex with circular border slightly depressed (Fig. 47A). It appears to us that it is a case of symphyosocery, when occurs a partial or total fusion of antennomeres, because the specimen lacks one of the antennomeres in the club (Fig. 47B). Due to some malformation, this segment may have ended up developed as this projection from pedicellum. The origin of teratological cases like that in Coleoptera are still not fully understood. Based on recent studies with

Diptera, environmental contaminants can induct mutation on larvae, pupae and adults (Shulman *et al.* 2017, Goretti *et al.* 2020). Even though cases of anomalies have been known since the beginning of the 20th century they are still scarce in the literature and probably subestimated (Ferreira 2015, Clavijo-Bustos *et al.* 2022).

***Minisiderus parecisensis* Sobral & Grossi sp. nov.**

(Figs. 40-41, 43, 48)

Diagnosis. Males of *M. parecisensis* sp. nov. can be distinguished from other species by: ocular canthi with slight protuberance on base of anterior margin (Fig. 40K). Clypeus semicircular with connection with cephalic horns slightly excavated near base (Fig. 40L). In frontal view base of pronotal tubercle narrow, 1.5 times wider than diameter of eye (Fig. 40L). Cephalic horns, in frontal view, with tips oblique and divergent (Fig. 40L). Parameres, in caudal view, with deep mesobasal notch on inner margin (Fig. 43J), basal region of parameres with inner portion almost straight (Fig. 43J). Parameres, in lateral view, with lateral margin strongly directed ventrally, covering ventral carina (Fig. 43K). In ventral view, parameres with ventral depression curved, with lateral margin of parameres projecting to depression, ventral portion of parameres apically sharp (Fig. 43L).

Description. Holotype Male. Color: Surface slightly lustrous; head and pronotum dark reddish brown; appendages, elytra and venter brown (Fig. 48A-B). **Head:** Cephalic horns transverse and directed forward, horns flat dorsally (Fig. 40J) and slightly convex ventrally, connection between horns deep at base; space between horns narrow, almost 4.5 times narrower than distance between apex of horns. Frons and vertex flat; vertex and frons with large ocellate punctures intertwined by thinner and denser punctures, punctures on sides coalescent. Clypeus semicircular, margins thick, dorsal surface depressed on sides with a slight longitudinal elevation medially near base, punctures large and dense (Fig. 40L). Ocular canthi transverse with base slightly protruded, anterior margin abruptly descending toward tip, tip sharp, surface densely punctate, punctures large, few setae on tip; presence of carinae basally, carinae curved with a short angulation posteriorly towards frons (Fig. 40K). **Mouthparts:** Mentum with sides slightly sinuous, but almost oblique, apical portion narrowing to apex. Cardum with outer edges reaching head margin near eyes, in ventral view. **Thorax:** Pronotum

convex, lateral margins slightly angulated towards anterior corners, presence of two short tubercles near anterior margin, tubercles with a slight longitudinal depression between them, fovea absent (Fig. 41J). Pronotal punctures moderate and dense on disc, becoming denser near posterior and anterior margins laterally, presence of few thin punctures medially, punctures coalescent on lateral sides of tubercles (Fig. 41J). Prosternum with medial carina thick between procoxae, prosternal posterior margin medially short and flat (Fig. 41K). Scutellum subtriangular, acute, surface with moderate punctures transversally distributed on middle, apex not punctate. **Elytra:** Form 2.2 times longer than wide. Surface glabrous, disc covered by ocellate punctures irregularly distributed, surface slightly rugose near humeral umbones (Fig. 48A). Apical and humeral umbones with thin sparse punctures, not ocellate. **Legs:** Protibia with four outer teeth increasing in size distally (Fig. 48A), margins of teeth darker than protibial surface, longitudinal row of setae near inner margin, presence of punctures thin and dense on entire dorsal surface, protibial apex distinctly curved medially near spur. Protarsi slender and simple, claws symmetric and thin. Mesotibiae with short row of thick setae longitudinally near inner margin. Distal portion of metacoxae slightly thickened. Metafemora with posterior row of setae almost reaching base. Metatibiae with three outer teeth, middle tooth bigger than others, apical margin slightly angulated towards apical tooth (Fig. 41L); surface between teeth with distinct large C-punctures (Fig. 41L). **Abdomen:** Tergite VIII round in lateral view; surface densely covered by wrinkles with few sparse punctures on disc; setae short transversally distributed near posterior margin. Sternite IV and VII with same length, sternites V-VI shorter than sternite IV. Sternites IV-VI with thin and sparse punctures transversally distributed on surface, presence of short setae on sides. Sternite VII slightly concave medially, surface with thin and dense punctures medially becoming sparser toward sides. Sternite VIII with posterior margin evenly concave, short setae on posterior margin, punctures thin and sparse on disc becoming denser near anterior margin. **Aedeagus:** Parameres slightly asymmetric. In caudal view, posterior phallobase with medial fissure long, reaching junction with anterior phallobase, inner margin of parameres with deep mesobasal notch (Fig. 43J), basal region of parameres with inner portion almost straight (Fig. 43J). In lateral view, parameres with elongated basal carina reaching upper portion of base (Fig. 43K). In ventral view, parameres with ventral depression curved, with lateral margin of parameres projecting to depression, ventral portion of parameres apically sharp (Fig. 43L).

Holotype Measurement. Body length: 23.5 mm. Elytral length: 14.6 mm. Elytral width: 8.1 mm. Head length: 3.8 mm. Pronotal width: 11.9 mm. Pronotal length: 7.6 mm. Protibial length: 6.2 mm.

Females. Unknown.

Geographic distribution. Brazil: Mato Grosso (Fig. 50).

Material examined. Holotype male (CERPE) labeled: a) “PARECIS/ M. Grosso, Brasil/ XI-1960/ M. Alvarenga leg.”, b) “*Minisiderus* M#/ *goyanus* (Ohaus)/ P. Grossi det. 2013”, c) “HOLOTYPE/ *Minisiderus/ parecisensis* Sobral/ & Grossi/ R. Sobral det. 2022”.

Etymology. The epithet is in reference to the Chapada dos Parecis, one of the iconic Brazilian plateaus located in the state of Mato Grosso, where the new species was collected.

Remarks. *Minisiderus parecisensis* is more similar to *M. martinae* and *M. furtadoi* than to other species. *M. parecisensis* differs from *M. martinae* by: males with ocular canthi distinctly projected basally, apex round (Fig. 40K), cephalic horns in frontal view with emargination near apex (Fig. 40L), tergite VIII with disc slightly elevated medially, densely wrinkled on anterior margin (Fig. 49C), whereas in *M. martinae* males with ocular canthi straight, with apex truncate (Fig. 40E), cephalic horns in frontal view simply curved to apex (Fig. 40F), tergite VIII with disc completely round, anterior margin with moderate and dense punctures (Fig. 49A). It also differs from *M. furtadoi* by: males with pronotal protuberance with base narrow in frontal view (Fig. 40L), tergite VIII with absence of setae on posterior margin (Fig. 49C), parameres in caudal view with distinct deep notch on inner margin (Fig. 43J), parameres in ventral view with anterior margin of ventral sclerite deeply emarginated, 4 times narrower than distance between anterior corners (Fig. 43L), parameres in ventral view with lateral margins distinctly projected to ventral depression (Fig. 43L), whereas in *M. furtadoi* males with pronotal protuberance with base wide in frontal view (Fig. 40I), tergite VIII with presence of short thin setae on posterior margin (Fig. 49B), parameres in caudal view with shallow notch on inner margin (Fig. 43G), parameres in ventral view with anterior margin of ventral sclerite shallow, 6 times narrower than distance between anterior corners (Fig. 43I), parameres in ventral view with lateral margins not projected ventrally (Fig. 43I).

Minisiderus parecisensis was found in the Chapada dos Parecis, a plateau ranging from 250 to 800 m of altitude with a top plain, acting as a watershed to the

rivers Paraguai, Guaporé and tributaries of Amazonas (Ross, 1991). This area is also mixed of native vegetation of Cerrado *sensu strictu* and Rupestrian fields with depleted areas by pasture. The Chapada dos Parecis in Mato Grosso is separated from the Chapada dos Guimarães by a large area of lowlands of Cuiabana and Paranatinga depressions, as if those two Chapadas are islands. The morphological similarity between *M. parecisensis* and *M. furtadoi* may be explained by a common ancestral population in these proximal areas. Also, as the morphotype of *M. parecisensis* was not found among specimens from the Chapada dos Guimarães, it may indicate that these species are isolated enough to be considered distinct species.

***Minisiderus rondoniensis* Sobral & Grossi sp. nov.**

(Figs. 24-25, 27-29, 50)

Diagnosis. Males: Ocular canthi with anterior margin completely straight (Fig. 24D). Connection between cephalic horns concave and shallow (Fig. 24E). Frons slightly depressed, depression wide, reaching frontal margins (Fig. 24F). Labrum with distinct medial round protuberance (Fig. 29D). Pronotal disc with paired oblique area of wrinkles from the anterior half of pronotum to sides of tubercles (Fig. 28B). Pronotal lateral margin straight to anterior corner (Fig. 28A). Parameres in caudal view as long as wide, outer margin evenly notched near apex, inner medial notch shallow, basal inner margin slightly curved (Fig. 25D). In lateral view, posterior phallobase with anterior margin concave and corners sharp, parameres with basal portion semicircular and lateral margin ending near the end of carina of ventral sclerite (Fig. 25E). In ventral view, lateral margins on basal portion distinctly open to sides, ventral sclerite with anterior corners blunt and medial area concave (Fig. 25F).

Description. Holotype. Male. **Color:** Surface slightly lustrous; head, pronotum, appendages, elytra and venter dark reddish brown (Fig. 27A-B). **Head:** Cephalic horns transverse and projected forward, united basally, connection between cephalic horns concave and shallow in frontal view (Fig. 24E). Frons slightly depressed with depression wide, reaching frontal margins (Fig. 24F); frons and vertex densely wrinkled and punctate, thin and sparse punctures among wrinkles. Clypeus subrectangular, sides suparallel with anterior corners round and tip truncate, dorsal surface straight with two lateral depressed areas, clypeal apex not deflected (Fig. 24E); clypeal punctures

moderate and dense, some punctures near horns coalescent. Ocular canthi with anterior margin completely straight, tip blunt, surface sparsely wrinkled, presence of short thick setae on apex, carinae inconspicuous (Fig. 24D). Antennal club 2.6 times longer than high, outer surface distinctly setose with short thin setae denser on base than on apex (Fig. 24F). **Mouthparts:** Labrum with distinct medial round protuberance, sides slightly prominent (Fig. 29D). Mandibles subtriangular with two subparallel main carinae, mandibular apex with distinct sharp tooth, presence of short carina on tooth between the two main carinae, in ventral view (Fig. 29A). Mandibles in lateral view with bump inconspicuous to ventral condyle, margin of dorsal socket distinctly prominent (Fig. 29C); in dorsal view, apex of mandibles distinctly emarginated, presence of depression medial, apical outer corner convex and densely covered by mesal brush, mesal brush as a thin stripe basally toward molar area (Fig. 29B). Maxillae with galea subtriangular, inner margin almost straight and oblique; stipes in ventral view with apical margin sinuous, inner margin straight, lateral border basally with outer portion short, cardum not crossing outer portion of lateral border (Fig. 29E); in dorsal view, subgalea crossing inner margin of stipes, maxillary palpomer III with inner corner round and not prominent (Fig. 29F). Mentum 1.3 times longer than wide, sides sinuous with basal portion wider than apical portion, densely setose on margins and base, apex round (Fig. 29G). **Thorax:** Pronotum slightly bordered, posterior margin almost continuously straight in dorsal view, pronotal disc convex, presence of two short tubercles near anterior margin; tubercles connected basally, space between apex distinctly notched, especially on posterior side. Pronotal disc densely punctate on anterior half, sparsely punctate on posterior half, punctures mainly moderate and sparse becoming denser on anterior half and corners; presence of paired oblique area of wrinkles from the anterior half of pronotum to sides of tubercles (Fig. 28B). Prosternum bordered, with medial protuberance as long as lateral protuberances on anterior margin, anterior corners with a slight depression. Scutellum subtriangular, apex blunt, surface sparsely punctate, punctures moderate medially, apex not punctate. **Elytra:** Form 2.2 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed (Fig. 27A). Punctures thin and sparse on humeral umbones, apical umbones with thin punctures densely distributed. **Legs:** Protibia with three outer teeth, medial tooth bigger than others, basal tooth smaller than others, shape of teeth flat, punctures thin and dense, sparser near base of tibia. Meso- and metatibiae with two oblique carinae on outer margin, presence of three teeth on outer margin. Mesotibia with medial tooth thin and

elongated, basal and apical teeth inconspicuous, anterior carina also inconspicuous (Fig. 27B). Metatibia, in lateral view, with large C-punctures from basal tooth to medial tooth; metatibial apex straight and oblique to apical tooth in lateral view (Fig. 27B).

Abdomen: Tergite VIII round, disc densely covered by coalescent punctures surrounded by wrinkles expanding to posterior and anterior margins, setae absent. Sternite VIII with surface wrinkled on corners, disc barely punctate and anterior margin with thin and sparse punctures, posterior margin densely covered by long setae, middle bare. Sternites IV-VI almost with same length, surface equally covered by thin punctures densely distributed near corners and anterior margins, presence of transverse row of setae laterally not reaching middle. **Aedeagus:** Parameres symmetric, in caudal view, with basal portion folded to middle, shape as long as wide, outer margin evenly notched near apex, inner medial notch shallow, basal inner margin slightly curved (Fig. 25D). In lateral view, posterior phallobase with anterior margin concave and corners sharp, parameres with basal portion semicircular and lateral margin ending near the end of carina of ventral sclerite (Fig. 25E). In ventral view, lateral margins on basal portion distinctly open to sides, ventral sclerite with anterior corners blunt and medial area concave (Fig. 25F).

Measurements. Body length: 25.5 mm. Elytral length: 15.7 mm. Elytral width: 8.3 mm. Head length: 4.1 mm. Pronotal width: 12.8 mm. Pronotal length: 8.1 mm. Protibial length: 6.4 mm.

Females. Unknown.

Geographic distribution. Brazil: Rondônia (Fig. 50).

Material examined. Holotype male (CERPE): a) “Vilhena, x.1988./ J. Becker & O Roppa”. **Paratypes** 9 males with same data as holotype; 2 males (CERPE) with same data as holotype except “19.x.1990”.

Etymology. The name is in reference to the Brazilian state of Rondônia, where the new species was collected.

Remarks. *Minisiderus rondoniensis* is very similar to *M. benjamini*. However these two species differ by: frons slightly depressed with depression wide, reaching frontal margins (Fig. 24F) [frons distinctly depressed with depression not touching frontal margins in *M. benjamini* (Fig. 9F)], ocular canthi with anterior margin completely straight (Fig. 24D) [ocular canthi with basal protuberance near horns in *M. benjamini* (Fig. 9D)], connection between cephalic horns concave and shallow (Fig. 24E) [concave and deep in *M. benjamini* (Fig. 9E)], labrum with distinct medial round

protuberance on anterior margin (Fig. 29D) [anterior margin straight in *M. benjamini* (Fig. 10H)], presence of paired oblique area of wrinkles from the anterior half of pronotal disc to sides of tubercles (Fig. 28B) [this area completely punctate in *M. benjamini* (Fig. 28E)], pronotal lateral margin straight to anterior corner (Fig. 28A) [curved dorsally to anterior corner in *M. benjamini* (Fig. 28D)], parameres in caudal view as long as wide, outer margin evenly notched near apex, basal inner margin oblique and slightly curved (Fig. 25D) [parameres in caudal view 1.2 times longer than wide, outer margin distinctly notched near apex, basal inner margin distinctly convex in *M. benjamini* (Fig. 12D)].

M. rondoniensis occurs within a great plateau known as Chapada dos Parecis. The vegetation in this part of Rondônia is a mosaic of different phytophysiognomies of Cerrado, such as Cerradão, Campo Sujo and Cerrado *sensu stricto*, intertwined with large areas of soybean monoculture. The proximity of this area with the Madeira-Tapajós moist forests allows the annual rainfall rate to range between 2000 to 2250 mm, with relative humidity index high above 70% (Miranda *et al.* 2006).

***Minisiderus veadeirensis* Sobral & Grossi sp. nov.**

(Figs. 23-25, 50)

Diagnosis. Males: Lateral margins of cephalic horns continuously connected with base of ocular canthi (Fig. 24A). Ocular canthi distinctly oblique, tip acute, base straight (Fig. 24A). Pronotal anterior margin, in lateral view, straightly connected to tubercles (Fig. 24C). Metatibia with outer margin between posterior carina and apical concavity 4 times longer than outer margin width (Fig. 23B). Parameres, in caudal view, with outer margin straight with a slight sinuosity at apex, inner margin of apical portion oblique with short notch medially, basal portion with inner margin oblique (Fig. 25A). In lateral view, lateral margin of parameres with posterior portion short not crossing margin of ventral sclerite at base; basal carina straight anteriorly and abruptly curved posteriorly (Fig. 25B), posterior phallobase with a distinct large depression on apical corners, 2.3 times longer than wide (Fig. 25B).

Description. Holotype. Male. **Color:** Surface slightly lustrous; head dark reddish brown, pronotum reddish brown, appendages, elytra and venter brown (Fig. 23A-B).

Head: Cephalic horns transverse and flat, apex sharp, base of horns connected, distance

between apex of horns 1.1 time wider than clypeal base (Fig. 24B); lateral margins of cephalic horns continuously connected with base of ocular canthi, lateral surface of horns distinctly excavated, surface densely punctate, punctures large and dense (Fig. 24C). Frons straight, densely punctate, frontal medial portion punctate by C-punctures, lateral portion near eyes with few wrinkles (Fig. 24A). Clypeus subrectangular, sides subparallel with anterior corners round and tip truncate (Fig. 24B); clypeal sides slightly deflected, tip not deflected; clypeal punctures thin and sparse with some moderate punctures near horns. Ocular canthi distinctly oblique, anterior margin straight, tip acute, base straight (Fig. 24A); surface densely punctate, C-punctures basally and round moderate punctures apically; presence of transverse round carinae basally. **Thorax:** Pronotum slightly bordered, lateral margin more round on posterior half than on anterior half, pronotal disc convex, presence of two short tubercles transverse and flat near anterior margin; tubercles slightly emarginated on apex (Fig. 23A); pronotal anterior margin, in lateral view, straightly connected to tubercles (Fig. 24C). Pronotal disc punctuation formed by moderate and sparse punctures on disc, becoming denser towards corners and sides, presence of thin punctures medially near tubercles, wrinkle present only on anterior margin below tubercles. Prosternum with anterior corners with oval depression, presence of few long setae on posterior margin and short setae on anterior margin near corners. Scutellum subtriangular, apex sharp, punctures moderate and dense medially and basally, punctures thin apically sparsely from medial punctures. **Elytra:** Form 2.1 times longer than wide. Surface glabrous covered by ocellate punctures irregularly distributed, margins of punctures distinctly dark (Fig. 23A). Humeral umbones discrete, not covering basal lateral margin of elytra in dorsal view (Fig. 23A); elytral lateral margins with thick borders, not flap-like (Fig. 23A). Apical and humeral umbones finely punctate. **Legs:** Protibia with three outer teeth, basal tooth short, medial and apical teeth almost with same size, both teeth downturned in lateral view; protibial punctures thin and sparse dorsally, becoming denser posteriorly to basal tooth and between teeth. Meso- and metatibiae with two oblique carinae at outer margin, presence of three outer teeth with basal and medial teeth connected to anterior and posterior carinae respectively. Mesotibiae, in lateral view, with anterior carina distinctly curved apically, almost hook-shaped, towards basal tooth (Fig. 23B). Metatibial apex, in lateral view, with deep concavity towards apical tooth. **Abdomen:** Tergite VIII round, presence of wrinkles on corners and anterior margin, almost reaching middle at posterior margin, disc densely punctate, punctures moderate,

becoming slightly sparser towards margins, microsetae present at middle on posterior margin. Sternite VIII with posterior margin covered by long setae with microsetae at middle, surface wrinkled on corners and sparsely punctate towards medial area. Sternite VII 2 times longer than sternite VI, sternite VI with almost same size as sternite V and IV; punctuation pattern similar to sternites IV-VI, wrinkles laterally and sparse punctures on anterior margin barely reaching middle. **Aedeagus:** Parameres symmetric, in caudal view, with basal portion folded to middle, outer margin straight with a slight sinuosity at apex, inner margin of apical portion oblique with short notch medially, basal portion with inner margin oblique (Fig. 25A). In lateral view, lateral margin with posterior portion short not crossing margin of ventral sclerite at base; basal carina straight anteriorly and abruptly curved posteriorly (Fig. 25B), posterior phallobase with a distinct large depression on apical corners, 2.3 times longer than wide (Fig. 25B). In ventral view, ventral sclerite with apical corners distinctly projected and blunt; parameres with ventrolateral depression between lateral and ventral carinae, depression almost reaching tip (Fig. 25C).

Measurements. Body length: 22.5 mm. Elytral length: 13.5 mm. Elytral width: 7.3 mm. Head length: 4 mm. Pronotal width: 10.7 mm. Pronotal length: 7.3 mm. Protibial length: 6 mm.

Measurements of paratypes. Body length: 21–22.6 mm. Elytral length: 13.5–13.6 mm. Elytral width: 7.2–7.4 mm. Head length: 3.5–4 mm. Pronotal width: 10.7–10.9 mm. Pronotal length: 7.1–7.3 mm. Protibial length: 6.2–6.3 mm.

Female. Unknown.

Geographic distribution. Brazil: Goiás and Distrito Federal (Fig. 50).

Material examined. Holotype male (CERPE): a) “BRASIL, GO, São João/D’Aliança, Chapada dos/ Veadeiros, Faz{enda}. Sendai/ 900 m – 14.XI.2007/ R.M. Koike Leg.”, b) “COLEÇÃO E./ & P. GROSSI”. **Paratypes.** 7 males (CERPE, EPGC) labeled: a) “São João D’Aliança, 10-15.xi.2006, 940m, R, Koike leg.”; 1 male (EPGC): a) “Distrito Federal, Brasília, x.1992, E.&P. Grossi legs.”; 3 males (EPGC): same data but “x.1993”; 1 male and 1 female (EPGC): same but “Luziânia, x.1973”; 2 males (EPGC): same but, “Campus UNB, 05-20.x.1970”; 2 males (EPGC): same but “Planaltina, Embrapa Cerrados, Cerrado Nativo 03.xi.2006, C. Oliveira leg.”; 2 males (EPGC): same but “Campus UNB, x.1980, Ana leg.”; 1 male (EPGC): “Luziânia, Estrela D’Alva, 27.ix.1981, Ana Paula leg.”; 1 male (EPGC): “Brasília, Faz. Água Limpa, 07.viii.1983”; 1 male (EPGC): “UNB, 08.xi.1975”; 1 male (EPGC): “Brasília,

S.M. Urbano, 04.xi.1978”; 1 male (EPGC): “Brasília, Asa Norte, 20.xi.1986”; 1 male (EPGC): “UNB, Campus, 30.x.1974, S. Kato leg.”; 1 male (EPGC): “Asa Sul, 30.ix.1980”.

Etymology. The name is in reference to the Chapada dos Veadeiros, an ancient Brazilian plateau located in the state of Goiás, near the municipality where the new species was collected.

Remarks. *Minisiderus veadeirensis* has a close resemblance to *M. minicola*, but it differs by: ocular canthi distinctly oblique, tip acute, base straight (Fig. 24A), distance from anterior margin to base of tubercles long, carina absent (Fig. 24B), outer margin of metatibia between posterior carina and apical concavity 4 times longer than wide (Fig. 23B), parameres, in caudal view, with outer margin straight with a slight sinuosity at apex, basal portion with inner margin oblique (Fig. 25A) whereas in *M. minicola*, ocular canthi slightly transverse, tip round, base protruded (Fig. 9A), distance from anterior margin to base of tubercles short, carina present (Fig. 9B), outer margin of metatibia between posterior carina and apical concavity 2.4 times longer than wide (Fig. 8B), parameres, in caudal view, with outer margin distinctly notched at apex, basal portion with inner margin curved (Fig. 12A).

The locality where this species was found is known as “The gateway to the Chapada dos Veadeiros”. The local relief is characterized by inselbergs and Chapadas, and it allows distinct phytophysionomies to coexist such as Rupestrian fields on the rocky terrain and open shrub trees on foothills (Souza *et al.* 2019).

Key to species of *Minisiderus* (Endrödi, 1970)

- 1. Head with pair of cephalic horns (Figs. 1A-B, 8A-B). Pronotum with pair of tubercles present on anterior margin (Figs. 1A-B, 8A-B) (males)..... 2
- Head with horns absent (Fig. 15C-D). Pronotum convex, tubercles on anterior margin absent (Fig. 15C-D) (females)..... 16
- 2. Protibiae with three outer teeth (Figs. 1, 2, 7, 8, 15A-B, 16A-B, 22A-B, 23, 26, 27)..... 3
- Protibiae with four outer teeth (Figs. 32A-B, 38, 39, 44 A-B, 46A-B, 48)..... 11

3. Elytra with color yellow and brown patches on humeral and apical umbones (Figs. 1, 2, 7).....	4
- Elytra with color brown to dark reddish brown, patches absent on humeral and apical umbones (Figs. 8, 15A-B, 16A-B, 22A-B, 23, 26, 27).....	5
4. Frons with wrinkles near sides (Fig. 3A), pronotal tubercles fused (Fig. 3A), cephalic horns with apex abruptly upturned (Fig. 3C), parameres in caudal view with apical portion medially carinated at inner margin (Fig. 6A), basal portion with left posterior margin angulated (Fig. 6A).....	<i>M. lenorae</i>
(Grossi, Dechambre & Grossi, 2012)	
- Frons with punctures on sides (Fig. 3I), pronotal tubercles distinctly emarginated (Fig. 3I), cephalic horns with apex continuously upturned (Fig. 3K), parameres in caudal view with apical portion medially not carinated at inner margin (Fig. 6E) and basal portion with left posterior margin round (Fig. 6E).....	<i>M. paranensis</i>
	(Arrow, 1902)
5. Clypeal base with two distinct lateral protuberances (Fig. 9G), cephalic horn with sides not touching sides of clypeus (Fig. 9H)...	<i>M. bertolossiorum</i>
	(Abadie, Godinho Jr & Koike, 2016)
- Clypeal base not protruded (Fig. 9A), cephalic horns with sides touching sides of clypeus (Fig. 9B).....	6
6. Head with frontal protuberance or protuberances.....	7
- Head with frons not protuberant.....	8
7. Frontal protuberance strong and transverse (Fig. 17B), area between cephalic horns wide, in frontal view, as wide as clypeal base (Fig. 17A), pronotal tubercles thick and moderate (Fig. 17B).....	<i>M. mielkeorum</i>
	(Grossi & Grossi, 2005)
- Frontal protuberances paired and short (Fig. 17G), area between cephalic horns narrow, in frontal view, 1.7 times narrower than clypeal base (Fig. 17F), pronotal tubercles flat and short (Fig. 17G).....	<i>M. elyanae</i>
	(Dechambre, 2009)
8. Cephalic horns with connection concave and shallow (Fig. 9E).....	9
- Cephalic horns with connection deep (Fig. 9B).....	10

9. Ocular canthi with short protuberance at base (Fig. 9D), frons distinctly depressed with depression not touching sides of frons (Fig. 9F), parameres in caudal view with inner margin distinctly notched medially (Fig. 12D), parameres with basal portion with inner margins convex (Fig. 12D)..... *M. benjamini*

(Abadie, 2014)

- Ocular canthi straight at base (Fig. 24D), frons slightly depressed with depression touching sides of frons (Fig. 24F), parameres in caudal view with inner margin shallow medially (Fig. 25D), parameres with basal portion with inner margins oblique (Fig. 25D)..... *M. rondoniensis* new

species

10. Ocular canthi with short protuberance at base (Fig. 9A), pronotal anterior margin with longitudinal carina touching base of tubercles (Fig. 9B), parameres in caudal view with outer margin distinctly notched (Fig. 12A)..... *M. minicola*

(Ohaus, 1930)

- Ocular canthi oblique and straight, protuberance absent at base (Fig. 24A), pronotal anterior margin without frontal carina (Fig. 24B), parameres in caudal view with outer margin straight (Fig. 25A)..... *M. veadeirensis* new

species

11. Pronotal anterior margin with elongated horn (Fig. 32B), presence of fovea on anterior margin of pronotum (Fig. 32B)..... 12

- Pronotal anterior margin with tubercles, horn absent (Fig. 39B), anterior margin of pronotum with fovea absent (Fig. 39B)..... 13

12. Clypeus subtrapezoidal with apex truncate (Fig. 33B), ocular canthi with base angulated towards sides of horns (Fig. 33C), fovea ellipsoid and big, 2 times wider than long, lateral sides evenly marked (Fig. 33A), posterior phallobase with apical corners short and round (Fig. 36E)..... *M.*

matogrossensis **(Ohaus, 1930)**

- Clypeus distinctly elongated with sides oblique and apex slightly round (Fig. 33F), ocular canthi with short convex protuberance near junction with sides of horns (Fig. 33G), fovea round and short, 1.5 times wider than long, lateral sides marked (Fig. 33E), posterior phallobase with apical corners long and acute (Fig. 36J)..... *M. cyclofoveatus*

new species

13. Ocular canthi with base protuberant and apical portion slender (Fig. 40B). Lateral margin of pronotum curved towards anterior corners (Fig. 40A). Aedeagus with parameres elongated (Fig. 43B) and asymmetric (Fig. 43A).....	<i>M. goyanus</i>
(Ohaus, 1930)	
- Ocular canthi with base straight (Fig. 40E) or slightly protuberant with apical portion thick (Figs. 40H, K). Lateral margin of pronotum straight to anterior corners (Fig. 40D, G, J). Aedeagus with parameres short (Fig. 43 E, H, K) and symmetric (Fig. 43 D, G, J).....	14
14. Frons flat (Fig. 40D), area between anterior margin and pronotal tubercles distinctly concave (Fig. 40D), cephalic horns in frontal view simply curved to apex (Fig. 40F), parameres in caudal view with posterior projections short and blunt (Fig. 40D)..	<i>M. martinae</i>
(Abadie, 2010)	
- Frons depressed (Figs. 40G, J), area between anterior margin and pronotal tubercles straight (Fig. 40G, J), cephalic horns in frontal view with emargination near apex (Fig. 40I, L), parameres in caudal view with posterior projections elongated (Figs. G, J).....	15
15. Pronotal protuberance with base narrow in frontal view (Fig. 40L), tergite VIII with absence of setae on posterior margin (Fig. 49C), parameres in caudal view with distinct deep notch on inner margin (Fig. 43J).....	<i>M. parecisensis</i>
new species	
- Pronotal protuberance with base wide in frontal view (Fig. 40I), tergite VIII with presence of short thin setae on posterior margin (Fig. 49B), parameres in caudal view with shallow notch on inner margin (Fig. 43G).....	<i>M. furtadoi</i>
new species	
16. Protibia with three outer teeth.....	17
- Protibia with four outer teeth.....	20
17. Frontal tubercles inconspicuous in lateral view (Fig. 21G).....	<i>M. elyanae</i>
(Dechambre, 2009)	
- Frontal tubercles conspicuous in lateral view (Figs. 14E, 21C, 31C).....	18
18. Clypeal base smoothly connected to ocular canthi (Fig. 14E). Frontal tubercles distinctly short and sharp (Fig. 14E).....	<i>M. benjamini</i>
(Abadie,	

2010)

- Clypeal base with connection to ocular canthi distinctly projected upward (Fig. 21C, 31C)..... 19

19. Frons and vertex strongly rugose, wrinkles distinctly projected in lateral view (Fig. 31C), clypeal base sharp, covering view of frontal tubercles in lateral view (Fig. 31C), ocular canthi with apex sharp (Fig. 31A)..... ***Minisiderus* sp.**

- Frons and vertex evenly rugose, wrinkles not projected in lateral view (Fig. C), clypeal base round, not covering view of frontal tubercles in lateral view (Fig. 21C), ocular canthi with apex truncate (Fig. 21A)..... ***M. mielkeorum* (Grossi & Grossi, 2005)**

20. Clypeal base not elevated on connection with ocular canthi (Fig. 37B), ocular canthi transverse with anterior corner distinctly angulated to apex (Fig. 37A)..... ***M. matogrossensis* (Ohaus, 1930)**

- Clypeal base elevated on connection with ocular canthi (Figs. 45B, F), ocular canthi oblique with anterior corner curved to apex (Fig. 45 A, E)..... 21

21. Vertex not punctate (Fig. 45A), frons rugose with border of rugosities weakly marked (Fig. 45A), ocular canthi slender (Fig. 45C), coxites with V-shaped emargination (Fig. 45D)..... ***M. martinae* (Abadie, 2010)**

- Vertex distinctly punctate (Fig. 45E), frons rugose with border of rugosities strongly marked (Fig. 45E), ocular canthi thick (Fig. 45G), coxites with distal margin not emarginated (Fig. 45H)..... ***M. furtadoi* new species**

Acknowledgments

We thank all the curators from the cited collections for their contributions of material for this study. We thank Max Barclay, Michael Geiser and Keita Matsumoto for all the support to RS during his time in the Natural History Museum (London, United Kingdom). We thank Dr. José Wellington de Moraes for all the support to RS during his time at INPA (Manaus, Brazil). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. RS acknowledge the Instituto Nacional de Pesquisas da Amazônia for research support;

the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for the PhD scholarship to RS and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Sandwich Doctorate scholarship to RS. PCG acknowledges the Universal Project, 449366/2014-6.

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Figures

FIGURE 1. Male of *Minisiderus paranensis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view.
Scale bars: 10 mm. Photo: Natural History Museum Data Portal

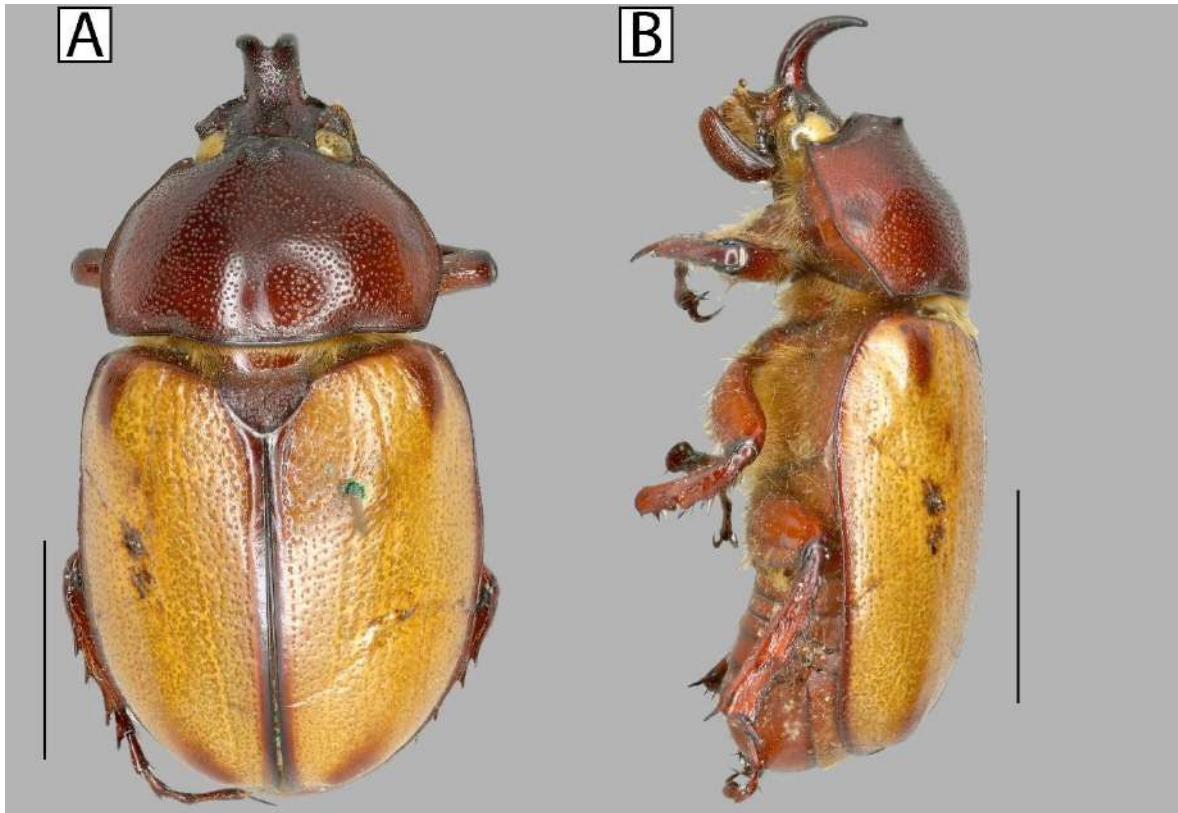


FIGURE 2. Male of *Minisiderus lenorae*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

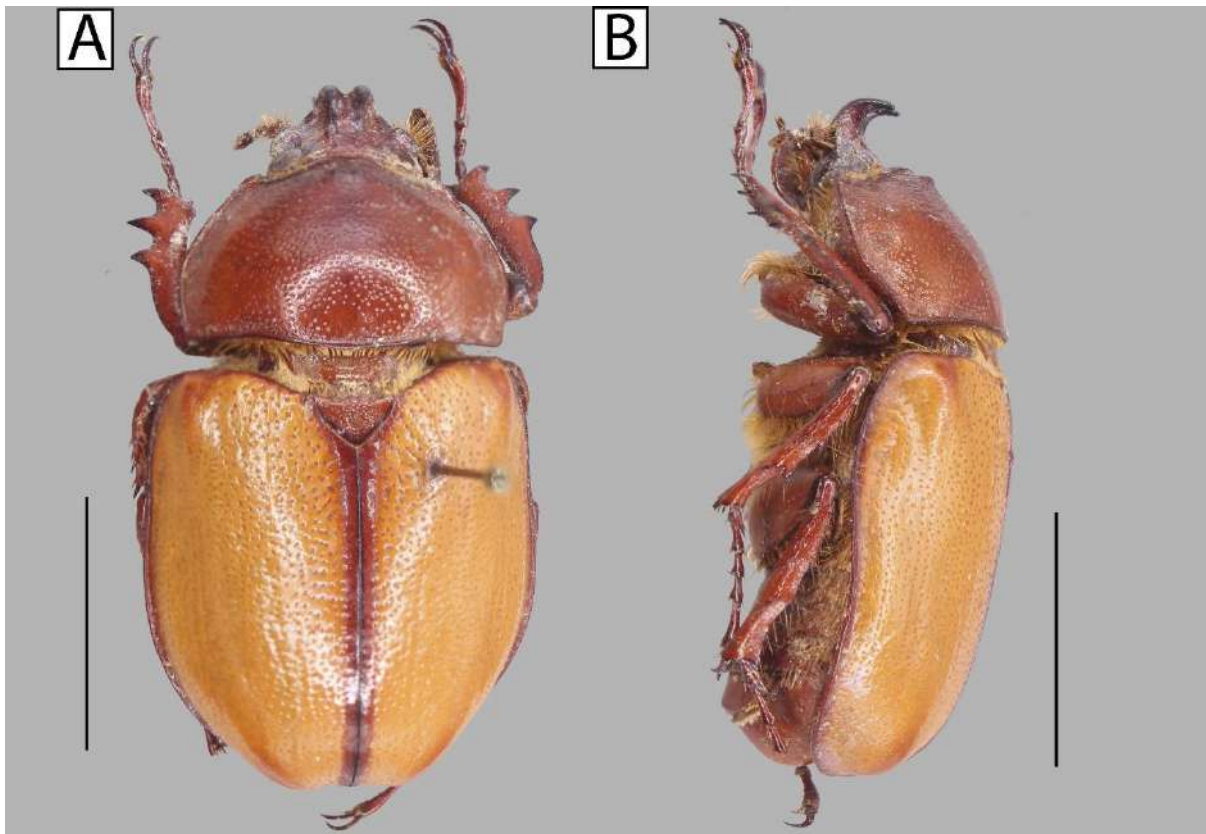


FIGURE 3. Head and pronotum of *Minisiderus lenorae* and *Minisiderus paranensis*. **A**, Head of *M. lenorae* in dorsal view. White arrows pointing to wrinkles. **B**, head of *M. lenorae* in frontal view. Double-headed white arrows showing width of horns and clypeal apex; black arrow pointing to lateral margin of clypeus. **C**, head of *M. lenorae* in lateral view. White arrow pointing to concavity on anterior margin. **D**, head of *M. lenorae* in frontolateral view. White arrows pointing to pronotal tubercles; black arrow pointing to clypeal apex. **E**, head of *M. paranensis* in dorsal view. Downside black arrow pointing to anterior margin of canthus; upside black arrow pointing to canthus apex. **F**, head of *M. paranensis* in frontal view. Double-headed white arrows showing width of horns and clypeal apex; black arrow pointing to lateral margin of clypeus. **G**, head of *M. paranensis* in lateral view. Black arrow showing apex of horn upturned; white arrow pointing to pronotal anterior margin. **H**, head of *M. paranensis* in frontolateral view. White arrows pointing to pronotal tubercles; black arrow pointing to clypeal apex. Scale bars: 1 mm.

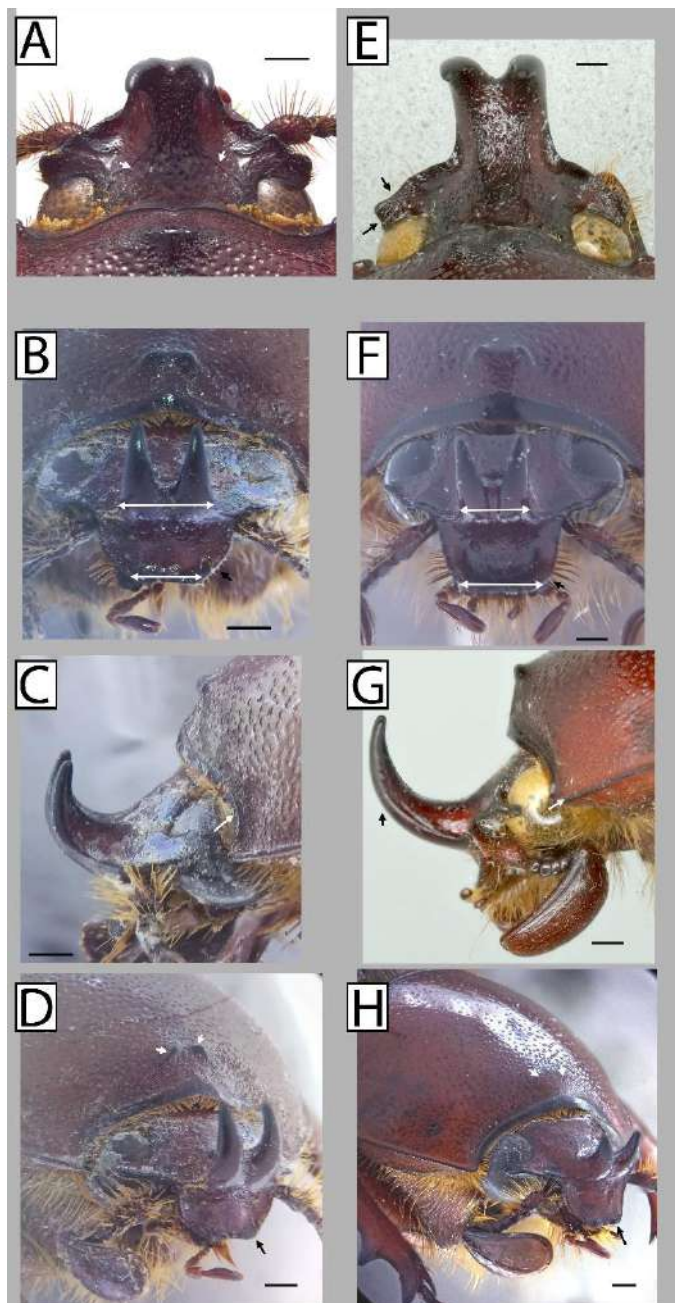


FIGURE 4. Mandible and Labrum of *Minisiderus lenorae*, *Minisiderus paranensis*. **A**, Mandible of *M. lenorae* in ventral view. Left black arrow pointing to lateral margin of molar area; right black arrow pointing to depression. **B**, Mandible of *M. lenorae* in dorsal view. White arrow pointing to limit of mesal brush; double-headed black arrows comparing sizes. **C**, Mandible of *M. lenorae* in lateral view. **D**, Labrum of *M. lenorae* in dorsal view. **E**, Mandible of *M. paranensis* in ventral view. Left black arrow pointing to lateral margin of molar area; right black arrow pointing to depression. **F**, Mandible of *M. paranensis* in dorsal view. White arrow pointing to limit of mesal brush; double-headed black arrows comparing sizes. **G**, Mandible of *M. paranensis* in lateral view. **H**, Labrum of *M. paranensis* in dorsal view. Scale bars: 1 mm.

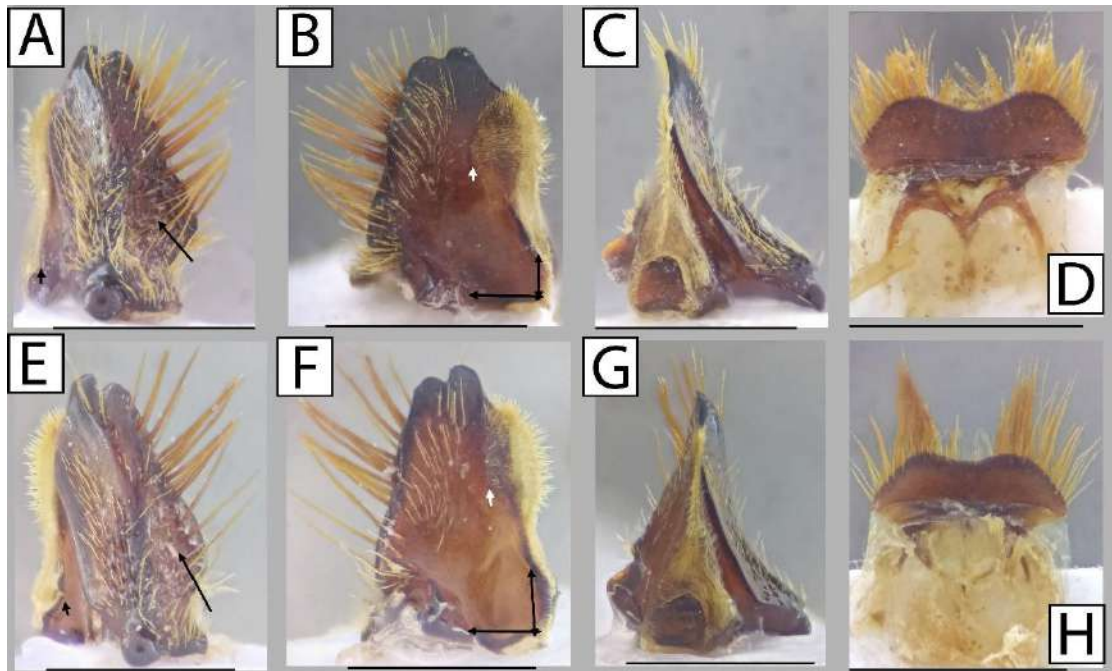


FIGURE 5. Maxilla and Mentum of *Minisiderus lenorae*, *Minisiderus paranensis*. **A**, Maxilla of *M. lenorae* in ventral view. Left black arrow pointing to apex of galea; double-headed white arrows comparing length to width of palpomere II. **B**, Maxilla of *M. lenorae* in dorsal view. Black arrow pointing to sensorial area in palpomere IV. **C**, Mentum of *M. lenorae* in ventral view. **D**, Maxilla of *M. paranensis* in ventral view. Left black arrow pointing to apex of galea; right black arrow pointing to lateral border of stipes; white arrows pointing to sinuosities on lateral border; double-headed black arrows comparing length to width of palpomere II. **E**, Maxilla of *M. paranensis* in dorsal view. Black arrow pointing to sensorial area in palpomere IV. **F**, Mentum of *M. paranensis* in ventral view. Scale bars: 1 mm.

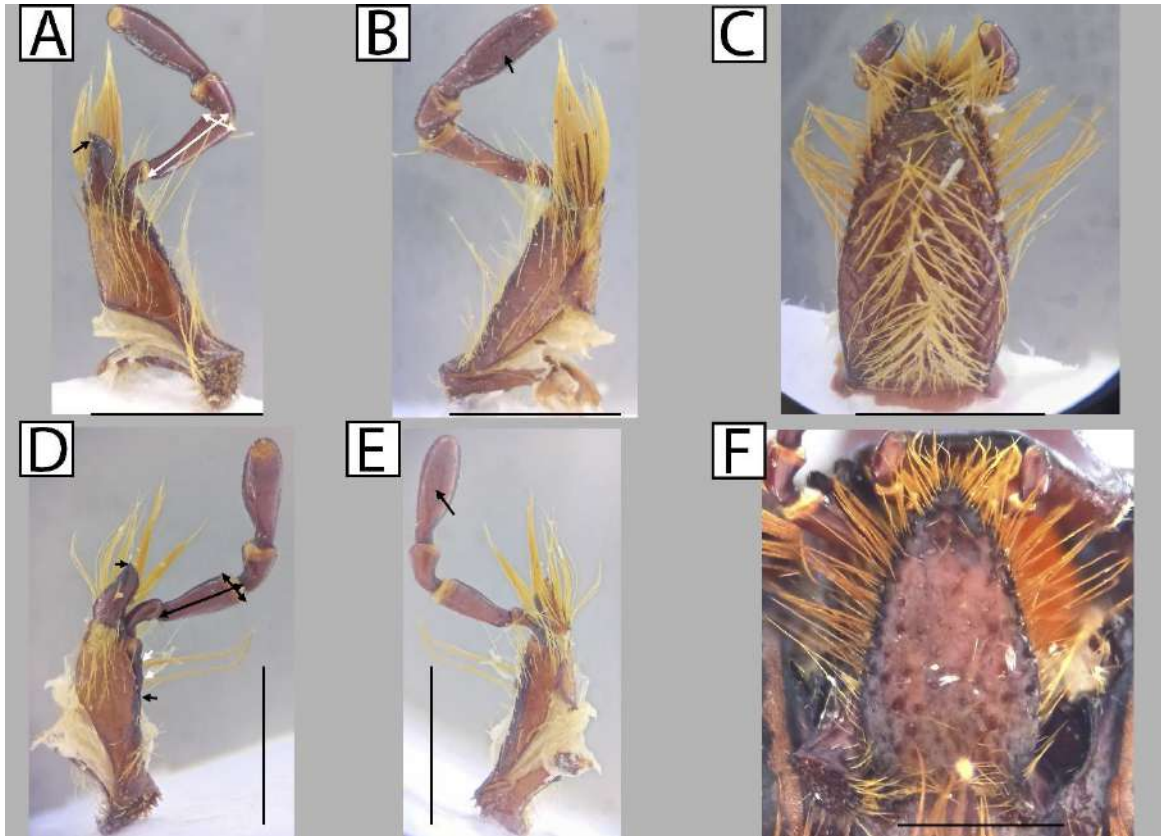


FIGURE 6. Male genitalia of *Minisiderus lenorae*, *Minisiderus paranensis*. **A**, Parameres of *M. lenorae* in caudal view. Upper white arrow pointing to carina on parameres; lower white arrow pointing to posterior base; upper black arrows pointing to ridges; lower black arrow pointing to depression of posterior phallobase. **B**, Parameres of *M. lenorae* in lateral view. Black arrow pointing to apex of depression. **C**, Parameres of *M. lenorae* in ventral view. Upper black arrow pointing to apex of parameres; lower black arrow pointing to ventral carina. **D**, Microscopy vision of parameres of *M. lenorae* in caudal view. White arrows pointing to ridges. **E**, Parameres of *M. paranensis* in caudal view. Left white arrow showing the lack of carina on parameres; right white arrows pointing to ridges; left black arrows pointing to posterior base; right black arrow pointing to depression of posterior phallobase. **F**, Parameres of *M. paranensis* in lateral view. Black arrow pointing to apex of depression. **G**, Parameres of *M. paranensis* in ventral view. Upper black arrow pointing to apex of parameres; lower black arrow pointing to ventral carina. **H**, Microscopy vision of parameres of *M. paranensis* in caudal view. White arrows pointing to ridges. Scale bars: 1 mm.

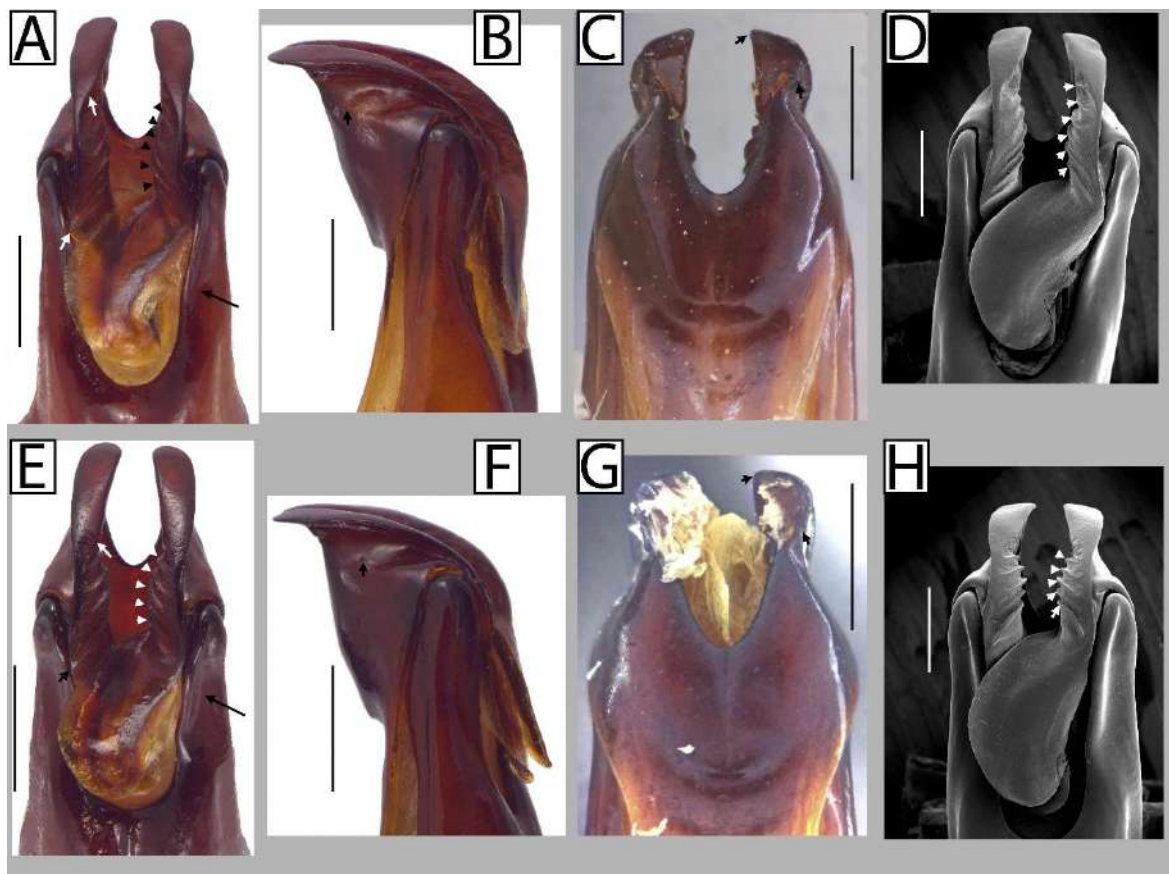


FIGURE 8. Male of *Minisiderus minicola*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. White lines comparing length to width of outer margin of metatibia; black arrow pointing to connection between apical margin to apical tooth. Scale bars: 10 mm.

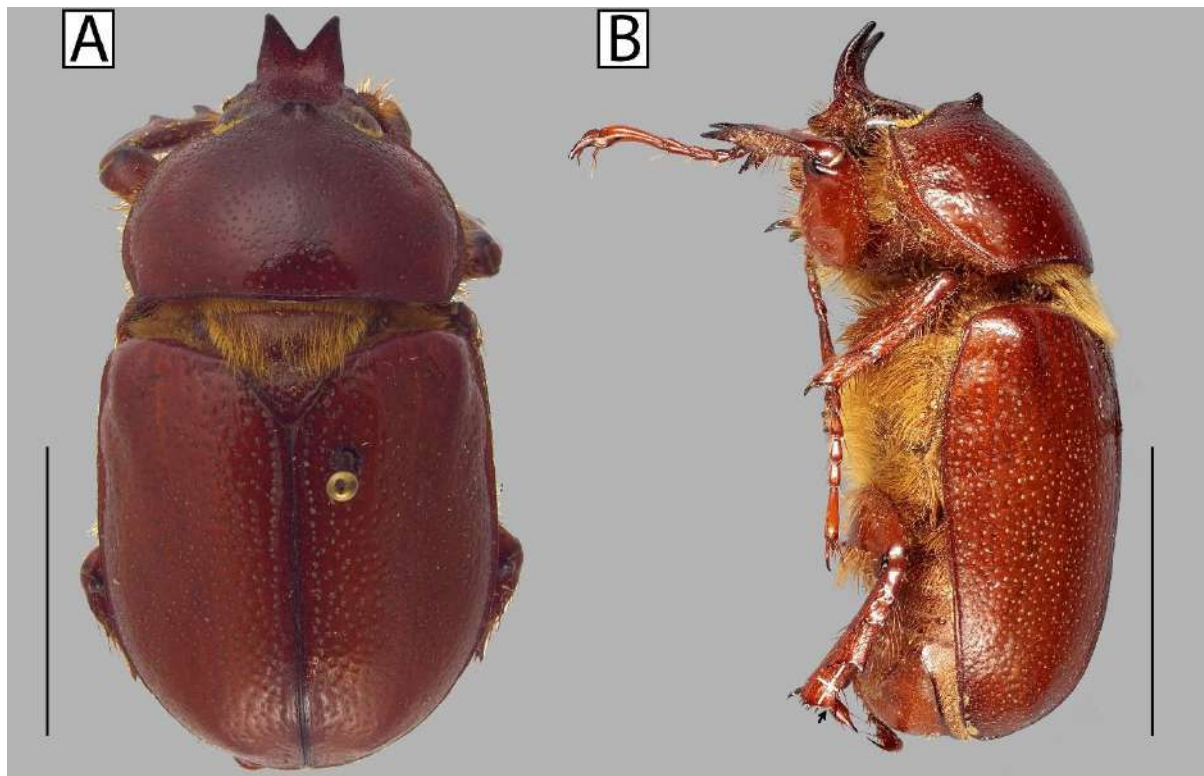


FIGURE 9. Head of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Head of *M. minicola* in dorsal view. White arrow pointing to protuberance on canthus base. **B**, Head of *M. minicola* in frontal view. Upper white arrow pointing to carina on anterior margin; lower white arrow pointing to connection between horns. **C**, Head of *M. minicola* in frontolateral view. **D**, Head of *M. benjamini* in dorsal view. Black arrow pointing to protuberance on canthus base. **E**, Head of *M. benjamini* in frontal view. White arrow pointing to connection between horns. **F**, Head of *M. benjamini* in frontolateral view. White arrow showing limits of frontal depression. **G**, Head of *M. bertolossiorum* in dorsal view. Black arrow pointing to protuberance on clypeal base. **H**, Head of *M. bertolossiorum* in frontal view. Upper black arrow pointing to tubercles; lower black arrow pointing to base of cephalic horns; white arrow pointing to sides of horns. **I**, Head of *M. bertolossiorum* in frontolateral view. Scale bars: 1 mm.

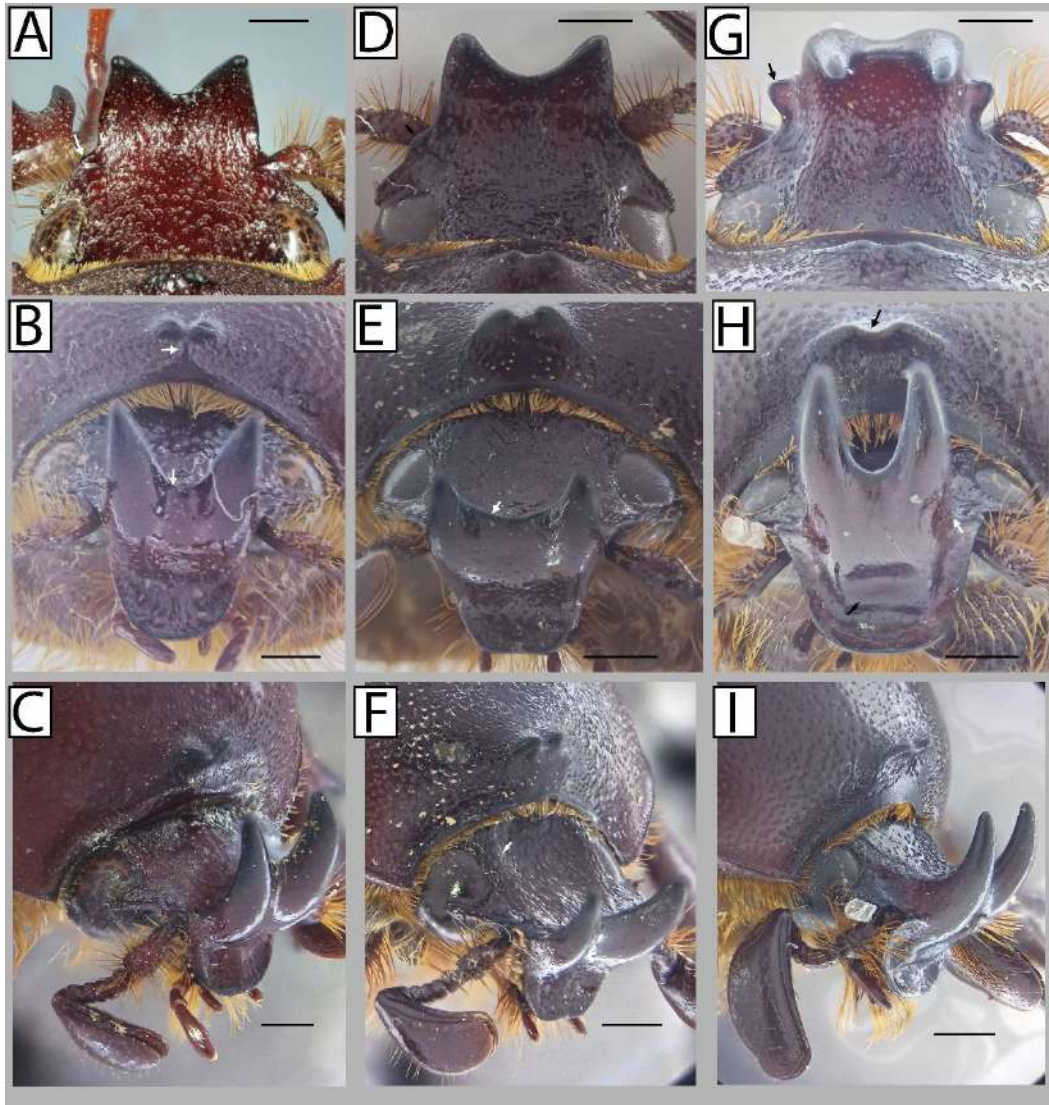


FIGURE 10. Mandible and Labrum of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Mandible of *M. minicola* in ventral view. **B**, Mandible of *M. minicola* in dorsal view. **C**, Mandible of *M. minicola* in lateral view. **D**, Labrum of *M. minicola* in dorsal view. **E**, Mandible of *M. benjamini* in ventral view. Left black arrow pointing to apex of mesal brush; right black arrow pointing to tooth. **F**, Mandible of *M. benjamini* in dorsal view. White arrow pointing to emargination of tooth; black arrows pointing to outer margin. **G**, Mandible of *M. benjamini* in lateral view. White arrow pointing to apex of molar area. **H**, Labrum of *M. benjamini* in dorsal view. **I**, Mandible of *M. bertolossiorum* in ventral view. White arrow pointing to inner carina; black arrow pointing to tooth. **J**, Mandible of *M. bertolossiorum* in dorsal view. Black arrow pointing to tooth; white arrow pointing to base of mesal brush. **K**, Mandible of *M. bertolossiorum* in lateral view. Black arrow pointing to ventral condyle. **L**, Labrum of *M. bertolossiorum* in dorsal view. Black arrow pointing to middle of anterior margin. Scale bars: 1 mm.

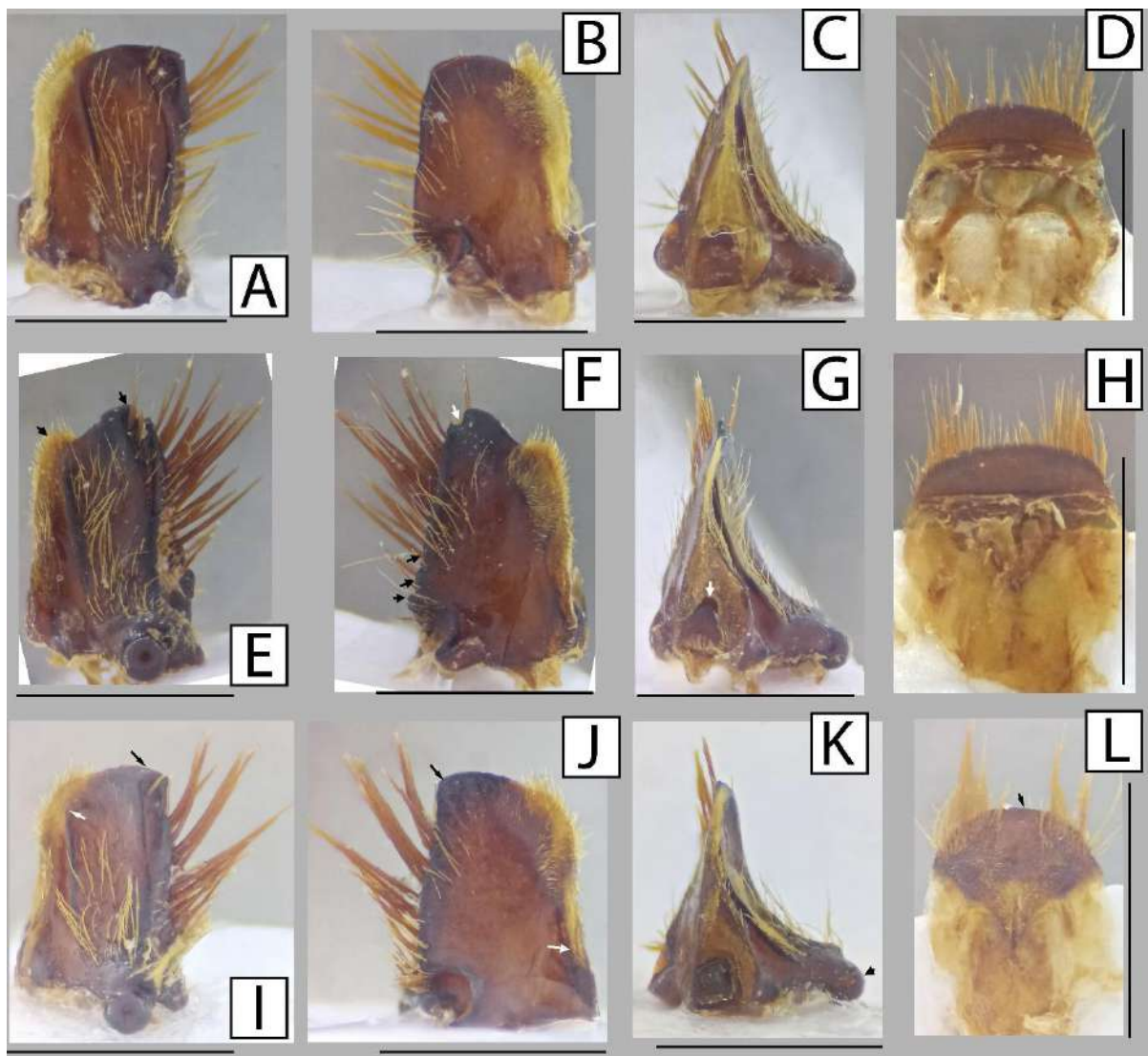


FIGURE 11. Maxilla and Mentum of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Maxilla of *M. minicola* in ventral view. **B**, Maxilla of *M. minicola* in dorsal view. **C**, Mentum of *M. minicola* in ventral view. **D**, Maxilla of *M. benjamini* in ventral view. White arrow pointing to posterior projection of ventral stipes. **E**, Maxilla of *M. benjamini* in dorsal view. Black arrow pointing to cardum. **F**, Mentum of *M. benjamini* in ventral view. Upper white arrow pointing to mentum apex; lower white arrows pointing to apical corners of mentum. **G**, Maxilla of *M. bertolossiorum* in ventral view. **H**, Maxilla of *M. bertolossiorum* in dorsal view. Black arrow pointing to subgalea crossing margin of stipes. **I**, Mentum of *M. bertolossiorum* in ventral view. Scale bars: 1 mm.

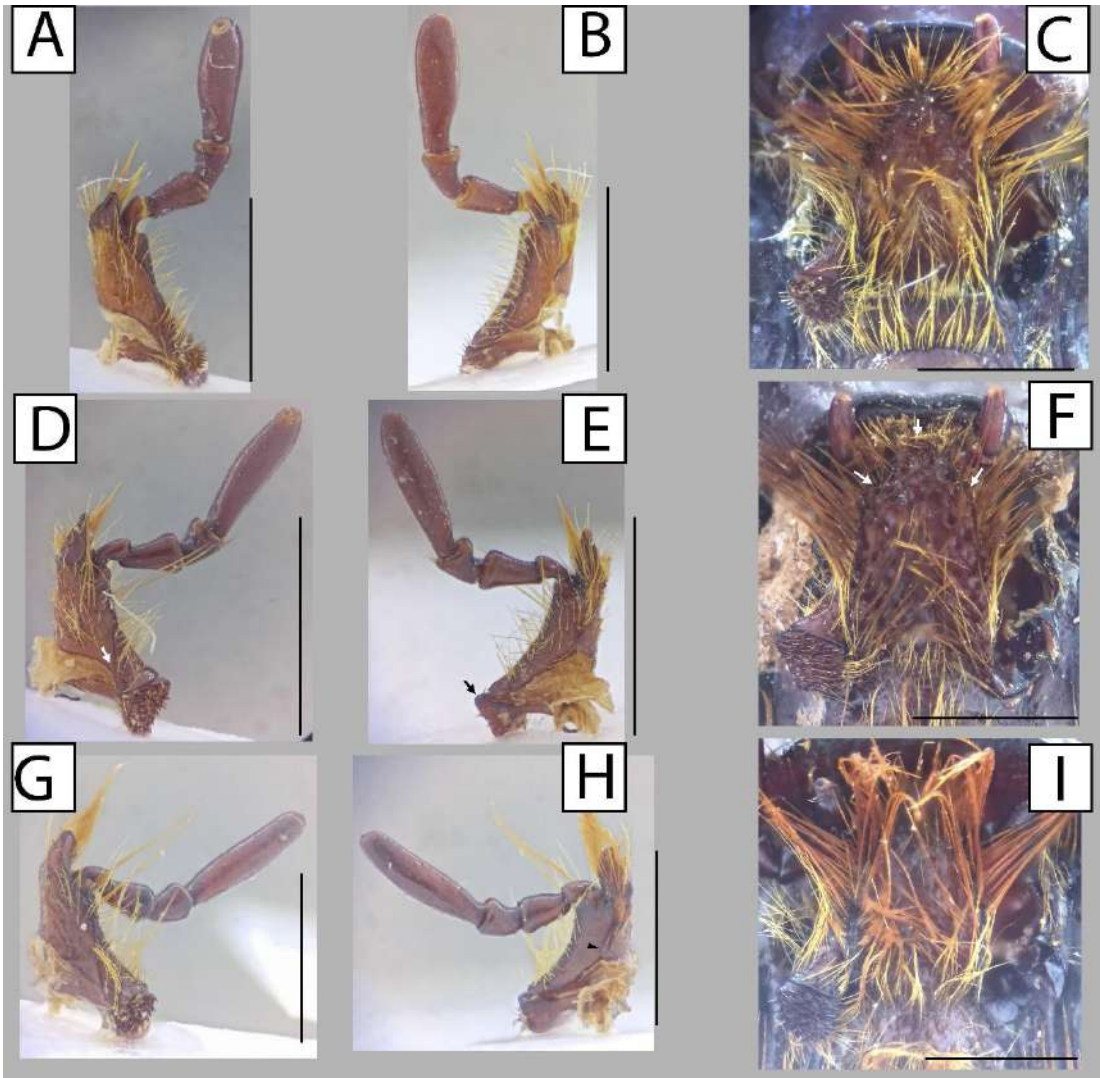


FIGURE 12. Male genitalia of *Minisiderus minicola*, *Minisiderus benjamini*, *Minisiderus bertolossiorum*. **A**, Parameres of *M. minicola* in caudal view. Black arrow pointing to outer margin. **B**, Parameres of *M. minicola* in lateral view. Left red arrow pointing to ventral carina. Right red arrow pointing to dorsal emargination. **C**, Parameres of *M. minicola* in ventral view. **D**, Parameres of *M. benjamini* in caudal view. Right black arrow pointing to outer margin; left black arrow pointing to notch at inner margin. **E**, Parameres of *M. benjamini* in lateral view. Black arrow pointing to lateral margin; white arrow pointing to apical margin of posterior phallobase. **F**, Parameres of *M. benjamini* in ventral view. Red arrow pointing to ventral depression. **G**, Parameres of *M. bertolossiorum* in caudal view. Black arrow pointing to outer margin; upper white arrow pointing to notch at inner margin; lower white arrow pointing to inner margin of basal portion. **H**, Parameres of *M. bertolossiorum* in lateral view. Left black arrow pointing to ventral carina; right black arrow pointing to lateral margin; white arrow pointing to basal carina. **I**, Parameres of *M. bertolossiorum* in ventral view. Black arrows pointing to anterior corners of ventral sclerite; white arrow pointing to lateral margin of ventral sclerite. Scale bars: 1 mm.

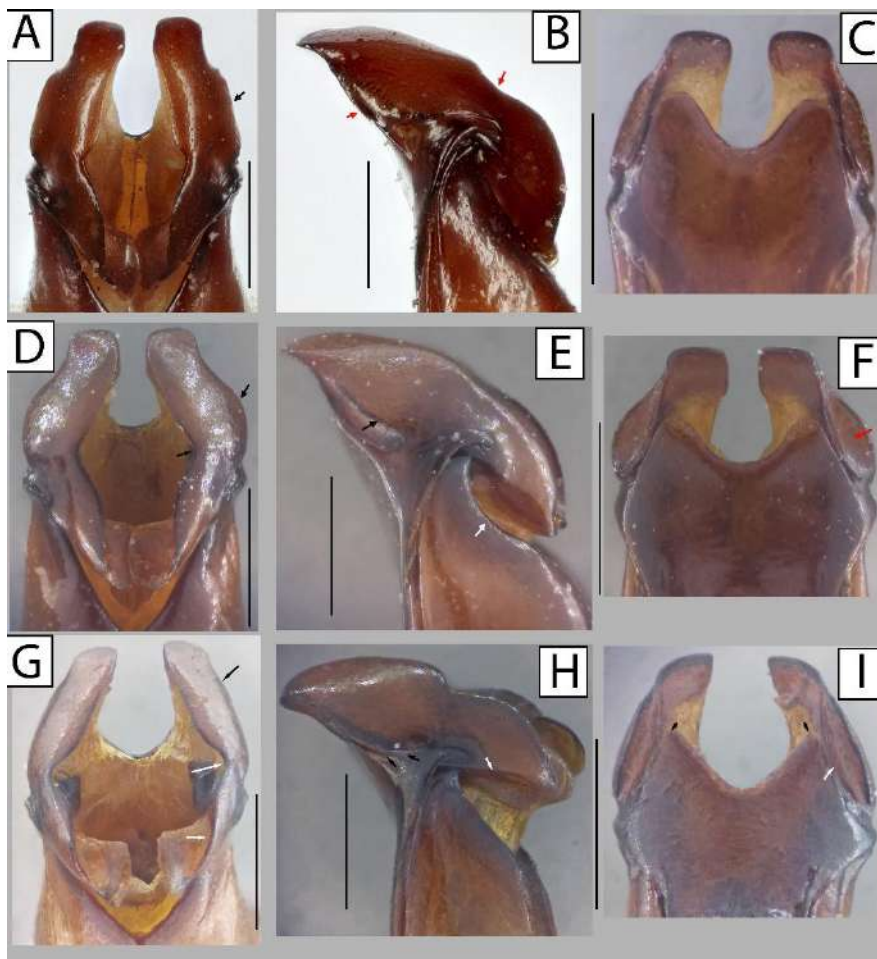


FIGURE 13. Male of *Minisiderus minicola* with antennal anomaly. **A**, Head in dorsal view. **B**, Head in ventral view. **C**, in ventral view, long-clubed left antennae. **D**, in ventral view, short-clubed right antennae. White arrows in C-D showing antennal insertion. Scale bars: 1 mm.

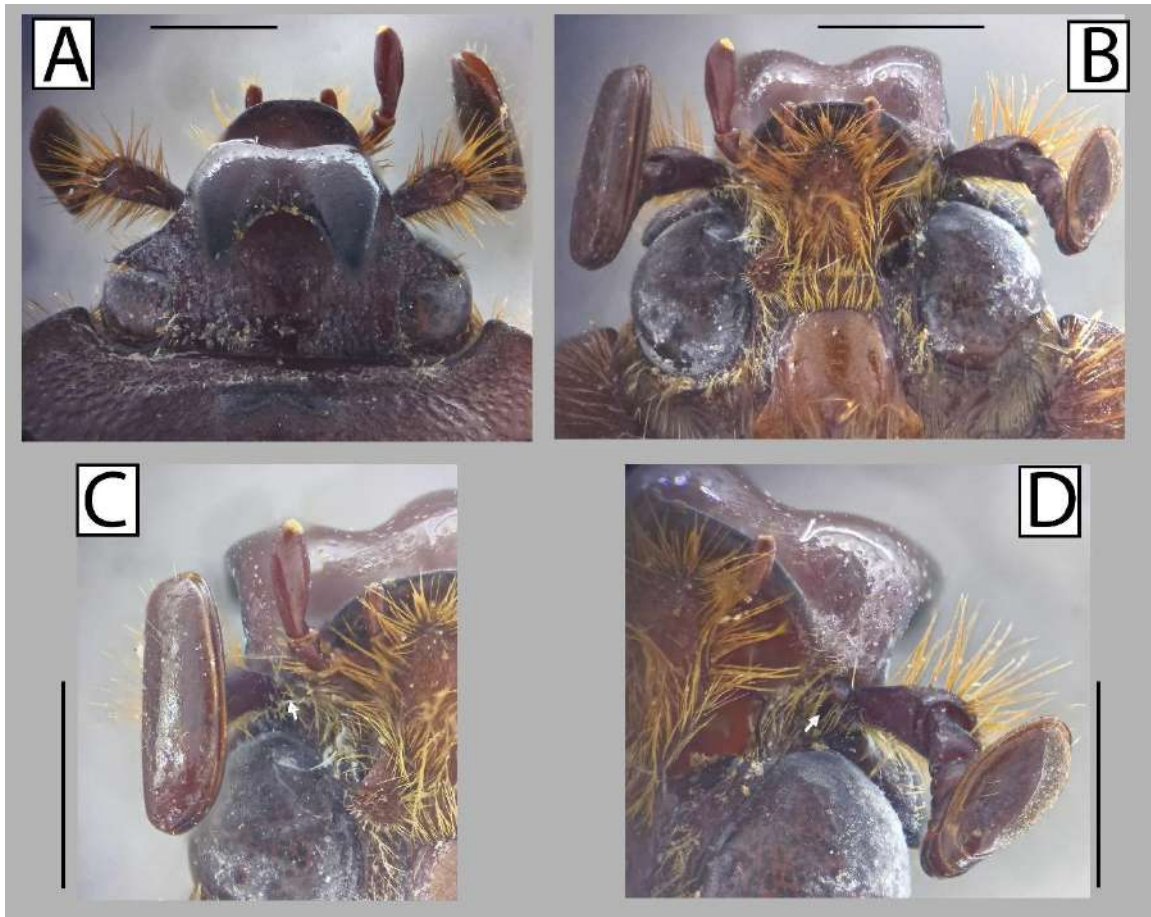


FIGURE 14. Head and metatibia of *Minisiderus benjamini*. **A**, Head of *M. benjamini* in dorsal view. Double-headed black arrow comparing clypeal length to width. **B**, Head of *M. benjamini* in lateral view. Black arrows pointing to frontal tubercles. **C**, Ocular canthus of *M. benjamini* in dorsal view. Black arrow pointing to canthus apex. **D**, Metatibia of *M. benjamini* in ventral view. Scale bars: A-C, 1 mm, D, 2 mm.

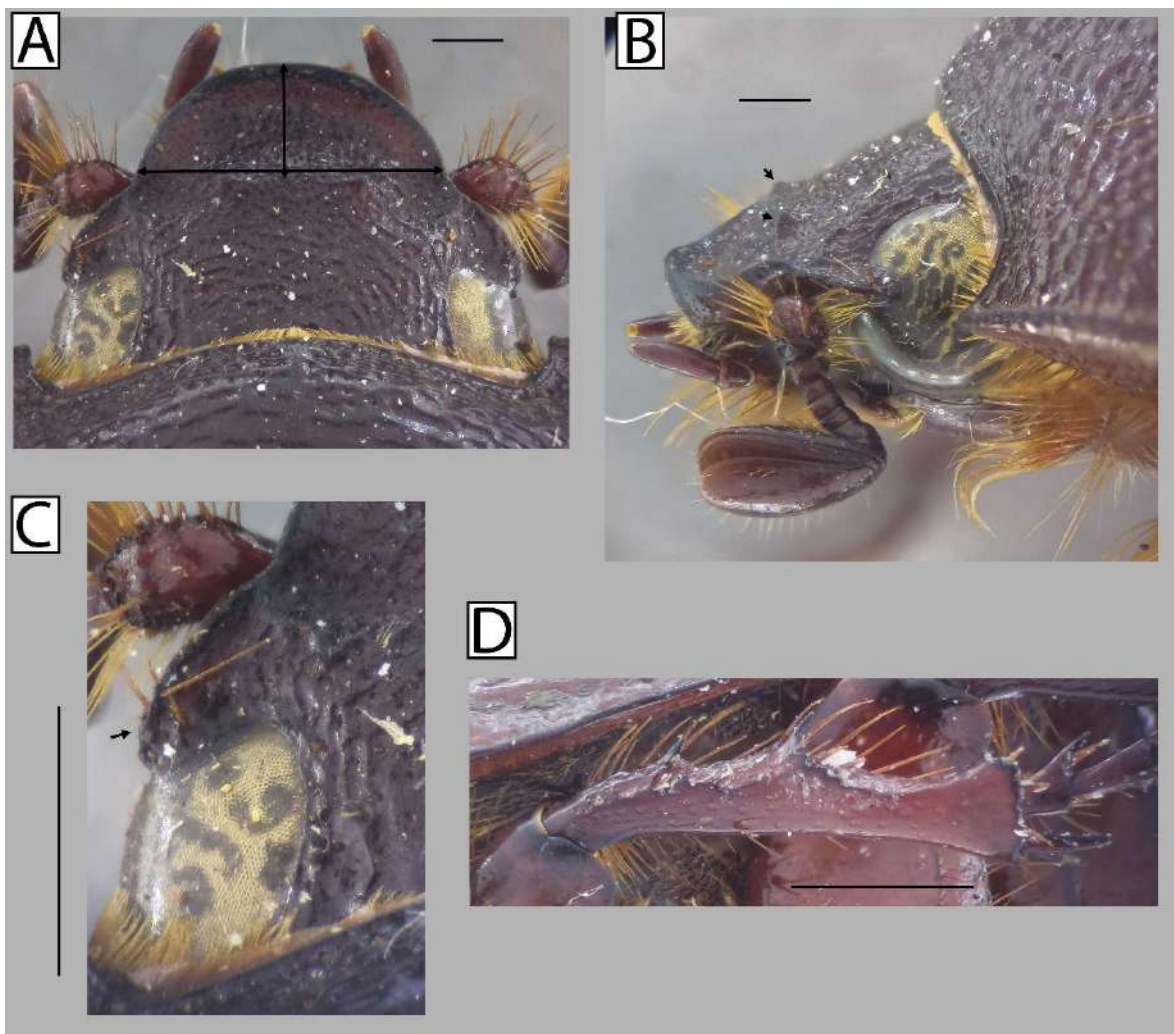


FIGURE 15. Male and female of *Minisiderus benjamini*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. White arrows pointing to pronotal wrinkles; Upper black arrow pointing to pronotal side flattened; lower black arrows showing elytral rugosities. **D**, habitus of female in lateral view. Black arrow pointing to posterior margin of tergite VIII. Scale bars: 10 mm.

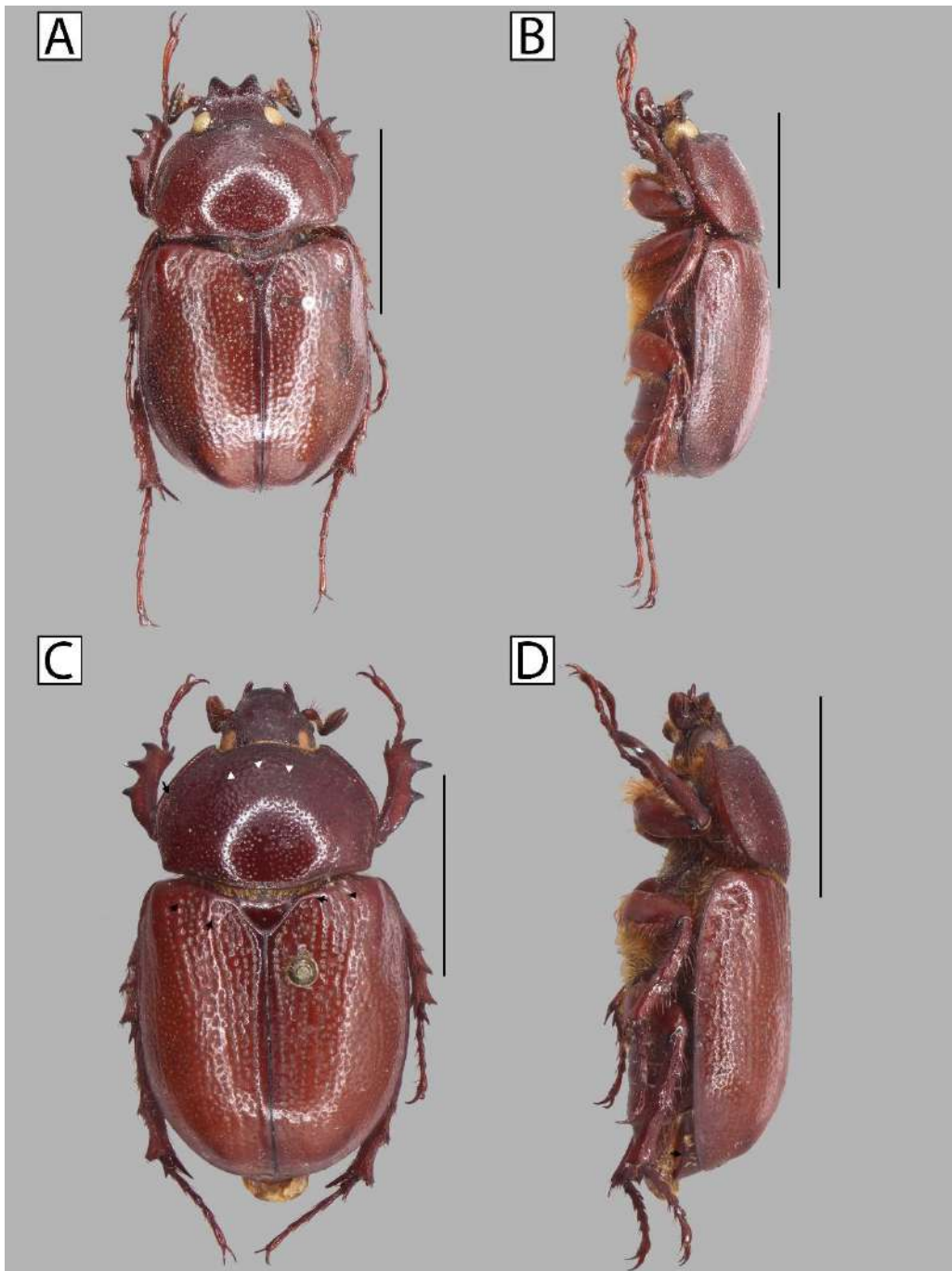


FIGURE 16. Male and female of *Minisiderus mielkeorum*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.

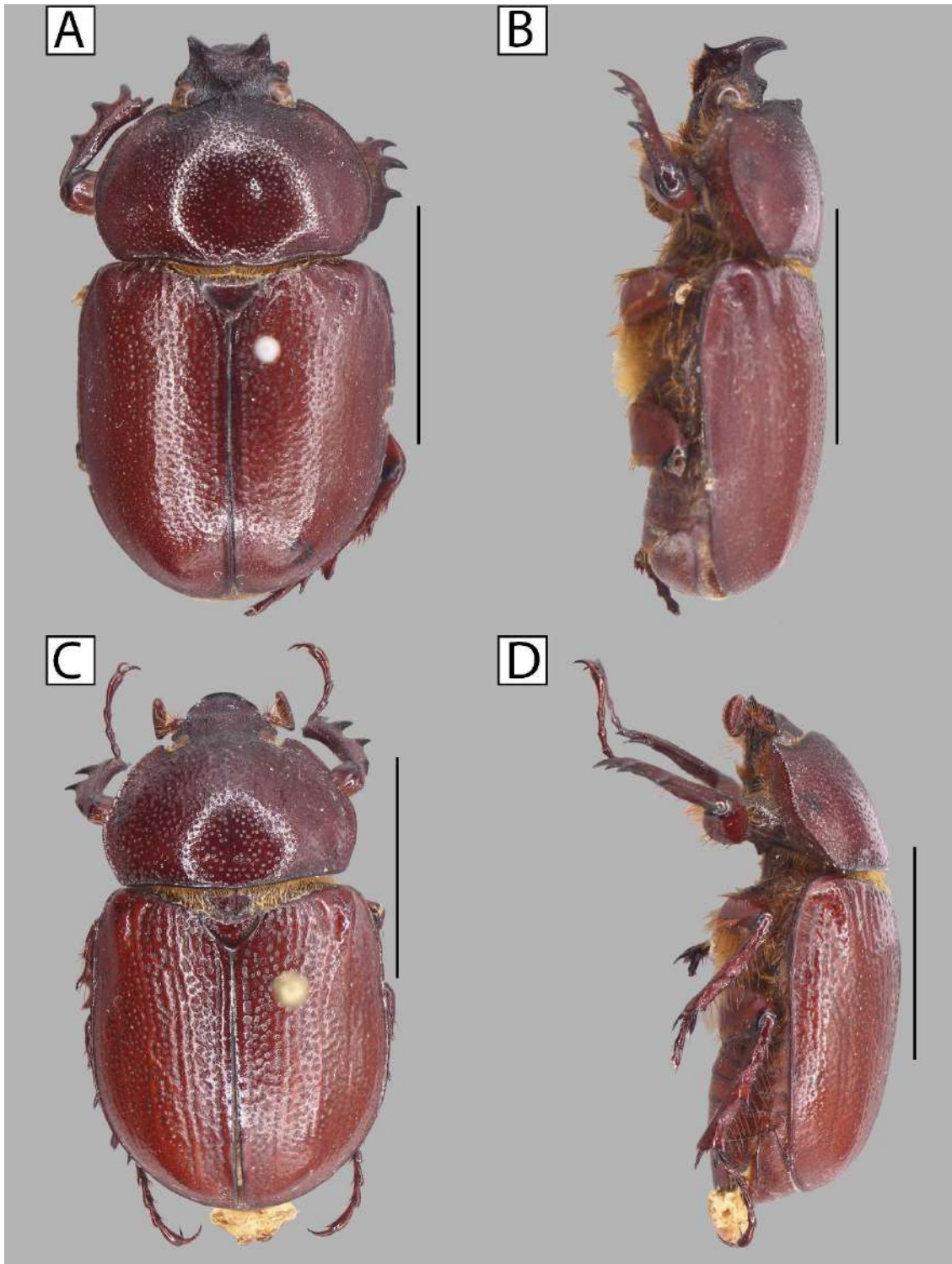


FIGURE 17. Male head, pronotum, metatibia and genitalia of *Minisiderus mielkeorum* and *Minisiderus elyanae*. **A**, Head and pronotum of *M. mielkeorum* in frontal view. White arrow pointing to space between tubercles. **B**, Head and pronotum of *M. mielkeorum* in lateral view. Black arrow pointing to horn carina; red arrow pointing to frontal tubercle; white arrow pointing to pronotal tubercles. **C**, Head and pronotum of *M. mielkeorum* in dorsal view. **D**, Metatibia of *M. mielkeorum* in ventral view. Upper white arrow pointing to anterior carina; lower white arrow pointing to posterior carina. **E**, Genitalia of *M. mielkeorum* in lateral view. **F**, Head and pronotum of *M. elyanae* in frontal view. Red arrow pointing to apex of pronotal tubercles. **G**, Head and pronotum of *M. elyanae* in lateral view. Red arrow pointing to frontal tubercles; white arrow pointing to pronotal tubercle. **H**, Head and pronotum of *M. elyanae* in dorsal view. **I**, Metatibia of *M. elyanae* in ventral view. Upper white arrow pointing to anterior carina; lower white arrow pointing to posterior carina; black arrow pointing to medial tooth. **J**, Genitalia of *M. elyanae* in lateral view. Scale bars: 1 mm.

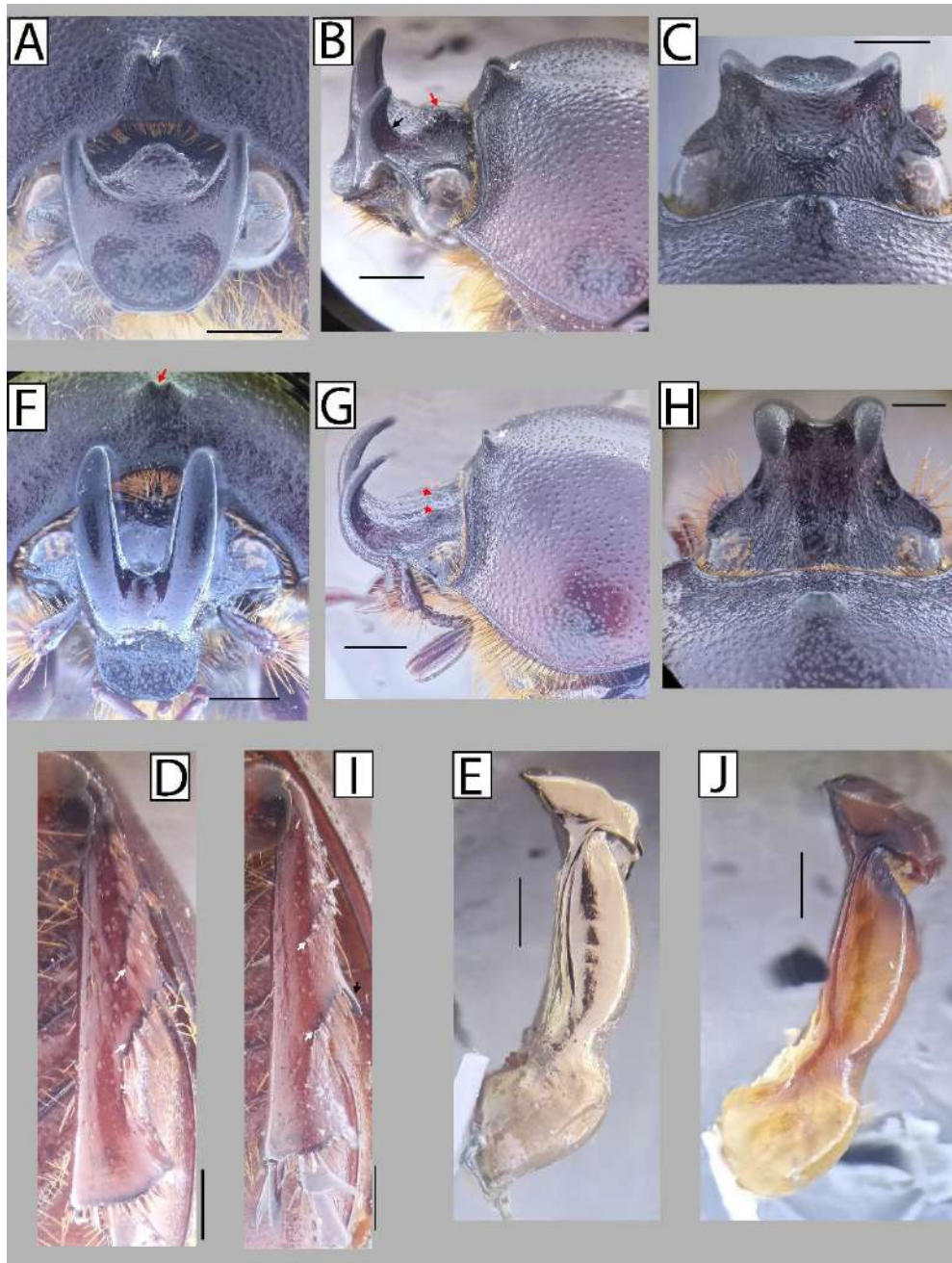


FIGURE 18. Mandible and Labrum of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Mandible of *M. mielkeorum* in ventral view. Black arrow pointing to tooth. **B**, Mandible of *M. mielkeorum* in dorsal view. Black arrow pointing to outer margin. **C**, Mandible of *M. mielkeorum* in lateral view. Black arrow pointing to ventral bump. **D**, Labrum of *M. mielkeorum* in dorsal view. **E**, Mandible of *M. elyanae* in ventral view. Upper white setae pointing to tooth; lower white setae pointing to lateral angulation of molar area margin. **F**, Mandible of *M. elyanae* in dorsal view. Black arrow pointing to outer margin. **G**, Mandible of *M. elyanae* in lateral view. Black arrow pointing to ventral bump. **H**, Labrum of *M. elyanae* in dorsal view. Scale bars: 1 mm.

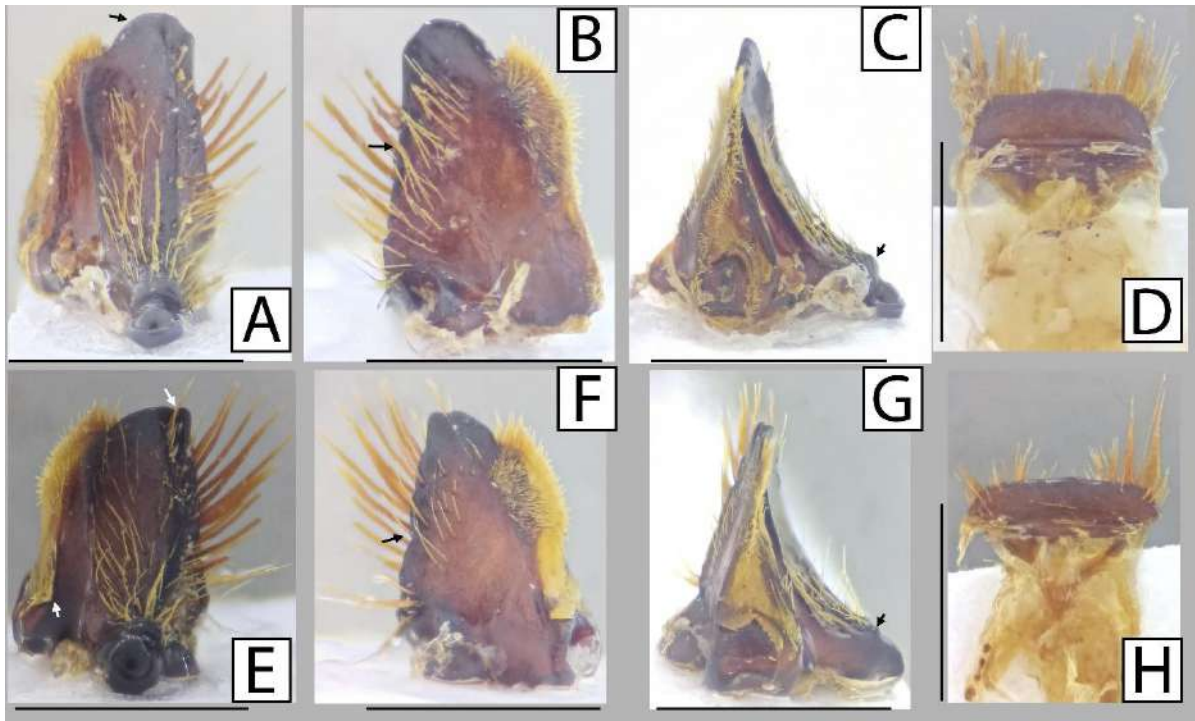


FIGURE 19. Maxilla and Mentum of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Maxilla of *M. mielkeorum* in ventral view. Black arrow pointing to inner margin of stipes. **B**, Maxilla of *M. mielkeorum* in dorsal view. Black arrow pointing to inner margin of stipes. **C**, Mentum of *M. mielkeorum* in ventral view. White arrow pointing to punctures. **D**, Maxilla of *M. elyanae* in ventral view. Black arrow pointing to lateral border. **E**, Maxilla of *M. elyanae* in dorsal view. Black arrow pointing to inner margin of stipes. **F**, Mentum of *M. elyanae* in ventral view. White arrow pointing to punctures. Scale bars: 1 mm.

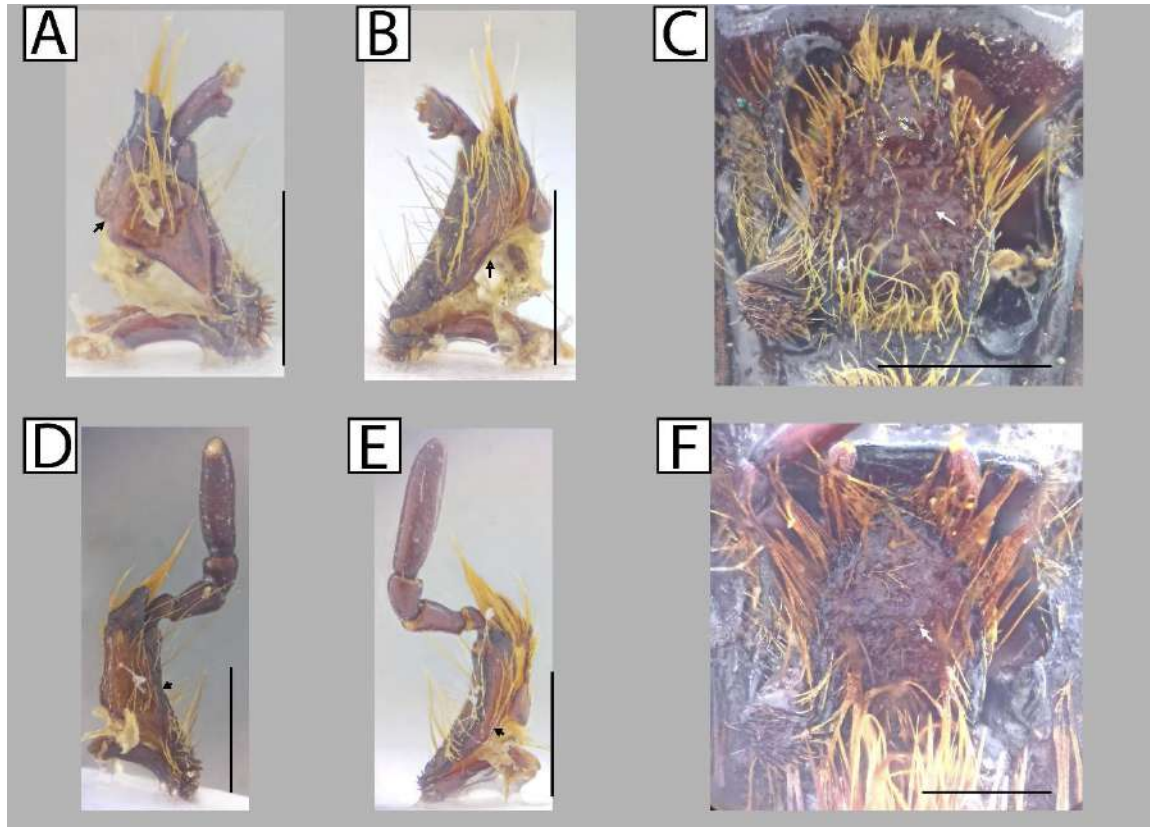


FIGURE 20. Male genitalia of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Parameres of *Minisiderus mielkeorum* in caudal view. White arrow pointing to outer margin; red arrow pointing to protrusion of inner margin at basal portion. **B**, Parameres of *Minisiderus mielkeorum* in lateral view. White arrow pointing to ventral carina; black arrow pointing to apical margin of posterior phallobase. **C**, Parameres of *Minisiderus mielkeorum* in ventral view. White arrow pointing to basal portion of margin of parameres; red arrow pointing to anterior emargination of ventral sclerite; black arrow pointing to apical inner margin. **D**, Parameres of *Minisiderus elyanae* in caudal view. White arrow pointing to notch at outer margin; red arrow pointing to inner margin at basal portion. **E**, Parameres of *Minisiderus elyanae* in lateral view. Upper white arrow pointing to ventral carina; lower white arrow pointing to apical margin of posterior phallobase. **F**, Parameres of *Minisiderus elyanae* in ventral view. White arrow pointing to basal portion of margin of parameres; red arrow pointing to emargination of ventral sclerite. Scale bars: 1 mm.

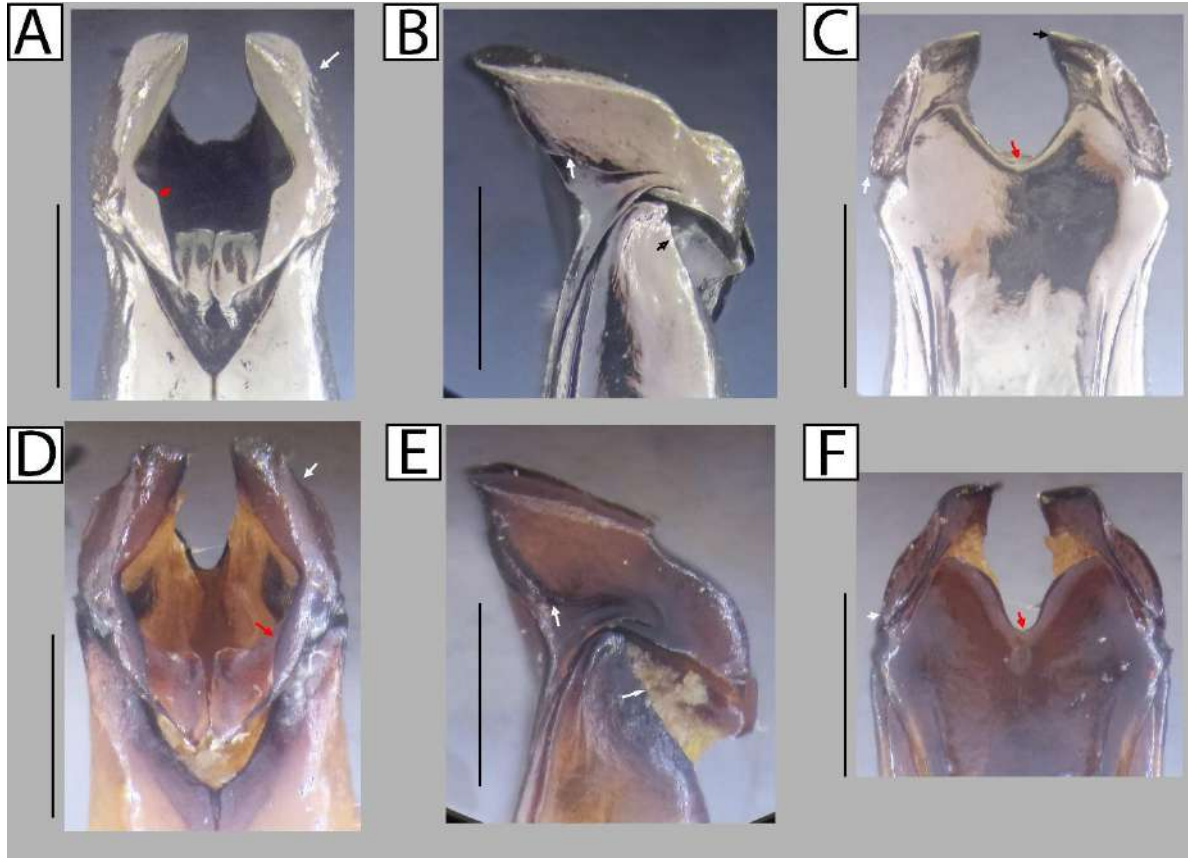


FIGURE 21. Female head, metatibia and genitalia of *Minisiderus mielkeorum*, *Minisiderus elyanae*. **A**, Head of *Minisiderus mielkeorum* in dorsal view. Black arrow pointing to canthus anterior margin; double-headed black arrows comparing clypeal length to width; white arrows pointing to punctures on clypeal apical portion. **B**, Coxites of *M. mielkeorum* in ventral view. Black arrows pointing to apical emargination. **C**, Head of *M. mielkeorum* in lateral view. Black arrow pointing to frontal tubercle; left white arrow pointing to clypeal base elevated; right white arrow pointing to pronotal anterior corner. **D**, Metatibia of *M. mielkeorum* in ventral view. **E**, Head of *Minisiderus elyanae* in dorsal view. Black arrows pointing to wrinkles on frons and vertex; double-headed arrows comparing clypeal length to width; white arrows pointing to clypeal apical portion. **F**, Coxites of *M. elyanae* in ventral view. Black arrows pointing to apical emargination. **G**, Head of *M. elyanae* in lateral view. Black arrow pointing to frontal tubercle; white arrow pointing to clypeal base. **H**, Metatibia of *M. elyanae* in ventral view. Scale bars: 1 mm.

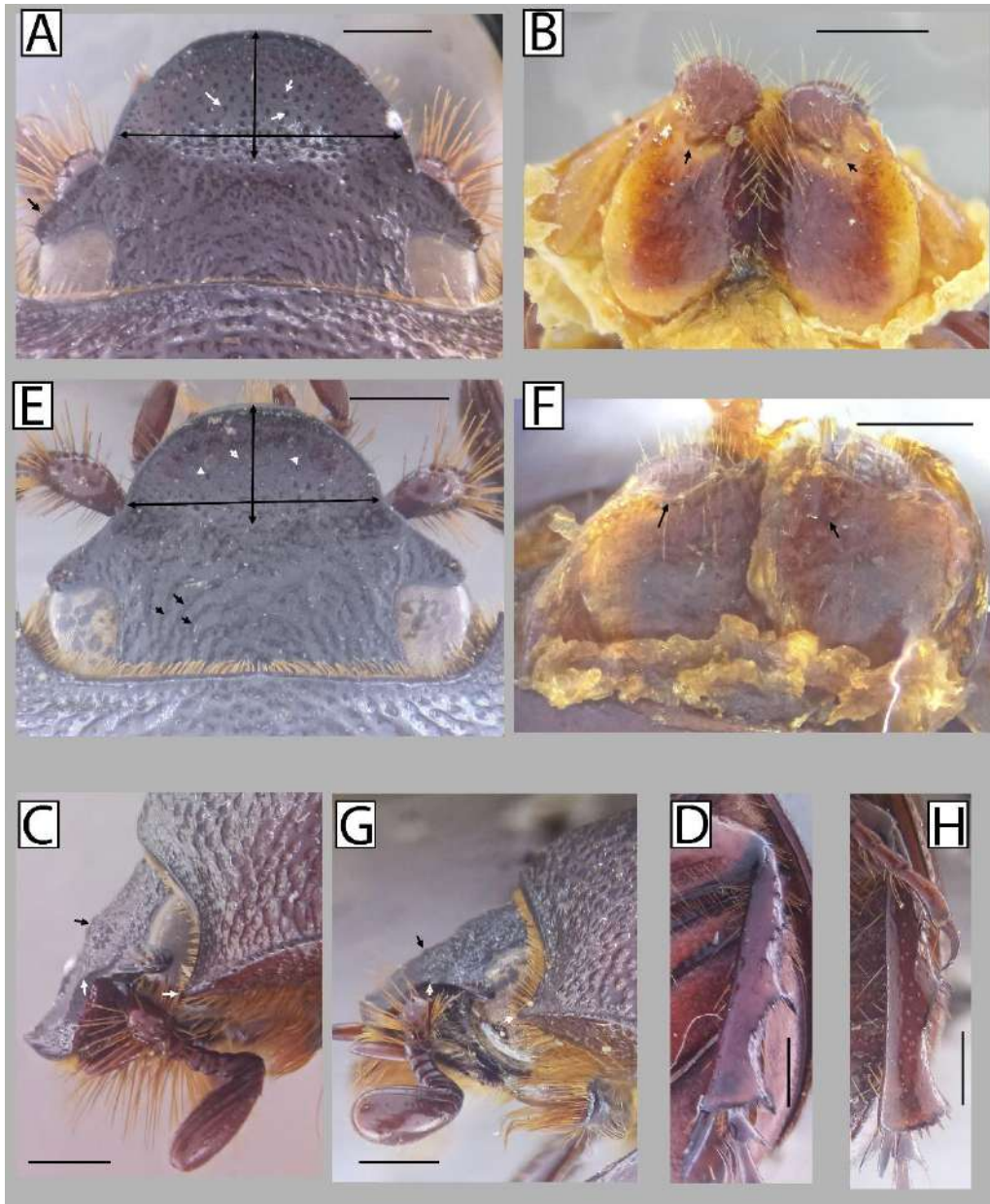


FIGURE 22. Male and female of *Minisiderus elyanae*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. Black arrow pointing to elytral apex. **D**, habitus of female in lateral view. Black arrow pointing to posterior margin of tergite VIII. Scale bars: 10 mm.

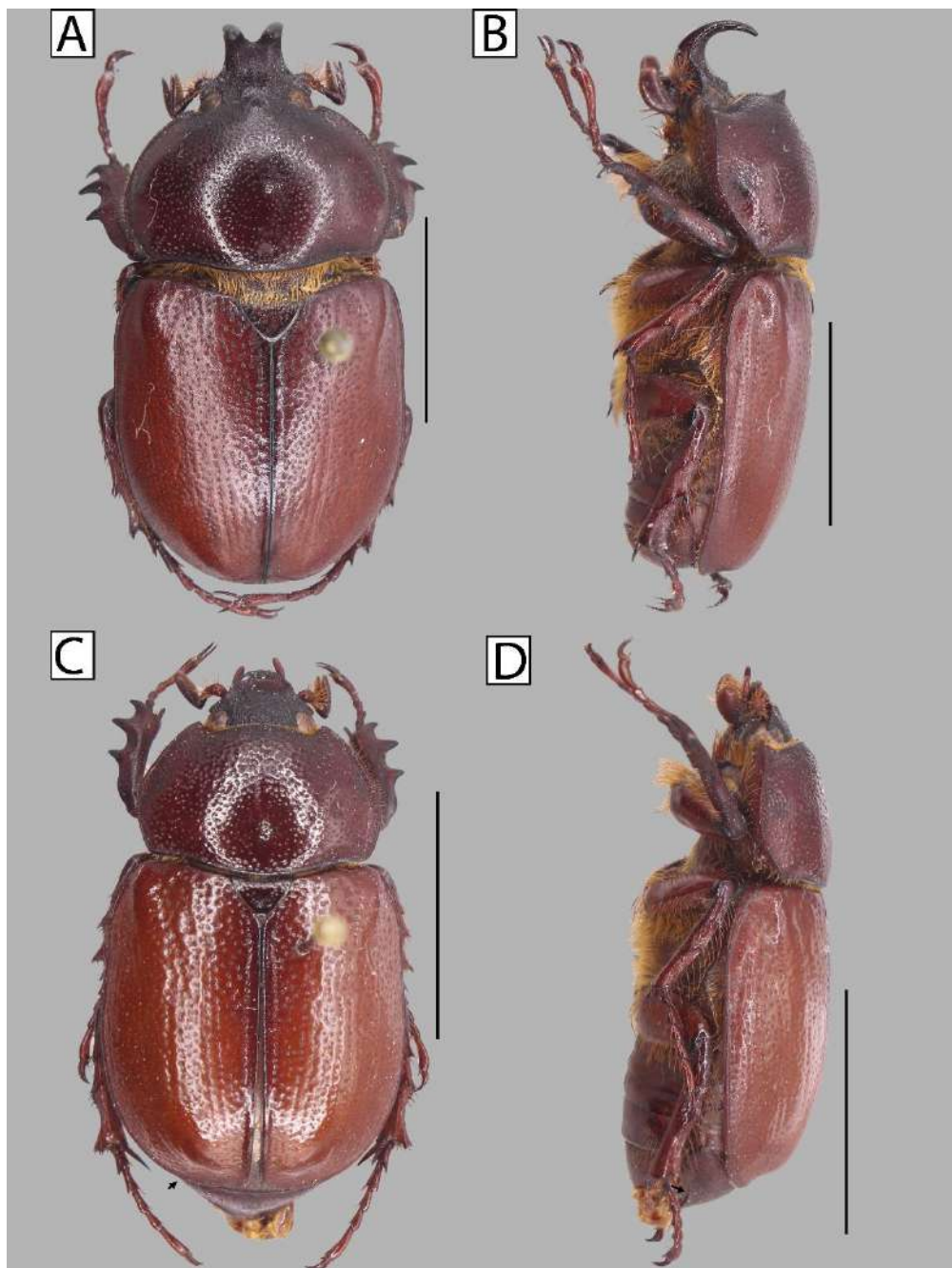


FIGURE 23. Male of *Minisiderus veadeirensis*. **A**, Habitus in dorsal view. Upper white arrow pointing to outer margin of humeral umbone; lower white arrow pointing to lateral margin of elytra. **B**, habitus in lateral view. Upper white arrow pointing to anterior carina of mesotibia; white stripes comparing length of outer margin of metatibia to width. Scale bars: 10 mm.

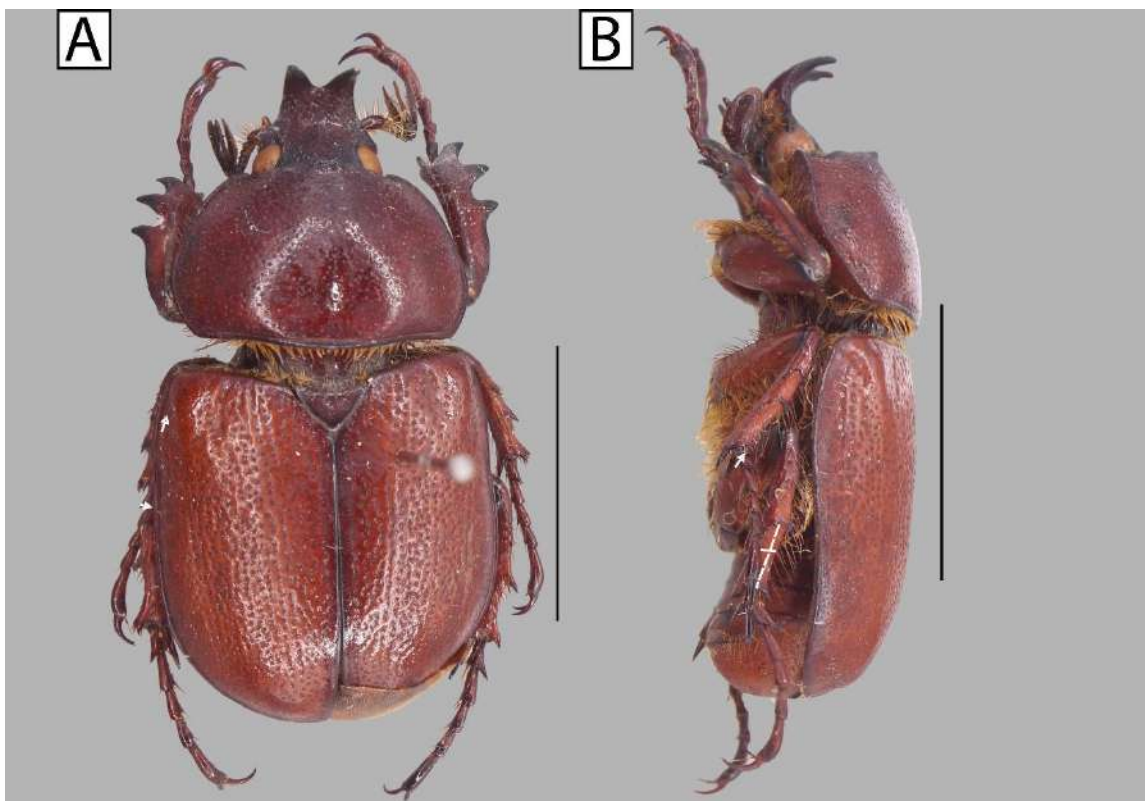


FIGURE 24. Male head and pronotum of *Minisiderus veadeirensis* and *Minisiderus rondoniensis*. **A**, Head of *M. veadeirensis* in dorsal view. White arrow pointing to connection between canthus and horn. **B**, Head of *M. veadeirensis* in frontal view. **C**, Head and pronotum of *M. veadeirensis* in lateral view. White arrow pointing to area between anterior margin of pronotum and pronotal tubercles. **D**, Head of *M. rondoniensis* in dorsal view. **E**, Head of *M. rondoniensis* in frontal view. White arrow pointing to connection between cephalic horns. **F**, Head and pronotum of *M. rondoniensis* in frontoateral view. Black arrow pointing to limit of depression on frons. Scale bars: 1 mm.

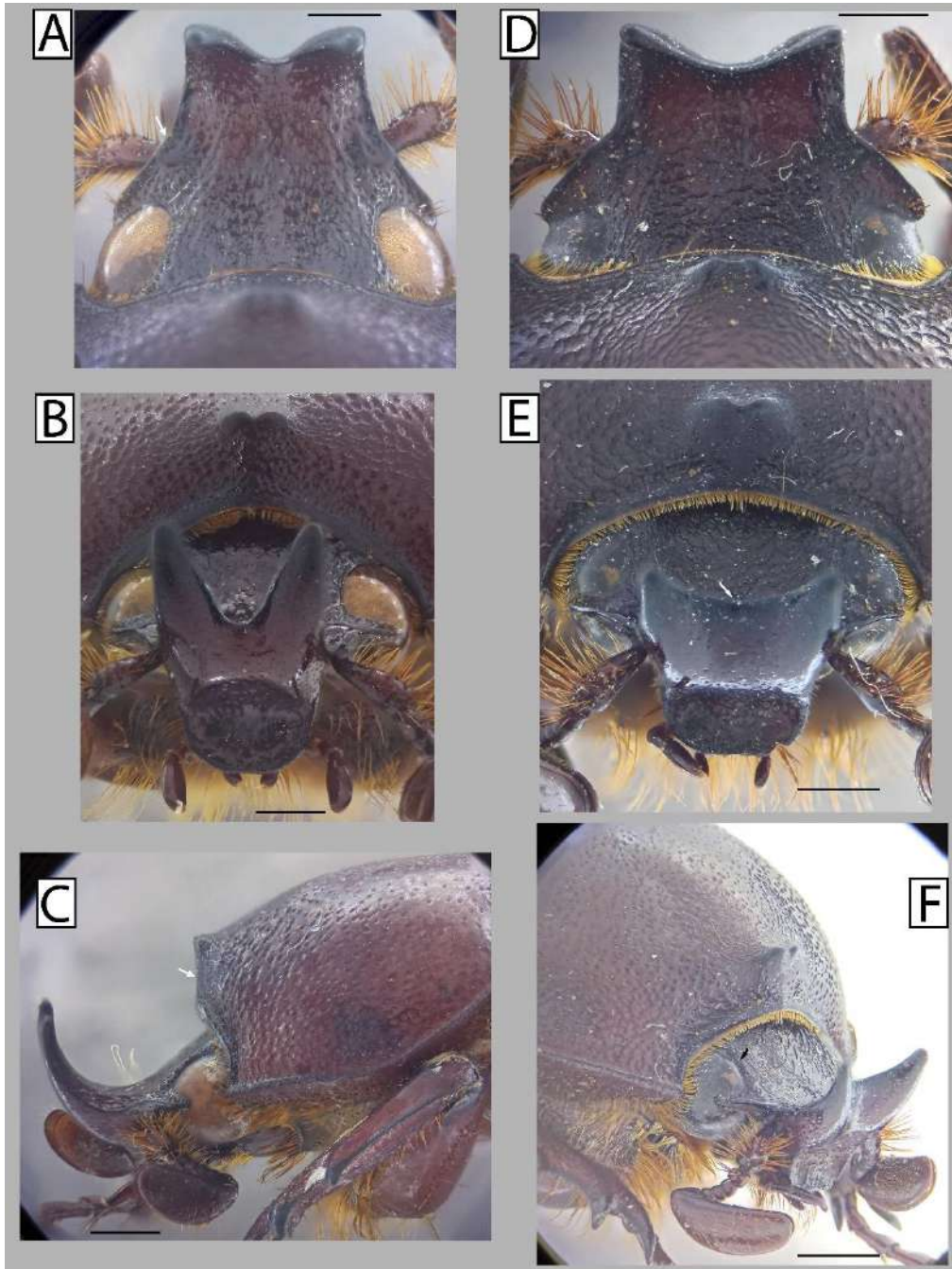


FIGURE 25. Male genitalia of *Minisiderus veadeirensis* and *Minisiderus rondoniensis*. **A**, Parameres of *M. veadeirensis* in caudal view. White arrow pointing to outer margin; black arrow pointing to notch at inner margin; red arrow pointing to inner margin at basal portion. **B**, Parameres of *M. veadeirensis* in lateral view. Upper white arrow pointing to end of lateral margin; lower white arrow pointing to end of ventral margin; black arrows pointing to basal carina; green arrow pointing to depression on posterior phallobase. **C**, Parameres of *M. veadeirensis* in ventral view. White arrows pointing to apex of ventral depression. **D**, Parameres of *M. rondoniensis* in caudal view. White arrow pointing to emargination at outer margin; red arrow pointing to medial notch; black arrow pointing to inner margin at basal portion. **E**, Parameres of *M. rondoniensis* in lateral view. Upper black arrow pointing to end of lateral margin; lower black arrow pointing to end of ventral margin; white arrow pointing to dorsal margin of basal portion; upper red arrow pointing to apex of posterior phallobase corner; lower red arrow pointing to apical margin of posterior phallobase. **F**, Parameres of *M. rondoniensis* in ventral view. White arrows pointing to anterior corners of ventral sclerite; black arrow pointing to basal portion of lateral margin. Scale bars: 1 mm.

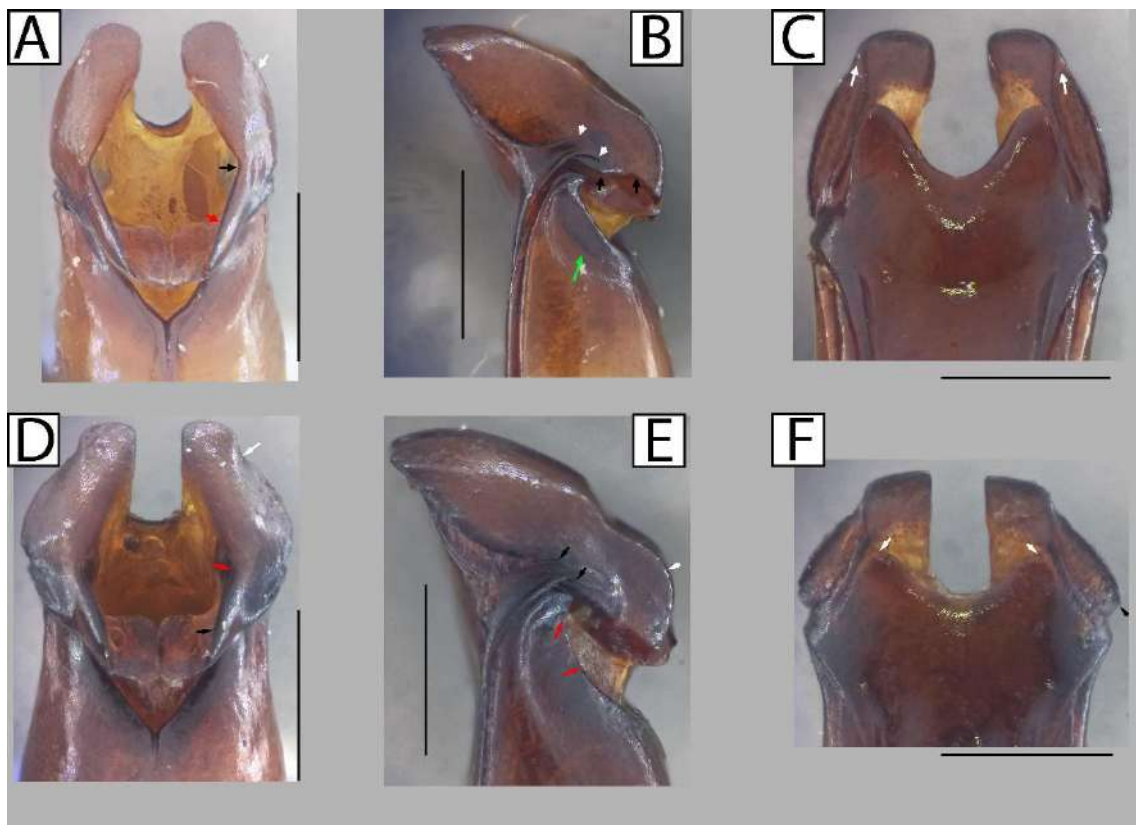


FIGURE 26. Male of *Minisiderus bertolossiorum*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Upper white arrows pointing to outer teeth of mesotibia; lower white arrow pointing to metatibial apex in connection to apical tooth; black arrow pointing to posterior carina of metatibia. Scale bars: 10 mm.

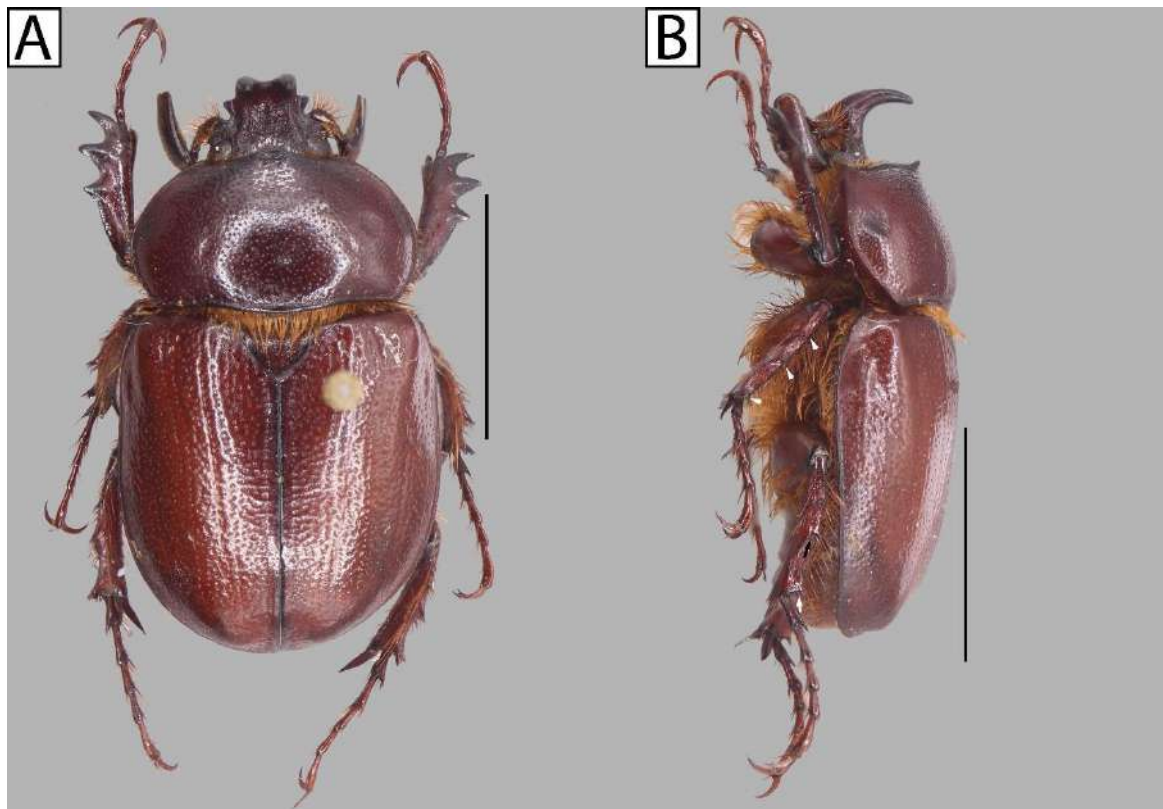


FIGURE 27. Male of *Minisiderus rondoniensis*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Upper black arrow pointing to medial tooth; lower black arrow pointing to metatibial apex in connection to apical tooth. Scale bars: 10 mm.

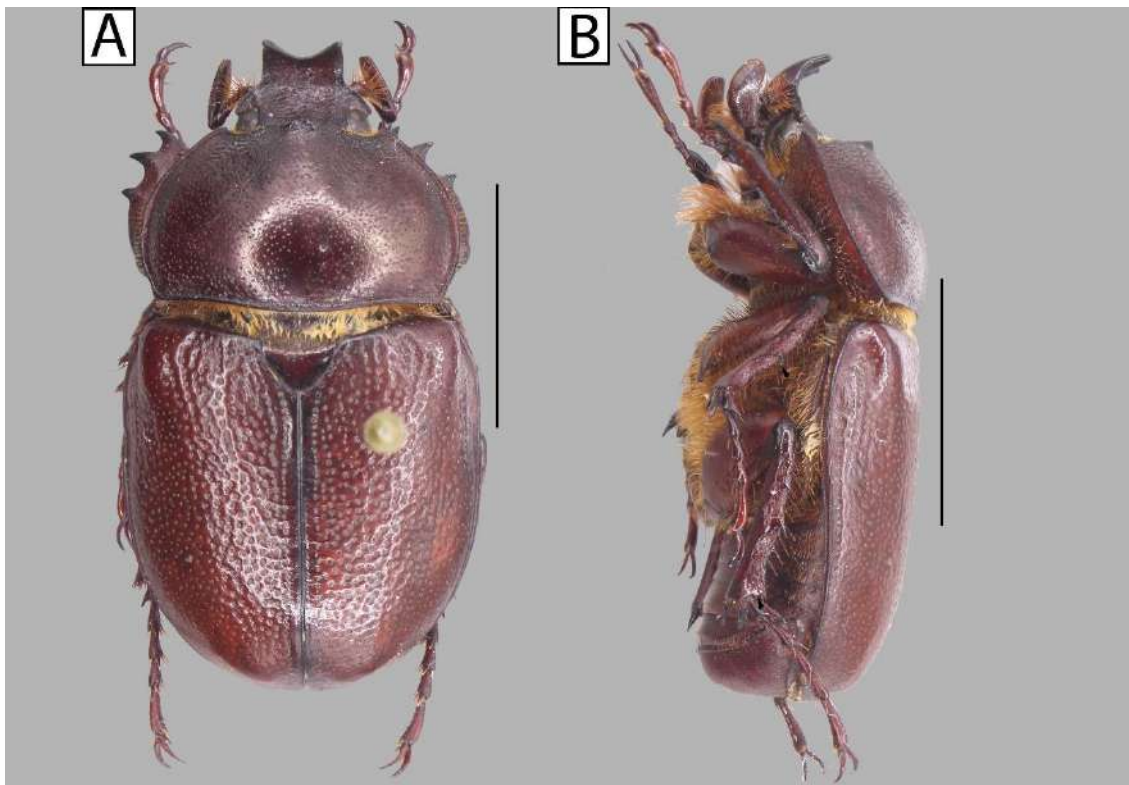


FIGURE 28. Male head, pronotum and tergite VIII of *Minisiderus rondoniensis* and *Minisiderus benjamini*. **A**, Head of *M. rondoniensis* in lateral view. White arrow pointing to apical portion of lateral margin. **B**, Head and pronotum of *M. rondoniensis* in dorsal view. White arrows pointing to wrinkles of pronotal disc. **C**, Tergite VIII of *M. rondoniensis* in posterior view. **D**, Head of *M. benjamini* in lateral view. **E**, Head and pronotum of *M. benjamini* in dorsal view. Scale bars: A, D, 1 mm, B-C, E, 5 mm.

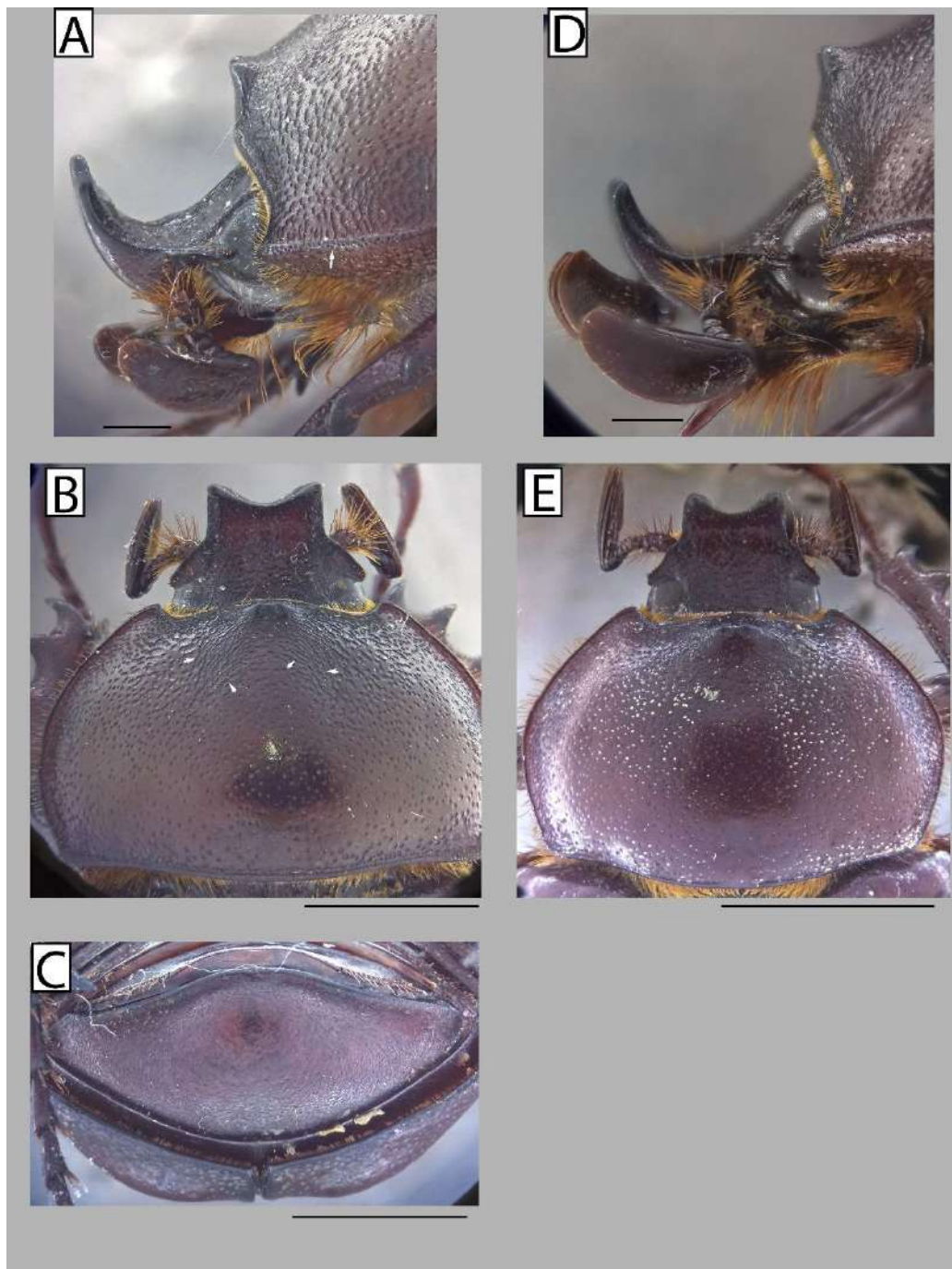


FIGURE 29. Male mouthparts of *Minisiderus rondoniensis*. **A**, Mandible in ventral view. White arrow pointing to tooth; black arrow pointing to short carina near tooth. **B**, Mandible in dorsal view. Upper black arrow pointing to emargination of tooth; lower black arrow pointing to mandibular depression. **C**, Mandible in lateral view. Left black arrow pointing to margin of socket; right black arrow pointing to condyle. **D**, Labrum in dorsal view. Black arrow pointing to bump on anterior margin. **E**, Maxilla in ventral view. Upper black arrow pointing to galea; lower black arrow pointing to cardum. **F**, Maxilla in dorsal view. Black arrow pointing to margin of palpomere III; white arrow pointing to outer margin of subgalea. **G**, Mentum in ventral view. Scale bars: 1 mm.

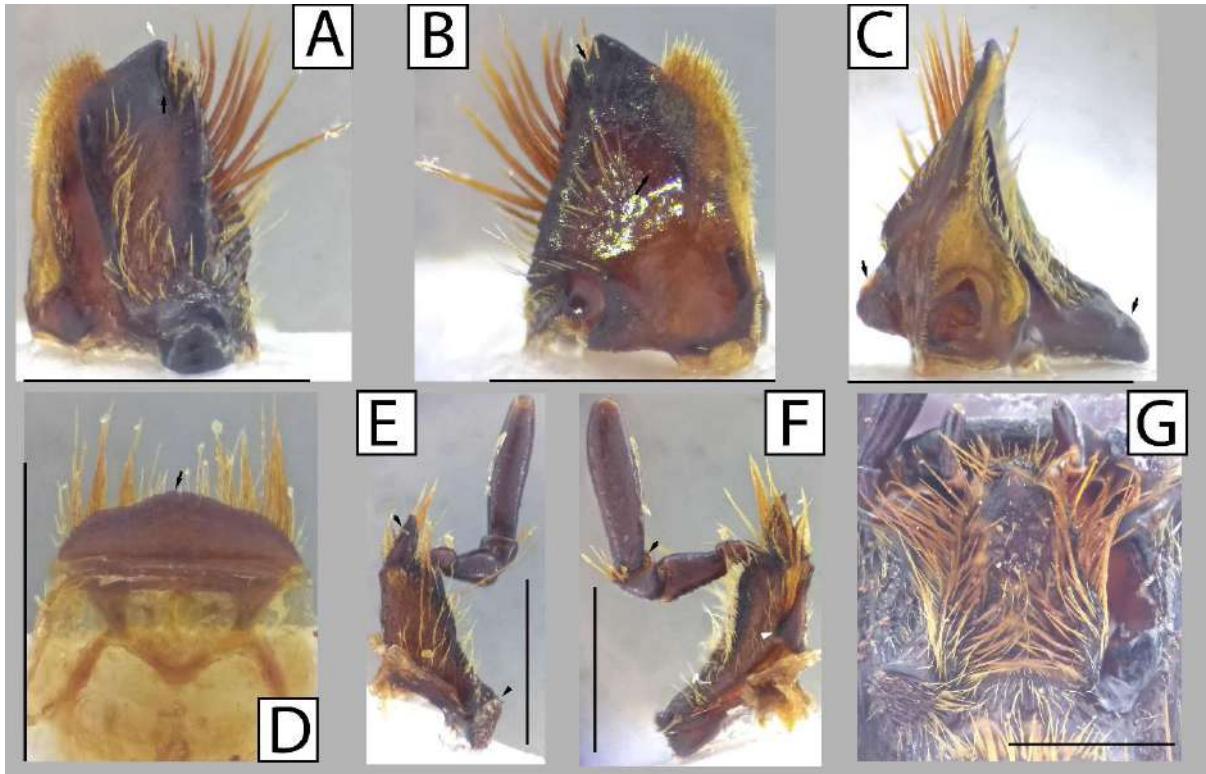


FIGURE 30. Female of *Minisiderus* sp. **A**, Habitus in dorsal view. Black arrow pointing to pronotal lateral margin; white arrows pointing to regular rows of setae on elytra. **B**, habitus in lateral view. White arrow pointing to basal tooth of metatibia. Scale bars: 10 mm.

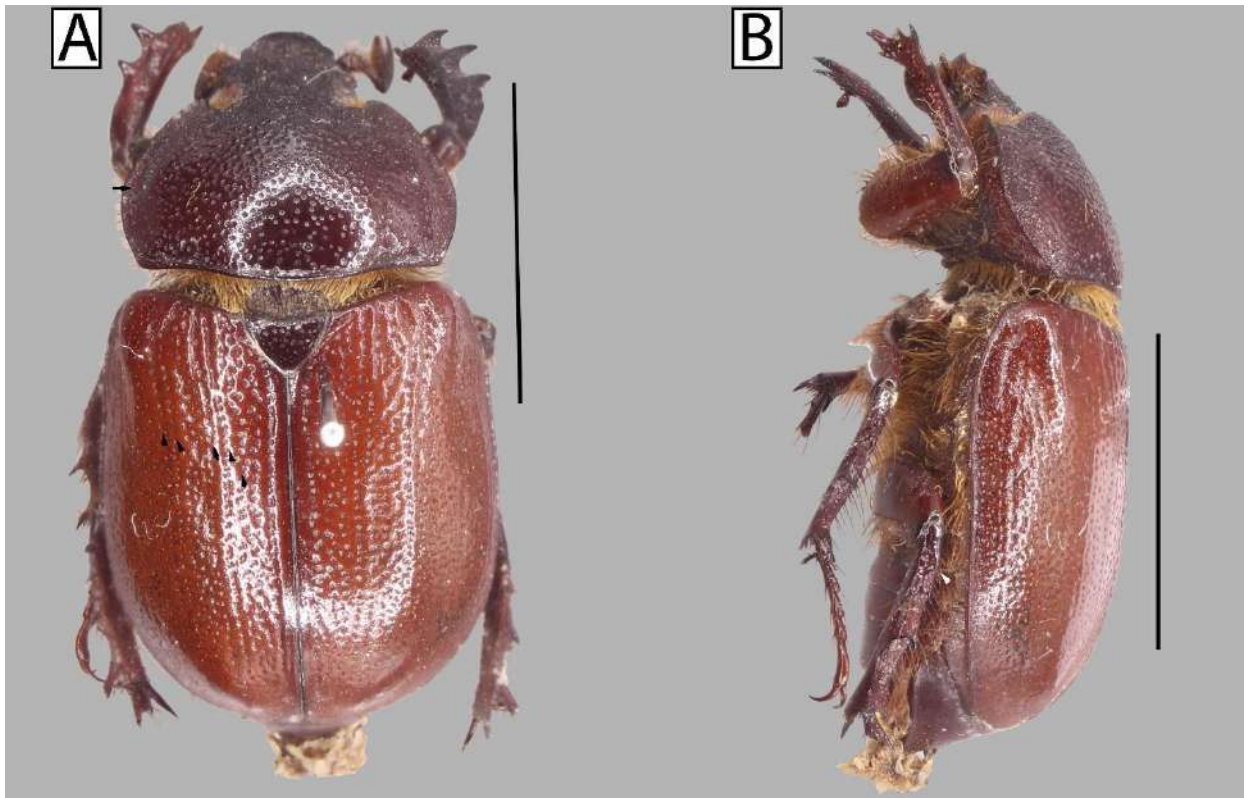


FIGURE 31. Head, abdomen, metatibia and genitalia of female of *Minisiderus* sp. **A**, Head in dorsal view. White arrows pointing to thin punctures near tubercles. **B**, Head in dorsolateral view. Left white arrow pointing to clypeal base elevated; right arrows pointing to tubercles. **C**, Head in lateral view. Black arrow pointing to projected wrinkle. **D**, Abdomen in ventral view. **E**, Mesotibia in ventral view. White arrow pointing to medial tooth. **F**, Coxites in ventral view. White arrow pointing to emargination. Scale bars: 1 mm.

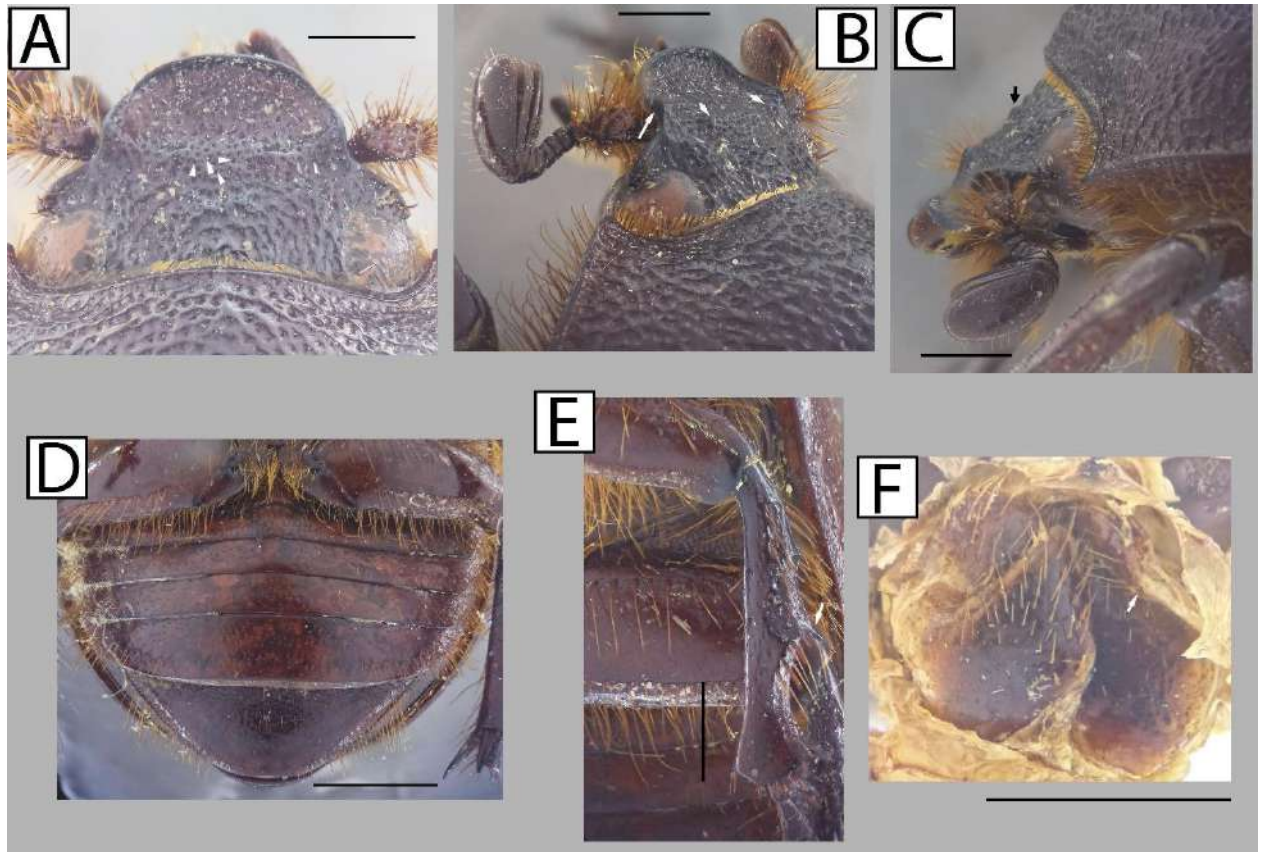


FIGURE 32. Male and female of *Minisiderus matogrossensis*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. White arrow pointing to pronotal anterior horn. **C**, habitus of female in dorsal view. Black arrow pointing to elytral apex. **D**, habitus of female in lateral view. Double-headed white arrows comparing the length between metatibial anterior and medial tooth to length between medial and apical tooth; black arrow pointing to connection between apical margin and apical tooth. Scale bars: 10 mm.

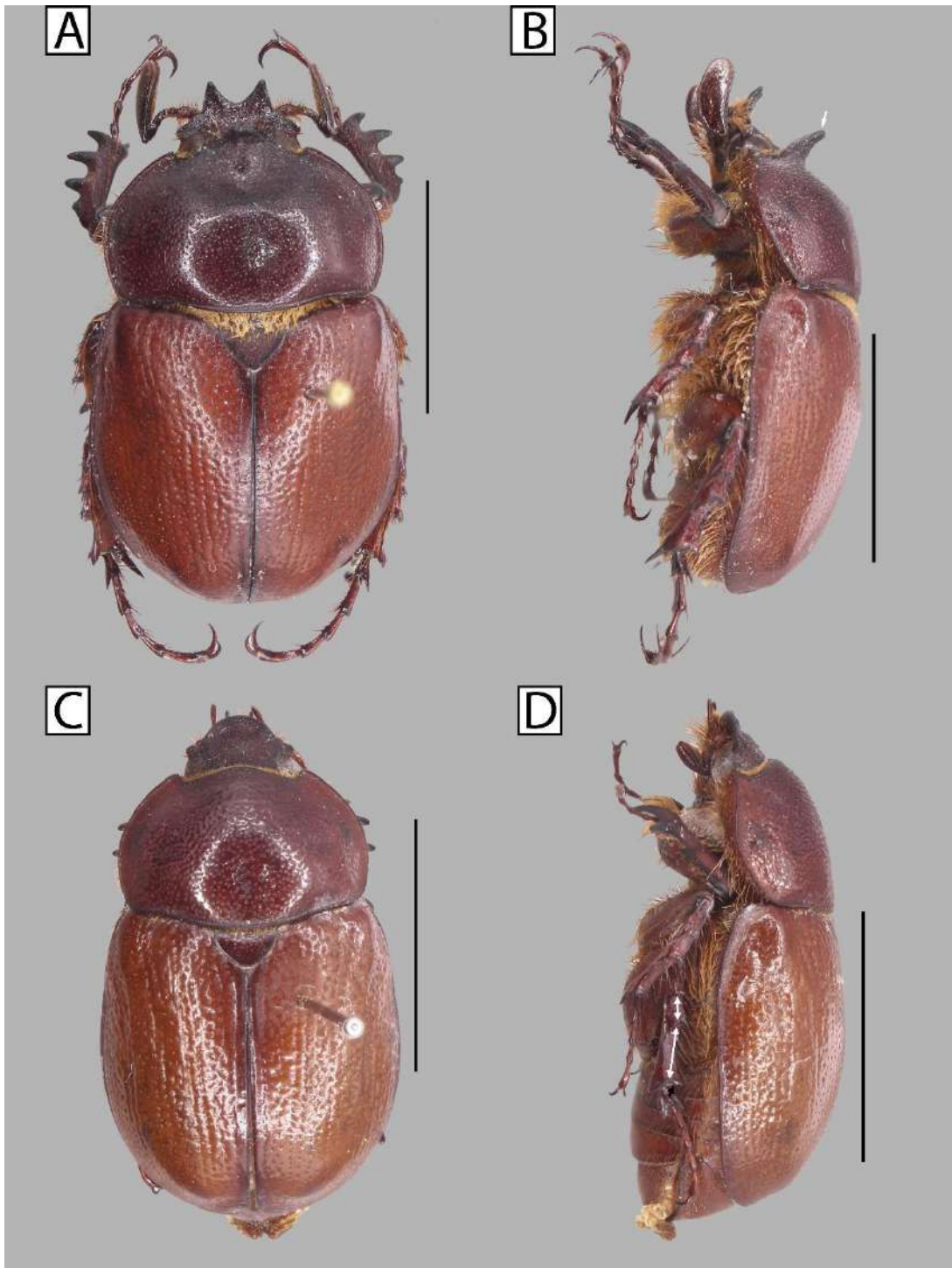


FIGURE 33. Male head, pronotum, canthus and mesotibia of *Minisiderus matogrossensis*, *Minisiderus cyclofoveatus*. **A**, Pronotal fovea of *M. matogrossensis* in dorsal view. **B**, Head of *M. matogrossensis* in frontal view. Double-headed red arrows showing clypeal length. **C**, Ocular canthus of *M. matogrossensis* in dorsal view. White arrow pointing to connection between canthus and horn. **D**, Mesotibia of *M. matogrossensis* in ventral view. White arrow pointing to space between anterior carina and basal tooth; red arrow pointing to metatibial apex. **E**, Pronotal fovea of *M. cyclofoveatus* in dorsal view. **F**, Head of *M. cyclofoveatus* in frontal view. Double-headed red arrows showing clypeal length. **G**, Ocular canthus of *M. cyclofoveatus* in dorsal view. Red arrow pointing to connection between canthus and horn. **H**, Mesotibia of *M. cyclofoveatus* in ventral view. Black arrow pointing to carina on inner margin. Scale bars: A, E, 5 mm, B-D, F-H, 1 mm.

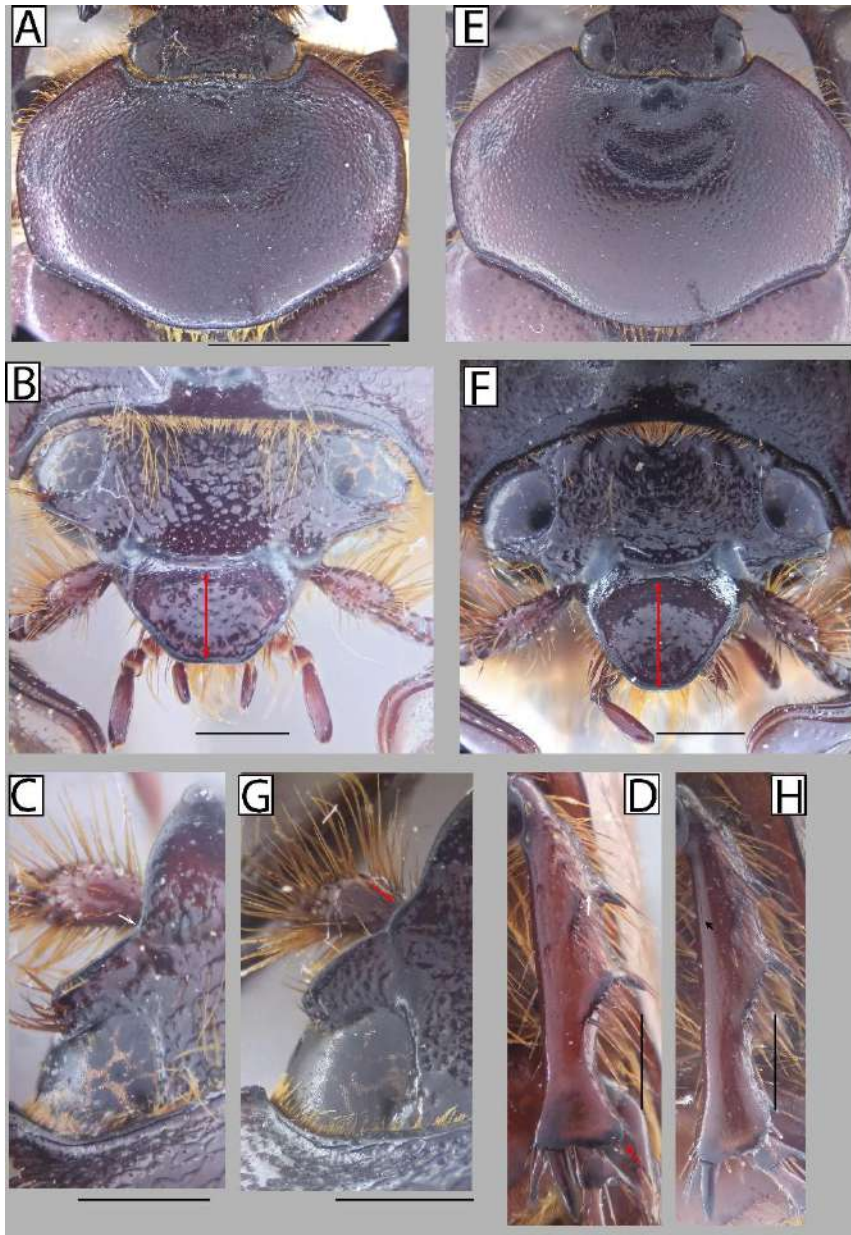


FIGURE 34. Mandible and Labrum of *Minisiderus matogrossensis*, *Minisiderus furtadoi*, *Minisiderus martinae*. **A**, Mandible of *M. matogrossensis* in ventral view. White arrow pointing to tooth; upper black arrow pointing to mesal brush apex; lower black arrow pointing to lateral margin near molar area. **B**, Mandible of *M. matogrossensis* in dorsal view. Upper black arrow pointing to emargination of tooth; lower black arrow pointing to protuberance of outer margin; white arrow pointing to end of mesalbrush. **C**, Mandible of *M. matogrossensis* in lateral view. Black arrow pointing to bump near condyle. **D**, Labrum of *M. matogrossensis* in dorsal view. **E**, Mandible of *M. furtadoi* in ventral view. Black arrow pointing to tooth. **F**, Mandible of *M. furtadoi* in dorsal view. Upper black arrow pointing to apex of mesal brush; lower black arrow pointing to basal insertion of mesal brush. **G**, Mandible of *M. furtadoi* in lateral view. Left black arrow pointing to base of mesal brush; right black arrow pointing to bump. **H**, Labrum of *M. furtadoi* in dorsal view. **I**, Mandible of *M. martinae* in ventral view. Left white arrow pointing to emargination on tooth; right white arrow pointing to round outer margin of tooth. **J**, Mandible of *M. martinae* in dorsal view. Black arrow pointing to base of outer margin; upper white arrow pointing to apex of mesal brush; lower white arrow pointing to basal insertion of mesal brush. **K**, Mandible of *M. martinae* in lateral view. Upper black arrow pointing to lateral margin of molar area; lower black arrow pointing to ventral condyle. **L**, Labrum of *M. martinae* in dorsal view. Black arrow pointing to middle of anterior margin. Scale bars: 1 mm.

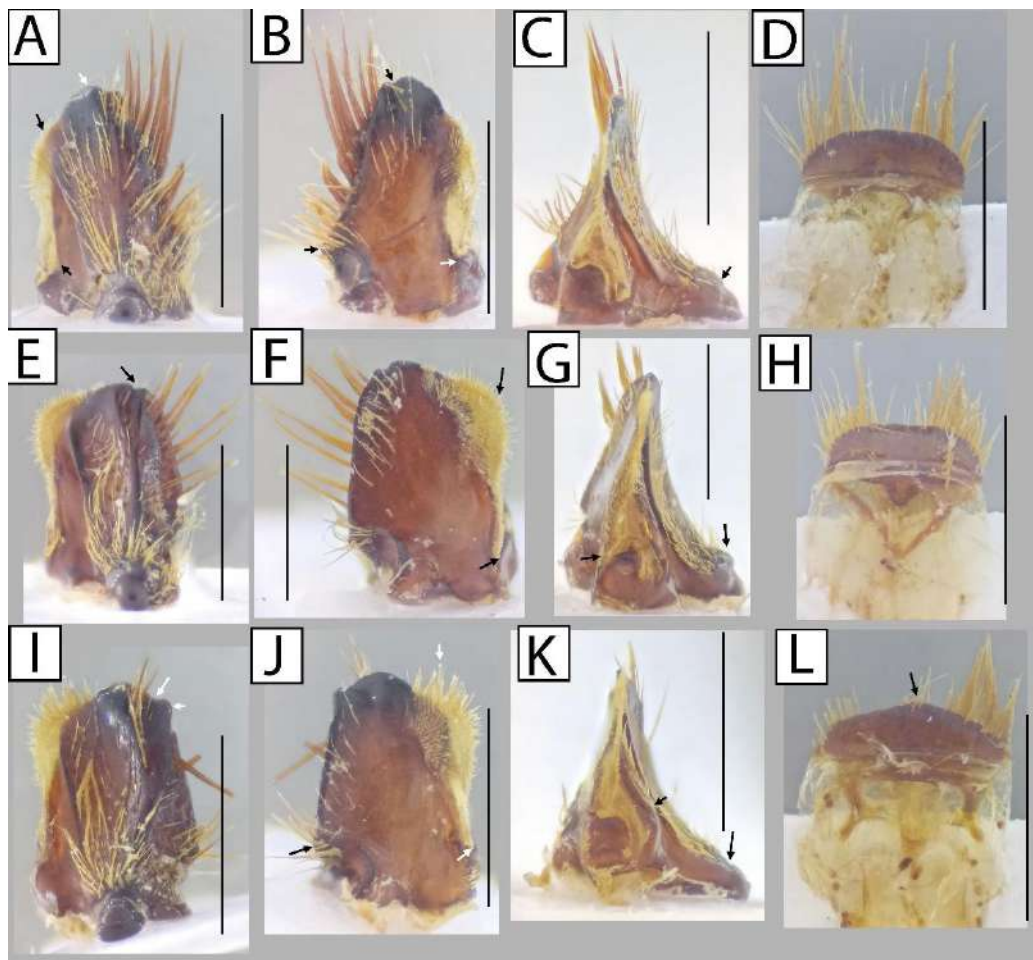


FIGURE 35. Maxilla and Mentum of *Minisiderus matogrossensis*, *Minisiderus furtadoi*, *Minisiderus martinae*. **A**, Maxilla of *M. matogrossensis* in ventral view. Left black arrow pointing to galea; right black arrow pointing to constriction of palpomere II. **B**, Maxilla of *M. matogrossensis* in dorsal view. Black arrow pointing to outer margin of subgalea. **C**, Mentum of *M. matogrossensis* in ventral view. Double-headed white arrows comparing width of base to apical corners. **D**, Maxilla of *M. furtadoi* in ventral view. **E**, Maxilla of *M. furtadoi* in dorsal view. **F**, Mentum of *M. furtadoi* in ventral view. **G**, Maxilla of *M. martinae* in ventral view. Black arrow pointing to inner margin of galea. **H**, Maxilla of *M. martinae* in dorsal view. Black arrow pointing to subgalea crossing margin of stipes. **I**, Mentum of *M. martinae* in ventral view. White arrow pointing to apex. Scale bars: 1 mm.

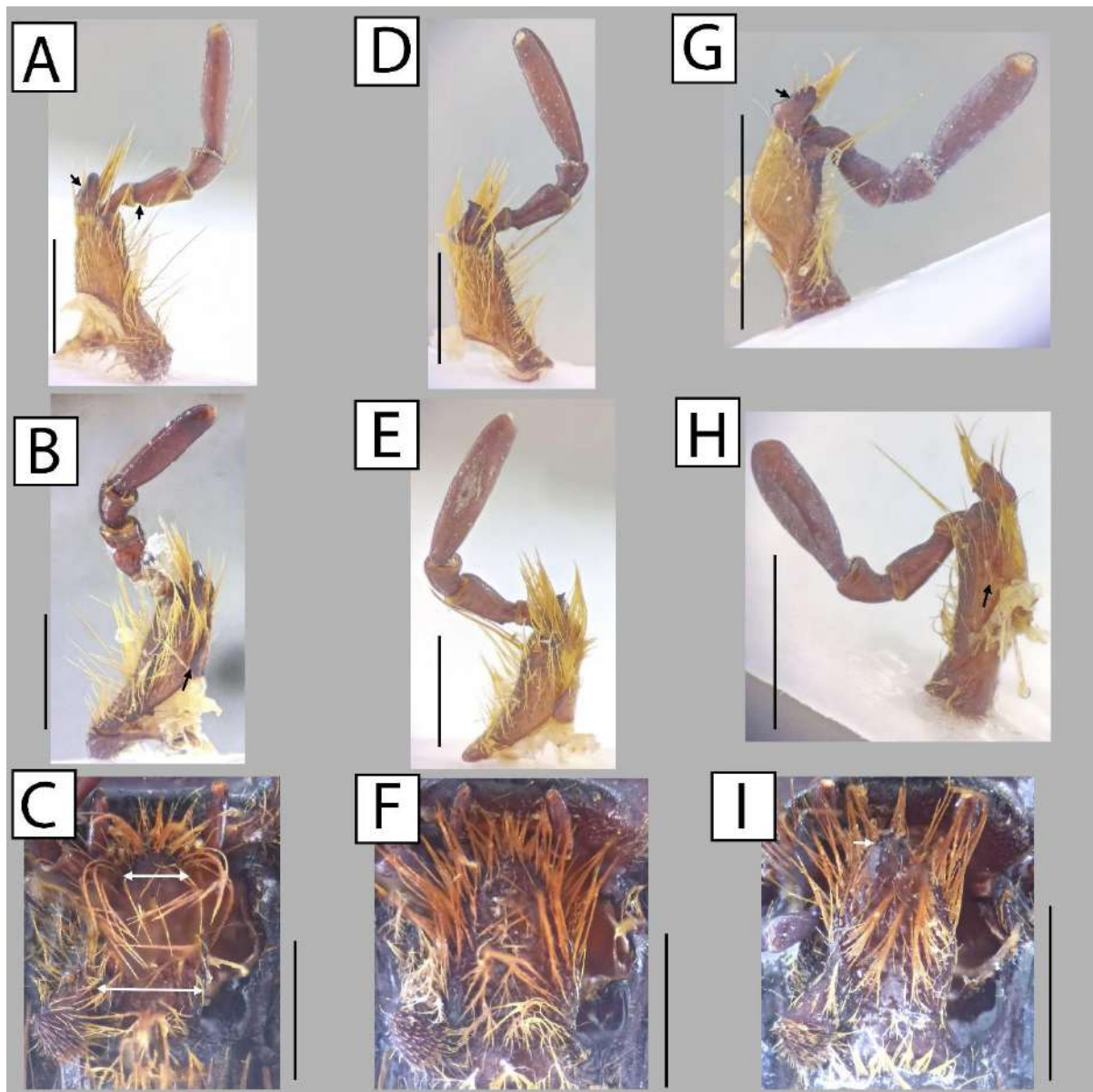


FIGURE 36. Genitalia of *Minisiderus matogrossensis*, *Minisiderus cyclofoveatus*. **A**, Parameres of *M. matogrossensis* in caudal view. Black arrows pointing to notch at inner margin. **B**, Parameres of *M. matogrossensis* in dorsolateral view. Black arrow pointing to end of lateral margin. **C**, Parameres of *M. matogrossensis* in lateral view. Upper black arrow pointing to lateral margin; lower black arrow pointing to ventral carina. **D**, Parameres of *M. matogrossensis* in ventral view. White arrow pointing to ventral depression. **E**, Genitalia of *M. matogrossensis* in lateral view. White arrow pointing to apical corner of posterior phallobase; double-headed white arrow showing thickness of posterior phallobase. **F**, Parameres of *M. cyclofoveatus* in caudal view. **G**, Parameres of *M. cyclofoveatus* in dorsolateral view. Black arrow pointing to end of lateral margin. **H**, Parameres of *M. cyclofoveatus* in lateral view. Upper black arrow pointing to lateral margin; lower black arrow pointing to ventral carina. **I**, Parameres of *M. cyclofoveatus* in ventral view. Black arrow pointing to ventral depression. **J**, Genitalia of *M. cyclofoveatus* in lateral view. White arrow pointing to apical corner of posterior phallobase; double-headed white arrow showing thickness of posterior phallobase. Scale bars: 1 mm.

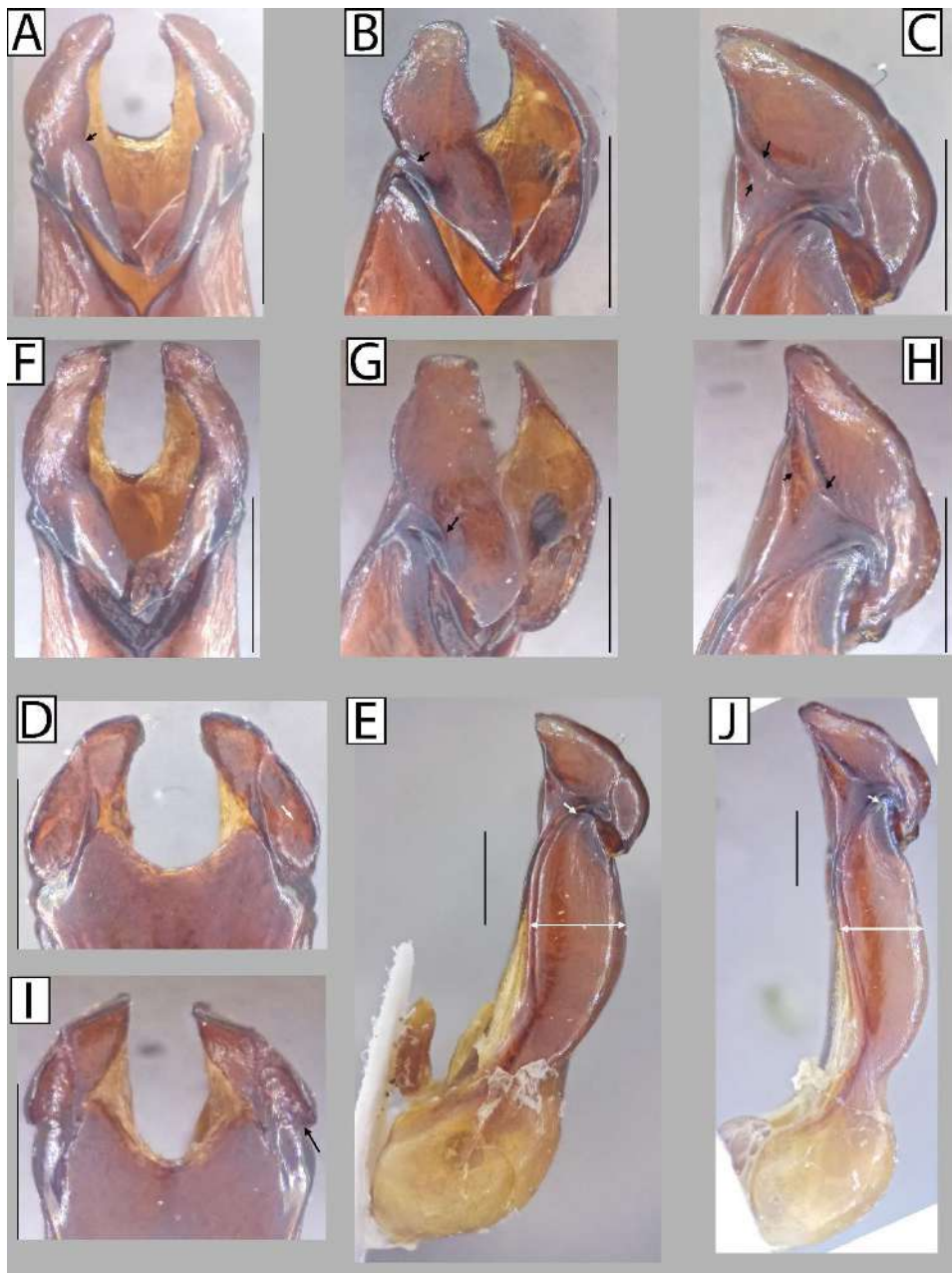


FIGURE 37. Head, abdomen, metatibia and genitalia of female of *Minisiderus matogrossensis*. **A**, Head in dorsal view. Black arrow pointing to apical corner of ocular canthus. **B**, Head in dorsolateral view. **C**, Head in lateral view. Black arrow pointing to frontal tubercles. **D**, Abdomen in ventral view. Black arrow pointing to sternite VIII covering elytra. **E**, Mesotibia in ventral view. Black arrow pointing to posterior carina. **F**, Coxites in ventral view. Scale bars: 1 mm.

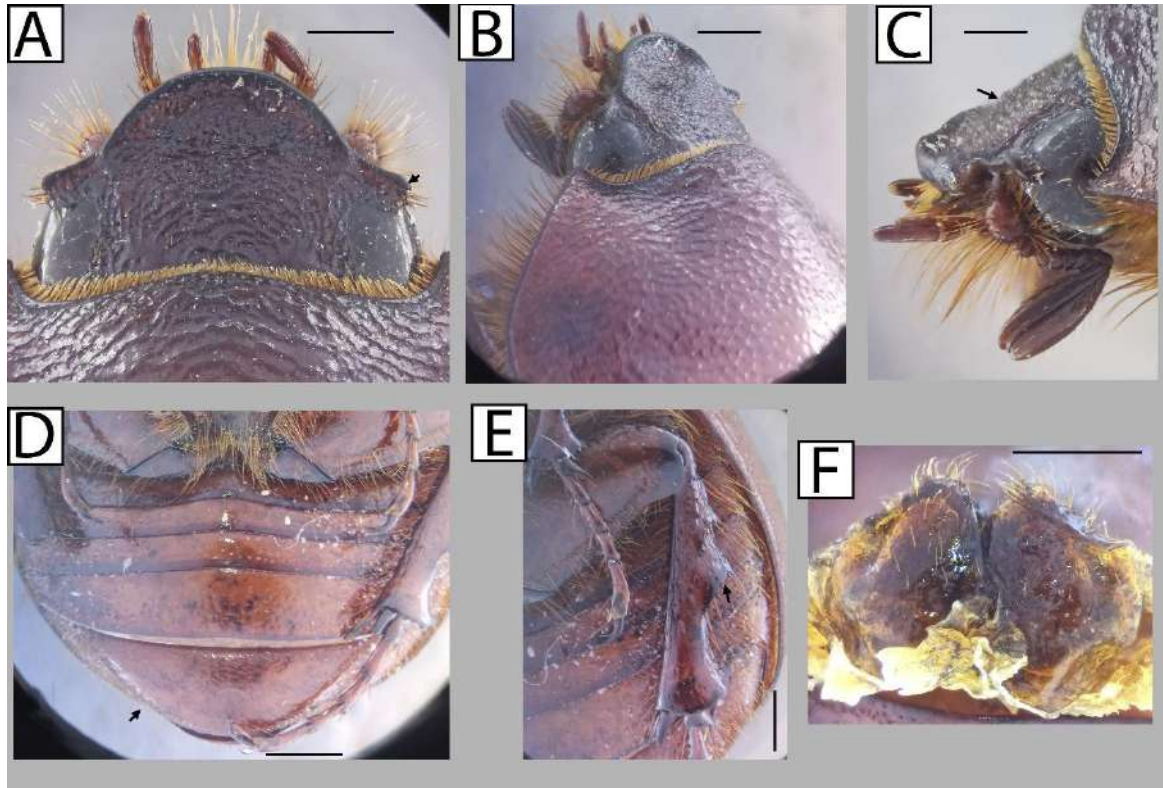


FIGURE 38. Male of *Minisiderus cyclofoveatus*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Black arrow pointing to pronotal horn on anterior margin. Scale bars: 10 mm.

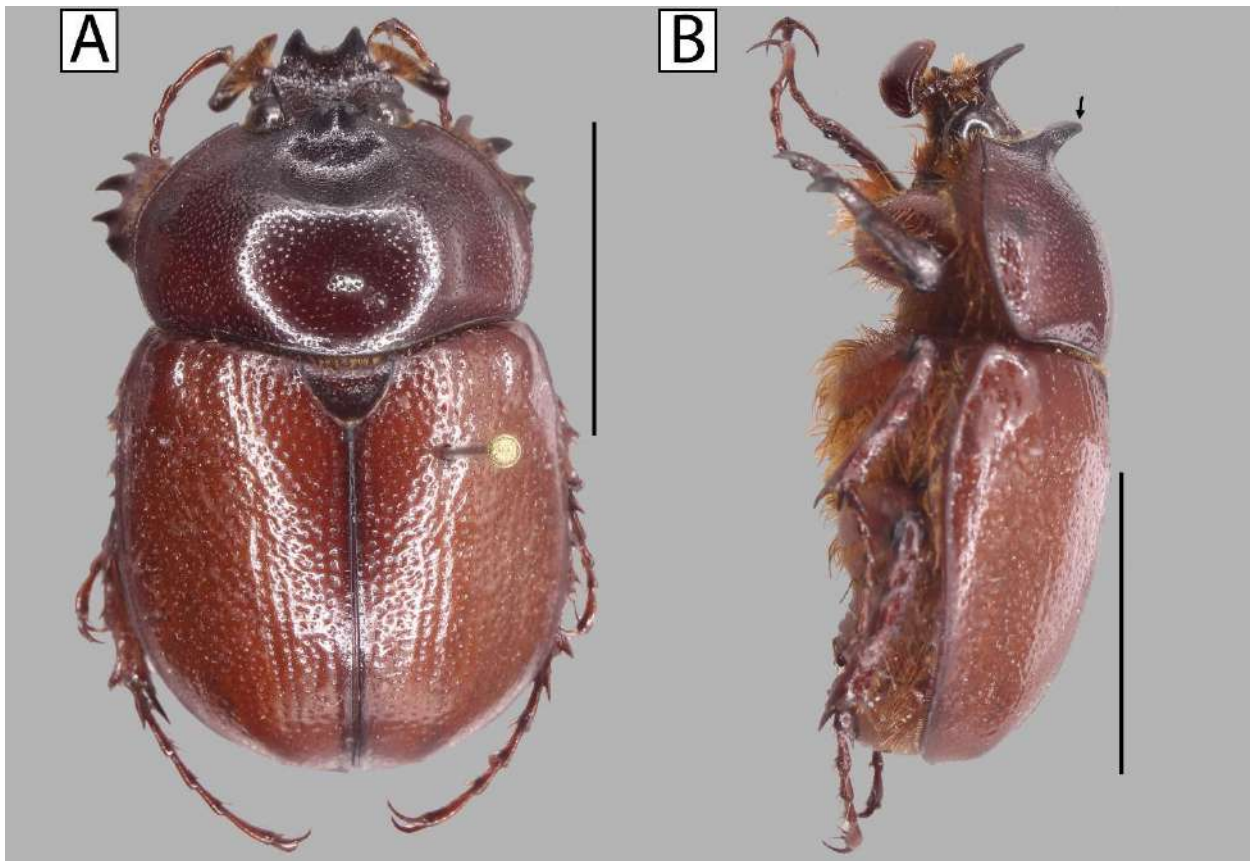


FIGURE 39. Male of *Minisiderus goyanus*. **A**, Habitus in dorsal view. **B**, habitus in lateral view. Scale bars: 10 mm.

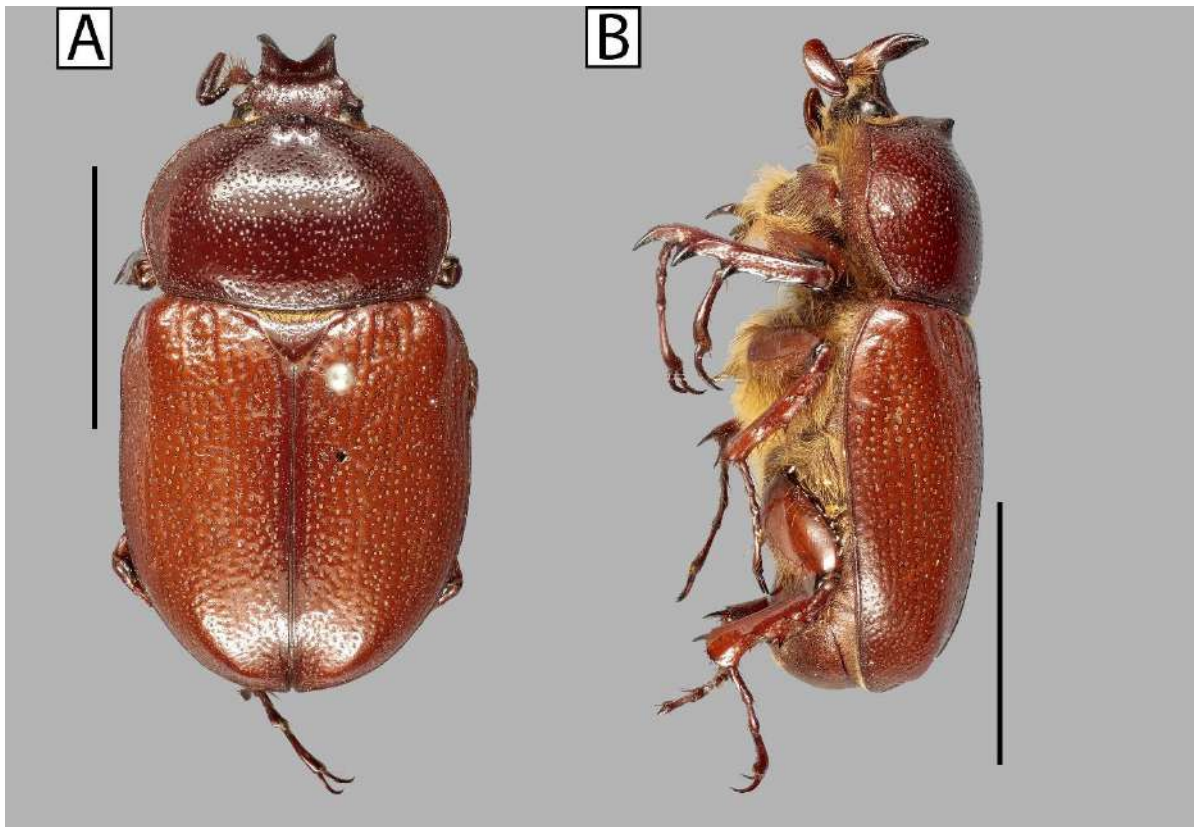


FIGURE 40. Head and pronotum of *Minisiderus goyanus*, *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Head of *M. goyanus* in lateral view. White arrow pointing to area between pronotal anterior margin and pronotal tubercles; upper black arrow pointing to pronotal tubercles; lower black arrow pointing to anterior portion of lateral margin. **B**, Ocular canthus of *M. goyanus* in dorsal view. Left white arrow pointing to basal protuberance of ocular canthus; right white arrow pointing to canthus carina. **C**, Head of *M. goyanus* in dorsal view. **D**, Head of *M. martinae* in lateral view. White arrow pointing to area between pronotal anterior margin and pronotal tubercles; black arrow pointing to tubercles. **E**, Ocular canthus of *M. martinae* in dorsal view. White arrow pointing to canthus carina. **F**, Head of *M. martinae* in dorsal view. **G**, Head of *M. furtadoi* in lateral view. Black arrow pointing to lateral margin of pronotal tubercles. **H**, Ocular canthus of *M. furtadoi* in dorsal view. Left white arrow pointing to basal connection between canthus and horns; right white arrow pointing to canthus carina. **I**, Head of *M. furtadoi* in dorsal view. Black arrow pointing to side of pronotal tubercles; upper white arrows showing margins of frontal depression; lower white arrow pointing to horn base in frontal view. **J**, Head of *M. parecisensis* in lateral view. **K**, Ocular canthus of *M. parecisensis* in dorsal view. Black arrow pointing to basal protuberance of ocular canthus. **L**, Head of *M. parecisensis* in dorsal view. Double-headed black arrows comparing width of pronotal tubercles and eye; white arrow pointing emargination of horn; lower black arrows pointing base of horn. Scale bars: 1 mm.

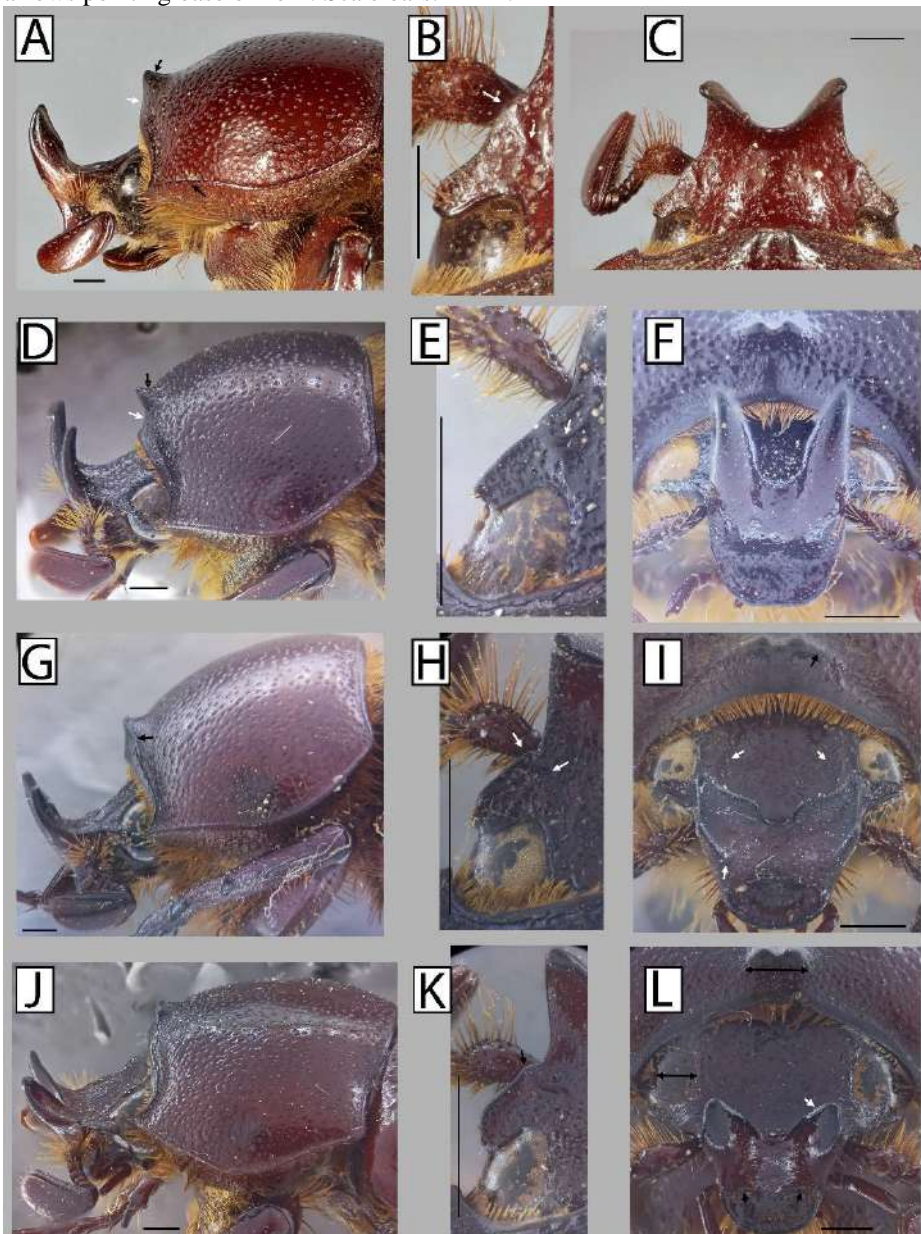


FIGURE 41. Pronotum, prosternum and metatibia of *Minisiderus goyanus*, *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Head and pronotum of *M. goyanus* in dorsal view. White arrows pointing to punctures shagrinated on posterior corners of pronotum. **B**, Prosternum and part of proleg of *M. goyanus* in ventral view. White arrows pointing to wrinkles on procoxa. **C**, Metatibia of *M. goyanus* in lateral view. White arrows pointing to outer teeth; black arrow pointing to setae on tergite VIII. **D**, Head and pronotum of *M. martinae* in dorsal view. **E**, Prosternum and part of proleg of *M. martinae* in ventral view. Upper black arrow pointing to prosternal anterior margin; lower black arrow pointing to femoral connection to protrocantheri. **F**, Metatibia of *M. martinae* in lateral view. Black arrows pointing to metatibial outer teeth. **G**, Head and pronotum of *M. furtadoi* in dorsal view. **H**, Prosternum and part of proleg of *M. furtadoi* in ventral view. **I**, Metatibia of *M. furtadoi* in lateral view. Upper black arrow pointing to basal tooth; lower basal tooth pointing to apical tooth. **J**, Head and pronotum of *M. parecisensis* in dorsal view. **K**, Prosternum and part of proleg of *M. parecisensis* in ventral view. Upper black arrows pointing to medial carina. **L**, Metatibia of *M. parecisensis* in lateral view. White arrows pointing to C-punctures on outer margin; black arrow pointing to connection between apical margin and apical tooth. Scale bars: A, D, G, J, 5 mm, B-C, D-E, H-I, K-L, 1 mm.

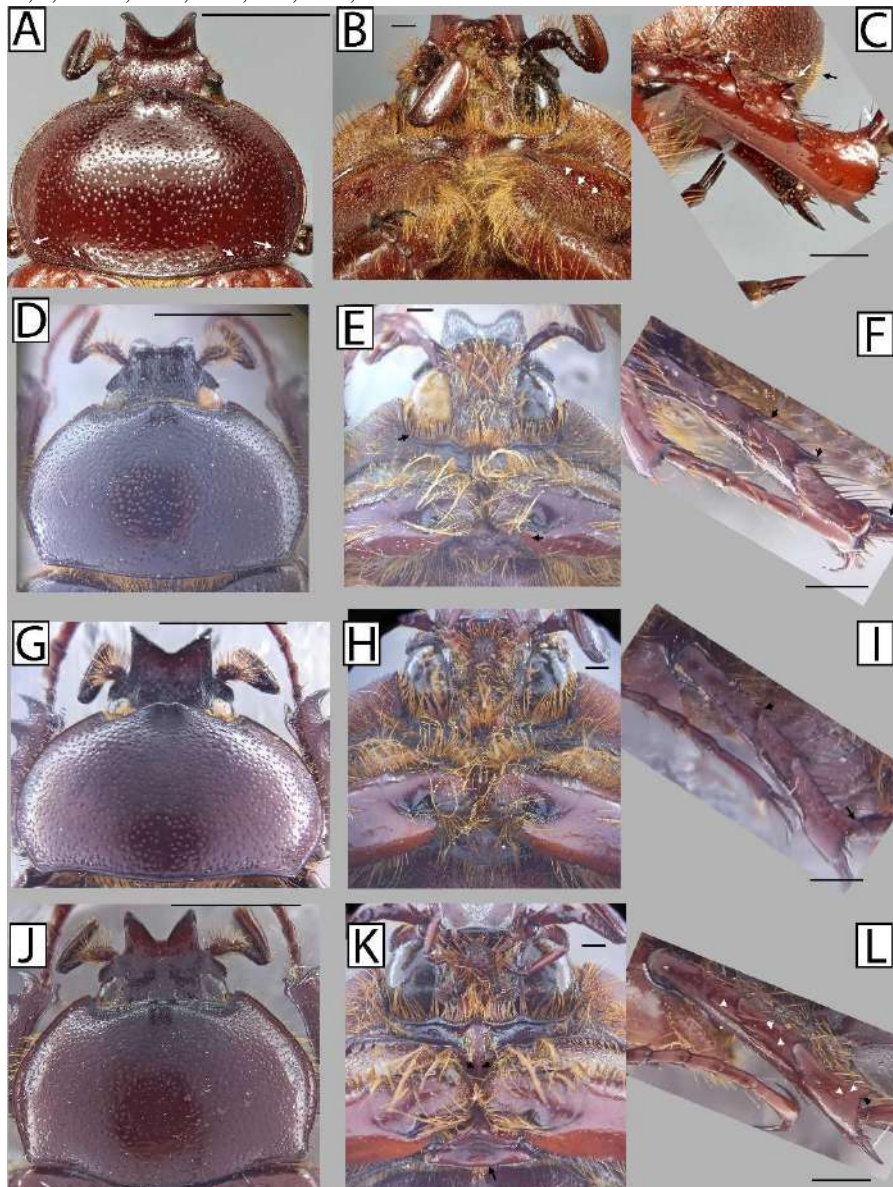


FIGURE 42. Mouthparts of *Minisiderus goyanus*. **A**, Mandible in dorsal view. Upper black arrow pointing to emargination of tooth; lower black arrow pointing to mesal brush; white arrows pointing to rows of short thin setae. **B**, Maxilla in dorsolateral view. Left black arrow pointing to palpomere III; right black arrow pointing to emargination at apex of galea. **C**, Mentum in ventral view. Double-headed white arrows comparing width of base to apical corners of mentum. Scale bars: 1 mm.

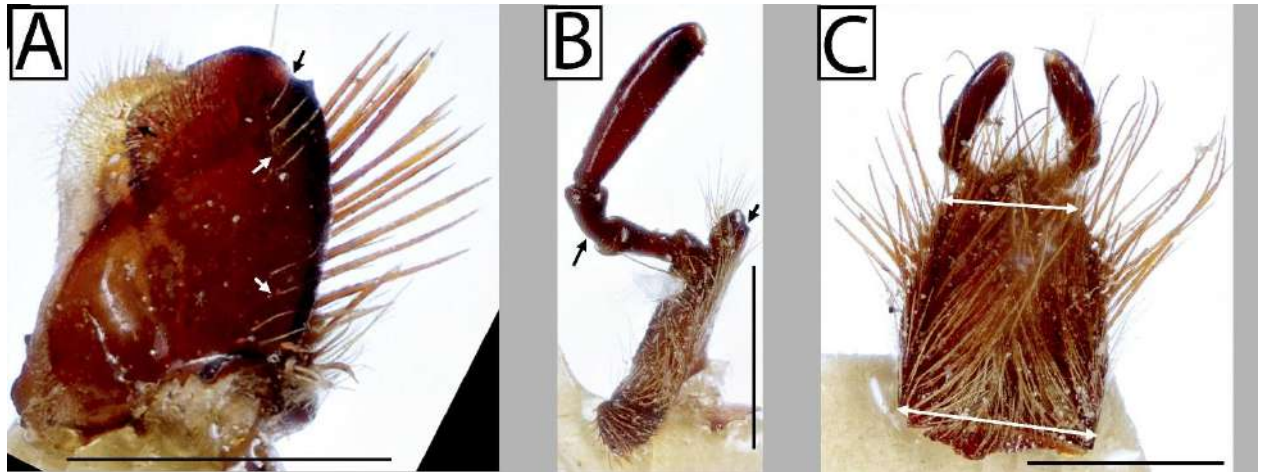


FIGURE 43. Male genitalia of *Minisiderus goyanus*, *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Parameres of *M. goyanus* in caudal view. Black arrow pointing to notch on outer margin; upper white arrow pointing to notch at medial inner margin; lower white arrow pointing to basal inner margin. **B**, Parameres of *M. goyanus* in lateral view. Upper white arrow showing apex elongated; lower white arrow pointing to lateral margin. **C**, Parameres of *M. goyanus* in caudal view. Black arrow pointing to margin of ventral sclerite; white arrow pointing to posterior phallobase apical corner. **D**, Parameres of *M. martinae* in caudal view. Red arrow pointing to angulation at apical inner margin; black arrow pointing to outer margin; white arrow pointing to posterior projection. **E**, Parameres of *M. martinae* in lateral view. Black arrow pointing to lateral margin. **F**, Parameres of *M. martinae* in ventral view. Upper black arrow pointing to apex of parameres; lower black arrow pointing to emargination of anterior margin of ventral sclerite. **G**, Parameres of *M. furtadoi* in caudal view. White arrow pointing to notch at medial inner margin; upper black arrow pointing to inner margin basally; lower black arrow pointing to posterior projection. **H**, Parameres of *M. furtadoi* in lateral view. Upper white arrow pointing dorsal surface of basal portion; lower white arrow pointing posterior projection. **I**, Parameres of *M. furtadoi* in ventral view. Left white arrow pointing to ventral depression; right white arrow pointing to lateral margin. **J**, Parameres of *M. parecisensis* in caudal view. White arrow pointing to notch at inner margin; upper black arrow pointing to basal inner margin; lower black margin pointing to posterior projection. **K**, Parameres of *M. parecisensis* in lateral view. Black arrow pointing to lateral margin. **L**, Parameres of *M. parecisensis* in ventral view. Black arrow pointing to apex of parameres; white arrow pointing to lateral margin. Scale bars: 1 mm.

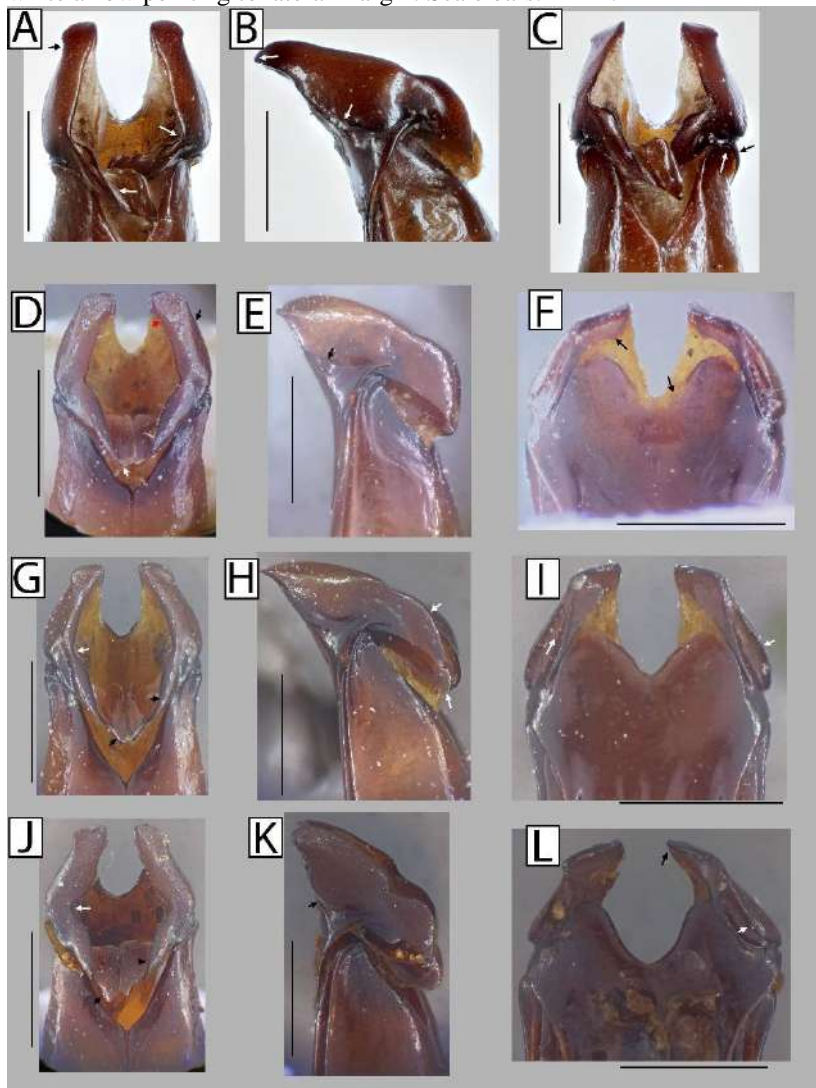


FIGURE 44. Male and female of *Minisiderus martinae*. **A**, Habitus of male in dorsal view. Black arrows pointing to fissures on elytra. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. Black arrows pointing to rugose surface of elytra. **D**, habitus of female in lateral view. Double-headed white arrows comparing the length between metatibial anterior and medial tooth to length between medial and apical tooth; black arrow pointing to connection between apical margin and apical tooth. Scale bars: 10 mm.

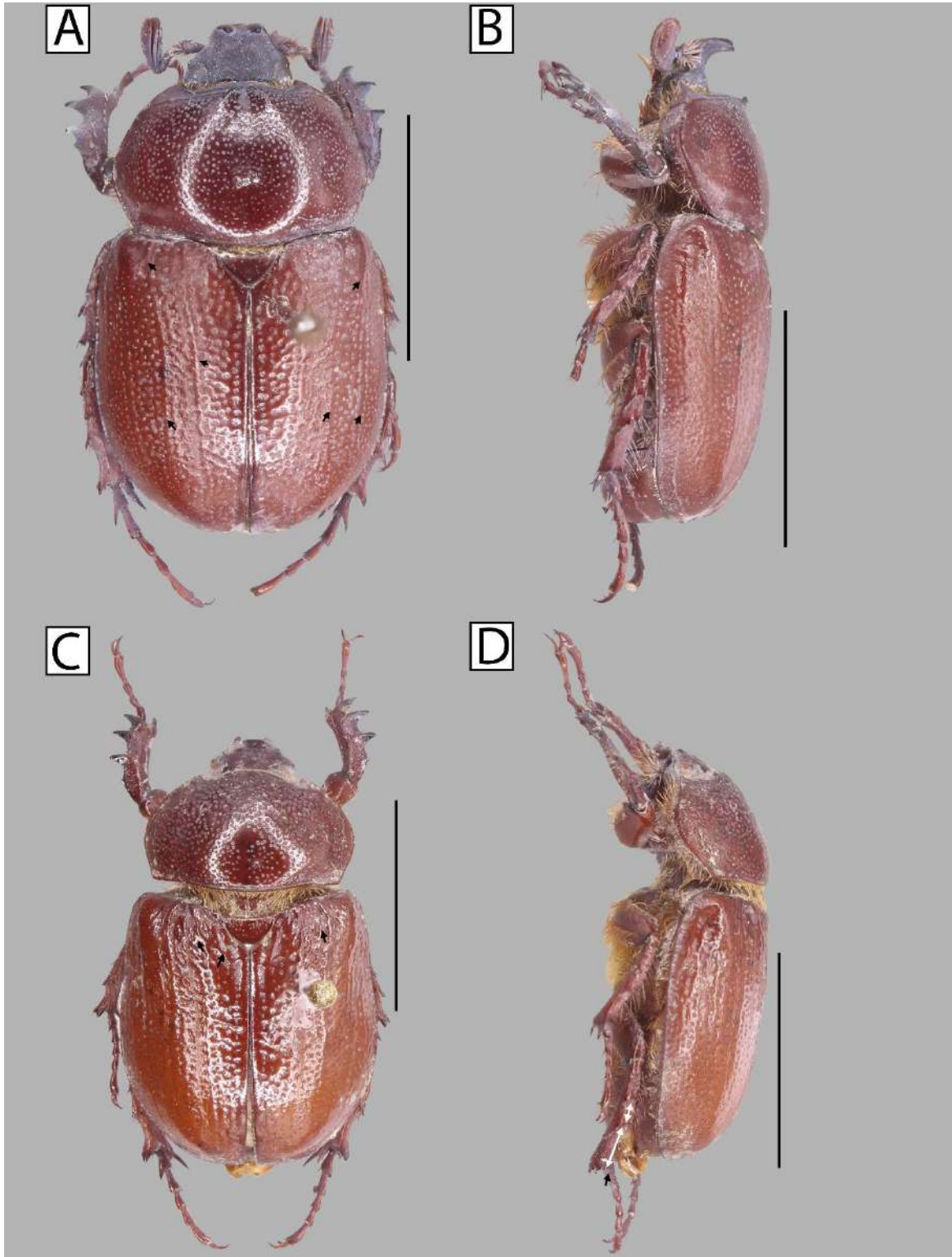


FIGURE 45. Female head and genitalia of *Minisiderus martinae*, *Minisiderus furtadoi*. **A**, Head of *M. martinae* in dorsal view. Left black arrow pointing to frontal wrinkles; right black arrow pointing to connection between canthus and clypeus; white arrow pointing to vertex. **B**, Head of *M. martinae* in dorsolateral view. Left white arrow pointing to clypeal base elevation; right white arrows pointing to tubercles. **C**, Ocular canthus of *M. martinae* in dorsal view. Black arrow pointing to apex. **D**, Coxites of *M. martinae* in ventral view. Black arrow pointing to V-shaped emargination. **E**, Head of *M. furtadoi* in dorsal view. Left black arrows pointing to frontal wrinkles; right black arrow pointing to connection between canthus and clypeus; white arrow pointing to vertex. **F**, Head of *M. furtadoi* in dorsolateral view. Left white arrow pointing to clypeal base elevation; right white arrows pointing to tubercles. **G**, Ocular canthus of *M. furtadoi* in dorsal view. Left black arrow pointing to apex; right black arrow pointing to carina. **H**, Coxites of *M. furtadoi* in ventral view. Scale bars: 1 mm.

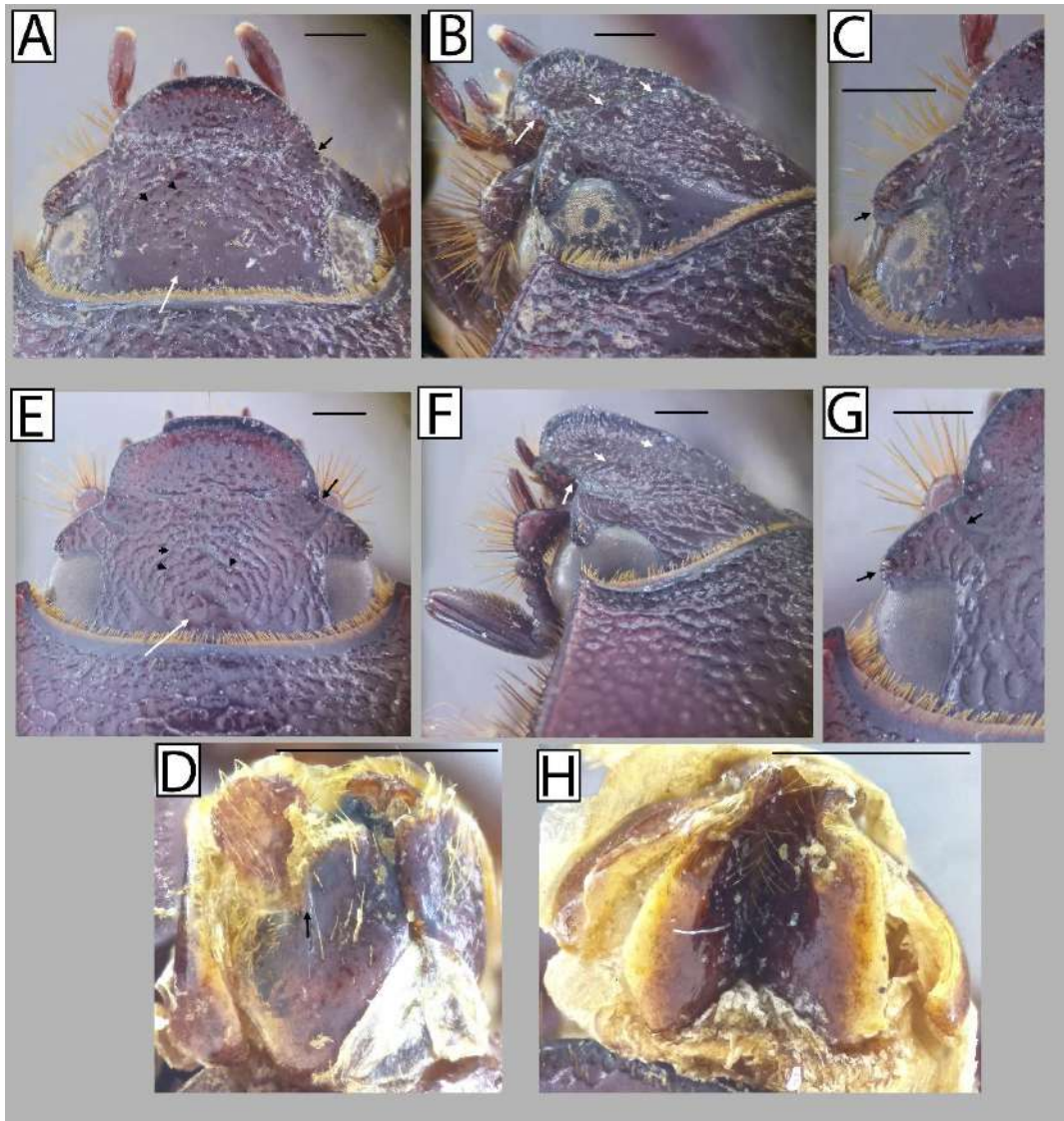


FIGURE 46. Male and female of *Minisiderus furtadoi*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, habitus of female in dorsal view. **D**, habitus of female in lateral view. Black arrow pointing to connection between metatibial apical margin and apical tooth. Scale bars: 10 mm.

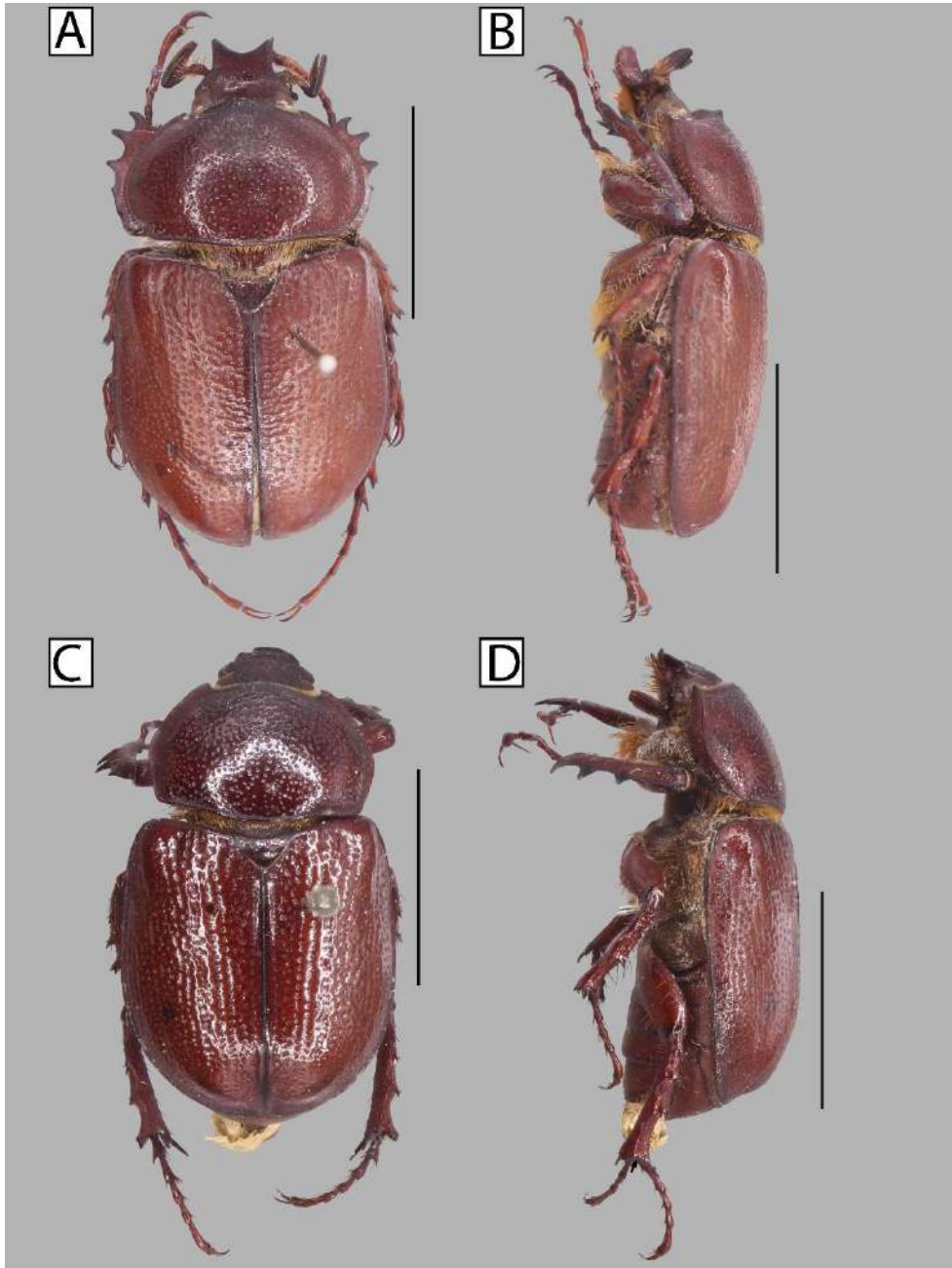


FIGURE 47. Antennal anomaly in male of *Minisiderus furtadoi*. **A**, Antennae and part of head in ventral view. Black arrow pointing to elongate projection from antenomere II; white arrow pointing to circular depression on apex of projection. **B**, Antennae and part of head slightly in ventrolateral view. Black arrows pointing to the two distal antenomeres. Scale bars: 1 mm.

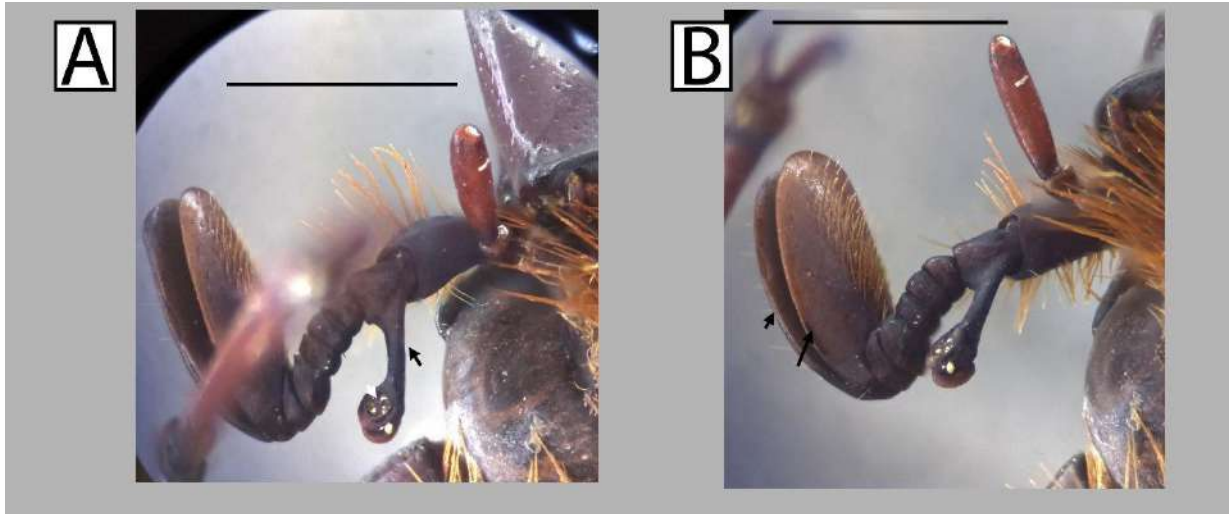


FIGURE 48. Male of *Minisiderus parecisensis*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. Scale bars: 10 mm.

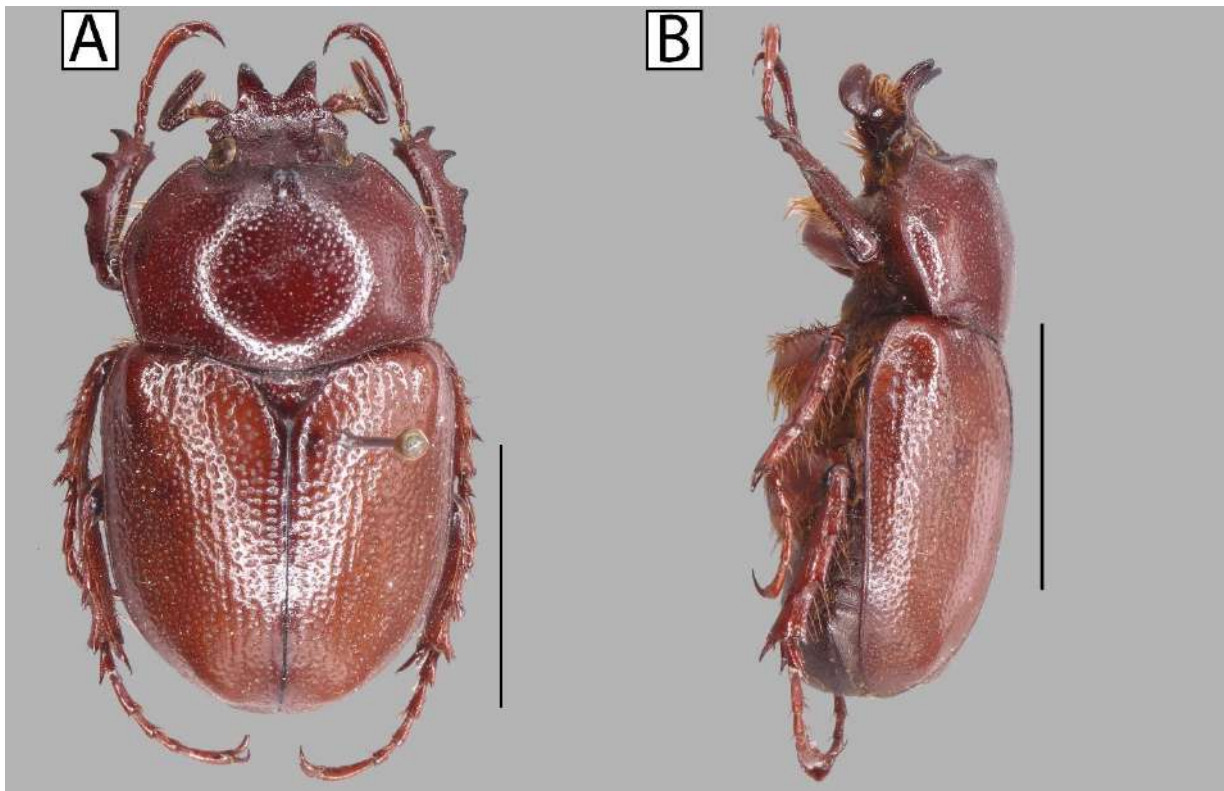


FIGURE 49. Male abdomen of *Minisiderus martinae*, *Minisiderus furtadoi*, *Minisiderus parecisensis*. **A**, Abdomen of male of *M. martinae* in ventroposterior view. Black arrows pointing to punctures on anterior margin of tergite VIII. **B**, Abdomen of male of *M. furtadoi* in ventroposterior view. Black arrows pointing to microsetae on posterior margin of tergite VIII. **C**, Abdomen of male of *M. parecisensis* in ventroposterior view. Black arrows pointing to wrinkles on anterior margin of tergite VIII. Scale bars: 5 mm.

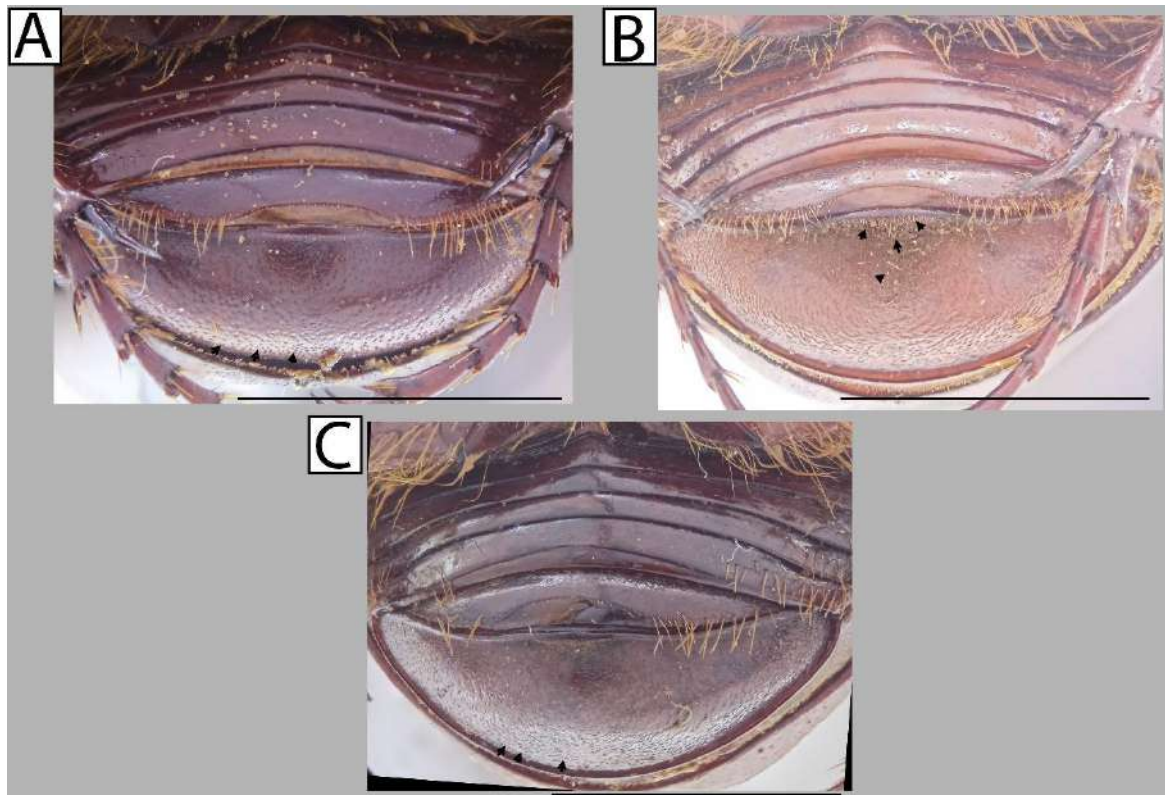


FIGURE 50. Distribution map of *Minisiderus*.

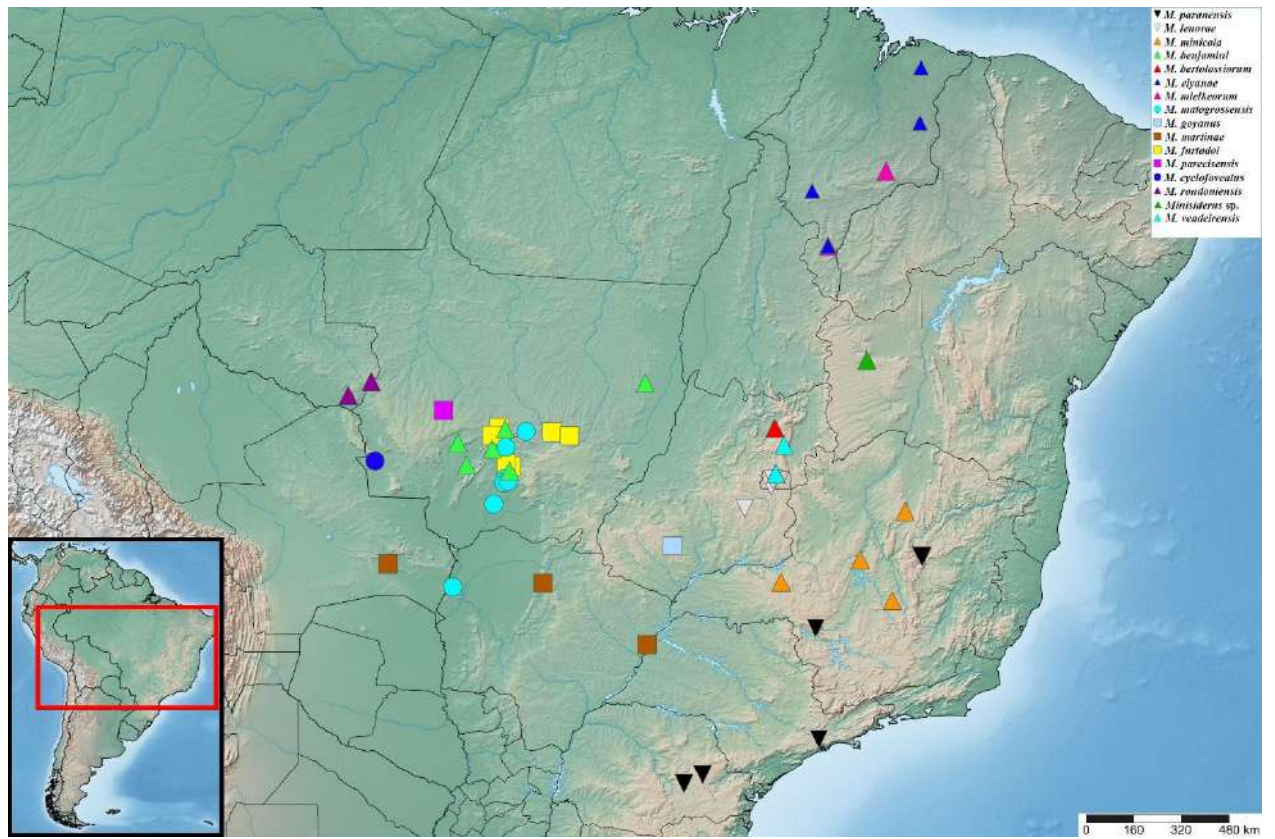


FIGURE 51. Comparison between male and female of *Minisiderus* and *Brachysiderus*. **A**, Head of *M. lenorae* in dorsal view. Black arrow pointing to apex of ocular canthus; white arrow pointing to apex of horns; lower white arrow pointing to anterior corner of ocular canthi. **B**, Head of *Brachysiderus* in dorsal view. Black arrow pointing to apex of ocular canthus; upper white arrow pointing to apex of horns; lower white arrow pointing to anterior corner of ocular canthi. **C**, Head of *M. benjamini* in dorsal view. Black arrow pointing to apex of ocular canthus; white arrow pointing to apex of horns; lower white arrow pointing to anterior corner of ocular canthi. **D**, Head and pronotum of female of *Minisiderus*. Black arrow pointing to connection between clypeal base and ocular canthus; upper white arrow pointing to apex of clypeus; lower white arrow pointing to base of ocular canthi. **E**, Head and pronotum of female of *Brachysiderus*. Left black arrow pointing to connection between clypeal base and ocular canthus; white arrow pointing to apex of clypeus; right black arrow pointing to base of ocular canthi. **F**, Elytra of female of *Minisiderus*. **G**, Elytra of female of *Brachysiderus*. **H**, Protarsus of male *Minisiderus*. Upper black arrow pointing to protarsal claw; lower black arrow pointing to inner margin of protarsomere V. **I**, Protarsus of male *Brachysiderus*. Upper black arrows pointing to protarsal claws; lower black arrow pointing to inner margin of protarsomere V. Scale bars: A-C, F-I, 1 mm, D-E, 5 mm.

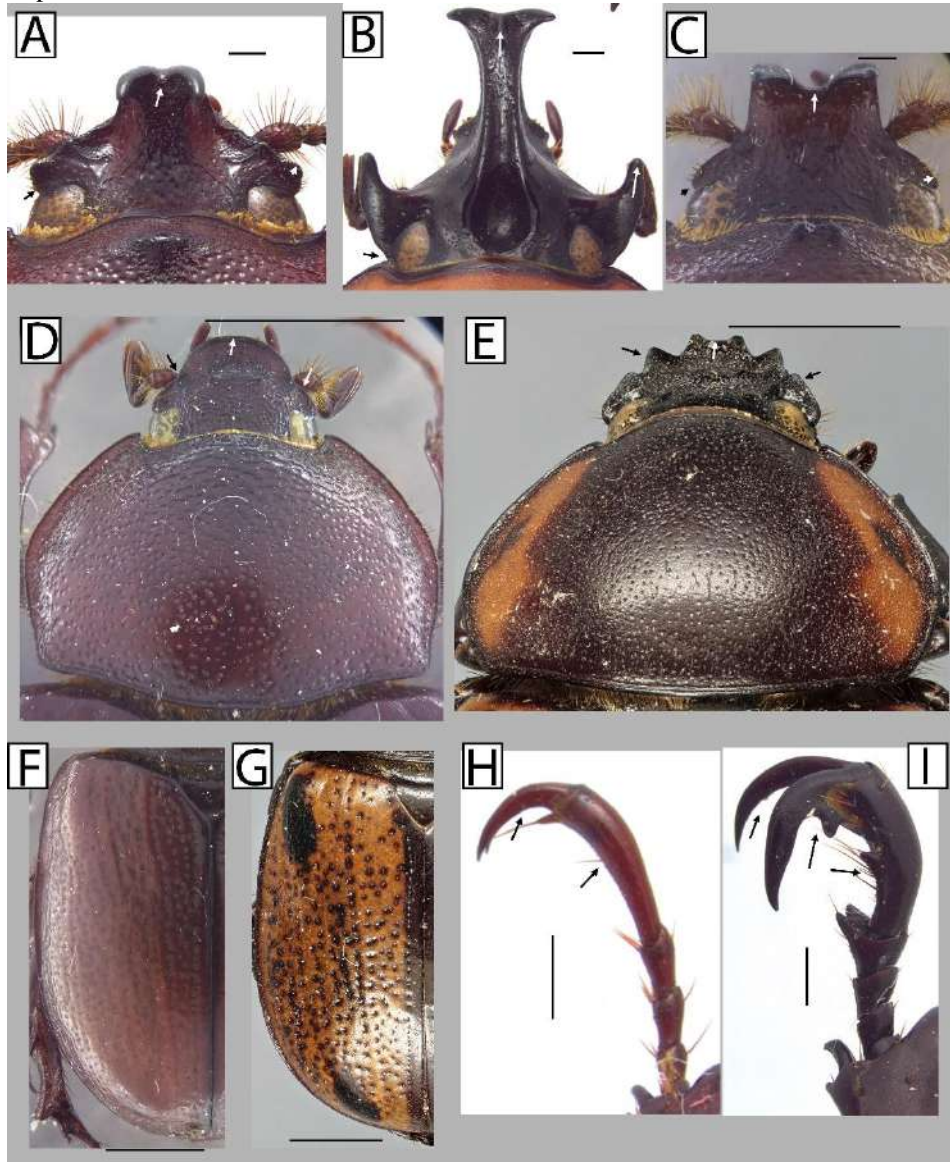
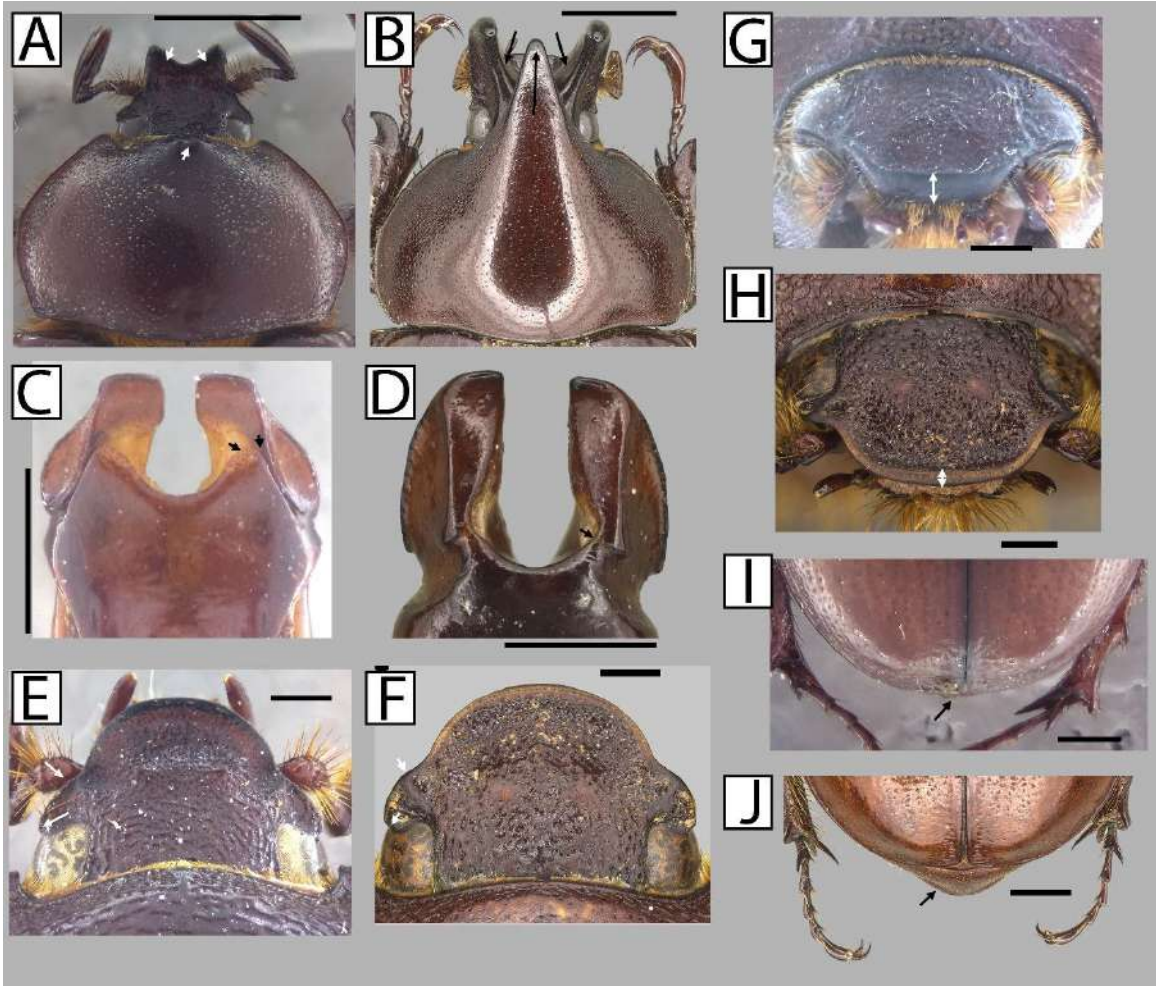


FIGURE 52. Comparison between male and female of *Minisiderus* and *Aegopsis*. **A**, Head and pronotum of male *Minisiderus* in dorsal view. Upper white arrows pointing to cephalic horns; lower white arrow pointing to pronotal tubercles. **B**, Head and pronotum of male *Aegopsis* in dorsal view. Upper black arrows pointing to cephalic horns; lower black arrow pointing to pronotal horn. **C**, Parameres of *Minisiderus* in ventral view. Left black arrow pointing to margin of ventral sclerite; right black arrow pointing to ventral margin of parameres. **D**, Parameres of *Aegopsis* in ventral view. Black arrow pointing to margin of ventral sclerite fused to ventral parameres. **E**, Head of female *Minisiderus* in dorsal view. Upper white arrow pointing to anterior margin of ocular canthus; lower white arrow showing apex of canthus elongated. **F**, Head of female *Aegopsis* in dorsal view. Upper white arrow pointing to anterior margin of ocular canthus; lower white arrow showing apex of canthus short. **G**, Head of female *Minisiderus* in frontal view. Double-headed white arrow showing thickness of anterior margin of clypeus. **H**, Head of female *Aegopsis* in frontal view. Double-headed white arrow showing thickness of anterior margin of clypeus. **I**, Elytral apex of female *Minisiderus* in dorsal view. Black arrow pointing to tergite VIII hidden under elytral apex. **J**, Elytral apex of female *Aegopsis* in dorsal view. Black arrow pointing to tergite VIII crossing elytral apex. Scale bars: A-B, 5 mm, C-J, 1 mm.



CAPÍTULO III

Sobral, R., Morais, J.W. de & Grossi, P.C. Review of *Brachysiderus* Waterhouse (Coleoptera, Scarabaeoidea, Dynastinae), revealing new species within old known specimens from Andes. Manuscrito em preparação para submeter à revista Zootaxa.

Review of *Brachysiderus* Waterhouse (Coleoptera, Scarabaeoidea, Dynastinae), revealing new species among historical specimens from Andes

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Abstract

Males and females of *Brachysiderus* Waterhouse, 1881 are revised, redescribed and illustrated. A new species traditionally treated in the collections and literature as *Brachysiderus quadrimaculatus* Waterhouse, 1881 is described to Peruvian Andes. *Brachysiderus tridentiger* (Prell, 1934) **stat. rev.** and *Brachysiderus breyeri* (Martínez, 1963) **stat. rev.** and **comb. nov.** are raised to species. A key to male and female species are provided as well as a new distribution map containing new records to Bolivia and Brazil.

Key words: Agaoccephalini, Melolonthidae, rhinoceros beetles, Scarabaeidae.

Introduction

The genus *Brachysiderus* Waterhouse, 1881 is a rhinoceros beetle commonly associated with the Andes and its surroundings, from where the majority of specimens deposited in the collections around the world were collected. However, the type species of the genus – *Brachysiderus quadrimaculatus* Waterhouse, 1881 – was described based on a specimen from the Amazon, in Brazil. In a recent past, the genus was divided in two subgenera: *Brachysiderus* (*Brachysiderus*) and *Brachysiderus* (*Minisiderus*), but Milani (2018) proposed the elevation of the former to genus *Minisiderus* Endrödi, 1970, which left *Brachysiderus* as a monotypic genus.

Brachysiderus is characterized by the distinctive sexual dimorphism, with males having a strong, elongate cephalic horn, and the distal protarsomere distinctly thick with asymmetrical claws, whereas in females the horn is absent and the distal protarsomere

slender with symmetrical claws. Also, the genus can be recognized by the absence of horn or tubercles on pronotum, ocular canthi with anterior corner distinctly sharp and projected forward, body lustrous but not metallic, head darker than body, pronotum with color ranging from yellow to reddish brown, elytra dark yellow to orange with darker patches on humeral and apical umbones (Endrödi 1970).

The genus can be found in western Amazon, in Brazil and Andine and Pré-andine forests through Colombia, Ecuador, Peru and Bolivia (Endrödi 1985; Milani 2018). The only species, *Brachysiderus quadrimaculatus*, was formerly divided in two subspecies: *B. quadrimaculatus quadrimaculatus* Waterhouse, 1881, and *B. quadrimaculatus tridentiger* (Prell, 1934). The populations occurring in the eastern side of the Andes and Brazil were treated as *B. q. quadrimaculatus*, while populations in the western side of the Andes are considered *B. q. tridentiger*. Recently, Ratcliffe *et al.* (2020) considered the late subspecies as a synonym, since they did not find morphological or geographical evidences sufficient to maintain those two subspecies as distinct populations. Information about the biology and immature stages of *Brachysiderus* is still unknown, but the adults can be found in a wide range of elevation, occurring from 200 to almost 2000 m of altitude, and are attracted to lights (Ratcliffe *et al.* 2020).

After the examination of the type specimen from Amazon and the specimens from distinct ecoregions along the Andes, we observed that the type specimen had distinct characters from those of the Andes (especially on head traits and genitalia) and that those specimens occurring across the Andes were not morphologically uniform, also occurring in different ecoregions. Therefore, herein we propose a review of *Brachysiderus*, with the description of one new species and the redescription of *B. quadrimaculatus*. Keys to males and females are provided and an actualized distribution map of these species is made.

Materials and methods

More than a hundred specimens were studied from the following collections (acronyms according Evenhuis (2009) when available).

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

CMNC Canadian Museum of Nature, Ottawa, Canada (François Génier)

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

(Everarado J. Grossi)

HNHM Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl)

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

NHM Natural History Museum, London, United Kingdom (Max Barclay)

RBINS Royal Belgian Institute of Natural Sciences, Brussels, Belgium (Alain Drumont)

ZMNB Museum für Naturkunde, Berlin, Germany (Bernd Jaeger)

Terminology follows in part Endrödi (1985) for the general traits of the body, Nel & Scholtz (1990) for mouthparts, Cristóvão & Vaz-de-Mello (2020) for abdomen and genitalia and Führmann (2010) for punctuation. The aedeagi were dissected after boiling specimens for 10 to 20 minutes in warm water with neutral soap, and then glued in card mount, and pinned just below each specimen. Images were obtained with a smartphone Xiaomi Redmi Note8 Pro attached at a stereoscopic microscope Digilab DI 106-T with stacked images made on software Helicon Focus 7, and edited using Adobe Photoshop CS6.

The map was made using SimpleMappr (<http://www.simplemappr.net>) (Shorthouse, 2010). For specimens whose latitude and longitude data were missing from the tags, a point was established using *GoogleMaps* within the limits of the most restricted location information available on the tag (reserve, park, district, municipality, etc.). For distribution records in the literature whose specimens were not found or could be examined, the original information was considered.

Results

Taxonomy

Brachysiderus Waterhouse, 1881

(Figs. 1-14)

Brachysiderus Waterhouse 1881: 410 (original description); Waterhouse 1882: 12 (cited); Arrow 1902: 146 (cited); Ohaus 1930: 261 (cited); Martínez 1963: 153 (description of new species, cited); Endrödi 1970: 57 (revision); Endrödi 1985: 216 (guidebook); Lachaume 1992: 22 (catalogue); Grossi & Grossi 2005: 25 (cited); Dechambre 2009: 99 (cited); Abadie (2010): 200 (cited); Grossi, Dechambre & Grossi 2012: 10 (cited); Abadie 2014: 126 (cited); McCullough, Ledger & Moore 2015: 813 (cited); Ratcliffe *et al.* 2015: 203 (checklist); Abadie, Godinho Jr. & Koike 2016: 232 (cited); Milani 2018: 75 (cited); Neita-Moreno & Ratcliffe 2019: 1049 (cited).

Type species: *Brachysiderus quadrimaculatus* Waterhouse, 1881.

Diagnosis. *Brachysiderus* differs from other genera of Agaoccephalini by the combination of the following characters. **Males:** body surface lustrous, head and tarsus dark reddish or black; pronotum with variety of patterns, might be completely dark yellow, orange or reddish or with sides dark yellow to orange and medial portion of disc red; elytra dark yellow with slightly darker shade than pronotum (when pronotum dark yellow), presence of dark reddish patches on humeral and apical umbones, some specimens with patches on apical umbones absent; legs and venter dark reddish, generally in lighter shade than head (Figs. 1A, 5A, 8A, 12A). Frons with medial fovea near base of cephalic horn (Fig. 2A, 2E, 9A, 9E). Cephalic horn elongated and bifid on apex, apex with (Fig. 9B, 9F) or without (Fig. 2B, 2F) medial tooth. Anterior base of cephalic horn connected to clypeal apical corners (Fig. 2D, 2H, 9D, 9H). Ocular canthi strong, shape thick, anterior margin with distinct tooth pointing forward, posterior margins covering part of eyes (Fig. 3A, 3F, 10A, 10F). Pronotum distinctly wide in dorsal view and convex in lateral view, absence of thoracic horn (Fig. 3D, 3I, 9D, 9I). Protarsi dilated, protarsomere V with outer margin distinctly convex, inner margin with mesobasal tooth (Fig. 3B, 3G, 9B, 9G). Protarsomere IV wider than long, with inner apical corner projected and emarginated (Fig. 3B, 3G, 9B, 9G). Protarsal claws asymmetric, inner claw distinctly longer and thicker than outer claw (Figs. 3B, 3G, 9B, 9G); inner claw pincer-like shaped with basal tooth while outer claw simply curved (Fig. 3B, 3G, 9B, 9G). Aedeagus with posterior phallobase short, more than 2 times shorter and narrower than anterior phallobase (Fig. 4D, 4H, 11D, 11H). Parameres symmetric with basal portion paddle-like shaped, medial portion distinctly thin and apical portion dilated only near tip, setae densely distributed on apex (Fig. 4A, 4E, 11A, 11E). **Females:** body shape oblong, less robust than males and with similar color pattern (Figs. 5C, 8C). Frons with medial fovea transverse (Fig. 6A, 6F). Horns absent, presence of pair of protuberances long or short near fovea (Figs. 6D, 6I). Clypeus with sides sinuous and apex emarginated (Fig. 6E, 6J). Clypeal base with margins projected upward and sharp (Fig. 6B, 6G). Clypeal apex with corners sharp (Fig. 6A, 6F). Elytra dark yellow with dark reddish spots on humeral and apical umbones, patches longitudinal on humeral umbones and oblique on apical umbones (Fig. 5C, 8C). Meso- and metatibia with outer margin with basal and medial sockets containing short thick setae and one outer apical tooth (Fig. 7B-C, 7F-G).

Male description. Color: Body surface lustrous, head and tarsus dark reddish or black; pronotum with variety of patterns, might be completely dark yellow, orange or reddish or with sides dark yellow to orange and medial portion of disc red; elytra dark yellow with slightly darker shade than pronotum (when pronotum dark yellow), presence of dark reddish patches on humeral and apical umbones, some specimens with patches on apical umbones absent; legs and venter dark reddish, generally in lighter shade than head (Fig. 1A, 5A, 8A, 12A). Frons with medial fovea near base of cephalic horn (Fig. 2A, 2E, 9A, 9E). **Head:** Cephalic horn elongated and bifid on apex, apex with (Fig. 9B, 9F) or without (Fig. 2B, 2F) medial tooth. Anterior base of cephalic horn connected to clypeal apical corners (Fig. 2D, 2H, 9D, 9H). Ocular canthi strong, shape thick, anterior margin with distinct tooth pointing forward, posterior margins covering part of eyes (Fig. 3A, 3F, 10A, 10F). **Thorax:** Pronotum distinctly wide in dorsal view and convex in lateral view, absence of thoracic horn (Fig. 3D, 3I, 9D, 9I). **Legs:** Protarsi dilated, protarsomere V with outer margin distinctly convex, inner margin with mesobasal tooth (Fig. 3B, 3G, 9B, 9G). Protarsomere IV wider than long, with inner apical corner projected and emarginated (Fig. 3B, 3G, 9B, 9G). Protarsal claws asymmetric, inner claw distinctly longer and thicker than outer claw (Fig. 3B, 3G, 9B, 9G); inner claw pincer-like shaped with basal tooth while outer claw simply curved (Fig. 3G, 9B, 9G). Protibia with three outer teeth, some specimens with a small bump posteriorly to basal tooth but never a true fourth tooth. Apical and medial teeth closer to each other than medial and basal teeth. Mesotibia with outer edge with three sockets of elongated thick setae, presence of two sockets almost medial paired with outer basal and medial sockets, carinae absent, mesotibial apex distinctly projected, surface finely punctate. Metatibia with same pattern of mesotibia but longer, metatibial apex not strongly projected as mesotibial apex. **Abdomen:** Tergite VIII short and round in lateral view, surface completely punctate, punctures thin densely distributed on entire surface. Sternite VIII short and wide with posterior margin emarginated medially, surface covered by thin punctures, punctures thinner medially than on sides. Sternites IV-VII with similar pattern of punctuation, punctures thin and dense on entire surface, sternite VII longer than others, presence of lateral row of setae near posterior margins. **Aedeagus:** Aedeagus with posterior phallobase short, more than 2 times shorter and narrower than anterior phallobase (Fig. 4D, 4H, 11D, 11H). Parameres symmetric with basal portion paddle-like shaped, medial portion distinctly thin and apical portion dilated only near

tip, setae densely distributed on apex (Fig. 4A, 4E, 11A, 11E).

Female description. Body: Shape oblong, less robust than males. Color pattern as in males (Figs. 5C, 8C). **Head:** Frons with medial fovea transverse (Fig. 6A, 6F), presence of pair of protuberances long (Fig. 6D) or short (Fig. 6I) near fovea. Horns absent. Clypeus with sides sinuous and apex emarginated (Fig. 6E, 6J), clypeal base with margins projected upward and sharp (Fig. 6B, 6G), clypeal apex with corners sharp (Fig. 6A, 6F), clypeal surface concave and densely punctate. Ocular canthi with anterior margin sharp and projected forward at base (Fig. 6C, 6H), surface densely punctate.

Thorax: Pronotum less wide and less convex than in males, discal punctures predominantly thin and sparse, becoming denser towards sides (Fig. 7A, 7E). Prosternal process absent. Prosternum with anterior margin medially convex and not protruded, anterior corners with dense aggregation of long thin setae, posterior margin medially projected. **Elytra:** Shape broad and convex. Elytra dark yellow with dark reddish spots on humeral and apical umbones, patches longitudinal on humeral umbones and oblique on apical umbones (Fig. 5C, 8C). Elytral surface irregularly punctate, punctures distinctly marked (Fig. 8C-D) or weakly marked (Fig. 5C-D). Elytral margins distinctly dark reddish, elytral suture with wide dark reddish stripes. **Legs:** Protibia with three outer teeth with same pattern as in males, but slightly thinner. Protarsi simple, not dilated as in males, protarsal claws symmetric and simply convex. Meso- and metatibia with outer margin with basal and medial sockets containing short thick setae and one outer apical tooth (Fig. 7B-C, 7F-G); presence of carina between medial sockets (Fig. 7C, 7G); meso- and metatibial apex projected (Fig. 7B-C, 7F-G). **Abdomen:** Tergite VIII with anterior portion convex and posterior portion slightly projected, surface densely punctate. Sternite VIII convex with short thin setae on posterior margin. Sternite VII bigger than sternite VI, sternite VI-IV with same size.

Geographical distribution. Neotropical region, recorded to the following countries: Bolivia, Brazil, Ecuador and Peru (Fig. 13).

Remarks. It was only recently that *Brachysiderus* was separated from *Minisiderus* (Milani 2018). Despite being part of the same genus for so long, those two genera bear less similarities than *Brachysiderus* to other Agaocephalini like *Spodistes* and *Lycomedes*. Differences between *Brachysiderus* and *Minisiderus* are detailed in remarks of *Minisiderus*. *Brachysiderus* resemble *Spodistes* and *Lycomedes* by males with one elongated cephalic horn, protarsomere V distinctly thick, protarsal inner claw pincer-like, aedeagus with posterior phallobase more than 2 times shorter than anterior

phallobase and the common distribution throughout the Andes. However, it differs from those two genera by: males with elytral surface smooth, not covered by tomentum (Fig. 14A), presence of fovea on frons (Fig. 14A), ocular canthi with horn-like projection on anterior corner (Fig. 14A) and pronotum disarmed (Fig. 14A) whereas in *Spodistes* and *Lycomedes* elytral surface tomentose (Fig. 14B-C), absence of fovea on frons (Fig. 14B-C), ocular canthi with anterior margin not projected as a short horn (Fig. 14B-C) and pronotum armed (Fig. 14B-C). Females differ by pronotal sculpture with thin and simple punctures (Fig. 14D), elytra lustrous, not tomentose with dark patches on umbones (Fig. 14D) and ocular canthi with anterior margin basally protruded forward (Fig. 14D) in *Brachysiderus*, whereas in *Spodistes* and *Lycomedes* pronotal sculpture is formed by large and tomentose punctures (Fig. 14E-F), elytra tomentose (Fig. 14E-F) and ocular canthi not projected basally (Fig. 14E-F).

When *Brachysiderus* was described by Waterhouse (1881), the author mentioned that this genus might be related to *Antodon* and *Mitracephala*, differing by the pronotum disarmed. Waterhouse (1881) did not give any more details on why he thought that those species were related, but we think that it might be linked to the shared presence of a single cephalic horn, protarsi distinctly dilated and elytra yellowish or dark yellowish with punctures deeply marked. Besides that, those genera do not have much more in common, except for the distribution of *Mitracephala* and *Brachysiderus* through the Andes while *Antodon* occurs in the Brazilian eastern Atlantic Forest. When Arrow (1902) described *Brachysiderus paranensis* [currently in *Minisiderus* (Milani 2018)], he considered only the general body shape and the coloration to describe it in the genus even that he mentioned that some main diagnostic traits are not compatible, i.e. the shape of cephalic horn, the ocular canthi and the short armature on pronotum in the new species. That description generated a butterfly effect that culminated in all the new species similar to *B. paranensis* from then on described in *Brachysiderus* until the proposition of Milani (2018) to separate them in two distinct genera, *Minisiderus* and *Brachysiderus*.

***Brachysiderus quadrimaculatus* Waterhouse, 1881**

(Figs. 1-4, 13)

Brachysiderus quadrimaculatus Waterhouse 1881: 410 (original description); Waterhouse 1882: 12 (cited); Arrow 1902: 147 (cited); Lachaume 1992: 22 (catalogue); Grossi & Grossi 2005: 28 (cited); McCullough, Ledger & Moore 2015: 813 (cited); Ratcliffe *et al.* 2015: 203

(checklist); Milani 2018: 75 (cited); Neita-Moreno & Ratcliffe 2019: 1052 (cited).

Diagnosis. Male: Frons with fovea subcircular short and deep, posterior margin with paired oblique protuberances (Fig. 2A). Foveal marginal protuberances acute in lateral view (Fig. 2C). Cephalic horn with apex bifid (Fig. 2B). Clypeus with base distinctly wide, about 2.1 times wider than apex (Fig. 2B). Lateral margin of clypeus distinctly notched near anterior corners (Fig. 2D). Pronotum completely or partially reddish with punctures thin intertwined by thinner punctures (Fig. 3D). Prosternum smooth near medial elevation, presence of dense thin setae near anterior corners (Fig. 3E). Protarsomere V with mesobasal slightly elongated tooth (Fig. 3B). Protibia with apical inner margin slightly concave, presence of seta on inner tooth of anterior corner (Fig. 3C). Parameres slender, in caudal view lateral margins with short bump medially, apical portion distinctly elongated (Fig. 4A). Parameres in ventral view with posterior margin strongly projected, sides distinctly concave and lateral corners convex and connected to ventrolateral carina (Fig. 4C).

Redescription. Male. **Color:** Surface slightly lustrous; head dark reddish brown; pronotum, appendages and venter reddish brown; elytra testaceous (Fig. 1A-B). **Head:** Frons more punctate near vertex than near horn, punctures moderate and dense. Cephalic horn oblique and long projected forward, subtrapezoidal in cross-section, apex bifid and concave (Fig. 2B). Frons with deep fovea posteriorly to horn base, fovea wider than long with shape subcircular (Fig. 2A), presence of two distinct protuberances on posterior margin of fovea (Fig. 2C). Vertex punctate, with a slight depressed area near base of ocular canthi. Clypeus with sinuous sides convergent to a subrectangular, truncate apex (Fig. 2B); clypeal anterolateral corners distinctly emarginate, presence of long carina connecting to horn apex (Fig. 2D); clypeal surface smooth, barely punctate. Ocular canthi horn-like shaped, anterior corner acute and projected forward, sides slightly round; dorsal surface with sparse striae, mainly concentrated near anterior projection, with few shallow large punctures sparse (Fig. 3A). **Thorax:** Pronotum transverse, 1.5 times wider than long, disc round in lateral view. Pronotal punctures thin and dense regularly distributed on disc and sides, some punctures bigger intertwined with minor punctures. Prosternum smooth near medial elevation, presence of dense thin setae near anterior corners (Fig. 3E). Mesepisternum with short thin setae sparsely distributed on surface, presence of large and coalescent punctures. Metasternum slightly

setose, punctures sparse and thin. Scutellum subtriangular, apex round; punctures thin and dense laterally and basally, sparse on disc. **Elytra:** Form 2.2 times longer than wide. Surface glabrous, covered by thin punctures; punctures almost inconspicuous, borders absent (Fig. 1A). Elytral margins darker than disc. Humeral umbone with same pattern of punctures as disc, presence of a distinct L-shaped dark patch (Fig. 1A). Apical umbone with same pattern of punctures as disc, presence of distinct oblique divergent patch (Fig. 1A). **Legs:** Protibia with three distinct external teeth (Fig. 3C). Protibial surface matte, densely covered by thin punctures; presence of straight row of large and deep punctures medially. In ventral view, apical emargination of protibia almost V-shaped (Fig. 3C). Protarsomere I–III slightly flattened antero-posteriorly, protarsomere IV with internal projection bifid with long ventral tooth and short dorsal tooth, protarsomere V with a rugose depression basally. Mesofemora with transverse fissure near posterior margin; surface completely punctate with thin and dense punctures. Mesotibia with external side slightly concave posteriorly, near projection. Metafemora basally larger than apically. Metatibial apex with a distinct toothed external projection, surface completely punctate with thin and dense punctures. **Abdomen:** Tergite VIII round, flattened in lateral view; surface glabrous, completely covered by thin and dense punctures, presence of some wrinkles near corners; posterior margin, in ventral view, distinctly thick and curved laterally towards sides. Sternites IV–VII densely covered by thin punctures, with rows of larger punctures on posterior margins; few short setae on lateral areas of posterior margins, not reaching middle. Sternite VIII as finely punctate as other sternites, but with no row of larger punctures on posterior margin. **Aedeagus:** Parameres symmetric, in caudal view basal portion wide, medial portion distinctly slender, apex globose and thick, long and thin setae densely on apex (Fig. 4A); in lateral view, posterior phallobase short, almost 2 times shorter than anterior phallobase (Fig. 4D), parameres with curved carina basally near posterior phallobase corner (Fig. 4B); in ventral view, ventral sclerites narrower than dorsal sclerites, lateral carinae visible, ventral sclerite with angulate projections basally (Fig. 4C).

Measurements. Body length: 29.7–30.1 mm. Cephalic horn length: 5.1–7.3 mm. Elytral length: 18.4–18.5 mm. Elytral width: 8.8–10.3 mm. Head length: 4.1–4.4 mm. Pronotal width: 14.3–14.5 mm. Pronotal length: 9.6–9.8 mm. Protibial length: 8.2–8.8 mm.

Female. Unknown.

Geographic distribution. Brazil: Amazonas (Fig. 13).

Material examined. Type male (RBINS) labeled: a) “Ex-Museo/ D.Sharp 1890”, b) “Amazona”, c) “*Brachysiderus/ 4-maculatus/ Type C. Waterh.*”, d) “A. Janssens vid, 1950/ *Brachysiderus/ quadrimaculatus/ Waterhouse m#/ Type/ Ex. Coll. R. Oberthür*”, e) “Guy Silvestre/ Vid. 2014”. **Other specimens:** 1 male (CMNC): a) “Brasil/ Benj. Constant/ rio Javary/ alto Amazonas/ Dirings”, b) “H. & A. Howden/ Collection/ ex. A. Martinez coll.”.

Remarks. *Brachysiderus quadrimaculatus* is the type-species of the genus. It was originally described by Waterhouse (1881) based on one male specimen labeled as from “Amazona”. Endrödi (1970) mentioned that the type-locality is Amazonas, Brazil, and considered the specimens from eastern Peru as *B. quadrimaculatus* as well. Ever since specimens from eastern portion of Peruvian Andes have been treated as *B. quadrimaculatus* and they are the main image that comes to mind when one think in *B. quadrimaculatus* especially because of the great amount of specimens collected from that region. However, when compared specimens from Peru to a specimen from Amazonas, Brazil, we realized that they are actually distinct species (more of that on the **remarks** of the new species below) and that the specimen from Amazonas was morphologically more similar to the type-specimen. Therefore, *B. quadrimaculatus* is until now composed only by specimens from Brazilian Amazon.

***Brachysiderus andinus* sp. nov. Sobral & Grossi**

(Figs. 2-7, 13)

Diagnosis. Male: Frons with fovea ellipsoid long and deep, reaching vertex (Fig. 2E). Posterior margin of fovea with distinct protuberances, protuberances convex in lateral view (Fig. 2G). Cephalic horn with apex bifid (Fig. 2F). Presence of parallel depression to dorsal carinae of cephalic horn (Fig. 2H). Clypeal base 1.7 times wider than apex (Fig. 2F). Lateral margins of clypeus with slight concavity near base and a distinct notch near anterior corners (Fig. 2F). Connection oblique between ocular canthi and clypeal base (Fig. 2F). Narrowest portion of cephalic horn in frontal view 3.7 times narrower than apical width (Fig. 2F). Prosternum with medial elevation distinctly slender towards procoxal connection (Fig. 3J). Protibial inner claw with basal tooth elongated, distal portion of claw distinctly swelling medially (Fig. 3G). Protibia with ventral carina not reaching line of basal tooth (Fig. 3H). Parameres in caudal view with

basal portion with lateral corners wide, apical portion dilated densely covered by long thin setae (Fig. 4E). Parameres in ventral view with posterior margin short and strongly projected, sides distinctly concave, lateral corners not reaching ventrolateral carinae (Fig. 4G).

Female: Clypeus with apical corners sharp and projected upward, with lateral short sharp protuberances pointing laterally (Fig. 6A). Frontal fovea deep and transverse reaching vertex (Fig. 6A). Presence of pair of sharp and long protuberances near fovea (Fig. 6B, 6D). Distance between apical corners 4 times narrower than distance between basal protuberances of ocular canthi (Fig. 6A). Distance between clypeal apex and anterior margin of fovea 1.3 times longer than clypeal width (Fig. 6E). Elytral punctures weakly marked on disc (Fig. 5C-D).

Description. Male. **Color:** Surface slightly lustrous; head and protarsi black, pronotum dark yellow with reddish patches on disc; appendages and venter reddish brown; elytra testaceous (Fig. 5A-B). **Head:** Frons sparsely punctate, punctures moderate, surface slightly rugose. Cephalic horn oblique and long projected forward, subtrapezoidal in cross-section, apex bifid, dorsal surface of horn slightly excavated (Fig. 2G). Frons with deep fovea posteriorly to horn base; fovea reaching vertex, shape ellipsoid longer than wide (Fig. 2E), presence of two distinct protuberances parallel to lateral margins of fovea (Fig. 2G). Vertex mainly punctate laterally, punctures shorter than punctures on frons. Clypeus with sinuous sides convergent to a subrectangular, truncate apex (Fig. 2F); clypeal anterolateral corners slightly concave, presence of long carina connecting to horn apex (Fig. 2H); clypeal surface covered by thin punctures and coalescent C-punctures. Ocular canthi horn-like shaped, anterior corner slender and projected forward, sides slightly oblique; dorsal surface with sparse striae, presence of large punctures irregularly distributed and thin punctures sparse near anterolateral corners (Fig. 3F). **Thorax:** Pronotum transverse, 1.5 times wider than long, disc round in lateral view. Pronotal punctures dense, thin and moderate punctures intertwined on entire surface, some thinner punctures coalescent (Fig. 3I). Prosternum with depression absent near anterior margin, medial connection between anterior and posterior margins slender near procoxae (Fig. 3J). Metepisternum densely covered by C-punctures, with short thin setae sparsely distributed on surface. Metasternum slightly setose, punctures sparse and thin more abundant anteriorly than posteriorly. Scutellum subtriangular, apex acute; punctures thin and dense on entire surface. **Elytra:** Form 2.2 times longer than

wide. Surface glabrous, covered by thin punctures; presence of micropunctures as a microsculpture between the major punctures on elytral disc (Fig. 5A). Elytral margins darker than disc. Humeral umbone with same pattern of punctures as disc, presence of a distinct oblique dark patch (Fig. 5A). Apical umbone with same pattern of punctures as disc, presence of distinct short oblique divergent patch (Fig. 5A). **Legs:** Protibia with three external teeth increasing in size anteriorly, no traces of a fourth tooth (Fig. 3H). Protibial surface lustrous, finely punctate; presence of straight row of large and deep punctures medially. In ventral view, apical emargination of protibia U-shaped (Fig. 3H). Protarsomere I–III slightly flattened antero-posteriorly, protarsomere IV with internal projection bifid with long ventral tooth and short dorsal tooth; protarsomere V thick with one strong tooth medially, internal margin distinctly concave (Fig. 3G); protarsal claws asymmetric, outer claw slender and curved, inner claw with elongate tooth basally and a smooth protuberance medially towards tip (Fig. 3G). Mesofemora with row of setae not connected transversally, fissure absent near posterior margin; surface densely punctate, punctures thin. Mesotibia with external side almost straight posteriorly, near projection. Metafemora with width subequal basally and anteriorly. Metatibial apex not projected externally, discretely angulate; surface covered by thin and dense punctures. **Abdomen:** Tergite VIII round, flattened in lateral view; surface glabrous, presence of punctures thin and dense on disc and sides; posterior margin, in ventral view, thick and nearly oblique towards sides. Sternites IV–VI densely covered by thin punctures, with rows of slightly larger punctures on posterior margins with microsetae. Sternites VII–VIII finely punctate, presence of coalescent thin punctures on disc. **Aedeagus:** Parameres in caudal view with basal portion with lateral corners wide, apical portion dilated densely covered by long thin setae (Fig. 4E). Parameres in lateral view with carina inconspicuous at base of lateral margin (Fig. 4F), ventrobasal margin slightly elongated (Fig. 4H). Parameres in ventral view with posterior margin short and strongly projected, sides distinctly concave, lateral corners not reaching ventrolateral carinae (Fig. 4G), apical portion as wide as posterior portion (Fig. 4G), ventrolateral carinae strongly marked (Fig. 4G).

Measurements of holotype. Body length: 33.7 mm. Cephalic horn length: 8.4 mm. Elytral length: 20.6 mm. Elytral width: 11.7 mm. Head length: 6.2 mm. Pronotal width: 17.6 mm. Pronotal length: 11.6 mm. Protibial length: 8.3 mm.

Variation, males. Males with medium size with apex of cephalic horn not as concave as in major males; minor males with apex bifid but apical corners turned to

sides; anterior corner of ocular canthi short, not longer than posterior area; pronotal lateral margins oblique towards anterior margin; pronotal disc completely dark yellow with no signs of reddish patch; protibial internal tooth pointing forward; mesotibia with row of setae near posterior margin dense; sides of sternites IV–VII setose, not reaching middle. Body length: 28.1–32.4 mm. Cephalic horn length: 2.7–8.4 mm. Elytral length: 17.3–20.2 mm. Elytral width: 9.9–11.9 mm. Head length: 4.4–5.7 mm. Pronotal width: 12.3–17.1 mm. Pronotal length: 8.3–10.3 mm. Protibial length: 6.9–8.7 mm.

Females. Body similar to male in color and in elytral and pronotal patterns (Fig. 5C-D). **Head:** Cephalic horn absent. Frons with deep fovea medially reaching vertex, less wide than eye diameter (Fig. 6A); presence of two prominent parallel tubercles near foveal lateral margins (Fig. 6B); presence of frontal depression anterior to fovea, reaching clypeal base; frontal punctures large and dense near fovea, punctures coalescent near clypeus, vertex with thin and sparse punctures more abundant laterally. Clypeus subtrapezoidal with margins strongly upward, lateral margins basally elevated, shape subtriangular sharp, apex truncate and short, apical corners triangular and prominent with one short tooth laterally at each corner (Fig. 6A); clypeal punctures large and coalescent basally, smaller and slightly sparse apically. Ocular canthi oblique with strong tooth forward near clypeal junction, tip oblique, external edge thinner than disc, almost as a flap (Fig. 6C); carina inconspicuous, not reaching vertex; surface punctate, punctures larger near frons, thinner and denser near external edge. **Thorax:** Pronotum convex but less round, in lateral view, than in male. In frontal view, anterior margin with medial concavity. Pronotal disc completely punctate, punctures moderate and thin intertwined densely on disc, sides with more thin punctures densely grouped (Fig. 7A). Proepisternum densely punctate, punctures thin, proepisternal suture slightly prominent posteriorly. Metepisternum sparsely hirsute, densely punctate. Metasternum sparsely hirsute and punctate, presence of two round depressions medially near metasternal suture, depressions sculturate. Scutellum subtriangular, punctures thin and sparse basally, barely reaching middle and absent on apex. **Legs:** Protibia similar to males, punctures thin and dense with few moderate punctures, presence of a slight indentation between medial and basal tooth. Profemoral ventral surface with longitudinal depression. Metafemora and metatibia thicker and shorter than in male. Metafemora with distinct row of setae near posterior margin, surface with moderate punctures sparse on disc, punctures bigger near anterior margin, presence of thin punctures between the moderate punctures on disc and near margins. Metatibial apex

slightly truncate, with external corner more prominent than in male, surface densely punctate, punctures thin and dense becoming sparser near apex (Fig. 7C). **Elytra:** Shape and color as in males, but shorter. Punctures thin with no border on disc, micropunctures absent between major punctures, punctures denser on sides near external edge (Fig. 5C). In lateral view, elytral edge deflected (Fig. 5D). Elytral epipleura flat near metacoxal external edge. **Abdomen:** Tergite VIII convex, medial portion of posterior margin prominent; surface glabrous, punctures thin and dense, punctures denser near corners. Sternites thicker than in male. Sternites IV–VII with anterior half with thin and dense punctures, and posterior half with bigger and sparser punctures. Sternite VIII with apex acuminate, surface densely punctate, punctures thin and denser near anterior margin and corners, apex with predominance of C-punctures; presence of short thin setae exactly on posterior margin.

Variation of females. Head: Cephalic horn absent. Frons with shallow fovea medially reaching vertex, as wide as eye diameter; presence of two prominent oblique tubercles near anterior margin of fovea; tubercles connected by strong carina with basal protuberance of clypeus; frontal punctures large and dense, vertex not punctate medially near pronotal margin. Clypeus subtrapezoidal with lateral margins distinctly upward and apical margins slightly upward, lateral margins subtriangular and sharp near ocular canthi, apex concave, apical corners triangular and slightly sharp; clypeal punctures shorter and sparser than frontal punctures. Ocular canthi oblique with short tooth near clypeal junction, tip oblique, carina distinct reaching vertex; punctures coalescent on disc, thin and dense near external edge. **Thorax:** Pronotum convex but less round, in lateral view, than in male. In frontal view, anterior margin convex. Lateral margins slightly prominent. Pronotal disc completely punctate, punctures moderate and dense with sparser areas near posterior margin, sides and corners with dense thin punctures, absence of microsculpture on disc. Prosternal medial protuberance with surface rugose. Metasternum sparsely hirsute and punctate, absence of depressions near metasternal suture. **Elytra:** Punctures thin with no border on disc, micropunctures present but fewer than in males, punctures denser on sides near external edge. In lateral view, elytral edge not deflected. Elytral epipleura slightly depressed near metacoxal external edge.

Measurements of females. Body length: 27.9–32.5 mm. Elytral length: 17.5–19.8 mm. Elytral width: 9.5–11.4 mm. Head length: 4.3–4.8 mm. Pronotal width: 12.8–15 mm. Pronotal length: 9–10.6 mm. Protibial length: 7.6–7.9 mm.

Geographic distribution. Peru: Cusco, Huánuco, Junín, San Martín (Fig. 13).

Material examined. Holotype male (CERPE): a) “PERU, San Martín,/ Janjuí, Saposoa, Monte/ Sacanche, 800 m./ VI.2009 – J.M.Z. Aguilé {leg.}”, b) “*Brachysiderus/ quadrimaculatus/* Waterhouse, 1881/ Det. E. & P. Grossi 2007”, c) “Coleção E./ & P. Grossi”. **Paratypes:** 1 male (CERPE): a) “PERU, Huanuco,/ Tingo Maria, 650 m./ 20.V.2006/ R.M. Koike”, b) “*Brachysiderus/ quadrimaculatus/* Waterhouse, 1881/ Det. E. & P. Grossi 2007”, c) “Coleção E./ & P. Grossi”; 1 male (CERPE): a) “PERU, Dep{artamento}. de/ Junin, 700m/ IV.1996/ P. Arnaud Leg.”, b) “*Brachysiderus/ quadrimaculatus/* Waterhouse, 1881/ Det. E. & P. Grossi 2007”, c) “Coleção E./ & P. Grossi”; 1 male (CERPE): a) “PERU, Dep./ de Junin, IV.{19}96”; 1 female (CERPE): a) “PERU, Huanuco,/ Tingo Maria, 650 m./ 01 – 17.V.2006/ Michael Buche Leg.”, b) “Coleção E./ & P. Grossi”; 1 female (CERPE): a) “PERU, Tingo Maria,/ Huanuco, 650 m/ V. 2012. Fva leg.”; 3 males and 1 female (RBINS): a) “Cordilière Andes/ Versant Est/ ex Schmidt/ de Lima”, b) “Ex Museo/ V. Mayet/ 1909”, c) “Coll. R. Oberthur/ R.I.Sc.N.B.17.647”; 1 male (RBINS): a) “La Merced/ Pérou, 1921”, b) “R.I.Sc.N.B. 21.418/ Coll. P. de Moffarts”, c) “*Brachysiderus/ 4-maculatus* m#/ J. Gillet det. Wath.”; 3 males and 3 females (RBINS): a) “Pérou/ Chanchamayo/ La Merced/ C. O. Schunke/ Reçu Novembre 1904”, b) “Coll. R. Oberthur:/ R.I.Sc.N.B. 17.647”; 1 female (RBINS): a) “Peru”, b) “*Cyclocephala/ endroedi/* Martinez”, c) “Coll. IRSNB/ ex coll. J. Roggeman/ I.G. 30.600”, d) “*Brachysiderus/ quadrimaculatus/* Waterhouse/ det. Y. Ponchel 2007”; 3 males (CMNC): a) “South America/ Peru/ 1977”, b) “Rod Parrott/ Collection/ Bequest 2019/ A2019.0135”; 1 male (CMNC): a) “Chanchamayo/ Peru iii.48/ F 6034”, b) “H. Bassler/ Collection/ Acc. 33591”, c) “*Brachysiderus/ quadrimaculatus/* Waterh./ Det. At B.M./ H.F. Howden 62”; 1 female (NHM): a) “Peru”, b) “*Brachysiderus/ 4-maculatus* Waterh{ouse}. f#/ comp{ared}. with type in Coll. Oberthur/ ident{ified}. m# and f# from Peru”; 1 female (NHM): a) “Peru/ Santa Ana/ J. Kalinowski/ 1902-276”. **Other specimens:** 1 male (MNHN): a) “Pérou{Peru}” b) “Ex Musaeo V. Mayet 1909”, c) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, d) “MNHN/ EC11762”; 1 male (MNHN): a) “Pérou/ Chanchamayo/ Ch. O. Schunke {collector}”, b) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, c) “MNHN/ EC11763”; 1 male (MNHN) with same data as previous specimen except: c) “MNHN/ EC11764”; 1 male (MNHN): a) “Pérou/ Prov. Huallaga/ Rio Mixiollo 1200 m/ G. A. Baer 7-8{VII-VIII}-1900”, b) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, c) “MNHN/ EC11765”; 1 female (MNHN) with same data as previous

specimen except: c) “MNHN/ EC11766”; 1 female (MNHN): a) “Pérou/ Moyobamba/ M. de Mathan/ 1888”, b) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, c) “MNHN/ EC11767”; 1 female (MNHN): a) “Pérou/ Chanchamayo/ Oswald Schunke/ Reçu 1912”, b) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, c) “MNHN/ EC11768”; 1 female (MNHN): a) “Pérou”, b) “Cordillère versant Est/ ex Schmidt de Lima”, c) “Ex Musaeo V. Mayet 1909”, d) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, e) “MNHN/ EC11769”; 1 female (MNHN): a) “Pérou/ Cumbase {San Roque de Cumbaza}”, b) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, c) “MNHN/ EC11770”; 1 male (MNHN): a) “Satipo (Pérou)/ 3.II.1989”, b) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2014”, c) “MNHN/ EC11773”.

Remarks. *Brachysiderus andinus* is a peculiar case of a new species that was extensively collected and well represented in entomological collections that has been treated for many years as another species. As mentioned in the **remarks** of *B. quadrimaculatus*, the image of specimens of *B. andinus* are so intricately related to *B. quadrimaculatus* that a search on internet for *Brachysiderus quadrimaculatus* will result in the majority of images showing specimens of what we are describing here as *B. andinus*. Actually, the image of a true *B. quadrimaculatus* is hard to find online. The new species can be distinguished from *B. quadrimaculatus* by: males with frontal fovea ellipsoid and reaching vertex (Fig. 2E), lateral margins of fovea with short round protuberances (Fig. 2G), clypeal base 1.7 times wider than apex (Fig. 2F), lateral margins of clypeus with slight concavity near base and slight emargination near anterior corners (Fig. 2F), parameres in lateral view with carina inconspicuous at base of lateral margin (Fig. 4F), ventrobasal margin slightly elongated (Fig. 4H), in ventral view with apical portion as wide as posterior portion (Fig. 4G), ventrolateral carinae strongly marked (Fig. 4G) whereas in *B. quadrimaculatus* frontal fovea subcircular and not reaching vertex (Fig. 2A), lateral margins of fovea with sharp protuberances (Fig. 2C), clypeus with base distinctly wide, about 2.1 times wider than apex (Fig. 2B), lateral margin of clypeus oblique basally and distinctly notched near anterior corners (Fig. 2B), parameres in lateral view with distinct curved carina at base of lateral margin (Fig. 4B), parameres in ventral view with apical portion narrower than posterior portion (Fig. 4C), ventrolateral carinae weakly marked (Fig. 4C), ventrobasal margin short (Fig. 4D).

There are only two species of *Brachysiderus* with known females, *B. andinus* and *B. tridentiger*. Females of these species can be distinguished by the following

characters: *B. andinus* with frontal fovea deep and transverse reaching vertex (Fig. 6A), presence of pair of sharp and long protuberances near fovea (Fig. 6B, 6D), ocular canthi thick (Fig. 6C), distance between apical corners 4 times narrower than distance between basal protuberances of ocular canthi (Fig. 6A), distance between clypeal apex and anterior margin of fovea 1.3 times longer than clypeal width (Fig. 6E) and elytral punctures weakly marked on disc (Fig. 5D), whereas in *B. tridentiger* frontal fovea shallow and transverse not reaching vertex (Fig. 6F), foveal margins with pair of round protuberances (Fig. 6G, 6I), ocular canthi slender (Fig. 6H), distance between apical corners 2.8 times narrower than distance between basal protuberances of ocular canthi (Fig. 6F), distance between clypeal apex and anterior margin of fovea 1.9 times longer than clypeal width (Fig. 6J) and elytral punctures distinctly marked on disc (Fig. 8D).

Brachysiderus andinus occurs in areas of Peruvian Yungas, Ucayali moist forests and Central Andean wet puna.

***Brachysiderus breyeri* (Martínez, 1963) stat. rev. and comb. nov.**

(Figs. 9-13)

Agacephala breyeri Martínez 1963: 153 (original description); Endrödi 1970: 57 (synonymized with *B. quadrimaculatus tridentiger*); Endrödi 1985: 217 (mentioned)

Diagnosis. Male: Frons with deep fovea posteriorly to horn base, shape circular and wide in dorsal view (Fig. 9E). Cephalic horn with apical margin tridentate with strong posterior tooth behind anterior medial tooth (Fig. 9F-G). Ocular canthi with anterior margin distinctly concave and sides distinctly round with slight posterior emargination near eyes (Fig. 10F). Pronotum transverse, almost 1.5 times wider than long, disc reddish brown and sides dark yellow with paired dark patches on lateral margins (Fig. 10I). Protarsal claws asymmetric, inner claw with basal short tooth and distal portion straight with no swelling near tip (Fig. 10G). Protibial inner margin, in ventral view, distinctly emarginated apically (Fig. 10H). Aedeagus in lateral view with anterior phallobase with outer margin angulated (Fig. 11H). Parameres in ventral view with posterior margin distinctly projected medially and slightly angulated towards sides (Fig. 11G), medial portion thick and densely punctate, inner margins narrow (Fig. 11G).

Description. Male. **Color:** Surface lustrous; head and protarsi dark reddish

brown almost black, pronotum dark yellow on sides and middle portion near anterior margin, with disc reddish and dark patches near lateral margins; appendages and venter reddish brown; elytra testaceous (Fig. 12A-B). **Head:** Cephalic horn oblique and long projected forward, subtrapezoidal in cross-section, apical margin tridentate with strong posterior tooth behind anterior medial tooth (Fig. 9H), dorsal surface of horn distinctly depressed with two subparallel carinae divergent basally towards frons (Fig. 9E). Frons with deep fovea posteriorly to horn base; fovea connected to dorsal depression of horn, shape circular and wide in dorsal view (Fig. 9E), lateral margins of fovea smooth, protuberances absent (Fig. 9G-H). Frons sparsely punctate, punctures thin. Vertex distinctly elevated in lateral view (Fig. 9G). Clypeus with base oblique and convergent, connection between anterolateral corners and clypeal base slightly angulated (Fig. 9F); clypeal apex slightly round; clypeal surface covered by thin and sparse punctures. Ocular canthi horn-like shaped, anterior margin distinctly concave, anterior corners thick, long and projected forward (Fig. 10F), sides distinctly round with slight posterior emargination near eyes (Fig. 10F); dorsal surface covered by thin and sparse punctures, presence of angulated carinae near eyes (Fig. 10F). In lateral view, apex of ocular canthi slightly pointing downward (Fig. 9G). **Thorax:** Pronotum transverse, distinctly large, almost 1.5 times wider than long (Fig. 10I); in lateral view, pronotal disc distinctly convex and robust (Fig. 12B); pronotal punctures thin and sparse on disc with micropunctures among them laterally, pronotal sculpture shagrinated on margins. Prosternum with anterior margin distinctly round at middle portion, prosternal surface depressed on sides (Fig. 10J); prosternal area between procoxae distinctly thick and hairless (Fig. 10J); prosternal posterior margin medially acuminate with ventral depression medially (Fig. 10J). **Legs:** Protibiae with three outer teeth, apical and medial teeth connected at base and more projected than basal tooth (Fig. 10H). In ventral view, protibial inner margin distinctly emarginated apically (Fig. 10H), presence of short thin setae at connection between protibiae and profemora (Fig. 10H). Protarsi distinctly thickened, protarsomeres I–III short and with inner corner simple, protarsomer IV short and with inner corner elongated and bifid (Fig. 10G); protarsomer V as long as protarsomeres II–IV together, presence of mesobasal tooth on inner margin of protarsomer V; protarsal claws asymmetric, inner claw thicker and longer than outer claw, inner claw pincer-like shaped with basal short tooth and distal portion straight with no swelling near tip (Fig. 10G). Mesotibia with three outer thick setae, mesotibial apex distinctly angulated towards apical outer seta, mesotibial surface finely punctate.

Metatibia with three outer thick setae, metatibial apex projected medially with short thick setae on tip. **Abdomen:** Tergite VIII round and short, surface distinctly punctate, punctures thin and dense. Sternite VIII short and emarginated medially, surface with thin and irregular punctures, less punctate than sternite VII. Sternite VII densely punctate, punctures thin and reaching medial portion, presence of row of short thin setae only near corners. Sternites IV-VI with same patten of punctures thin and dense, barely reaching middle, row of setae shorter than on sternite VII. **Aedeagus:** Parameres symmetric; in caudal view, basal portion paddle-like shaped distinctly narrowing on medial portion, apex dilated with dense aggregation of setae (Fig. 11E), inner margin concave and apical portion distinctly touching internally (Fig. 11E); in lateral view, lateral surface slightly depressed and ventrolateral projection slender towards middle (Fig. 11F), posterior phallobase distinctly shorter than anterior phallobase, posterior phallobase with surface round, anterior phallobase with outer margin angulated (Fig. 11H); in ventral view, parameres with posterior margin distinctly projected medially and slightly angulated towards sides (Fig. 11G), medial portion thick and densely punctate, inner margins narrow (Fig. 11G).

Measurements. Body length: 29–35.9 mm. Cephalic horn length: 6.5–9.8 mm. Elytral length: 17.6–20.6 mm. Elytral width: 10–11.9 mm. Head length: 5.5–6.3 mm. Pronotal width: 14.9–19.5 mm. Pronotal length: 10.5–12.1 mm. Protibial length: 8.3–8.6 mm.

Female. Unknown.

Geographic distribution. Bolivia: Cochabamba, Santa Cruz (Fig. 13).

Material examined. Paratype male (HNHM): a) “Bolivia, Santa Cruz/, Ibáñez, El Espejo/, Campamento Zischka-Canela/, II-1962/ A.F. Prosen y A. Martínez leg.”.

Other specimens: 1 male (CERPE): a) “Bolivia, Chapará/, San Jacinto/ 5 – 15.II.2003/ A. Chaminade {leg.}”, b) “*Brachysiderus/ tridentiger/* Prell, 1934/ Det. E. & P. Grossi 2008”, c) “Coleção E./ & P. Grossi”; 1 male (CERPE): a) “BOLIVIA, Arani, Prov./ Cochabamba, 1400 m/ XII. 2006/ P. Arnaud {leg.}”, b) “*Brachysiderus/ tridentiger/* Prell, 1934/ Det. E. & P. Grossi 2008”, c) “Coleção E./ & P. Grossi”.

Remarks. *Brachysiderus breyeri* was originally described by Martínez (1963) as a species of *Agacephala* forming a distinct group with *B. tridentiger* in that genus. It is curious that Martínez (1963) considered *B. breyeri* and *B. tridentiger* as being *Agacephala* but did not synonymize *Brachysiderus* to *Agacephala* and kept *B. quadrimaculatus* in a distinct genus even that the three species are clearly more similar

to each other than to any species of *Agacephala*. Despite the confusion with the genus in which these species were put by Martínez (1963), the author had a keen eye to notice the subtle differences between the two species. *B. breyeri* is more similar to *B. tridentiger* than to the other species of *Brachysiderus* but males of these species can be distinguished by the following characters: *B. breyeri* with frontal fovea with shape circular as wide as long (Fig. 9E), cephalic horn with strong posterior tooth on apex (Fig. 9G), vertex distinctly elevated in lateral view (Fig. 9G), ocular canthi with sides distinctly round with slight posterior emargination near eyes (Fig. 10F), protibial inner margin in ventral view distinctly emarginated apically (Fig. 10H), protarsal inner claw with distal portion straight and not swelling (Fig. 10G), parameres in ventral view with posterior margin distinctly projected medially (Fig. 11G) and with inner margins narrow (Fig. 11G). whereas in *B. tridentiger* frontal fovea with shape ellipsoid longer than wide (Fig. 9A), cephalic horn with posterior tooth absent on apex (Fig. 9C), vertex not elevated (Fig. 9C), ocular canthi convex near eyes (Fig. 10A), protibial inner margin straight apically (Fig. 10C), protarsal inner claw with distinct medial swelling before tip (Fig. 10B), parameres in ventral view with posterior margin not projected (Fig. 11C) and with inner margins wide (Fig. 11C). *Brachysiderus breyeri* occurs in the oriental portion of Bolivia near the foothills of Andes, in areas corresponding to the Dry Chaco and the Bolivian montane dry forests.

***Brachysiderus tridentiger* (Prell, 1934) stat. rev.**

(Figs. 6-11, 13)

Brachysiderus quadrimaculatus tridentiger Endrödi 1970: 57 (new status); Endrödi 1985: 217 (cited); Lachaume 1992: 22 (cited); Grossi & Grossi 2005: 25 (cited); Milani 2018: 75 (cited)

Agacephala tridentiger Martínez 1963: 153 (new combination);

Lycotharses tridentiger Prell, 1934: 59 (original combination).

Diagnosis. Male: Frons with fovea ellipsoid, shape longer than wide (Fig. 9A). Lateral margins of fovea with paired short protuberances (Fig. 9C). Cephalic horn with apical margin tridentate, medial tooth distinctly shorter than lateral teeth, posterior tooth absent on apex (Fig. 9B). Narrowest portion of cephalic horn in frontal view 2.4 times narrower than apical width (Fig. 9B). Vertex straight to frontal fovea margin (Fig. 9C). Ocular canthi with anterior margin distinctly concave, sides convex from apex to base near eyes (Fig. 10A). Pronotal sculpture with moderate punctures intertwined by thinner

and denser punctures (Fig. 10D). Protibial inner margin straight apically, in ventral view (Fig. 10C). Protarsal claws asymmetric, inner claw with distinct medial swelling before tip, base with short tooth (Fig. 10B). Aedeagus in lateral view with anterior phallobase round dorsally (Fig. 11D). Parameres in ventral view with posterior margin not projected (Fig. 11C) and with inner margins wide (Fig. 11C).

Female: Clypeus with apical corners sharp and projected upward, sides oblique (Fig. 6F). Frontal fovea shallow and transverse not reaching vertex (Fig. 6F, 6I). Foveal margins with pair of round protuberances (Fig. 6I). Distance between apical corners 2.8 times narrower than distance between basal protuberances of ocular canthi (Fig. 6F). Distance between clypeal apex and anterior margin of fovea 1.9 times longer than clypeal width (Fig. 6J). Elytral punctures distinctly marked on disc (Fig. 8D).

Description. Male. **Color:** Surface slightly lustrous; head dark reddish brown, appendages and venter reddish brown; pronotum dark yellow with small brown patches near lateral margins; elytra testaceous (Fig. 8A-B). **Head:** Frons and vertex punctate, punctures sparse moderate and thin; rugose patterns larger on frons near canthi than on vertex. Cephalic horn oblique and long, projected upward, subtrapezoidal in cross-section, apex bifid with a small tooth at middle between apical corners, dorsal surface of horn flat (Fig. 9B). Frons with deep fovea posteriorly to horn base; fovea barely reaching vertex, shape acute longer than wide, presence of two discrete protuberances parallel to lateral margins of fovea (Fig. 9A). Clypeus with sinuous sides convergent to a subrectangular, slightly round apex (Fig. 9B); presence of long carina connecting to horn apex; in frontal view, space between carinae smoothly widening towards apex; clypeal surface densely rugose on sides, punctate frontally between carinae, punctures moderate and dense. Ocular canthi horn-like shaped, anterior corner acute not as long as posterior corner, sides slightly round, presence of curved carinae from anterior corners to frons (Fig. 10A); dorsal surface rugose with large punctures on outer area of anterior corner. **Thorax:** Pronotum transverse, 1.4 times wider than long, disc round in lateral view. Pronotal punctures dense, thin and moderate punctures intertwined on entire surface; bigger punctures irregularly sparse with bigger areas of thinner punctures between each big puncture, thin punctures coalescent in some areas (Fig. 10D). Pronotal margins smoothly dark brown. Proepisternum densely punctate, punctures moderate and large touching margins with punctures of same size, thinner punctures filling the gaps among bigger punctures. Prosternum with a depression between middle portion of

anterior margin and medial area of prosternal disc; prosternal disc medially thick with some ridges near anterior margin (Fig. 10E). Metepisternum densely covered by large round punctures, with short thin setae sparsely on surface. Metasternum hirsute, with anterior and lateral external areas densely setose; punctures thin and sparse on disc. Scutellum subtriangular, apex acute; punctures thin and dense basally and medially, sparse apically. **Elytra:** Surface glabrous, covered by thin punctures with distinct whitish border; presence of micropunctures as microsculpture between the major punctures on elytral disc (Fig. 8A). Elytral margins darker than disc. Humeral umbone punctate as disc, presence of distinct L-shaped patch. Apical umbone with small punctures but less micropunctures than disc, presence of distinct short oblique divergent patch (Fig. 8A). **Legs:** Protibia with three external teeth increasing in size anteriorly, no traces of a fourth tooth. Protibial surface densely covered by thin punctures; in ventral view, surface thick medially, apical emargination slightly U-shaped (Fig. 10C). Protarsomere I–III slightly flattened antero-posteriorly. Protarsomere IV with internal projection bifid with long ventral tooth and short dorsal tooth; in dorsal view, anterior margin slightly concave (Fig. 10B). Protarsomere V thick with one strong tooth medially, internal margin distinctly concave (Fig. 10B); protarsal claws asymmetric, outer claw slender and curved, inner claw with elongate tooth basally and a smooth protuberance medially towards tip (Fig. 10B). Mesotibia with external side almost straight posteriorly, near projection; mesotibial apex widely concave. Metafemora densely punctate, punctures thin near anterior margin with some bigger punctures sparsely distributed transversely from base to apex. Metatibial apex not projected externally, discretely angulate; surface covered by thin and dense punctures. **Abdomen:** Tergite VIII round, slightly protruded in lateral view; surface glabrous, completely covered by thin and dense punctures; posterior margin, in ventral view, slightly curved toward sides. Sternites IV–VIII densely covered by thin punctures, with rows of slightly larger punctures on posterior margins with microsetae. Sternites IV–VII with sparse short setae only on sides. Sternites VIII with microsetae on posterior margin. **Aedeagus:** Parameres symmetric; in caudal view, apex with outer margin dilated narrowing to medial portion, medial portion slightly sinuous, basal portion paddle-like shaped with distal part almost as narrow as proximal part (Fig. 11A); in lateral view, anterior phallobase with dorsal margin round, posterior phallobase round and distinctly shorter than anterior phallobase (Fig. 11D), parameres with apex densely covered by long thin setae, lateral surface slightly depressed with ventrolateral projection with tip

blunt (Fig. 11B). Parameres in ventral view with medial portion slender and punctate, posterior margin not distinctly projected with sides not reaching ventrolateral carina (Fig. 11C).

Measurements of holotype. Body length: 33.8 mm. Cephalic horn length: 7 mm. Elytral length: 20.7 mm. Elytral width: 9.7 mm. Head length: 5.9 mm. Pronotal width: 17.3 mm. Pronotal length: 10.2 mm. Protibial length: 6.8 mm.

Variation, males. Males with medium size with apex of cephalic horn not as concave as in major males; minor males with frontal fovea shorter and shallower than in bigger males; anterior corner of ocular canthi short, not longer than posterior area; pronotal lateral margins oblique towards anterior margin; pronotal disc completely dark yellow with smooth dark patch medially. Body length: 27.7–30.1 mm. Cephalic horn length: 6.7–7.3 mm. Elytral length: 16.9–20.2 mm. Elytral width: 9.7–10.3 mm. Head length: 5.1–6 mm. Pronotal width: 13.3–17.9 mm. Pronotal length: 8.7–10.4 mm. Protibial length: 7.3–7.5 mm.

Females. Body similar to males in color and in elytral and pronotal patterns (Fig. 8C-D). **Head:** Cephalic horn absent. Frons with shallow fovea medially, almost as wide as eye diameter; presence of two inconspicuous oblique tubercles at foveal lateral margins (Fig. 6F); frontal punctures large and dense, some punctures coalescent towards clypeus, punctures on vertex almost absent. Clypeus subtrapezoidal with margins slightly upward, lateral margins slightly acuminate towards apex, apex slightly truncate, apical corners triangular and prominent (Fig. 6F); clypeal punctures large and dense, but smaller than frontal punctures. Ocular canthi oblique with short tooth near clypeal junction, tip smoothly round, presence of thin carina from clypeal junction to vertex (Fig. 6H); surface punctate, punctures large and dense. **Thorax:** Pronotum convex but less round, in lateral view, than in male. In frontal view, anterior margin convex medially (Fig. 7E). Pronotal disc completely punctate, punctures moderate sparse from punctures of same size, thinner punctures between moderate punctures, presence of coalescent thin punctures near lateral margins (Fig. 7E). Prosternum with posterior margin slightly excavated and with transverse row of setae (Fig. 7H). Proepisternum densely punctate, punctures thin. Metepisternum sparsely hirsute, densely punctate, punctures ocellate shallow. Metasternum sparsely hirsute and punctate, presence of two small round depressions medially near metasternal suture, depressions sculpturate. Scutellum subtriangular, punctures thin and sparse not reaching apex. **Legs:** Protibia similar to males, with moderate punctures intertwined by thin and dense punctures,

presence of a slight indentation between medial and basal tooth. Profemoral ventral surface flat, with no signs of depression. Mesotibia with anterior carina distinct and posterior carina inconspicuous (Fig. 7F), outer margin with C-punctures and coalescent punctures, ventral surface finely punctate. Metafemora and metatibia thicker and shorter than in male. Metafemora with a distinct row of setae near posterior margin, surface densely punctate. Metatibial apex with outer corner more prominent than in male, surface densely covered by thin punctures (Fig. 7G). **Elytra:** Shape and color as in males, but shorter. Punctures moderate with dark thick border and micropunctures between them (Fig. 8C). Punctures near lateral edges bigger than discal punctures (Fig. 8D). In lateral view, elytral edge not deflected. Elytral epipleura with longitudinal depression near metacoxal external edge. **Abdomen:** Tergite VIII convex, medial portion of posterior margin slightly prominent; surface glabrous, densely punctate. Sternites thicker than in male. Sternites IV–VI with punctures thin and dense, presence of short setae near lateral margins. Sternite VII almost with same punctuation as previous sternites but with longitudinal row of sparser punctures near posterior margin. Sternite VIII with apex acuminate, surface with thin punctures denser near anterior margin and sparser on disc and posterior margin, presence of row of setae near posterior margin.

Measurements of female. Body length: 27–29.1 mm. Elytral length: 17.1–18.6 mm. Elytral width: 8.4–9.6mm. Head length: 4.4–4.5 mm. Pronotal width: 12.5–13.5 mm. Pronotal length: 8.3–9.1 mm. Protibial length: 6.3–6.7 mm.

Geographic distribution. Ecuador: Loja, Morona-Santiago, Pastaza (Fig. 13).

Material examined. Type male (ZMNB) labeled: a) “413”, b) “Zarayaku{Sarayaku}/ Ecuador or.”, c) “*Lycotharses/ tridentiger/* Prell m#-Type”, d) “Lectotypus/ *Brachysiderus/ tridentiger* Prell”. **Other specimens:** 1 male and 1 female (RBINS): a) “Ecuator/ Loja/ Abbe Gaujon”, b) “G.J. Arrow/ Vidit 1901”, c) “Coll. R. Oberthur:/ R.I.Sc.N.B. 17.647”; 1 male (MNHN): a) “Zarayaku{Sarayaku}/ Ecuador or{iental}.”, b) “*Brachysiderus/ quadrimaculatus* Waterhouse/ F. Dupuis det. 2011”, c) “MNHN/ EC11771”; 1 female (ZMNB): a) “662”, b) “Sucula/ Macas 800m/ Ecuador”, c) “*B. qu. Prell/ tridentiger/* det. Dr. Endrödi 1968”; 1 male (CERPE): a) “Ecuador/ Chugchilam, II.83”.

Remarks. *Brachysiderus tridentiger* **stat. rev.** and **comb. nov.** was described in a then new genus *Lycotharses* by Prell (1934). Prell (1934) considered that that new genus is closer to *Lycomedes* and did not mention the similarities to *Brachysiderus*

quadrимaculatus described by Waterhouse (1881). Endrödi (1970) synonymized *Lycotharses* to *Brachysiderus* and considered the former *L. tridentiger* as a subspecies of *B. quadrимaculatus*, becoming *Brachysiderus quadrимaculatus tridentiger*. Also, *Lycotharses* is a preoccupied name of a genus of spiders so even that it was in fact a distinct genus it would have to change the name. It is possible that Prell did not have knowledge of *B. quadrимaculatus* and for that reason his description of *L. tridentiger* have more generic diagnostic traits than specific traits.

Since Endrödi (1970) the two morphotypes have been treated as subspecies of *B. quadrимaculatus*. *B. quadrимaculatus quadrимaculatus* including specimens from Brazil and eastern Peru with elytral sculpture formed by thin punctures distinctly marked and tegument shining; and *B. quadrимaculatus tridentiger* with specimens from Ecuador, western Peru and Bolivia with elytral punctures sparser and thin but weakly marked and tegument oily. We propose here the revalidation of the status of species to *Brachysiderus tridentiger* based on the morphological differences and distinct geographical distribution in relation to *B. quadrимaculatus*. *B. tridentiger* can be distinguished by the following characters: frontal fovea ellipsoid, longitudinally elongated (Fig. 9A) [frontal fovea round and short in *B. quadrимaculatus* (Fig. 2A)], lateral margins of fovea posteriorly with short round protuberances (Fig. 9C) [lateral margins of fovea with sharp protuberances in *B. quadrимaculatus* (Fig. 2C)], cephalic horn with apical margin tridentate (Fig. 9B) [cephalic horn with margin bifid in *B. quadrимaculatus* (Fig. 2B)], mesobasal tooth of protarsomere V short and thick (Fig. 10B) [tooth elongated and slender in *B. quadrимaculatus* (Fig. 3B)], parameres in caudal view with distal part of basal portion thinner in *B. tridentiger* (Fig. 11A) than in *B. quadrимaculatus* (Fig. 4A), ventral inner margins shorter in *B. tridentiger* (Fig. 11A) than in *B. quadrимaculatus* (Fig. 4A), parameres in ventral view with posterior margin not projected and oblique towards sides (Fig. 11C) [parameres with posterior margin distinctly projected and concave towards sides in *B. quadrимaculatus* (Fig. 4C)].

Martínez (1963) described a new species from Bolivia with close resemblances to *B. tridentiger*. By the time, Martínez (1963) used only three characters as diagnostic to distinguish the two species, the shape of protarsal inner claw and differences in color and pronotal sculpture. Differences between these two species are mentioned in the **remarks** of *B. beyeri* below.

Brachysiderus tridentiger is found in Ecuador, in areas of moist forests ranging the Northwest Andean montane forests, Eastern Cordillera Real montane forests and

Napo moist forests. Considering the occurrence data, it appears to us that the Cordillera is not an obstacle to the distribution of this species as it occurs both in eastern and western sides of Andes.

Key to species of *Brachysiderus* Waterhouse, 1881

1. Head with elongated cephalic horn (Fig. 2C). Protarsomere V distinctly dilated, protarsi with inner claw pincer-like shaped (Fig. 10G) (males)..... 2
 - Head with horn absent (Fig. 6A). Protarsomere V thin, protarsi with claws symmetric and simply curved (females)..... 5
2. Cephalic horn with presence of thick tooth posteriorly to apex (Fig. 9H). Vertex distinctly elevated (Fig. 9G)..... ***B. breyeri* (Martínez, 1963) comb. nov.**
 - Cephalic horn with posterior tooth absent on apex (Fig. 9C). Vertex not elevated (Fig. 9C)..... 3
3. Fovea with shape subcircular and short (Fig. 2A). Margins of fovea with pair of sharp protuberances (Fig. 2C)..... ***B. quadrimaculatus* Waterhouse, 1881**
 - Fovea with shape ellipsoid and long (Fig. 2E, 9A). Margins of fovea with pair of round protuberances (Fig. 2G, 9C)..... 4
4. Cephalic horn with presence of small tooth medially on apex (Fig. 9B). Clypeal lateral margin with middle portion not protruded (Fig. 9B). Protarsomere V with mesobasal tooth short and thick (Fig. 10B). Ocular canthi with anterior apical corner directed inward (Fig. 10A). Parameres in ventral view with posterior margin shortly projected and ventrolateral carinae sinuous (Fig. 11C)..... ***B. tridentiger* (Prell, 1934)**
 - Cephalic horn bifid, medial tooth absent (Fig. 2F). Clypeal lateral margin with middle portion protruded (Fig. 2F). Protarsomere V with mesobasal tooth long and thin (Fig. 3G). Ocular canthi with anterior apical corner directed outward (Fig. 3F). Parameres in ventral view with posterior margin distinctly projected and ventrolateral carinae oblique

(Fig. 4G)..... *B. andinus*

new species

5. Frontal fovea deep and transverse reaching vertex (Fig. 6A). Presence of pair of sharp and long protuberances near fovea (Fig. 6B, 6D). Ocular canthi thick (Fig. 6C).

Distance between clypeal apex and anterior margin of fovea 1.3 times longer than clypeal width (Fig. 6E). Elytral punctures weakly marked on disc (Fig. 5D).....

***B. andinus* new species**

- Frontal fovea shallow and transverse not reaching vertex (Fig. 6F). Presence of pair of round and short protuberances near fovea (Fig. 6G, 6I). Ocular canthi slender (Fig. 6H).

Distance between clypeal apex and anterior margin of fovea 1.9 times longer than clypeal width (Fig. 6J). Elytral punctures distinctly marked on disc (Fig.

8D)..... *B. tridentiger* (Prell, 1934)

Acknowledgments

We thank all the curators from the cited collections for their contributions of material for this study. We thank Max Barclay, Michael Geiser and Keita Matsumoto for all the support to RS during his time in the Natural History Museum (London, United Kingdom). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. RS acknowledge the Instituto Nacional de Pesquisas da Amazônia for research support; the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for the PhD scholarship to RS and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Sandwich Doctorate scholarship to RS. PCG acknowledges the Universal Project, 449366/2014-6.

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Figures

FIGURE 1. Male of *Brachysiderus quadrimaculatus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view.
Scale bars: 10 mm.

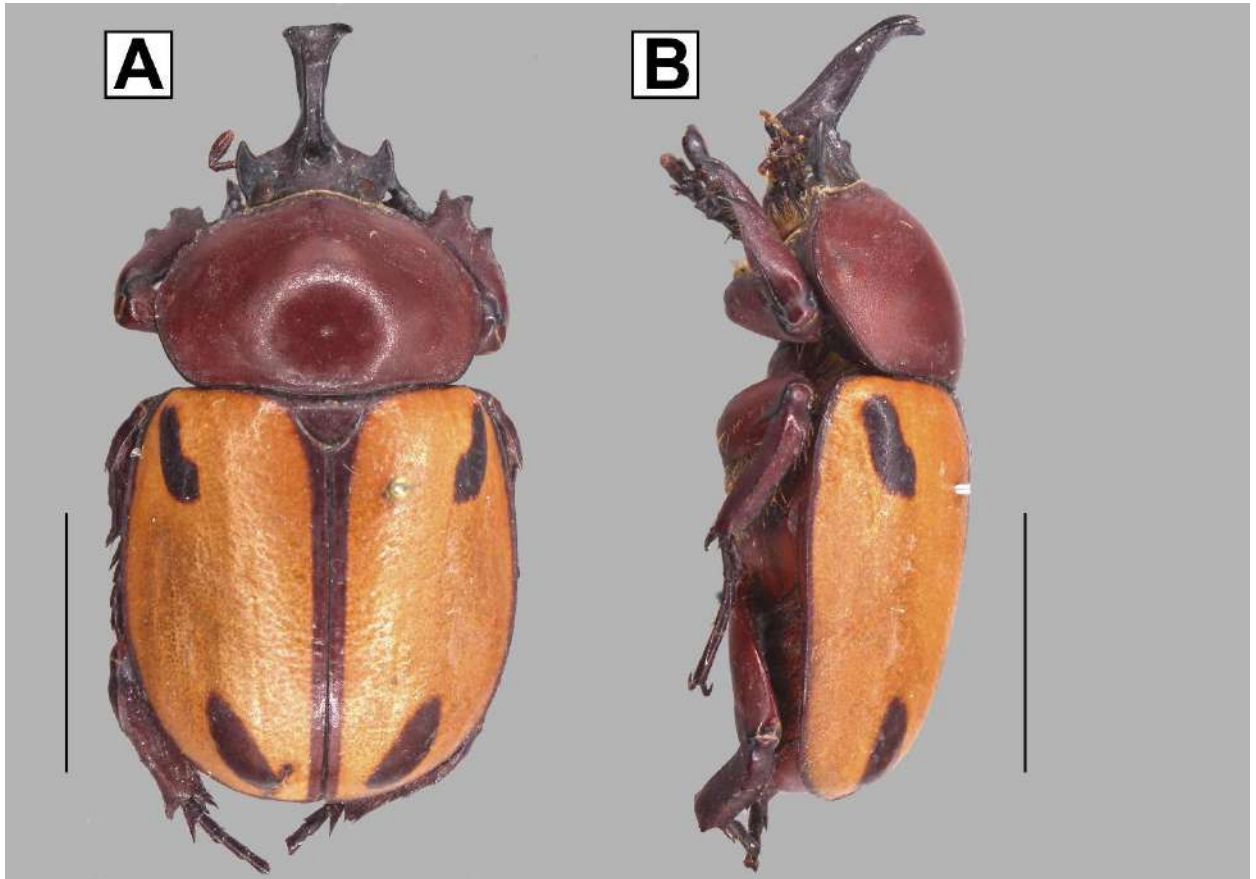


FIGURE 2. Male head of *Brachysiderus quadrimaculatus* and *Brachysiderus andinus*. **A**, Head of *B. quadrimaculatus* in dorsal view. White arrow pointing to fovea. **B**, Head of *B. quadrimaculatus* in frontal view. Simple white arrow pointing to apex of horn; double-headed white arrows comparing clypeal base width with clypeal apex. **C**, Head of *B. quadrimaculatus* in lateral view. White arrows pointing to foveal protuberances. **D**, Head of *B. quadrimaculatus* in dorsolateral view. White arrow pointing to emargination near anterior corner of clypeus. **E**, Head of *B. andinus* in dorsal view. White arrow pointing to fovea. **F**, Head of *B. andinus* in frontal view. Superior simple white arrow pointing to apex of horn; inferior simple white arrow pointing to lateral protuberance of clypeus; double-headed white arrows comparing clypeal base width with clypeal apex; simple black arrow pointing to concavity on clypeal base; double-headed black arrows comparing width of cephalic horn middle with apex. **G**, Head of *B. andinus* in lateral view. Black arrows pointing to foveal protuberances. **H**, Head of *B. andinus* in dorsolateral view. Superior white arrow pointing to depression on horn; inferior white arrow pointing to emargination near anterior corner of clypeus. Scale bars: 1 mm.

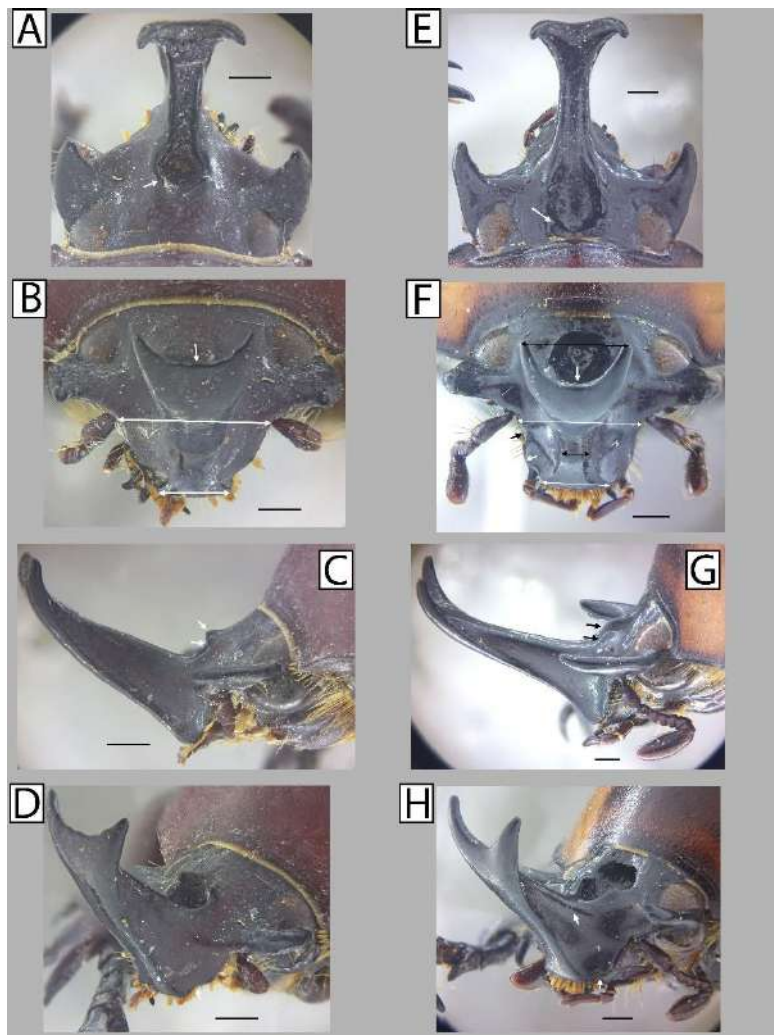


FIGURE 3. Male ocular canthus, thorax and legs of *Brachysiderus quadrimaculatus* and *Brachysiderus andinus*. **A**, Canthus of *B. quadrimaculatus* in dorsal view. **B**, Protarsus of *B. quadrimaculatus* in dorsal view. White arrow pointing to mesobasal tooth. **C**, Protibia of *B. quadrimaculatus* in ventral view. White arrow pointing to V-shaped margin; black arrow pointing to apical concavity of protibia. **D**, Pronotum of *B. quadrimaculatus* in dorsal view. **E**, Prosternum of *B. quadrimaculatus* in ventral view. White arrows pointing to setae. **F**, Canthus of *B. andinus* in dorsal view. Black arrow showing direction of ocular canthi tooth. **G**, Protarsus of *B. andinus* in dorsal view. Superior white arrow pointing to protuberance on distal inner claw; inferior white arrow pointing to basal tooth. **H**, Protibia of *B. andinus* in ventral view. Left white arrow pointing to U-shaped margin; right white arrow pointing to carena. **I**, Pronotum of *B. andinus* in dorsal view. **J**, Prosternum of *B. andinus* in ventral view. White arrow pointing to medial elevation of prosternum. Scale bars: A-C, E, F-H, J, 1 mm; D, I, 5 mm.

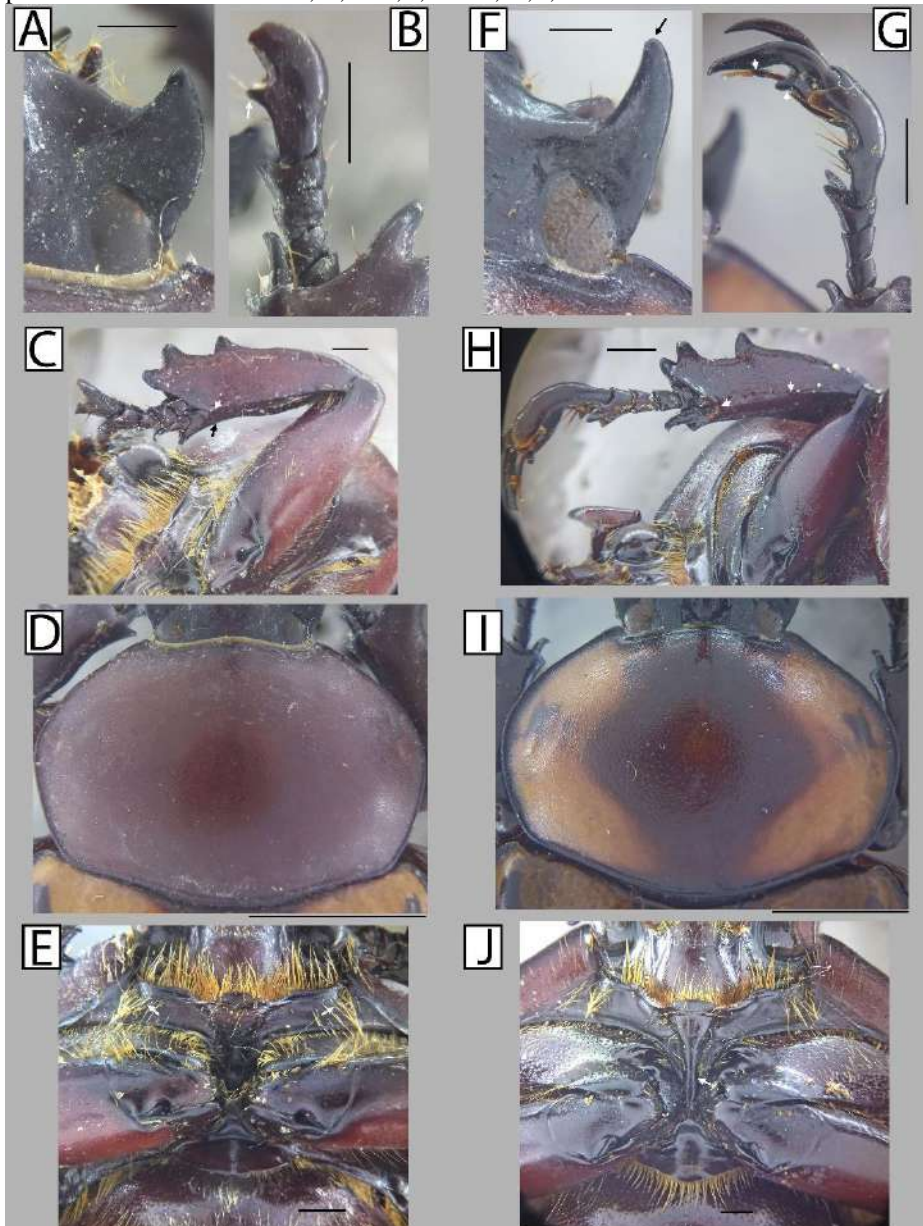


FIGURE 4. Male genitalia of *Brachysiderus quadrimaculatus* and *Brachysiderus andinus*. **A**, Parameres of *B. quadrimaculatus* in caudal view. Black arrows pointing to bump on medial portion of parameres; double-headed white arrows comparing distal part to proximal part of basal portion of parameres. **B**, Parameres of *B. quadrimaculatus* in lateral view. White arrow pointing to carina. **C**, Parameres of *B. quadrimaculatus* in ventral view. Left white arrow pointing to ventrolateral carina; right white arrow pointing to projection of posterior margin; simple black arrow pointing to concavity of posterior margin of parameres; double-headed arrows comparing width of apical and basal portions. **D**, Aedeagus of *B. quadrimaculatus* in lateral view. **E**, Parameres of *B. andinus* in caudal view. White arrow pointing to corner expanded. **F**, Parameres of *B. andinus* in lateral view. **G**, Parameres of *B. andinus* in ventral view. Simple black arrow pointing to ventrolateral carina; left white arrow showing posterior margin not touching carina; right white arrow pointing to projection of posterior margin; double-headed black arrows comparing width of apical and basal portions. **H**, Aedeagus of *B. andinus* in lateral view. Black arrow pointing to ventrobasal margin. Scale bars: 1 mm.

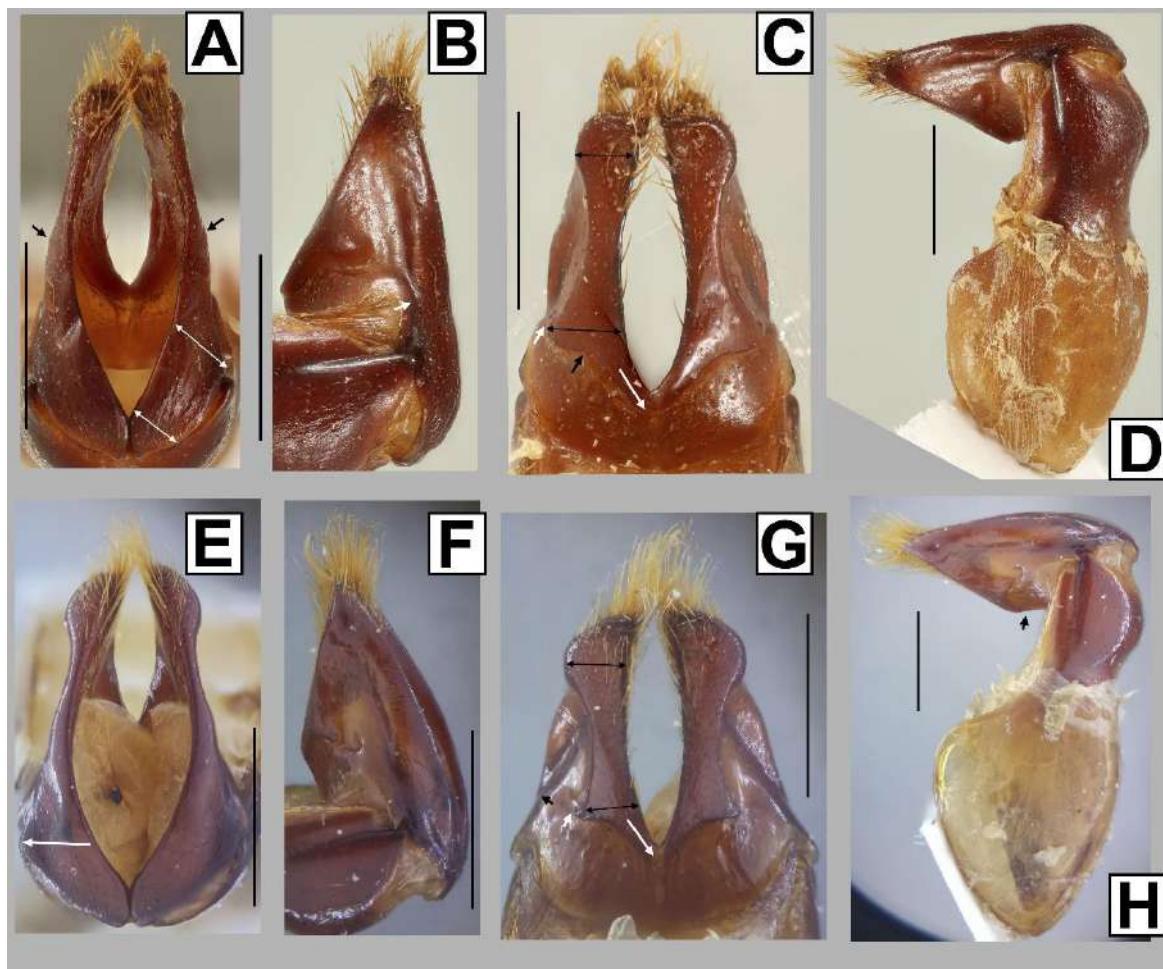


FIGURE 5. Male and female of *Brachysiderus andinus*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, Habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.

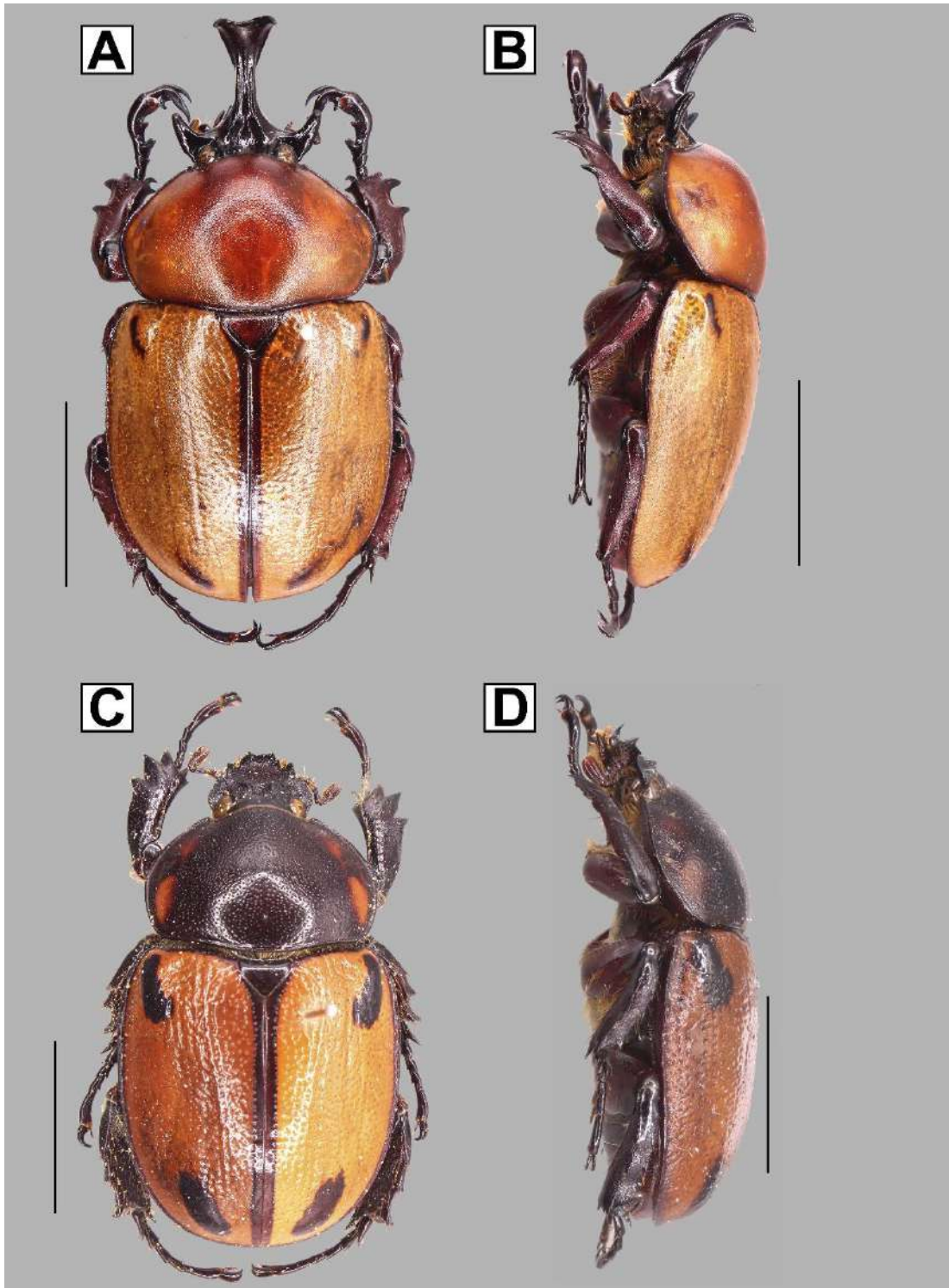


FIGURE 6. Female head of *Brachysiderus andinus* and *Brachysiderus tridentiger*. **A**, Head of *B. andinus* in dorsal view. Superior simple white arrows pointing to lateral protuberances of clypeal apex; inferior white arrows pointing to fovea; double-headed white arrows comparing width of clypeal apex to basal protuberance of ocular canthi. **B**, Head of *B. andinus* in lateral view. White arrows pointing to foveal protuberances. **C**, Canthus of *B. andinus* in dorsal view. Simple white arrow pointing to basal protuberance of canthus; double-headed white arrow showing thickness of canthus. **D**, Head of *B. andinus* in dorsolateral view. White arrows pointing to foveal protuberances. **E**, Head of *B. andinus* in frontal view. Double-headed white arrows for comparisons. **F**, Head of *B. tridentiger* in dorsal view. White arrow pointing to fovea; double-headed red arrows comparing width of clypeal apex to basal protuberance of ocular canthi. **G**, Head of *B. tridentiger* in lateral view. White arrows pointing to foveal protuberances. **H**, Canthus of *B. tridentiger* in dorsal view. Double-headed white arrow showing thickness of canthus. **I**, Head of *B. tridentiger* in dorsolateral view. White arrows pointing to foveal protuberances. **J**, Head of *B. tridentiger* in frontal view. Double-headed white arrows for comparisons. Scale bars: 1 mm.

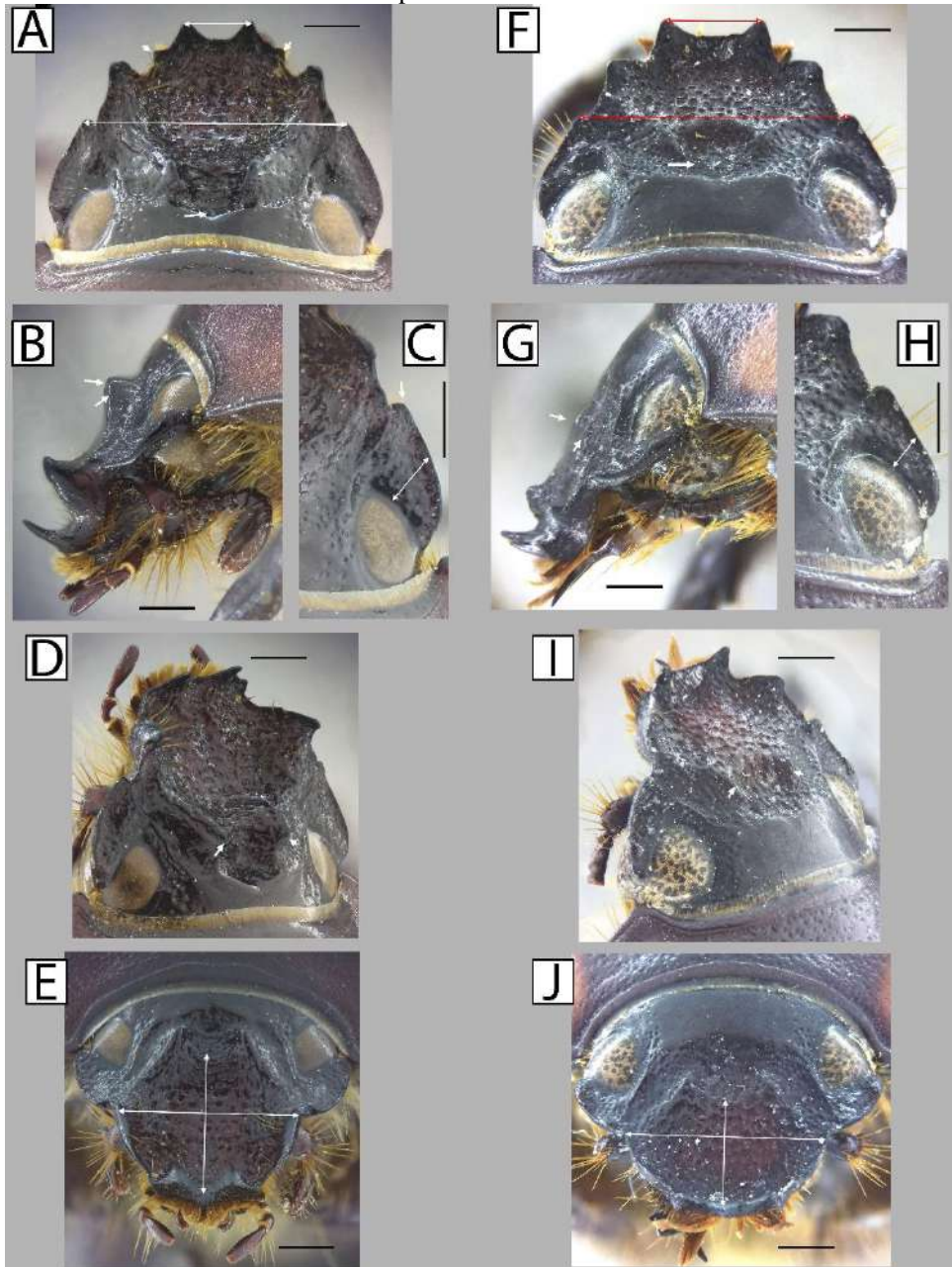


FIGURE 7. Female thorax and legs of *Brachysiderus andinus* and *Brachysiderus tridentiger*. **A**, Pronotum of *B. andinus* in dorsal view. **B**, Mesotibia of *B. andinus* in lateral view. **C**, Mesotibia of *B. andinus* in lateral view. Black arrow pointing to apical tooth of outer margin. **D**, Prosternum of *B. andinus* in ventral view. **E**, Pronotum of *B. tridentiger* in dorsal view. **F**, Mesotibia of *B. tridentiger* in lateral view. Black arrow pointing to anterior carina. **G**, Metatibia of *B. tridentiger* in lateral view. Black arrow pointing to apical tooth of outer margin. **H**, Prosternum of *B. tridentiger* in ventral view. Black arrow pointing to transverse row of setae near posterior margin of prosternum. Scale bars: A, E, 5 mm; B-D, F-H, 1 mm.

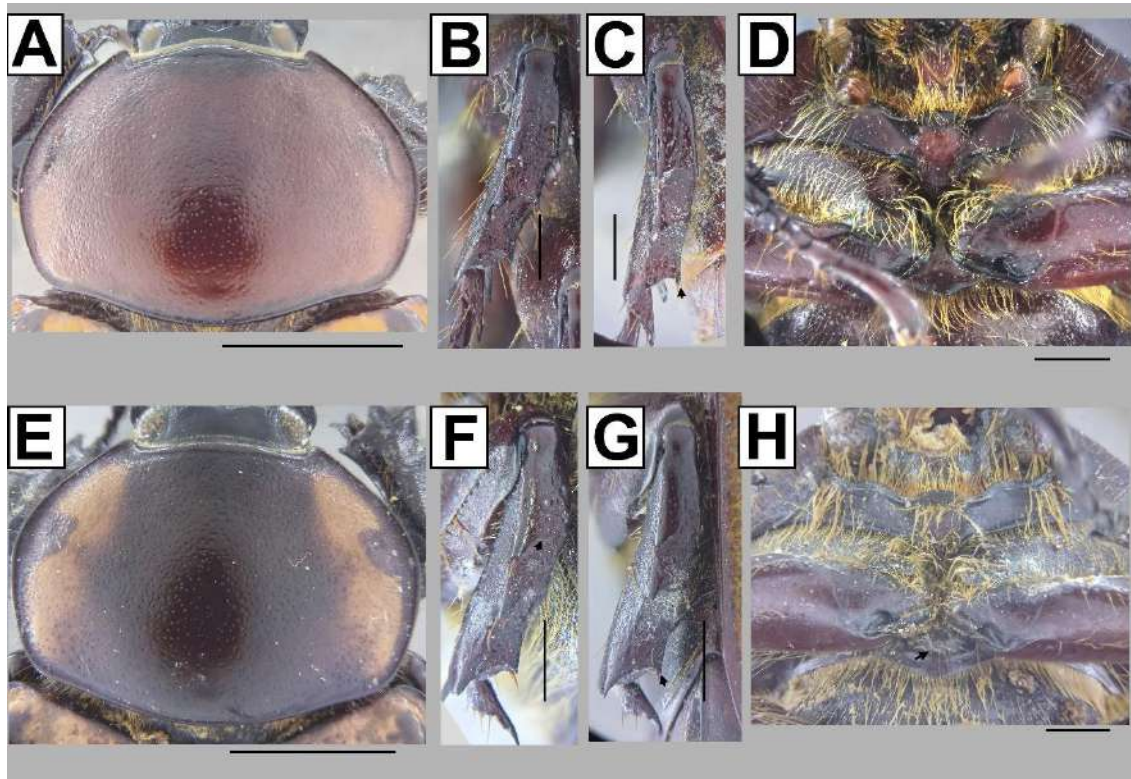


FIGURE 8. Male and female of *Brachysiderus tridentiger*. **A**, Habitus of male in dorsal view. **B**, habitus of male in lateral view. **C**, Habitus of female in dorsal view. **D**, habitus of female in lateral view. Scale bars: 10 mm.

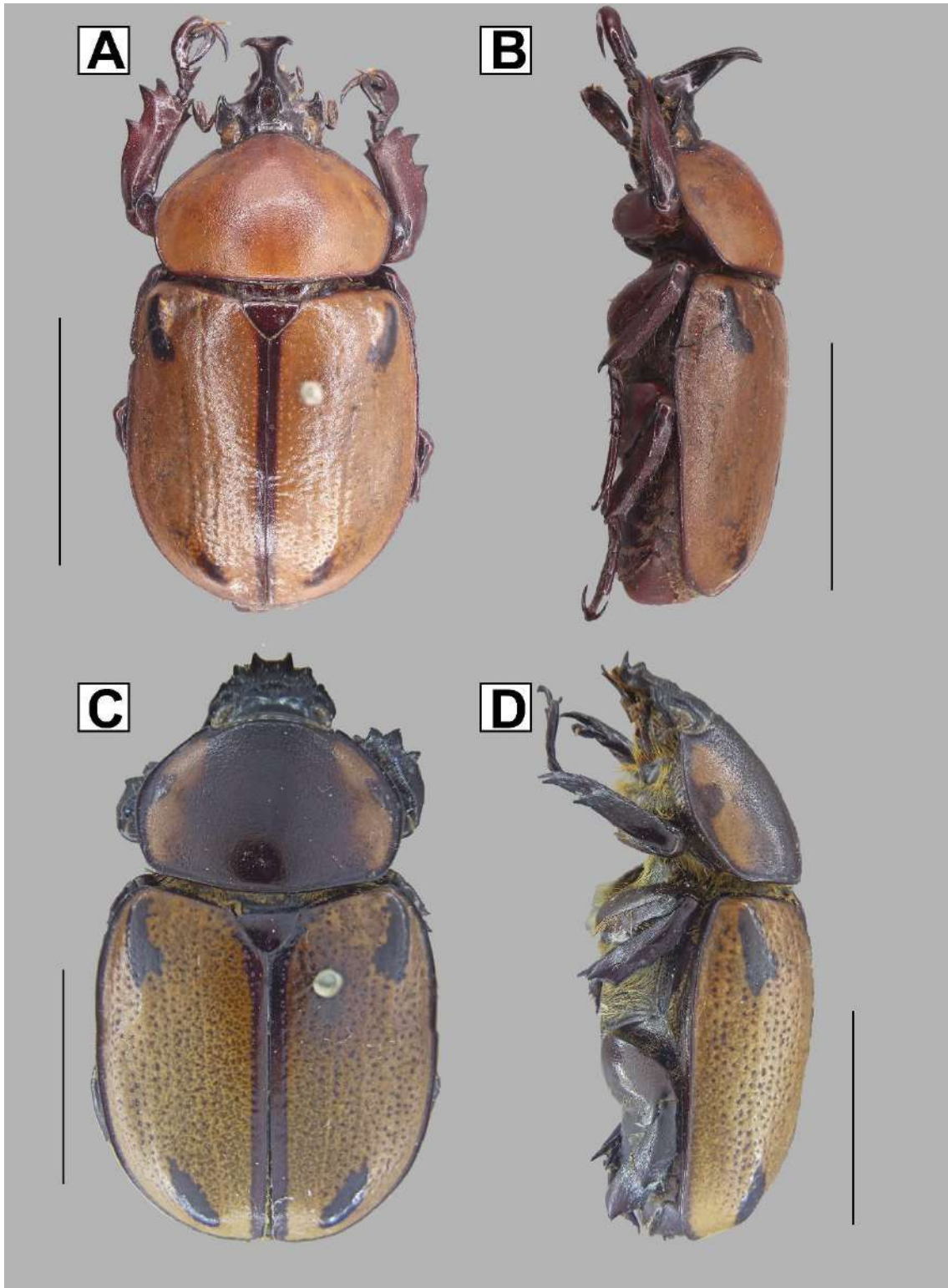


FIGURE 9. Male head of *Brachysiderus tridentiger* and *Brachysiderus breyeri*. **A**, Head of *B. tridentiger* in dorsal view. White arrow pointing to fovea. **B**, Head of *B. tridentiger* in frontal view. Simple white arrow pointing to apex of horn; simple black arrow pointing to medial portion of clypeal lateral margin; double-headed white arrows comparing width of horn middle to horn apex. **C**, Head of *B. tridentiger* in lateral view. Black arrows pointing to foveal protuberances. **D**, Head of *B. tridentiger* in dorsolateral view. **E**, Head of *B. breyeri* in dorsal view. White arrow pointing to fovea. **F**, Head of *B. breyeri* in frontal view. White arrow pointing to apex of horn; black arrow pointing to medial portion of clypeal lateral margin. **G**, Head of *B. breyeri* in lateral view. White arrow pointing to posterior tooth of cephalic horn; black arrow pointing to vertex elevated. **H**, Head of *B. breyeri* in dorsolateral view. White arrow showing the elevation of apex of horns. Scale bars: 1 mm.

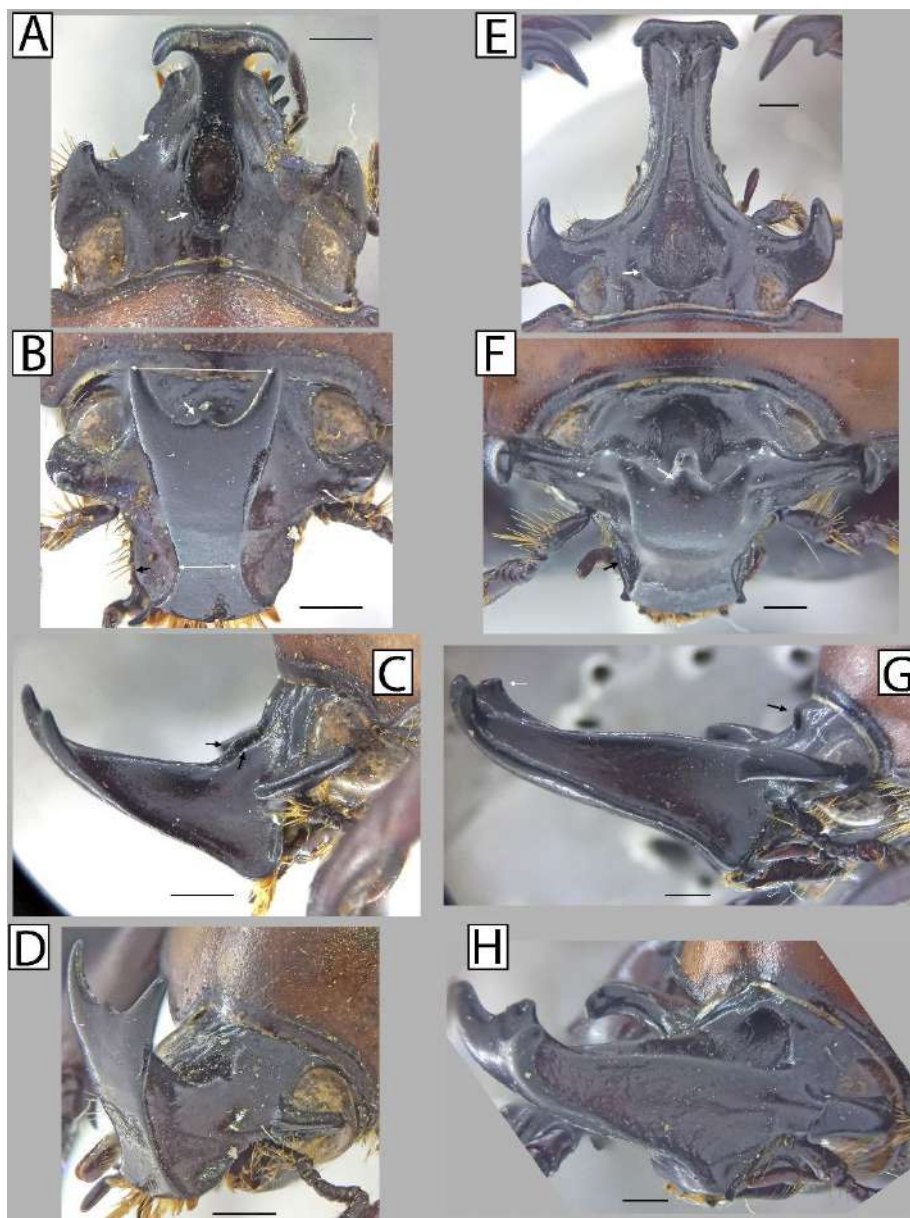


FIGURE 10. Male ocular canthus, thorax and legs of *Brachysiderus tridentiger* and *Brachysiderus breyeri*. **A**, Canthus of *B. tridentiger* in dorsal view. Black arrow showing direction of ocular canthi basal tooth; white arrows pointing to carina. **B**, Protarsus of *B. tridentiger* in dorsal view. White arrow pointing to protuberance of distal inner claw; black arrow pointing to mesobasal tooth. **C**, Protibia of *B. tridentiger* in ventral view. Black arrow pointing to apical portion of protibia. **D**, Pronotum of *B. tridentiger* in dorsal view. **E**, Prosternum of *B. tridentiger* in ventral view. White arrow pointing to medial elevation on prosternum. **F**, Canthus of *B. breyeri* in dorsal view. White arrow pointing to emargination on canthus. **G**, Protarsus of *B. breyeri* in dorsal view. Left black arrow pointing to distal inner claw disarmed; right black arrow pointing to basal tooth. **H**, Protibia of *B. breyeri* in ventral view. Black arrow pointing to apical concavity of protibia. **I**, Pronotum of *B. breyeri* in dorsal view. **J**, Prosternum of *B. breyeri* in ventral view. Simple white arrow pointing to depression near prosternal posterior margin; double-headed arrow showing thickness of medial portion of prosternum. Scale bars: A-C, E, F-H, J, 1 mm; D, I, 5 mm.

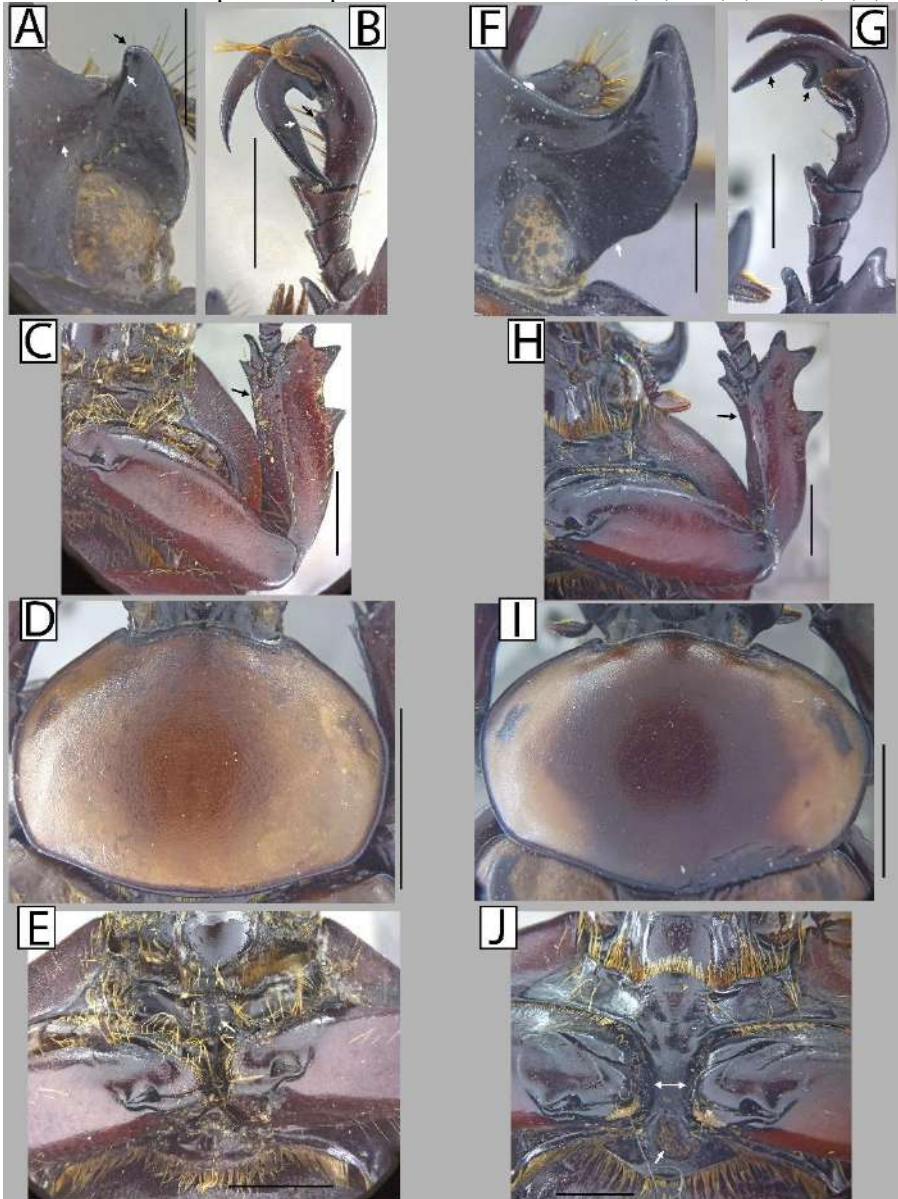


FIGURE 11. Male genitalia of *Brachysiderus tridentiger* and *Brachysiderus breyeri*. **A**, Parameres of *B. tridentiger* in caudal view. Double-headed arrows comparing distal and proximal parts of basal portion. **B**, Parameres of *B. tridentiger* in lateral view. Black arrow pointing to ventrolateral projection. **C**, Parameres of *B. tridentiger* in ventral view. Superior black arrow pointing to ventrolateral carina; inferior black arrow pointing to outer edge of posterior margin; simple white arrow pointing to posterior margin projection; double-headed white arrow showing width of medial portion of parameres. **D**, Aedeagus of *B. tridentiger* in lateral view. White arrow pointing to outer edge of anterior phallobase. **E**, Parameres of *B. breyeri* in caudal view. **F**, Parameres of *B. breyeri* in lateral view. Black arrow pointing to ventrolateral projection. **G**, Parameres of *B. breyeri* in ventral view. Black arrow pointing to emargination of posterior margin; simple white arrow pointing to posterior margin projection; double-headed white arrow showing width of medial portion of parameres. **H**, Aedeagus of *B. breyeri* in lateral view. White arrow pointing to outer edge of anterior phallobase. Scale bars: 1 mm.

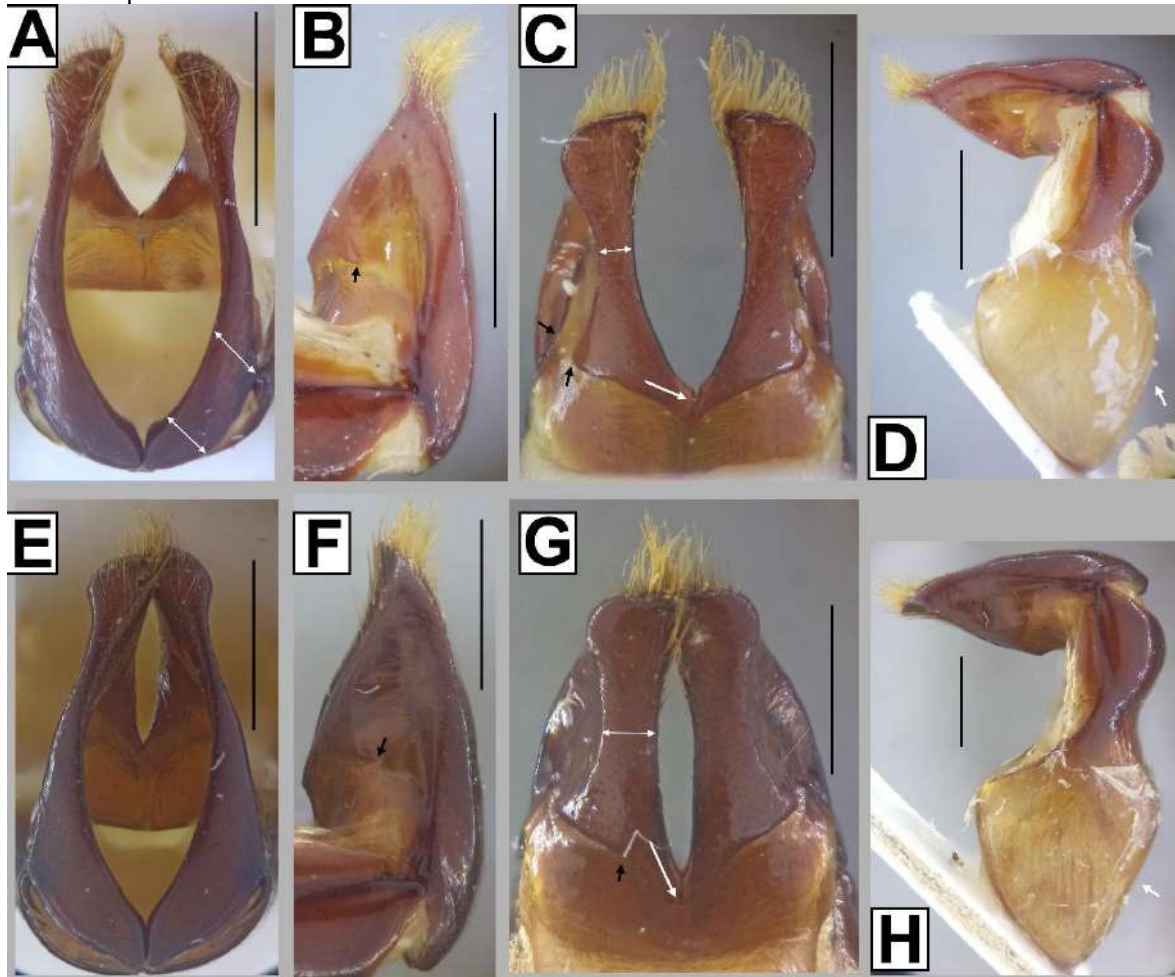


FIGURE 12. Male of *Brachysiderus breyeri*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

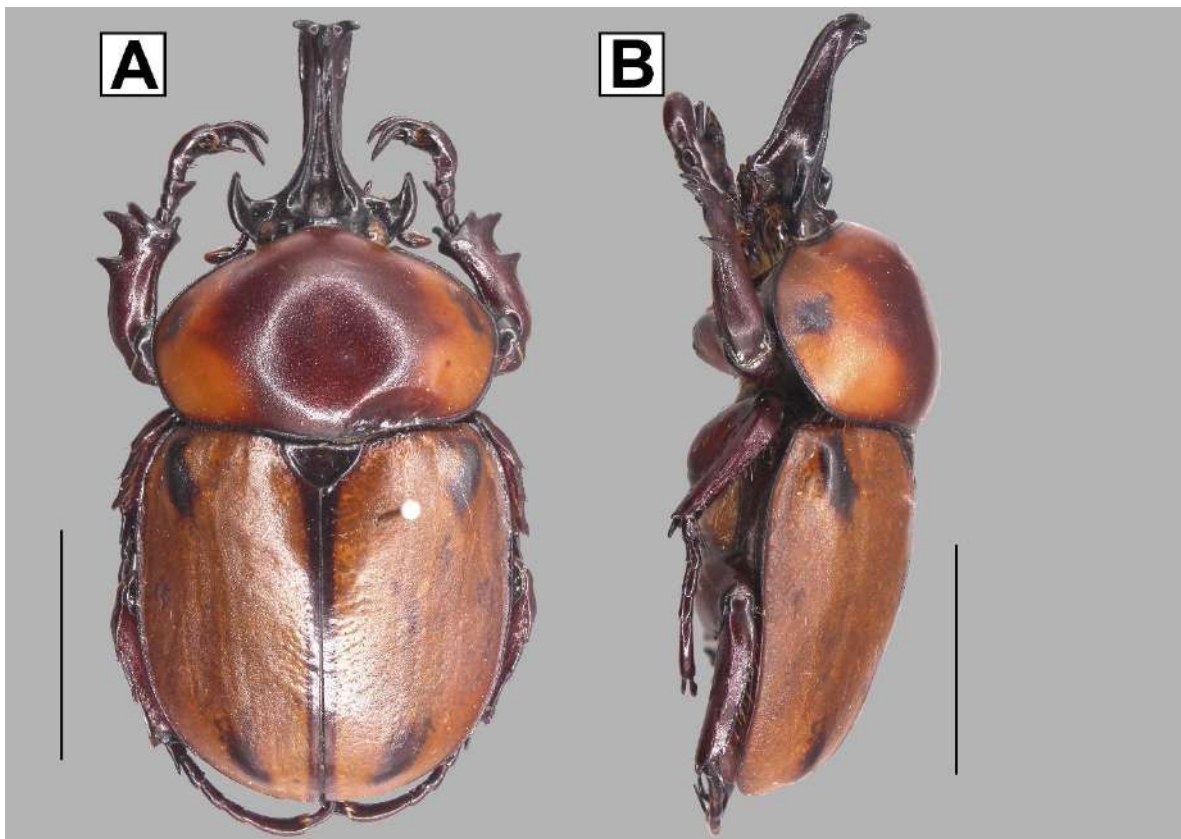
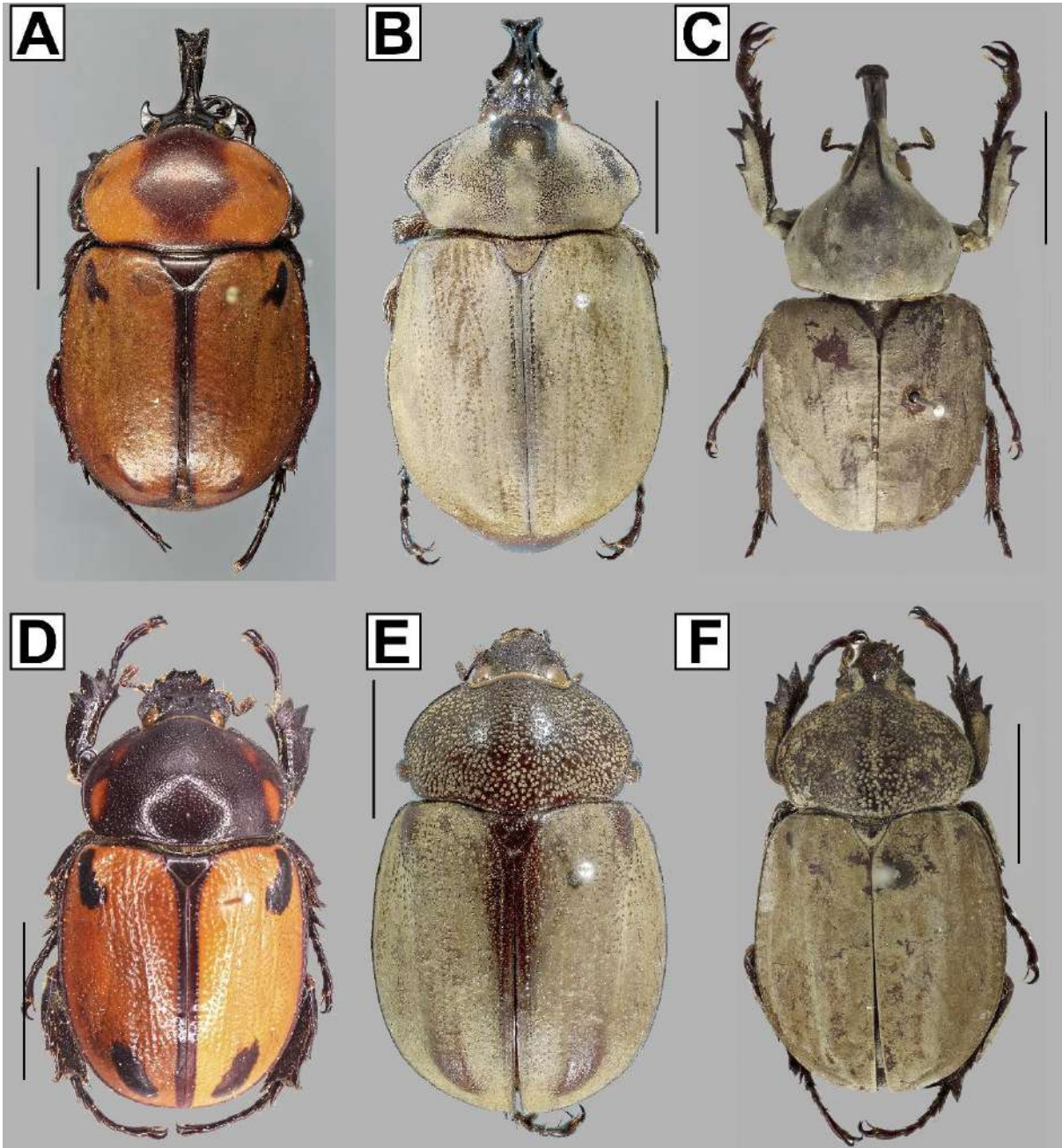


FIGURE 13. Distribution map of *Brachysiderus*.



FIGURE 14. Male and female of *Brachysiderus*, *Lycomedes* and *Spodistes*. **A**, Habitus of *Brachysiderus tridentiger* male in dorsal view. **B**, Habitus of *Lycomedes buckleyi* male in dorsal view. **C**, Habitus of *Spodistes hopei* male in dorsal view. **D**, Habitus of *Brachysiderus tridentiger* female in dorsal view. **E**, Habitus of *Lycomedes buckleyi* female in dorsal view. **F**, Habitus of *Spodistes hopei* female in dorsal view. Scale bars: 10 mm.



CAPÍTULO IV

Sobral, R., Morais, J.W. de, Choi, W., & Grossi, P.C. Review of *Spodistes* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae) with notes on mating behavior of *Spodistes grandis* Sternberg, 1903. Manuscrito em preparação para submeter à revista Zootaxa.

Review of *Spodistes* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae) with notes on mating behavior of *Spodistes grandis* Sternberg, 1903

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Abstract

Males and females of *Spodistes* Burmeister, 1847 are revised, redescribed and illustrated with emphasis in the addition of characters of mouthparts. New diagnosis are proposed to males and females, and remarks regarding the taxonomy and geographic distribution of each species are discussed. The first description of a female of *Spodistes angulicollis* Dechambre, 1992 is provided. The mating behavior of *Spodistes grandis* Sternberg, 1903 in captivity is described. Distribution maps and an identification key to male and female species in the genus are provided.

Key words: Agaoccephalini, rhinoceros beetles, Melolonthidae, Neotropical region

Resumo

Machos e fêmeas de *Spodistes* Burmeister, 1847 são revisados, redescritos e ilustrados com ênfase na adição de caracteres do aparelho bucal. Novas diagnoses são propostas para machos e fêmeas, e comentários acerca da taxonomia e distribuição geográfica de cada espécie são discutidos. A primeira descrição da fêmea de *Spodistes angulicollis* Dechambre, 1992 é fornecida. O comportamento de acasalamento de *Spodistes grandis*

Sternberg, 1903 em cativoiro é descrito. Mapas de distribuição e uma chave de identificação para machos e fêmeas do gênero são fornecidos.

Introduction

Spodistes Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae: Agaocephalini) is a Neotropical genus of rhinoceros beetles distributed along the continental America from southern Mexico to western Ecuador. The genus has eight known species: *S. hopei* Arrow, 1902, *S. batesi* Arrow, 1902, *S. mniszewski* (Thomson, 1860), *S. beltianus* (Bates, 1888), *S. grandis* Sternberg, 1903, *S. angulicollis* Dechambre, 1992, *S. monzoni* Warner, 1992, *S. armstrongi* Dechambre, 1994 (Ratcliffe 2003; Ratcliffe & Cave 2006). *Spodistes* attracts a lot of attention from collectors worldwide for the rarity of some species and the general appearance of the genus, resembling a tiny version of a *Dynastes* Kirby, 1825 (Warner 1992). Male adults are characterized mainly by the greyish tomentum covering the body, the prominent, elongate thoracic horn forward-oriented, and the prominent cephalic horn directed forward but with apical portion slightly upward (in lateral view, forming a pincer-like shape together with thoracic horn). As in other horned rhinoceros beetles, both horns can be reduced in minor males (appearing as a short triangular tubercle in some smaller specimens). Females, on the contrary, are completely different from the males, sharing only the presence of the greyish tomentum on elytra and some other body parts, but they can be recognized by the sharp cephalic tubercles and the pronotum hornless with large and dense tomentose punctures.

In literature, few information is known about the biology of *Spodistes*. The most common data is about the elevations (with species occurring both in lowlands and in highlands, ranging from sea level to almost 3000m of altitude) and the type of vegetation where some species can be found (Ratcliffe, 2003; Ratcliffe & Cave, 2006; Ratcliffe, Cave & Cano, 2013; Ratcliffe, Cave & Paucar-Cabrera, 2020). Immatures are unknown and there is a huge taxonomical problem regarding the females. Female species of this genus are practically identical and their identification in entomological collections throughout the time has been made based mainly on association with males from the same collect locality or on nearby country records (R.S. personal observation). Also, some species are sympatric, i.e. *S. mniszewski* and *S. monzoni* in Honduras and El Salvador; *S. mniszewski* and *S. batesi* in Costa Rica; and *S. batesi* and *S. hopei* in Panama, which makes the association based on country records dubious. Ratcliffe

(2003) created an identification key to adult females of *Spodistes* from Costa Rica and Panama, but despite being a great improving tool to distinguish the females, the key only deals with four of the eight species in the genus.

Traditionally, the original descriptions of the females of *Spodistes* were restricted to nothing or a few lines of some traits of dorsal habitus (i.e. details in pronotal shape or ocular canthi) and consequently had no diagnosis. Based on our recent experience with the use of mouthparts as diagnostic characters to females of *Aegopsis* Burmeister, 1847 (Dynastinae: Agaoccephalini) (Sobral *et al.* 2018), we made in the present work a review of *Spodistes*. In this work, we propose a Diagnosis for the females, add morphological characters of mouthparts and ventral habitus to both sexes, register for the first time notes on the mating behavior of *S. grandis* in captivity, and provide a key to males and females of *Spodistes* species modified from Ratcliffe (2003). Also, a distribution map of these species is provided.

Material and methods

Specimens in this study were examined or borrowed from the following institutional and private collections. Acronyms are according to Evenhuis (2021) if available:

BMNH	Naturhistorisches Museum Basel, Basel, Switzerland (Cristoph Germann)
CMNC	Canadian Museum of Nature, Ottawa, Canada (François Génier)
HNHM	Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl)
MNHN	Muséum National d'Histoire Naturelle, Paris, France (Antoine Mantillieri)
MSUC	Michigan State University Albert J. Cook, Arthropod Research Collection, East Lansing, USA (Anthony Cognato and Gary Parsons)
NHM	Natural History Museum, London, United Kingdom (Max Barclay)
NMPC	National Museum (Natural History), Prague, Czech Republic (Jiří Hájek)
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom (Zoë Simmons)
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium (Alain Drumont)
ZMNB	Museum für Naturkunde, Berlin, Germany (Johannes Frisch and Bernd Jaeger)

The male genitalia was dissected through an aperture between tergite VI and tergite VII with forceps, and the aedeagi were then glued onto a paper point and pinned below the specimen. The mouthparts were dissected with an entomological stylet adapted with a sharp hypodermic needle on tip, and then glued on a small card according to Ohaus (1934) and pinned below the specimen. Terminology follows in part Endrödi (1985) and Ratcliffe (2003) for general aspects of the body, Nel & Scholtz (1990) for mouthparts, and Cristóvão & Vaz-de-Mello (2020) for genitalia. The nomenclature for biogeographic regionalisation follows Morrone (2014) and for ecoregions follows Dinnerstein (2017). The occurrence records were based on the labels of the specimens examined by the authors, and on literature records. The distribution map of the species was made using SimpleMappr (Shorthouse 2010).

Taxonomy

Spodistes Burmeister, 1847

(Figs. 1–27, 29–30)

Spodistes Arrow 1902: 142 (redescription, description of new species); Burmeister 1847: 285 (original description misidentified as *Lycomedes*); Thomson 1860: 16 (description of new species as *Lycomedes*); Bates 1888: 338 (description of new species as *Lycomedes*); Sternberg 1903: 300 (description of new species); Blackwelder 1944: 260 (checklist); Endrödi 1970: 83 (revision); Endrödi 1985: 226 (catalogue, characters in key); Lachaume 1992: 25 (catalogue, description of new species); Warner 1992: 378 (description of new species); Dechambre 1994: 149 (description of new species); Ratcliffe 2002: 36 (checklist to Panama); Ratcliffe 2003: 416 (catalogue to Costa Rica and Panama); Restrepo-Giraldo *et al.* 2003: 262 (catalogue to Colombia); Krajcik 2005: 5 (checklist); Ratcliffe & Cave 2006: 349 (catalogue to Honduras, Nicaragua and El Salvador); Gillett 2009: 6 (new record to Belize); Gasca-Álvarez *et al.* 2010: 179 (list of species to Colombia); Neita-Moreno 2011: 19 (cited); Neita-Moreno & Ratcliffe 2019: 1049 (key to Colombia); Ratcliffe, Cave & Paucar-Cabrera 2020: 479 (catalogue to Ecuador).

Type species: *Spodistes hopei* Arrow, 1902: 146.

Diagnosis. *Spodistes* differs from other genera of Agaoccephalini by the combination of following characters. **Males:** presence of greyish tomentum covering the whole body except the tarsi, apical portion of cephalic and thoracic horns, and mesosternum (Figs.

1A, 9A, 12A, 13A, 18A, 21A, 25A, 26A). Presence of cephalic horn prominent, with or without tooth near base, projected forward with tip slightly upward, apex bifid or acute, with or without a tooth near apex (Fig. 1B, 13B, 18B). Mandibles with two distinct teeth and two ventral carinae, inner carinae reaching apical tooth, outer carinae reaching basal tooth, outer edge with tomentum ventrally and shape round, acuminate, semicircular or truncate (Fig. 4A–E). Protarsi dilated, protarsomere IV with inner corner elongate reaching basal tooth of protarsomere V, protarsomere V with basal acuminate tooth and distinctly concave medially on inner side (Fig. 1A, 9A, 12A). Protarsal claws distinct, dorsal claw pincer-like shaped with distinct basal tooth and distinct round protuberance medially, ventral claw simply curved (Fig. 1A, 9A, 12A). Pronotum convex, bordered, lateral margins medially wider than posterior margin, anterior corners narrowing to anterior margin, shape subtrapezoidal to subhexagonal (Fig. 1A, 12A, 18A, 23A). Thoracic horn prominent and elongate, directed forward, with or without ventral tooth (Fig. 18B, 21B). **Females:** Head with two acute cephalic tubercles slightly oblique towards base of ocular canthi (Fig. 6A–C, 16A–C). Presence of tomentose stripes on tubercles reaching vertex (Fig. 6A–C, 16A–C). Clypeus subtrapezoidal, margins deflected, apex emarginated or concave, anterior corners toothed (Fig. 6A–C, 16A–C). Mandibles with two distinct teeth, outer edge protruded apically [almost looking like a third tooth], tomentum on ventral surface absent, mesal brush dense apically almost reaching second tooth (Fig. 8A–F). Maxillae densely hirsute on dorsal surface of galea, galea shape slightly drop-like, apex curved inwards with two strong teeth parallel, galea almost as long as stipes (Fig. 16G–I). Mentum pear-shaped, in ventral view tomentum absent, apical corners toothed in dorsal view (Fig. 7A–F). Pronotal shape broad and convex, disc with large and dense tomentose punctures, margins bordered with row of tomentose punctures along lateral margins and anterior and posterior corners (Fig. 5A, 10A, 17A, 19A, 22A, 25A). Prosternal process reduced, with a short tomentose area basally. Meso- and metatibae with outer edge distinctly prominent and acute (Fig. 27A–B).

Male description. Color: Body covered by greyish tomentum except the tarsi, apical portion of cephalic and thoracic horns, and mesosternum. **Head:** Shape elongate, finely punctate, ocular canthi elongate, base of ocular canthi slightly prominent. Presence of cephalic horn prominent, with or without tooth near base, projected forward with tip slightly upward, apex bifid or acute, with or without a tooth near apex (Fig. 1B, 13B,

18B). Clypeus almost as long as frons, sides oblique, concave or emarginated, apex simply round, bilobate, round with corners laterally acute (Fig. 2C–E). Antennae 10-segmented, scape longer than pedicel and flagellum (excluding the lamella), pedicel caliciform with apex wider than base, antenomere III slightly caliciform, antenomere V with inner margin not acute as antenomeres VI–VII, antenomeres VIII–X lamellate. Presence of long and thin setae mainly on scape and lamellae. **Mouthparts:** Labrum acuminate or subtriangular, with sides round or oblique, densely hirsute on ventral surface and on anterior margin of dorsal surface (Fig. 14A–B). Mandibles with two distinct tooth and two ventral carinae, inner carinae reaching apical tooth, outer carinae reaching basal tooth, outer edge with tomentum ventrally and shape round, acuminate, semicircular or truncate (Fig. 4A–E). Mandibles in dorsal view with mesal brush dense apically almost reaching second tooth, presence of long and thin setae on outer edge. Maxillae densely hirsute on dorsal surface of galea, galea shape slightly drop-like, apex curved inwards with two strong teeth parallel, galea almost as long as stipes, palpomere II almost two times longer than III, palpomere IV bastoniform as long as galea. Mentum pear-shaped, in ventral view covered by tomentum at least on sides, long setae on sides and near margins; in dorsal view apex densely hirsute, presence of one teeth at each side of apical corners (Fig. 14C–D). **Legs:** Protarsi dilated, protarsomeres I–IV wider than long, protarsomere IV with inner corner elongate reaching basal tooth of protarsomere V, protarsomere V with basal acuminate tooth and distinctly concave medially on inner side (Fig. 1A, 9A, 12A). Protarsal claws distinct, dorsal claw pincer-like shaped with distinct basal tooth and distinct round protuberance medially, ventral claw simply curved (Fig. 1A, 9A, 12A). Protibiae with three outer teeth and one inner tooth near protibial spur (Fig. 1A). Mesofemora with short and minute setae on surface, presence of rows of setae medially and near anterior margin, with or without irregular shorter setae on surface, apex of posterior margin distinctly excavated. **Thorax:** Pronotum convex, bordered, lateral margins medially wider than posterior margin, anterior corners narrowing to anterior margin (Fig. 1A, 12A, 18A, 23A). Thoracic horn prominent and elongate, directed forward, with or without ventral tooth (Fig. 1B, 9B). In minor males, horn reduced ranging from short horn barely crossing pronotal anterior margin to conspicuous tubercle (Fig. 20A–B). Prosternal process reduced. Mesosternum barely punctate, generally densely hirsute with short or long bristles. Elytral punctures thin and dense homogeneously distributed on surface. **Abdomen:** Tergite VIII convex, in ventral view visible area narrower than Sternite VIII. Parameres of aedeagi in caudal view with

base subrectangular transverse and apex paddle-like (Fig. 3G), in lateral view with a depression basally and apex acute with tip straight or hooked (Fig. 3E).

Female description. Head: Dorsal surface with two acute cephalic tubercles slightly oblique towards base of ocular canthi (Fig. 6A–C, 16A–C). Presence of tomentose stripes on tubercles reaching vertex (Fig. 6A–C, 16A–C). Clypeus subtrapezoidal, margins deflected, apex emarginated or concave, anterior corners toothed (Fig. 16A–C). Presence of punctures large and dense, and coalescent punctures on clypeus and frons. Antennae 10-segmented, pedicel caliciform with apex wider than base, antenomere III–V subquadrate as long as wide, antenomere V with inner margin not acute as antenomerens VI–VII, lamellae with antenomere VIII thicker than IX–X together. **Mouthparts:** Labrum densely hirsute ventrally and on anterior margins dorsally, in some species bristles reaching the surface medially; shape acuminate with sides roundly oblique or round, proportion ranging from 3.4 to 4 times wider than long. Mandibles with two distinct teeth, outer edge protruded apically [almost looking like a third tooth], tomentum on ventral surface absent; in dorsal view mesal brush dense apically almost reaching second tooth, presence of long and thin setae on outer edge (Fig. 8D–F). Maxillae densely hirsute on dorsal surface of galea, galea shape slightly drop-like, apex curved inwards with two strong teeth parallel, galea almost as long as stipes, palpomere II almost with same size as III, palpomere IV bastoniform slightly shorter than galea (Fig. 16G–I). Mentum pear-shaped, in ventral view tomentum absent, long setae on sides and near margins; in dorsal view apex densely hirsute, presence of one tooth at each side of apical corners (Fig. 7A–F). **Thorax:** Pronotum hornless, shape broad and convex, disc with large and dense tomentose punctures, margins bordered with row of tomentose punctures along lateral margins and anterior and posterior corners (Fig. 5A, 10A, 17A, 19A, 22A, 25A). Scutellum acuminate with tomentose punctures basally and V-shaped tomentose stripe apically or slightly medially. Hypomeron smooth, only with thin and long setae (Fig. 27C–D). Prosternal process reduced, with a short tomentose area basally. **Legs:** Protarsi simple, protarsal claws curved and similar (Fig. 5A). Protibiae with three outer teeth and one short inner tooth near protibial spur, presence of an indentation between medial and basal teeth (Fig 5A.). Pro-, meso- and metacoxae distinctly marked by the sockets of setae, tomentose areas near apex. Meso- and metatibae with outer edge distinctly prominent and acute (Fig. 27 A–B). **Abdomen:** Sternite VIII shorter than sternite VII or almost with same size.

Geographical distribution. Neotropical region, recorded to the following countries: Mexico, Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia and Ecuador. Regarding biogeographical regions (Morrone 2014), the distribution of *Spodistes* range from the Veracruz province on southern Mexico to the Cauca province on western Ecuador and the Paramo province on eastern Cordillera of the Andes in Colombia (Fig. 29).

Remarks. *Spodistes* is only similar to other two genera of Agaocephalini: *Lycomedes* Brême, 1844 and *Horridocalia* Endrödi, 1974. Those three genera resemble each other for sharing the tomentose body, strong sexual dimorphism, males with distinct and prominent cephalic and thoracic horns, male protarsi dilated with basal tooth and distinct protarsal claws. However, male *Spodistes* differs from them in the shape of thoracic horn directed forward (Fig. 1B) [directed upwards in *Lycomedes* (Fig. 28B) and *Horridocalia*], prosternal process reduced (see Fig. 6D in Neita-Moreno & Ratcliffe (2019) [prominent in *Lycomedes* (see Fig. 6E–F in Neita-Moreno & Ratcliffe (2019), and *Horridocalia*], pronotal shape subtrapezoidal to subhexagonal (Fig. 1A, 12A) [discoidal in *Lycomedes* (28A) and *Horridocalia*]. Female *Spodistes* differs from the other two genera in elytral punctures thin with rows irregular and almost inconspicuous (Fig. 5A) [punctures large with rows regular in *Horridocalia*; deep with rows irregular and conspicuous in *Lycomedes* (Fig. 28C)], cephalic tubercles with tomentose stripes (Fig. 6A) [absence of tomentum in *Lycomedes* (Fig. 28C)], cephalic tubercles distinctly prominent and pointed (Fig. 5B) [slightly prominent and acuminate in *Lycomedes* (Fig. 28D) and *Horridocalia*], mentum pear-shaped (Fig. 7A–F) [droplike-shaped in *Lycomedes* (Fig. 28E)].

The taxonomic history of *Spodistes* is directly linked to *Lycomedes*. In Burmeister (1847), the author reveals he had identified specimens from Hope's collection and Dupont's collection that he classified as a new genus and had baptized as *Spodistes*. However, he stepped back of that decision because he thought that those specimens of his new genus were actually individuals of *Lycomedes reichei* De Brême, 1844, giving them a full description as variations of *L. reichei* (Burmeister, 1847). For that reason, Thomson (1860) and Bates (1888) were the ones who described the first species of what we know today as *Spodistes* (*S. mniszehi* and *S. beltianus* respectively) but within *Lycomedes*. However, it was Arrow (1902) who created a new genus to group Thomson's species and Bates' species with the two new species he had found – after a hint by Mr. René Oberthür – and decided that the description in Burmeister

(1847) could be applied to those specimens, and retained the name *Spodistes* idealized originally by Burmeister.

***Spodistes hopei* Arrow, 1902**

(Figs. 1–8, 27, 29–30)

Spodistes hopei Arrow 1902: 146 (original description); Burmeister 1847: 285 (redescription, mislabeled identification). Sternberg 1903: 301 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 84 (revision); Endrödi 1985: 226 (catalogue, characters in key); Lachaux 1992: 26 (catalogue); Warner 1992: 382 (cited); Ratcliffe 2002: 36 (checklist to Panama); Ratcliffe 2003: 424 (catalogue to Costa Rica and Panama); Krajcik 2005: 5 (checklist); Gasca-Álvarez *et al.* 2010: 179 (list of species to Colombia); Neita-Moreno & Ratcliffe 2019: 1053 (citation).

Diagnosis. *Spodistes hopei* differs from the majority of the other species of *Spodistes* by the cephalic horn of males bifurcate with a strong tooth posteriorly near the bifurcation (Fig. 1A, B). This previous trait is shared only with *Spodistes grandis* and with *Spodistes angulicollis*. However, males of *S. hopei* differs from *S. angulicollis* by the clypeal corners strongly protruded laterally (Fig. 2C), shape of pronotum with lateral margins round (Fig. 1A), parameres in caudal view with apical half strongly curved, shape almost like a boomerang, tips obliquely convergent (Fig. 3A) whereas in *S. angulicollis*, clypeal corners are slightly protruded laterally (Fig. 2E), lateral margins of pronotum acute (Fig. 12A), and parameres in caudal view with apical half broad, tips almost parallel (Fig. 3G). Also, males of *S. hopei* differs from *S. grandis* by the base of cephalic horn simple (Fig. 1B), clypeal apex round (Fig. 2C), mandibles with outer edge round (Fig. 4A), whereas in *S. grandis* base of cephalic horn with a protuberance (Fig. 9A), clypeal apex emarginated (Fig. 2D), mandibles with outer edge acuminate (Fig. 4B).

Females of *S. hopei* occurs in the same locality as females of *S. batesi* (Chiriqui, Panama) but can be separated by clypeal apex 2.5 times narrower than transverse distance of cephalic tubercles (Fig. 6A), mentum with basal half more than 1.2 times longer than apical half (Fig. 7A), presence of short thin setae medially on mentum in ventral view (Fig. 7A), shape of mandibles short (Fig. 8A) while in *S. batesi* clypeal apex almost 2 times narrower than transverse distance of cephalic tubercles (Fig. 16B), mentum with basal half less than 1.2 times longer than apical half (Fig. 7D), absence of short thin setae medially on mentum in ventral view (Fig. 7D), shape of mandibles

elongate (Fig. 8D). Also, *S. hopei* is similar to *S. grandis* but differs by mandibles with outer edge perpendicularly protruded (Fig. 8A), apex of mentum round (Fig. 7A), clypeal apex 2.5 times narrower than transverse distance of cephalic tubercles (Fig. 6A), whereas in *S. grandis* mandibles have outer edge obliquely protruded (Fig. 8B), apex of mentum acuminate (Fig. 7B), clypeal apex more than 2.5 times narrower than transverse distance of cephalic tubercles (Fig. 6E).

Redescription. Holotype. Male. **Color:** Body mainly tomentose, color gray. Distal portion of cephalic horn, portions of legs and tarsi smooth, reddish brown (Fig. 1A, B). **Head:** Frons and vertex with punctures thin and moderately dense. Cephalic horn projected forward, with medioapical portion strongly curved upwards, 1.5 times longer than head; basally straight, apex bifurcate with a strong tooth posteriorly almost reaching apex (Fig. 1B); tomentum only reaching medial portion of horn, wrinkles on distal portion of tomentum, medioapical portion bare, punctures thin and dense on ventral surface of horn, punctures moderately dense on dorsal surface. Clypeus strongly concave laterally, apex round, anterior corners distinctly acute pointing laterally (Fig. 2C); punctures thin and sparse laterally, thin and moderately dense apically. Ocular canthi sinuous and angulate at anterior margin, oblique basally, straight medially and oblique towards tip, with a short protuberance on anterior corner, tip acute, posterior margin almost straight; canthi carinae sinuous, basal region of canthi anteriorly prominent. **Mouthparts:** Labrum acuminate medially. Mandibles oblong with two strong and thick teeth on apex; in ventral view, outer edge round thicker medially than apically, presence of tomentum from apex to middle, not reaching base (Fig. 4A). In lateral view, mesal brush thinner medially than basally above internal lobe; middle region more hirsute and protuberant than apical region. In dorsal view, absence of carina on teeth, presence of thin and long setae near outer edge, setae denser apically and medially, sparse near base. Maxilla with galea subtriangular and elongate, apex oblique with two teeth parallel, base oblique; ventrostipes sinuous, thin on apex, wide progressively medially and basally. Mentum pear-shaped, basal half 1.8 times longer than apical half, ventral surface with sides tomentose forming oblong areas, presence of long and thick setae on lateral region. **Thorax:** Pronotum transverse, slightly narrowing towards anterior margin, convex and with a strong horn projected forward (Fig. 1A). Thoracic horn thick and moderately short, not crossing nor reaching cephalic horn apex, in lateral view, shape conical, apex acute (Fig. 1B). Pronotal disc with thin and dense

punctures, weakly carved on tomentum, punctures with same size on non-tomentose areas of horn; presence of two small round regions laterally non-tomentose (Fig. 1A). Prosternal process completely tomentose, apex with thin and dense setae. Metepisternum tomentose except by a thin inner area with non-tomentose punctures covering the surface, short and thin setae moderately dense. Metasternal plate covered by short thin setae moderately dense, punctures thin and moderately dense. **Elytra:** Form 2 times longer than wide. Punctures annular, thin and dense on disc, moderately dense basally near humeral umbones; humeral umbones short, almost inconspicuous; punctures denser on apical umbones, covered by microsetae. **Legs:** Protibia with 3 external teeth increasing in size distally, and 1 short tooth near protibial spur, almost with same length as protarsi. In dorsal view, tomentum covering from protibial base to base of protibial apical teeth on outer edge, punctures thin and sparse; inner edge of protibia bare, with large and sparse punctures, row of short thick setae near protibial spur, not reaching basal tooth. In ventral view, presence of short carinae basally not reaching basal tooth, tomentum covering medial region of protibia, inner and outer sides mainly non-tomentose. Profemora with inconspicuous carinae not reaching profemoral apex, tomentum covering almost all surface, except by posterior corner near apex. Distal protarsomere strongly curved internally, tarsal claws asymmetric with inferior claw curved and superior claw with a short round tooth basally and a strong protuberance medially. Meso- and metafemora thick, with short thin setae on surface from base to apex. **Abdomen:** Tergite VIII transverse and convex, 2.6 times wider than long; surface tomentose, densely covered by microsetae and thin punctures. Sternites IV–VII tomentose, densely covered by short thin setae, sternite VII with C-punctures posteriorly weakly carved. Sternite VIII almost completely tomentose except by a longitudinal are at the middle, C-punctures medially, sides densely covered by short thin setae, posterior edge with longer setae than disc. **Aedeagus:** Parameres symmetric. In caudal view, slender, apical half longer than basal half, apical half strongly curved, tips round and obliquely convergent (Fig. 3A). In lateral view, posterior phallobase short and round, parameres with lateral carinae short, tips curved downward (Fig. 3B). In ventral view, parameres strongly prominent laterally, narrowing apically and basally; basal area with a distinct latero-basal depression (Fig. 3C).

Measurements of holotype. Body length: 34.4 mm. Cephalic horn length: 8.7 mm. Elytral length: 21.3 mm. Elytral width: 10.6 mm. Pronotal width: 15.2 mm. Protibial length: 9.4 mm. Thoracic horn length: 7.6 mm.

Male variation. Thoracic horn tip slightly downturned, sides of pronotum less acuminate, protibia thinner than in holotype, meso- and metafemora completely tomentose. Scutellar plate subtriangular, apex round; surface wrinkled, with punctures thin and sparse. Body length: 33.7–34.4 mm. Cephalic horn length: 8.4–8.7 mm. Elytral length: 21.3–21.4 mm. Elytral width: 10.4–10.6 mm. Pronotal width: 15–15.2 mm. Protibial length: 9.4–9.8 mm. Thoracic horn length: 7.2–7.6 mm.

Females. Body oblong, pronotum wider than in males (Fig. 5A). **Head:** Cephalic horns absent. Frons with two strong triangular tubercles near ocular canthi, tomentose dorsally, forming two slightly oblique stripes (Fig. 6A); frontoclypeal surface concave; punctures large and coalescent towards vertex. Distance between the tubercles equivalent to 1.2 times eye diameter, in dorsal view. Clypeus trapezoidal, two teeth apically at corners; punctures large and dense, more coalescent near tubercles and less coalescent near apex; clypeal apex 2.5 times narrower than transverse distance of cephalic tubercles. Ocular canthi as in males, less oblique, anterior protuberance stronger than in males, presence of a short anterior area tomentose. **Mouthparts:** Labrum transversely elongate, convex anteriorly and slightly concave posteriorly, sides round. Mandibles with apical corner strongly protruded, becoming straight towards the base, tomentum absent; distance between inner and outer tooth longer than in males, mesal brush less protruded medially (Fig. 8A). Maxilla slightly thinner than in males, ventrostipes thinner apically than in males and almost straight on outer edge, galea less curved apically than in males. Mentum non-tomentose, labial palpomere III shorter and rounder than in males, setae on sides thicker than in males. **Thorax:** Pronotum convex, but slightly flattened, anterior margin slightly protruded, covering part of vertex. Pronotal surface densely covered by tomentose punctures; punctures large and dense, forming a longitudinal row medially, punctures becoming more coalescent laterally with some sparse aggregations on disc and denser aggregations on sides. Prosternal process only tomentose basally with long and short thin setae on tomentose area. Scutellum tomentose apically and laterally, with tomentose punctures on disc near lateral edges and non-tomentose annular punctures moderately dense basally. **Legs:** Surface of legs ventrally mainly not covered by tomentum, having short tomentose areas near apex of pro-, meso-, and metafemora and on outer edge of all tibiae. Protibial carina, in ventral view, reaching middle tooth area; long thin setae parallel to carina. Profemora with two transverse rows of long thin setae. Mesofemora covered by long and short thin setae intercalated, presence of thin and sparse punctures basally. Metafemora mainly covered

by microsetae medially and long thin setae anteriorly and posteriorly; presence of tomentose punctures apically. **Elytra:** Shape narrower than in male. Row of punctures parallel to elytral suture better visible in females, punctures on disc smaller than these punctures near elytral suture. Elytral apex more tapered, while in males it is more round. **Abdomen:** Tergite VIII weakly convex, narrowing apically, surface tomentose; punctures thin and dense, with some wrinkles near anterior margin. Sternites II–V completely tomentose. Sternites II–III completely covered by short thin setae. Sternite IV densely covered by short thin setae laterally, only with some sparse short setae medially. Sternite V with short thin setae densely distributed on sides near posterior margin, microsetae on disc laterally, microsetae medially inconspicuous. Sternite VI tomentose apically and laterally, smooth basally; surface wrinkled basally; short thick setae on apical margin.

Measurements of females. Body length: 25.6–28.3 mm. Elytral length: 16.4–17.5 mm. Elytral width: 8.6–9.1 mm. Head length: 3.5–3.8 mm. Pronotal width: 12.4–12.6 mm. Protibial length: 7.4–7.5 mm.

Geographic distribution. Panama: Chiriqui, Colón, Panama (Fig. 30B).

Material examined. Type male (OUMNH) labeled: a) “N. Gr.”, b) “M. S. G. J. Arrow/ Descr. of type in Ann./ Mag. Nat. Hist., Ser 7, v 10,/ Aug. 1902 p. 146”, c) “*Spodistes/ curvidipennis/* Burm.”, d) “TYPE/ Arrow/ Ann. Mag. Nat./ Hist. Ser7-V10/ Arg. 1902 P.146/ Coll. Hope Oxon.”, e) “TYPE COL: 652/ *Lycomedes/ hopei* Arrow/ HOPE DEPT. OXFORD”. **Other specimens:** 1 male (ZMNB) labeled: a) “Chiriqui/ (Boucard)”, b) “*Hopei/* Arrow”, c) “*Spodistes/ hopei/* det. Dr. Enrödi 19_”, d) “1991/ Comparé au type/ par R-P. Dechambre/ *Spodistes hopei* Arrow”; 1 female (ZMNB): a) “Chiriqui”, b) “Coll. Boucard”, c) “*S. Arr./ hopei/* det. Dr. Enrödi 1968”; 1 female (ZMNB): a) “PANAMA”, b) “Coll./ Hohne”, c) “*S. Thoms./ mniszzechi ?/* det. Dr. Enrödi 1968”; 1 male and 1 female (CERPE): a) “C. America, Panama,/ West Panama prov.,/ San Carlos distr./ 8.62986N, 80.05716W/ h=870 m. 13.vi.2017/ A. Kozlov & Yu. Kovaleva leg.”.

Remarks. In Lachaume (1992) the author discuss about the assumption by Arrow (1902) that the holotype of *Spodistes hopei* would be from Colombia based on the label where is written “N.Gr.”, an abbreviation to “New Grenade” or “Nueva Granada” – in its original spanish spelling. Nueva Granada was a republic from 1830 to 1858 containing the majority of territories that nowadays are part of Colombia, Panama, Costa Rica, and some smaller portions of today’s Brazil, Ecuador, Peru and Venezuela.

The dissolution of Nueva Granada gave origin to what we know today as Colombia but, until 1903, Panama was part of Colombian republic. Therefore, according to Lachaume (1992) it is possible that the holotype of *S. hopei* actually came from Panama as this country only became independent from Colombia in 1903, one year after the description of *S. hopei*. Regarding the material of *S. hopei* examined in this work, only the specimens from Panama have a detailed location (at least with the name of the administrative division where they were found). Through the analysis of material deposited in ZMNB, we find one male and two females of *S. hopei* collected from Chiriqui, which are the first records of this species to that region. Hitherto, *S. hopei* was only recorded to the Isthmian-Atlantic moist forests, not crossing the isthmus of Panama (Ratcliffe, 2003). Now its distribution is updated to occurring in Isthmian-Pacific moist forests (Dinnerstein, 2017), reaching areas of higher altitude.

***Spodistes grandis* Sternberg, 1903**

(Figs. 2–4, 6–11, 29–30)

Spodistes grandis Sternberg 1903: 302 (original description); Blackwelder 1944: 260 (checklist); Endrödi 1970: 86 (revision); Endrödi 1985: 227 (catalogue, characters in key); Lachaume 1992: 25 (catalogue); Restrepo-Giraldo *et al.* 2003: 262 (catalogue to Colombia); Krajcik 2005: 5 (checklist); Neita-Moreno & Ratcliffe 2019: 1055 (cited); Ratcliffe, Cave & Paucar-Cabrera 2020: 479 (catalogue to Ecuador).

Diagnosis. *Spodistes grandis* is the bigger species in the genus, in terms of robustness. It differs from the other *Spodistes* (except *S. hopei* and *S. angulicollis*) by the cephalic horn of males bifurcate with a strong tooth posteriorly near the bifurcation (Fig. 9A, B). For differences between *S. grandis* and *S. hopei* see the Diagnosis section of *S. hopei*. Males of *S. grandis* have clypeus acuminate with apex emarginated and sides oblique (Fig. 2D), ocular canthi transversally projected, anterior edge slightly sinuous, tip round, posterior edge straight (Fig. 2A), whereas *S. angulicollis* have clypeus with apex round and sides slightly concave (Fig. 2E), ocular canthi subtrapezoidal, anterior edge oblique basally, becoming sinuous to the tip (Fig. 2B).

Females of *S. grandis* can be characterized by: clypeus bidentate subtrapezoidal with apex more than 2.5 times narrower than distance between cephalic tubercles (Fig. 6E), ocular canthi subrectangular, anterior and posterior margins slightly sinuous basally, tip slightly emarginated (Fig. 6E), frontal surface almost straight (Fig. 10B),

mandibles with outer edge protruded at corner, round apically and straight medially (Fig. 8B), apical tooth of mandibles with a strong carina, in dorsal view (Fig. 8B), mentum with apex acute (Fig. 7B).

Redescription. Holotype. Male. **Color:** Body mainly non-lustrous, covered by a yellowish gray tomentum, except by parts of both horns, ventral surface of head, all the tarsi and pro-, meso-, and metasternal plate. The lustrous parts not covered by tomentum (Fig. 9A, B). **Head:** Frons and vertex sparsely punctate, punctures thin and deep, mixed with short bristle-like stripes on tomentum mainly on vertex. Cephalic horn projected forward, 2.5 times longer than head; basally with a short protuberance, barely noticeable; apex bifurcate, with one strong posterior tooth dorsally (Fig. 9B); tomentum reaching middle of horn dorsally, not reaching the tooth; frontal and ventral surfaces of horn not covered by tomentum, punctures thin and moderately dense. Clypeus acuminate with apex bilobate, apex not covered by tomentum (Fig. 2D); clypeal punctures thin and dense. Ocular canthi transversally projected, anterior edge slightly sinuous, tip round, posterior edge straight (Fig. 2A); canthi carinae slightly sinuous, ending near canthi anterior margin basally, at a triangular black spot. **Mouthparts:** Labrum subtriangular, apex and sides acute, base slightly concave. Mandibles oblong, with two strong and elongate teeth on apex; in ventral view, presence of two carinae, inner carina stronger than outer carina, reaching apical tooth; outer edge of mandible acuminate medially, narrowing to apex, covered by tomentum, tomentum reaching tooth (Fig. 4B). In lateral view, mesal brush as thick medially as basally above internal lobe, mesal region more hirsute apically than basally. In dorsal view, mesal brush basally covering partially internal lobe, more hirsute basally than medially. Maxilla with galea triangular and elongate, apex twisted externally with two teeth parallel; ventral tooth longer than dorsal tooth, presence of a short protuberance near teeth. Sensorial area of maxillary palpomere IV densely striate, shape oblong, almost reaching palpomere basally. Mentum pear-shaped, sides slightly sinuous; ventral surface tomentose on sides, presence of short thick setae basally and few long thick setae near corners. Apex bilobate in dorsal view, with two pointed lobes. **Thorax:** Pronotum convex and transverse with a strong thoracic horn projecting forward; form 3.8 times wider than head. Thoracic horn slightly flattened dorsoventrally at base, becoming cylindrical and sharp near apex; frontally with an almost inconspicuous protuberance near anterior margin of pronotum (Fig. 9B). Thoracic horn with a pair of non-tomentose stripes

finishing at horn base. Pronotal punctures thin and dense on disc, clearly visible even on tomentose surface. Prosternal process with a large tomentose area on disc, not reaching the edges; apex with short thin setae. Metepisternum tomentose except on basal corners, with short thin setae on surface, punctures thinner near outer edge and larger near metasternal plate. Metasternal plate covered by short thin setae moderately dense, punctures ocellate denser near anterior corners. Scutellar plate subtriangular, apex round; surface completely punctate, punctures thin and dense, disc more punctate than edges. **Elytra:** Form 2 times longer than wide. Surface velutinous, with some irregular patterns of stripes slightly visible on disc; punctures thin and dense on disc, larger and sparser rows of punctures between external edges and humeral umbone. Short setae on elytral apex surrounding and covering apical umbones. **Legs:** Protibia with 3 external teeth increasing in size distally, and 1 short internal tooth near protibial spur. Dorsal surface of protibia tomentose, except on edges, punctures thin and dense on the tomentose portion, punctures shallow and large on protibial teeth. Ventral surface with same pattern of punctures as dorsal surface; presence of a short carina not reaching basal tooth. Profemora with a strong transversal carina not reaching profemoral apex, surface completely tomentose. Distal protarsomere strongly curved internally; thickened setae basally on inner edge; tarsal claws asymmetric, inferior claw curved, superior claw with a short round tooth basally and a strong protuberance medially. Meso- and metafemora with short thin setae basally on posterior edge, setae sparsely distributed. **Abdomen:** Tergite VIII transverse, simply convex in lateral view, 2.4 times wider than long; surface tomentose, densely covered by thin punctures and short thin setae. Sternites IV–VII tomentose, sternite VIII mainly tomentose except on apex medially; surface of sternites IV–V covered completely by short thin setae moderately dense; sternites VI–VII with denser setae on sides and with a row of short thin setae at posterior edges not reaching the middle. Surface of sternite VIII mainly rugose, row of short thin setae only at posterior edge, punctures thin and sparse on tomentose portion. **Aedeagus:** Parameres symmetric. In caudal view, basal half with shape like a hockey stick narrowing to reach apical half, apical half almost parallel, dilated apically, internal edge concave, slightly convex only near tips (Fig. 3D). In lateral view, apex of phallobase angulate at apical corners; lateral carina almost inconspicuous, ending at the middle of paramere; presence of a semicircular prominence near phallobase corners; inferior edge of parameres oblique and straight basally (Fig. 3E). In ventral view,

inferior edge of parameres V-shaped; ventral carina slightly sinuous medially, narrowing basally (Fig. 3F).

Measurements of holotype. Body length: 36.9 mm. Cephalic horn length: 14.8 mm. Elytral length: 23.9 mm. Elytral width: 12.6 mm. Pronotal width: 16.4 mm. Protibial length: 10.3 mm. Thoracic horn length: 18.1 mm.

Male variation. Major males with cephalic horn basally less covered by tomentum than holotype, horn tooth slightly upwards; in ventral view, base of cephalic horn slightly narrower than apex, with a depression covered by large and dense punctures near clypeus; basal region of ocular canthi slightly more protruded than in holotype; elytra with no pattern of stripes on disc. Minor males with cephalic horn tips thinner than major males, basal protuberance on dorsal surface of horn conspicuous; thoracic horn short and curved at tip, pronotal disc with large punctures moderately dense intermixed with thin punctures densely distributed among the large ones. Elytra and scutellum in some specimens lacking tomentum. Body length: 29.6–35.4 mm. Cephalic horn length: 5.6–11.6 mm. Elytral length: 19.6–23.9 mm. Elytral width: 10.7–12.1 mm. Pronotal width: 12.4–15.3 mm. Protibial length: 9.4–10.1 mm. Thoracic horn length: 3.7–17.7 mm.

Females. Body oblong, pronotum wider than in males (Fig. 10A). **Head:** Cephalic horns absent. Frons with two strong triangular tubercles near ocular canthi, tomentum covering surface from edges of vertex to clypeal edges basally, forming two strong oblique stripes (Fig. 6E); frontoclypeal surface slightly concave; punctures large and dense, deeply marked, punctures coalescent near tubercles and clypeal corners. Clypeus trapezoidal with two teeth at apical corners, clypeal apex more than 2.5 times narrower than distance between cephalic tubercles (Fig. 6E); same pattern of punctures than frons. Ocular canthi subrectangular, anterior and posterior margins slightly sinuous basally, tip slightly or strongly bilobated (Fig. 6E); surface split in half by an anterior transversal stripe of tomentum, posterior region not tomentose with large and shallow punctures. **Mouthparts:** Labrum as in males, but apically less sharp. Mandibles with teeth slender than in males, apical corner obliquely protruded; outer edge straight medioapically, becoming sinuous basally (Fig. 8B). Outer carina strongly sinuous, not reaching apical corner. Tomentum absent. Maxillae with same shape and general morphology as in males, long thin setae on ventral side of stipes almost reaching outer edge of stipes, short thick setae basally on cardo less dense than in males. Mentum with same shape as in males, tomentum absent, long thin setae moderately dense on sides

ventrally; apex, in ventral view, more acuminate and elongate than in male (Fig. 7B); apex, in dorsal view with lobes less sharp. **Thorax:** Pronotum convex, thoracic horn absent, anterior margin simply round. Pronotal surface glabrous, coloration black to darkish red, covered by large tomentose punctures; presence of a longitudinal depression medially covered by a row of tomentose punctures; punctures becoming larger and sometimes forming aggregations near pronotal sides, anterior margin medially with thin and sparse non-tomentose punctures. Scutellum covered by tomentum apically and laterally, forming a V-shaped zone; disc partially covered by tomentum near apex, basally bare with thin and moderately dense tomentose punctures. **Legs:** Profemur with an inconspicuous carina. Pro-, meso-, and metatrocantheri apically with an aggregation of tomentose punctures and few long setae. Metafemur densely tomentose, except by a transverse bare zone from the base to the middle, with large and thin tomentose punctures becoming denser distally. Metatibial apex with a triangular projection at outer edge crossing basal tarsomere; metatibial spurs almost 2 times longer and more robust than in males. **Elytra:** Surface with no pattern of stripes, just tomentose. Row of punctures parallel to elytral suture larger than in males, punctures on disc thin and moderately dense, becoming larger near outer edges and denser near apical umbones. **Abdomen:** Tergite VIII slightly convex, almost straight near apex, surface tomentose; punctures thin and dense on disc and sides. Sternites IV–VIII completely tomentose. Sternite IV with surface covered by short thin setae, shorter setae medially. Sternites V–VII with short thin setae not reaching the middle, medially with microsetae almost indistinguishable on thin punctures. Sternite VIII covered by microsetae on disc, apical margin densely covered by short thin setae.

Measurements of females. Body length: 30.8–31.3 mm. Elytral length: 19.6–20 mm. Elytral width: 10.6–10.9 mm. Head length: 4.3–4.4 mm. Pronotal width: 14.4–14.8 mm. Protibial length: 8.1–8.4 mm.

Geographic distribution. Colombia: Valle del Cauca. Ecuador: Bolívar, Cañar, Esmeraldas, Guayas, Imbabura, Napo (Fig. 30B).

Material examined. Type male (ZMNB) labeled: a) “Cachabé/ low c., 1_97./ (Rosenberg).”, b) “*Spodistes grandis*/ *type! Sternberg”, c) “Holotypus/ *Spodistes grandis*/ Sternb.”. **Other specimens:** 2 males (ZMNB) labeled: “Cali, Kolumbia/ V. 1971”; 1 female (ZMNB) labeled: a) “Kolumbia/ Cali, VI.1970”, b) “*Spodistes mniszehi* f#”; 1 male (NHM): a) “Cali, 01.1975/ Colombie”, b) “Brit. Mus. 1975, 284”, c) “ex coll. R.-P. Dechambre”, d) “*Spodistes* m#/ *hopei* Arrow/ R.-P. Dechambre det.

1975”, e) “*Spodistes grandis*/ R. Sobral det. 2020”; 1 male (NHM): a) “Cali, Colombie”, b) “1976 ex coll./ R.-P. Dechambre”, c) “*Spodistes/ hopei* Arrow/ R.-P. Dechambre det. 1975”, d) “*Spodistes grandis*/ R. Sobral det. 2020”; 1 female (NHM): a) “Valle del Cauca/ Colombie”, b) “1976 ex coll./ R.-P. Dechambre”, c) “*Spodistes/ hopei* Arrow/ R.-P. Dechambre det. 1975”, d) “*Spodistes grandis*/ R. Sobral det. 2020”; 1 female (NHM): a) “Cali, 1500 m/ Colombie, Dec, 70”, b) “Brit. Mus./ 1975, 284”, c) “ex coll./ R.-P. Dechambre”, d) “*Spodistes f#/ hopei* Arrow/ R.-P. Dechambre det. 1974”, e) “*Spodistes grandis*/ R. Sobral det. 2020”; 1 male (RBINS): a) “Veragua/ ex coll./ Janson”, b) “*Lycomedes/ reichei*/ Br./ det. L. Candeze”, c) “Collection/ E. Candeze”, d) “Veragua s. Am./ Warsweiz.”, e) “*reichei*/ Br./ Veragua”, f) “*Spodistes/ grandis*/ Sternberg/ det. Y. Ponchet, 2004”.

Biology. The mating of *S. grandis* in captivity was observed in Japan and registered in video on the YouTube channel “AKIRA RISING”. The specimens were over a small log when the male approaches the female and mounts on it while exposing its aedeagus. With the hooked tip of parameres, the male lifts tergite VIII of female and introduces the aedeagus in female’s genital opening. While in coupling, the male uses its metalegs to hold to the log, and the meso- and prolegs to hold the female. The male mesotibia grab on sides of female elytra, whereas the male protarsus at first hold the female metatibia but after becomes loose. Also, the male grab the female proleg fitting the tarsal dorsal claw of protarsus into the junction between female protibia and profemur (Fig. 11). When finished the copulation, the male dismounted the female and walks away. During the entire copulation, the female remained immobile and the male had the antennae frequently moving. The author of the video gave us permission to use his images in this work. The whole video can be seen through the link:

<https://www.youtube.com/watch?v=DZBpkBFHgnY> (accessed 2 May 2021).

This is the first record of mating behavior to *Spodistes*. The constant movement of the male antennae might indicate the detection of sexual pheromones by the antennal sensillae, which is hypothesized to other Dynastinae species (Rodrigues *et al.* 2018; Saldanha *et al.* 2020). The method used by the male to hold the female in *Spodistes* is different from what is known to other Dynastinae with dilated protarsi (i.e. *Cyclocephala* Latreille, 1829). The male *Spodistes* uses its pincer-like claw to fit in the articulation between female profemur and protibia, whereas in *Cyclocephala* species use the protarsal claw to hold on different areas of female elytra (Moore 2012; Souza *et al.* 2013).

Remarks. *Spodistes grandis* is the largest and one of the longest species in the genus. The distribution of the species occurs throughout the Western Cordillera of the Andes, on Cauca province, habiting the Northwestern Andean montane forests (Ecuador and Colombia) – which can range from 1000-4000m of altitude, with a wetter climate on foothills than in upper mountain – and in the Cauca Valley montane and dry forests (Colombia). The Cauca Valley forests are located between the western and the northern central Cordillera of the Andes and have two types of vegetation where *S. grandis* can be found: the dry forests and the montane forests. The majority of specimens of *S. grandis* were found in areas of dry forests (ca. 1500m of altitude), but little is known about the endemic vegetation due to the high deforestation rate (Kattan 2021).

***Spodistes angulicollis* Dechambre, 1992**

(Figs. 2–3, 12, 29–30)

Spodistes angulicollis Dechambre in Lachaume 1992: 79 (catalogue, original description); Restrepo-Giraldo et al. 2003: 262 (catalogue to Colombia); Krajcik 2005: 5 (checklist); Gasca-Álvarez *et al.* 2010: 179 (list of species to Colombia).

Diagnosis. Males: clypeus sinuous, apex round, lateral corners protruding laterally, with a slightly concave connection with basal portion of ocular canthi (Fig. 2E); ocular canthi subtrapezoidal, anterior margin oblique basally, becoming sinuous to the tip (Fig. 2B); mandibles with two strong apical teeth, with a strong truncate protuberance at apical corner (Fig. 2F); shape of pronotum almost hexagonal, sides strongly acute (Fig. 12A, B). It differs from the other *Spodistes* (except *S. grandis* and *S. angulicollis*) by the cephalic horn of males bifurcate with a strong tooth posteriorly near the bifurcation (Fig. 12A, B). For comparisons with *S. grandis* and *S. hopei* see the Diagnosis section of the two species.

Female differs from *S. hopei* by clypeal base slightly round (Fig. 32D), clypeal sculpture formed by deep and large punctures from base to apex (Fig. 32E), antennomere I distinctly thicker than in *S. hopei* (Fig. 33F), clypeal basal tooth distinctly closer to clypeal apical teeth than to vertex (Fig. 32F), tomentum on profemora widely covering anterior portion in ventral view (Fig. 33E), prosternal anterior portion slightly longer than in *S. hopei* (Fig. 33D), whereas in *S. hopei* clypeal base concave (Fig. 32A), clypeal sculpture formed by thin and sparse punctures near apex (Fig. 32B), antennomere I thinner than in *S. angulicollis* (Fig. 33C), clypeal basal

tooth with almost same distance to clypeal apical teeth and to vertex (Fig. 32C), tomentum on profemora shortly restricted to distal portion (Fig. 33B), prosternal anterior portion shorter than in *S. angulicollis* (Fig. 33A).

Redescription. Holotype. Male. **Color:** Body tomentose, yellowish grey, non-lustrous. Pronotum more tomentose than elytra. Tarsi, some lateral portions of pro-, meso-, and metalegs, frontal surface of cephalic horn and part of head ventrally lustrous, reddish brown (Fig. 12A, B). **Head:** Vertex medially with a more greyish zone than sides, punctures absent near anterior margin of pronotum, present towards frons and horn; punctures large and moderately dense on vertex and frons, with some zone non-punctate near ocular canthi. Cephalic horn projected forward, but abruptly curving upward, as long as head; basal surface straight to vertex; apex bifurcate with a strong tooth posteriorly to the bifurcation (Fig. 12B); tomentum barely reaching middle of cephalic horn; surface of horn with rough areas dorsally, ventral surface smooth, punctures thin and moderately dense on tips and smooth parts. Clypeus sinuous, apex round, lateral corners protruding laterally, with a slightly concave connection with basal portion of ocular canthi (Fig. 2E); clypeal punctures thin and moderately dense medially, tomentum wrinkled on sides near clypeal protrusions. Ocular canthi subtrapezoidal; anterior margin oblique basally, becoming sinuous to the tip, posterior margin almost straight; surface punctate, punctures thin and moderately dense, tomentose basally and medially, tomentum not reaching tip nor posterior margin (Fig. 2B). **Mouthparts:** Mentum pear-shaped, apex round, ventral surface tomentose on sides not reaching apex nor middle, long thin setae on large sockets on sides (Fig. 2F). Mandibles with two strong apical teeth, with a strong protuberance at apical corner, punctures thin and moderately dense on teeth; outer edge protruded and truncate, surface completely covered by tomentum (Fig. 2F). **Thorax:** Pronotum convex, shape almost hexagonal, sides strongly pointy, with a short thoracic horn projecting forward; form 4.2 times wider than head. Thoracic horn slightly sinuous at apex, with a black frontal carina ending before reaching pronotal anterior margin (Fig. 12B); non-tomentose from middle to apex. Pronotal disc mainly tomentose, presence of two mediolateral zones less tomentose than sides and not smooth as horn apex; punctures thin and dense on main tomentose areas; shades of tomentose punctures on mediolateral zones (Fig. 12A). Prosternal process mainly bare, only with a small tomentose area near procoxae. Metepisternum partially covered by a weak tomentum, C-punctures large and dense on

surface with medium thin setae on them. Metasternal plate densely hirsute, setae long and slender; punctures coalescent near corners. Scutellum tomentose, except by a transversal thin area basally; punctures thin and dense, two rows of short thin setae on disc, not reaching apex. **Elytra:** Form 1.9 times longer than wide. Surface weakly tomentose, parts of brown surface of elytra visible under the light; punctures large and dense near elytral suture, becoming thinner on disc, and large again intermixed with thin punctures near outer edges and humeral umbone, punctures large and dense near apical umbone, thin on apical umbone. Short setae on elytral apex, becoming shorter near apical umbone. **Legs:** Protibia with 3 external teeth increasing in size distally, and 1 short internal tooth near protibial spur. Dorsal surface of protibia only not tomentose on inner edge and on apex of teeth, puncture thin and dense near outer edge, larger near inner edge, two rows of short thick setae dorsally, long thick setae on apex. Ventral surface of protibia with a weak layer of tomentum medially, sides bare with sparse rows of long thin setae. Distal protarsal tarsomere strongly curved internally, tarsal claws asymmetric, inferior claw simply curved, superior claw with an acuminate tooth basally and a strong protuberance medially. Wrinkles on surface from the protuberance to apex of claw. Profemora with a short transversal row of short thin setae not reaching base nor apex. Meso- and metafemora tomentose, covered by short thin setae, with 3 transversal rows of long thin setae. **Abdomen:** Tergite VIII transverse, convex in lateral view, crossing elytral apex, 2.5 times wider than long; surface tomentose, completely covered by short thin setae. Sternites IV–VII completely tomentose, sternite VIII with a tomentose area not reaching the middle nor basal margin; surface of sternites IV–VI densely hirsute, covered by short thin setae; sternite VII with short thin setae denser on sides, becoming microsetae towards middle, coalescent punctures near corners. Sternite VI wrinkled basally, with thin and moderately dense punctures on middle, surface with short thin setae not reaching the middle. **Aedeagus:** Parameres symmetric. In caudal view, basal half oblique towards middle, apical half almost parallel, tips acuminate (Fig. 3G). In lateral view, parameres distinctly depressed latero-ventrally near base, inferior edge of parameres oblique and straight basally, tip slightly hooked (Fig. 3H). In ventral view, inferior edge of parameres V-shaped, inner edge concave (Fig. 3I).

Measurements of holotype. Body length: 31.1 mm. Cephalic horn length: 4.9 mm. Elytral length: 19 mm. Elytral width: 9.4 mm. Pronotal width: 13.1 mm. Protibial length: 7.9 mm. Thoracic horn length: 4.2 mm.

Male variation. Ocular canthi more excavated medially, apical protuberance more conspicuous; clypeal corners more angulate, lateral margins more concave than in holotype; sides of scutellum straight. Body length: 30.2–31.1 mm. Cephalic horn length: 4.9–5.3 mm. Elytral length: 19–20.3 mm. Elytral width: 9.4–10.2 mm. Pronotal width: 13.1–13.4 mm. Protibial length: 7.9–8.3 mm. Thoracic horn length: 4.2–5.1 mm

Females. Shape of the body oblong, pronotum wider than in males (Fig. 31A). **Head:** Cephalic horns absent. Frons dense punctate, punctures circular and dense near vertex, C-punctures on frons near clypeus, presence of two tomentose stripes oblique from vertex to clypeal base. Connection between frons and clypeal base with pair of strong triangular projections. Clypeus campaniform, clypeal base slightly round in dorsal view (Fig. 32D), clypeal sculpture formed by deep and large punctures from base to apex (Fig. 32E), apex of clypeus with two paired teeth pointing upward, clypeal lateral margin thick, clypeal basal tooth distinctly closer to clypeal apical teeth than to vertex (Fig. 32F). Ocular canthi transversal and subrectangular, anterior margin almost straight with anterior corner slightly thick, tip straight, presence of transversal tomentose area covering $2/3$ of canthi. Antennal club shorter than antennomeres II-VII together, antennomere I distinctly thick and covered by long thin setae (Fig. 33F), antennal club densely covered by setae on antennomere VIII, antennomere IX with longitudinal row of setae sparse, antennomere X only setose near apex. **Mouthparts:** Mandibles with two long teeth projecting upwards and over clypeal apex, visible in dorsal view, presence of distinct and projected apical protuberance on outer margin near teeth. Mentum non-tomentose, ventral surface with deep punctures on sides, thin punctures medially, lateral margins densely covered by thin and thick long setae. **Thorax:** Pronotum convex and slightly flattened, medial portion slightly more elevated than sides; presence of tomentose punctures on entire surface, punctures forming a longitudinal line from posterior margin to anterior margin, almost touching anterior marginal line, presence of few spaces not punctate near posterior half and anterior half, punctures denser near margins (Fig. 31A). Prosternum with pair of swollen areas near anterior corners, presence of long thin setae densely aggregated on that areas, prosternal anterior portion slightly longer (Fig. 33D), medial elevation slender and setose near procoxal junction; prosternal process absent, prosternal posterior margin medially indistinctly projected anteriorly (Fig. 33D), ventral surface completely tomentose. Scutellum subtriangular with apex blunt, surface with apex completely tomentose, medial and basal portions densely covered by tomentose punctures. **Legs:** Protibia with

tomentose stripe from base of leg to basal tooth, surface finely punctate in dorsal view; in ventral view, punctures shallow and coalescent near medial tooth. Profemur with tomentum widely covering anterior portion in ventral view (Fig. 33E). Meso- and metatibia completely tomentose on lateral margins. **Elytra:** Surface more flattened than in male. Elytral disc completely tomentose, presence of thin punctures irregularly distributed, only regular near elytral suture. Lateral margins of elytra with slight rugosities from base to apex. Apical and humeral umbones densely covered by punctures thinner than on disc. **Abdomen:** Tergite VIII convex, with apical portion slightly narrowing medially, surface completely tomentose, densely covered by short thin setae on entire surface. Sternites IV-VII completely tomentose and equally covered by short thin setae on disc and corners, with thicker setae on posterior margin not reaching middle. Sternite VIII only with thin stripe near anterior margin not continuously tomentose, surface densely wrinkled near anterior margin, disc and sides covered by short thin setae, posterior margin with dense setae longer than those on disc.

Measurements of female. Body length: 29.2 mm. Elytral length: 17.6 mm. Elytral width: 8.8 mm. Head length: 3.2 mm. Pronotal width: 14.4 mm. Protibial length: 6.9 mm.

Geographic distribution. Colombia: Cundinamarca, Meta, Santander (Fig. 30B).

Material examined. Type male (ZMNB) labeled: a, frente) “Columbia/ Rio Negro”, a, verso) “III.10 1200 m”, b) “1-43”, c) “Coll./ Jul. Moser”, d) “S. Arr./ *hopei*/ det.Dr.Endrödi 1968”, e) “HOLOTYPE”, f) “*Spodistes* m#/ *angulicollis* n. sp./ Holotype/ R.-P. Dechambre det. 1991”. **Paratype** (HNHM) labeled: a, frente) “Columbia/ Villavicencio”, a, verso) “col. Jul./ I.11 440 m”, b) “*S. hopei* Arr./ det. Dr. Endrödi 1968”, c) “*Spodistes* m#/ *angulicollis* n. sp./ Paratype/ R.-P. Dechambre det. 1991”, d) “PARATYPE” [on red label]. **Other specimens.** 2 males and 1 female (Wonseok Choi private Collection) labeled: a) “Colombia, Santander, La India”.

Remarks. *Spodistes angulicollis* is extremely rare to find and as far as we know only two specimens were recorded (the holotype and the paratype). We think that its rarity may be explained by the scarcity of collects in the easternmost areas of Eastern Cordillera of the Andes, compared to other areas in Colombia. At first, the label data of the holotype confused us as it is just written “Columbia, Rio Negro” and there are three different places in Colombia with that same name, which misled authors for years to consider *S. angulicollis* occurring in Antioquia where there is a city named Rionegro

(Restrepo-Giraldo *et al.* 2003; Gasca-Álvarez *et al.* 2010). We choose the province of Rio Negro (in Cundinamarca) as the right type locality due to the proximity with the paratype locality (Villavicencio, Meta). Only after that, we realized that the other two homonymous Colombian localities are spelled as “Rionegro” instead of “Rio Negro”, which reinforced our decision.

The female of *S. angulicollis* that we describe here for the first time was acquired by Wonseok Choi from Santander, Colombia, which is a new record to that side of the Cordillera. We also have seen in the website *iNaturalist* (a social media focused on nature photography for amateur and professional naturalists) other male specimens of *Spodistes* sp. from Santander, Colombia but in different localities. These specimens have clearly the cephalic horn bifurcate with a strong tooth posteriorly near the bifurcation, and the clypeal apical margin angulate, a characteristic of *S. angulicollis*. Considering the morphological match and the proximity with the specimens acquired by Choi, we identified them as *S. angulicollis* as well. The specimens were found in northern and central Magdalena Valley montane forests, a different ecoregion than previous records of *S. angulicollis* (Fig. 30B). The Magdalena Valley montane forests are seasonally wet forests, with two rainy seasons annually, located in the Magdalena province, a zone flanked at west by the Northern Central Cordillera of the Andes and at east by the Eastern Cordillera (Morrone, 2014; Constantino, 2018). Also, *S. angulicollis* occurs in the Paramo province, part of the South American transition zone, but in areas comprising the Cordillera Oriental montane forests (at ca. 1200m of altitude) and the Apure-Villavicencio dry forests (at 440m of altitude). The Cordillera Oriental montane forests have a dense and moist vegetation but with some traits of the dry forests on its foothills, interchanging fauna along the altitudinal gradient (Naranjo 2021). The area of Apure-Villavicencio dry forests where *S. angulicollis* was found is the narrowest area of that ecoregion, which is a transitional zone to the Llanos at east and the Amazon at southeast (Locklin 2021), and is suffering a severe loss of vegetation (Sánchez-Cuervo *et al.* 2012).

***Spodistes mniszehi* (Thomson, 1860)**

(Figs. 4, 7–8, 13–17, 27, 29–30)

Spodistes mnizechi Arrow 1902: 143 (new combination); Blackwelder 1944: 260 (checklist); Endrödi 1970: 91 (revision); Endrödi 1985: 228 (catalogue, characters in key); Lachaume 1992: 25 (catalogue); Warner 1992: 378 (cited, key to species); Krajcik 2005: 5 (checklist); Ratcliffe

2003: 426 (catalogue to Costa Rica and Panama); Restrepo-Giraldo *et al.* 2003: 262 (cited); Ratcliffe & Cave 2006: 351 (catalogue to Honduras, Nicaragua and El Salvador); Gillett 2009: 6 (new record to Belize); Gasca-Álvarez *et al.* 2010: 179 (list of species to Colombia).
Lycomedes mnizechi Thomson 1860: 16 (original description); Bates 1888: 337 (new records).

Diagnosis. *Spodistes mnizechi* differs from other species by the cephalic horn bifurcate apically, without a tooth near the bifurcation (Fig. 13A, B). This previous trait is shared only with *Spodistes batesi* and *Spodistes monzoni*. However, males of *S. mnizechi* differ from *S. batesi* by absence of carinae on both sides of cephalic horn (Fig. 13B); mandibles with outer edge thick and round (Fig. 4C); mentum not as long as wide (Fig. 14D); labrum distinctly triangular (Fig. 14A); parameres in caudal view with apex dilated, straightly connected to basal region, internal edge straight basally becoming diagonal and convergent apically (Fig. 15A); parameres in lateral view with ventral surface slightly round apically (Fig. 15B). In *S. batesi* presence of carinae on both sides of cephalic horn (Fig. 18B); mandibles with outer edge truncate (Fig. 4D); mentum almost 2 times longer than wide (Fig. 14C); labrum subtrapezoidal (Fig. 14B); parameres in caudal view with distal half widening progressively to apex, internal edges concave (Fig. 15D); parameres in lateral view with ventral edge slightly concave apically, dorsal apex slightly depressed (Fig. 15E); posterior phallobase almost 2 times shorter than parameres (Fig. 15E). Also, males of *S. mnizechi* differ from *S. monzoni* by disc of pronotum completely tomentose (Fig. 13A); mandibles with corner of outer edge round (Fig. 4C); parameres in lateral view with ventral edge round near apex (Fig. 15B); parameres in ventral view with inner edge almost parallel (Fig. 15C). In *S. monzoni* the disc of pronotum is not tomentose medially (Fig. 21A); mandibles with corner of outer edge oblique (Fig. 4E); parameres in lateral view with ventral edge straight near apex (Fig. 15H); parameres in ventral view with inner edge concave (Fig. 15I).

Females of *S. mnizechi* are very similar to females of *S. batesi* and *S. monzoni* but can be separated by clypeal apex 1.5-1.7 times wider than transverse eye diameter (Fig. 16A); tergite VIII in lateral view with a small concavity near anterior margin (Fig. 16D); mandibles with outer edge round apically, concave basally (Fig. 8C); galea with base sinuous (Fig. 16G); mentum with apex round (Fig. 7C) in *S. mnizechi*, whereas in *S. batesi* clypeal apex 1.3 times wider than transverse eye diameter (Fig. 16B); tergite VIII in lateral view smoothly convex (Fig. 16E); mandibles with outer edge protruded

apically, with a notch medially, straight basally (Fig. 8D); galea with base distinctly convex (Fig. 16H), and in *S. monzoni* tergite VIII in lateral view straight (Fig. 16F); mandibles with outer edge evenly round apically, straight medially and basally (Fig. 8D); galea with base slightly convex (Fig. 16I); mentum with apex acuminate (Fig. 7E).

Redescription. Paralectotype. Male. **Color:** Surface velutinous, not shining; head, and pronotal disc light gray; elytra, scutellum, meso- and metafemora, and abdominal sternites gray; apical and medial portions of cephalic horn, side and venter of pronotal horn, parts of the legs and tarsi brown (Fig. 13A, B). **Head:** Cephalic horn triangular in cross-section, almost 2 times longer than head, apex slightly thickened in lateral view; presence of a small bumping dorsally at base (Fig. 13B). Punctures almost not visible on head, covered by tomentum; punctures on horn thin and dense. Clypeus acuminate with apex round. Ocular canthi halteriform, anterior margin distinctly concave, canthi apex diagonally round; tomentum covering surface only anteriorly. **Mouthparts:** Labrum distinctly triangular (Fig. 14A). Mandibles with two strong teeth, outer edge thick and convex (Fig. 4C); in ventral view, inner carina from inner tooth to basal region of mandible, almost reaching condyle, outer portion of mandible barely setose. In dorsal view, mesal brush apically covering part of inner tooth basally, presence of long thick setae covering outer edge of mandible but not reaching outer tooth. Maxillae with galea as long as stipes, apex with two strong and slender teeth transverse, presence of a long diagonal carina ventrally on galea, surface of galea covered with long and dense setae in dorsally; cardo with base densely covered by short and thick spine-like setae on outer region, and long slender setae on outer ventral region. Mentum pear-shaped, apical portion shorter than basal portion; dorsally with two prominent oblique corners longer than palpomere I and inner portion of palpomere II together; in ventral view, presence of two spots of tomentum laterally, long and thick setae mixed with few short and thick setae on sides, bare medially (Fig. 14D). **Thorax:** Pronotum convex with a strong thoracic horn projecting forward, arched medially, and with a distinct acuminate protuberance near pronotal anterior margin (Fig. 13B); lateral and ventral portions of horn not covered by tomentum, with punctures thin and dense from horn apex to base, some punctures coalescent on areas not covered by tomentum near pronotal disc. Metasternal plate hirsute, with punctures thin and dense more visible near metasternal suture; metepisternum almost completely covered by tomentum, except by a thin inner area, surface covered by short thin setae. Scutellar plate subtriangular, slightly round

laterally, surface tomentose; punctures bigger near basal corners, thinner to apex.

Elytra: Form 2.1 times longer than wide. Surface tomentose, presence of thin and dense punctures becoming denser near outer margin. Humeral umbones basally with transverse thin stripes not covered by tomentum. Short bristles on elytral apex. **Legs:** Protrocanter with a smooth depression covered by tomentum near profemur. Protibia with 3 external teeth increasing in size distally, and one short internal tooth at apex. In dorsal view, surface covered by tomentum near basal and medial teeth. Ventral surface of protibia not covered by tomentum, presence of few medium thick setae parallel to ventral carinae. Distal tarsomere of protarsi with inner portion strongly concave, basally with long and dense thick bristles; tarsal claws asymmetric, inferior claw sharp and slightly curved, superior claw completely wrinkled ventrally with a round protuberance medially. Metafemora with two long and sharp spines distally. **Abdomen:** Tergite VII crossing superior margin of Tergite VIII posteriorly. Tergite VIII transverse, round in lateral view, inferior edge bordered and thickened medially, surface tomentose; punctures thin and dense on disc and sides, presence of thin and short setae on entire surface. Sternites IV–VII completely tomentose. Sternite IV–V with surface completely covered by short thin setae decreasing in size medially. Sternites VI–VII less setose than IV–V. Sternite VIII mainly bare medially and near anterior margin, with tomentose areas on posterior corners. **Aedeagus:** Parameres symmetric. In caudal view, apex dilated, straightly connected to basal region, internal edge straight basally becoming diagonal and convergent apically (Fig. 15A). In lateral view, posterior phallobase almost with same size as parameres; parameres with tip hook-shaped, ventral surface slightly round apically, almost straight towards base with presence of a short protuberance (Fig. 15B). In ventral view, apex of parameres truncate near medial edge; basal portion of parameres with presence of an angulate protuberance laterally (Fig. 15C).

Measurements of paralectotype. Body length: 35.1 mm. Cephalic horn length: 11.2 mm. Elytral length: 21 mm. Elytral width: 11.1 mm. Pronotal width: 14.6 mm. Protibial length: 10.1 mm. Thoracic horn length: 15.3 mm.

Male variation. Major males with cephalic protuberance acute; frontal area of pronotum with no protuberance, simply round; lateral edges of clypeus more round when cephalic horn is thicker than common major males; lateral margin of pronotum slightly emarginated near posterior corners. Minor males with thoracic horn reduced as a short triangular horn not crossing anterior margin of pronotum in lateral view;

cephalic horn shorter or with same length as head; apex of cephalic horn almost 2 times narrower than base on frontal view, bifurcate corners almost parallel; absence of the frontal protuberance of pronotum; protibiae longer than pronotum; apical umbones more protruded than in major males. Body length: 24.5–35 mm. Cephalic horn length: 5.1–11.1 mm. Elytral length: 12.9–21.2 mm. Elytral width: 9.8–11.6 mm. Pronotal width: 8.9–13.3 mm. Protibial length: 9.2–9.9 mm. Thoracic horn length: 3.3–16.1 mm.

Females. Body oblong, pronotum wider than in males (Fig. 17A, B). **Head:** Cephalic horns absent. Frons with two conspicuous oblique triangular tubercles near ocular canthi, presence of triangular stripes of tomentum covering tubercles and reaching vertex (Fig. 16A). Punctures large and deep, dense near vertex and coalescent towards tubercles, presence of spots of tomentum in some punctures on vertex and frons. Clypeus trapezoidal with two teeth at apical corners, clypeal apex 1.5–1.7 times wider than transverse eye diameter (Fig. 16A); punctures deep and dense, but smaller than frontal punctures. Ocular canthi narrowing apically, tip oblique; presence of tomentose area mediobasally near anterior edge. **Mouthparts:** Labrum as in males, but not so protuberant medially, surface densely hirsute ventrally with long bristles reaching anterior edge even dorsally. Mandibles with teeth slender than in males, apical corner protruded as a round area at outer edge, concave towards base (Fig. 8C). Maxillar with general shape similar as in males but with galea more robust and round on outer edge. Mentum shorter than in males, but with same shape; tomentum absent, setae longer than in males, apical corners short (Fig. 7C). **Thorax:** Pronotum convex, thoracic horn absent, pronotal anterior margin acuminate; in lateral view, lateral margin medially acute. Pronotal margins bordered, completely covered by tomentum except medial portion of anterior margin. Disc covered by large tomentose punctures; punctures larger and denser towards lateral edges and corners; presence of a medial row of punctures not straightly aligned (Fig. 17A). Scutellum triangular, apex acute, with a U-shaped tomentose area not reaching apex, basal portion bare with few tomentose punctures shorter than pronotal punctures. Metepisternum thinner than in males, not covered by tomentum, and densely hirsute with short setae and long bristles. **Legs:** Protarsi not distinguishably dilated. Protibiae shorter than in male, apical tooth with shape like equilateral triangle; ventral surface rugose mainly near outer edge. Profemora mainly bare, only with a tomentose boomerang-shaped area ventrally near apical junction. Metafemora with two stripes of tomentum on apical half, main surface non-tomentose with sparse long and thin setae marginally, and microsetae medially. Metatibial apex

with a triangular projection at outer edge crossing basal tarsomere. Metatarsi with tarsomere V 2 times longer than tarsomere IV. **Elytra:** General shape similar to males, but slender in lateral view. Disc surface more rugose in females, punctures on disc slightly bigger than in males. Elytral apex simply round. **Abdomen:** Tergite VIII less round than in males, posterior margin thickened with medial portion thicker than sides. Sternites IV-V non-tomentose, covered by short setae denser on sides and sparser medially. Sternites VI-VII tomentose, sternite VI with short setae only on sides; sternite VII longer than sternite VIII, surface with short setae near posterior margin, with microsetae on disc. Sternite VIII with posterior half tomentose, anterior half bare, surface of anterior half rugose.

Measurements of females. Body length: 30.4–31.1 mm. Elytral length: 19.5–19.7 mm. Elytral width: 9.4–9.6 mm. Head length: 4.7–5.1 mm. Pronotal width: 14.4–14.6 mm. Protibial length: 7.3–7.6 mm.

Geographic distribution. Costa Rica: Cartago, Guanacaste. El Salvador: Ahuachapán, Cabañas, Chalatenago, La Libertad, La Paz, San Salvador, Santa Ana. Guatemala: (local desconhecido). Honduras: Atlantida, Choluteca, Comayagua, Copán, Cortés, El Paraiso, Francisco Morazán, Lempira, Olancho, Santa Bárbara, Yoro. Mexico: Chiapas, Hidalgo, Oaxaca, Veracruz. Nicaragua: Matagalpa, Chontales (Fig. 30A).

Material examined. Type male (MNHN): a) “*Mniszechi*/ Thoms{on}./ Mexico”, b) “Type/ J. Thom”, c) “G.J. Arrow”/ Vidit 1901”, d) “*Spodistes*/ *Mniszechi* Thoms/ Mexique Type”, e) “Muséum Paris/ 1952/ Coll R. Oberthur”, f) “M254”, g) “Lectotypus/ *Spodistes*/ *mniszechi* Thoms”, h) “LECTOTYPE”, i) “MNHN/ EC2468”.

Other specimens: 1 female (ZMNB) labeled: a) “Mexico”, b) “*Batesi*/ Arrow F#”, c) “*S. Toms.*/ *mniszechi*/ det Dr. Endrödi 1968”; 1 female (ZMNB): a) “Mexico, 8{viii}. {19}79/ Veracruz”, b) “*Spodistes*/ *mniszechi*”, c) “*Spodistes*/ *mniszechi*”; 1 male (ZMNB): a) “988”, b) “Motzorango/ Veracruz”, c) “*S. Toms.*/ *mniszechi*/ det Dr. Endrödi 1968”; 1 male (ZMNB): a) “Guatemala”, b) “*Mniszechi*/ Thomson”, c) *S. Toms.*/ *mniszechi*/ det Dr. Endrödi 1968”; 1 male (ZMNB): a) “Nicaragua/ Matagalpa/ Rothschild”, b) “7{vii}-{18}90”, c) *Spodistes*/ *mniszechi*/ det Dr. Endrödi 1968”; 1 male (CMNC) labeled: a) “MEXICO: Chiapas,/ Laguna Belgica,/ 16kmNW Ocozocoautla/ 970m. 7.vi.1990/ H. & A. Howden”, b) “FIT: Flight/ Intercept trap”, c) “Ratcliffe & Cave/ db Dynastine/ Mexico, Belize & Guatemala”; 1 female (CMNC) labeled: a) “HONDURAS: Olancho/ Montaña del Malacate, 900 m/ N15°08'04”

W85°35'36"/ vi-18-2001/ B. Ratcliffe, M.L. Jameson, R. Cave"; 1 male (NHM) labeled: a) "BELIZE, Cayo District/ 88°59'W, 16°43'N/ Las Cuevas Field St./ H.Mendel&MVI.Barclay/ 500-700m, v.2010, at light", b) "BMNH(E)/ 2010 54", c) "*Spodistes/ mniszzechi* (Thomson)/ S. Pokorny det. 2010"; 1 male (NHM): a) "B.C.A. Col. II. (2)/ *Lycomedes/ mniszzechi*", b) "Chontales./ Janson", c) "*Lycomedes/ mniszzechi*/ Thoms."; 1 female (NHM) labeled: a) "BELIZE (Cayo)/ Chiquibul Forest Reserve/ Las Cuevas Research Station/ 16°44'N, 88°59'W/ June 2006/ BMNH (E) 2006-141/ C. Gillett & J. Kitson"; 1 female (NHM): a) "BELIZE, vi.1997/ Chiquibul Forest Res./ Las Cuevas field station/ 88°59'W, 16°44'N/ 500-700m, D. Inward/ BMNH (E) 2005-78", b) "Ratcliffe & Cave/ db Dynastine/ Mexico, Belize & Guatemala" 1 female (ZMNB) labeled: a) "MEXICO/ J. Flohr G."; b) "*S./ batesi* Arr./ det. Dr. Endrödi 1968"; 2 females (ZMNB) labeled: a) "Mexico", b) "*Batesi/ Arrow*", c) "*Spodistes/ batesi* Arr./ det. Dr. Endrödi 1968"; 1 male (MSUC) labeled: a) "MEXICO/ Veracruz St./ Fortin/ July 1979", b) "Purchased from/ Combined/ Scientific Supply/ Sept{ember} 1981", c) "*Spodistes/ mniszzechi* (Thomson)/ det. G. Parsons 1984"; 1 male and 1 female (MSUC) labeled: a) "GUATEMALA/ Zacapa/ La Union/ +850m elev{ation}/ July 1979", b) "Purchased from/ Eduardo C./ Welling M. 1981", c) "*Spodistes/ mniszzechi* (Thomson)/ det. G. Parsons 1984"; 1 male (MSUC): a) "GUATEMALA Izabal/ Morales, Cerro Negro Norte/ Finca Firmeza el{evation}. 2220m/ 18-19 August 2006/ N15°22'53.7", W88°43'02.4"/ A.M. & F.M. West coll.", b) "*Spodistes/ mniszzechi* (Thomson)/ det. G. Parsons 1984".

Remarks. *Spodistes mniszzechi* can be found from southeastern Mexico, Belize, Honduras, El Salvador, to northwestern Nicaragua. Despite I could not see specimens from Guatemala, their occurrence is almost certain at least in the northern portion of the country as that region shares the same vegetation as in Belize, and also because *S. mniszzechi* is widely recorded along the neighbor countries of Honduras and El Salvador. In Mexico, the distribution of *S. mniszzechi* is almost parallel with *S. monzoni* but whereas *S. monzoni* occurs in lowlands of Pacific coast, *S. mniszzechi* occurs in lowlands of coast of the Gulf of Mexico corresponding to Veracruz province in areas of Petén-Veracruz moist forests. In Central American, *S. mniszzechi* extends its distribution along Petén-Veracruz moist forests in Belize, and reaches areas of Central American Atlantic moist forests (in lowlands of Mosquito province) in Honduras. Apparently, the mountain ranges of Chiapas Highlands province do not act as a geographical barrier to *S. mniszzechi* since it can be found in various habitats in highlands, as Central American

montane forests, pine-oak forests and patches of dry forests, and even reaching the lowlands of Pacific coast in El Salvador, being sympatric to *S. monzoni* in these areas. The southernmost distribution of *S. mniszewi* is in Talamancan montane forests on the Cordillera de Talamanca, Costa Rica. There are records in literature to Panama and Colombia but we did not see any specimen of *S. mniszewi* from these countries. The occurrence in Panama is more plausible due to the montane forests continuous to Costa Rica.

***Spodistes batesi* Arrow, 1902**

(Figs. 4, 7–8, 14–16, 18–20, 29–30)

Spodistes batesi Arrow 1902: 145 (original description); Sternberg 1903: 301 (key to species); Blackwelder 1944: 260 (checklist); Endrödi 1970: 89 (revision); Endrödi 1985: 228 (catalogue, characters in key); Lachaume 1992: 26 (catalogue); Warner 1992: 378 (key to species); Ratcliffe 2002: 36 (checklist to Panama); Ratcliffe 2003: 420 (catalogue to Costa Rica and Panama); Krajcik 2005: 5 (checklist).

Diagnosis. *Spodistes batesi* differs from other species (except *S. mniszewi* and *S. monzoni*) by the cephalic horn of males bifurcate apically, without a tooth near the bifurcation (Fig. 18A, B). For differences between males of *S. batesi* and *S. mniszewi* see the Diagnosis section of *S. mniszewi*. Males of *S. batesi* have carinae on both sides of cephalic horn basally near base of ocular canthi (Fig. 18B), pronotal disc tomentose with punctures thin and dense (Fig. 18A), mandibles with apical corner slightly round (Fig. 4D), outer edge of parameres in ventral view round at base (Fig. 15F), basal half of parameres subrectangular longer than wide (Fig. 15F), whereas *S. monzoni* have carinae absent on cephalic horn (Fig. 21B), pronotal disc not tomentose medially with tomentose punctures large and dense (Fig. 21A), mandibles with apical corner oblique (Fig. 4E), outer edge of parameres in ventral view angulate at base (Fig. 15I), basal half of parameres subquadrangular wider than long (Fig. 15I).

Females of *S. batesi* can be characterized by: clypeus bidentate subtrapezoidal, with apex 1.3 times wider than transverse eye diameter, and almost 2 times narrower than distance between tips of cephalic tubercles (Fig. 16B), tergite VIII in lateral view smoothly convex (Fig. 16E), mandibles with apical corner protruded, with a notch medially, straight basally (Fig. 8E), galea with base distinctly convex (Fig. 16H), mentum with basal half less than 1.2 times longer than apical half (Fig. 7D).

Comparison with females of *S. mniszewi* and *S. monzoni* were made in Diagnosis section of *S. mniszewi*.

Redescription. Holotype. Male. **Color:** Surface mainly dull, velutinous; head, elytra, abdominal sternites and the main part of the legs gray; pronotum greyish brown; parts of both horns, carinae of horns, thoracic sternites, parts of the legs and tarsi reddish brown (Fig. 18A, B). **Head:** Shape subrectangular; frons with punctures thin and sparse, almost indistinguishable. Cephalic horn triangular in cross-section, base extending from vertex to clypeus, almost 3 times longer than head; apex bifurcate, tips slender and sharp; horn with a sharp dorsal protuberance at the middle (Fig. 18B); punctures thin and sparse basally, becoming denser near apex. Clypeus acuminate with sides slightly sinuous, almost parallel, apex truncate; lateral depressions between the cephalic horn and ocular canthi carinae; clypeal punctures thin and denser on apex, sparser near horn. Ocular canthi subtriangular, slightly protruded on anterior margin near apex. Presence of longitudinal carinae from the base of ocular canthi reaching cephalic horn basally; carinae 1.2 times longer than canthi (Fig. 18B). **Mouthparts:** Labrum subtrapezoidal, corners smoothly convex, sides acute (Fig. 14B). Mandibles oblong, with two strong long teeth, outer edge protruded at apical corner and straight laterally (Fig. 4D); inner ventral carina from inner tooth to middle of mandible, outer ventral carina sinuous reaching apical corner. In lateral view, mesal brush surrounding internal lobe, reaching it basally. In dorsal view, mesal brush apically not covering inner tooth, but extending to the base on inner edge. Maxillae with galea as long as stipes, apex with two strong and thick teeth transverse and densely hirsute dorsally; maxillary palpomere IV with a narrow base, widening apically, apex blunt and acuminate, sensorial area ellipsoid and large with surface striate. Mentum pear-shaped, apical portion longer than basal portion; in dorsal view, apex with two pointy oblique corners, concave at middle; in ventral view, few long thin setae basally, presence of two short stripes of tomentum on sides, not reaching the middle of mentum (Fig. 14C). **Thorax:** Pronotum convex with a strong thoracic horn projecting forward. Thoracic horn triangular in cross-section, with a sharp protuberance frontally near anterior margin of pronotum (Fig. 18B); surface of horn velutinous on base, smooth from middle to apex. Anterior corners of pronotum not reaching the middle of eyes. Punctures thin and sparse on disc, barely visible due to the tomentose surface; punctures thin and dense on dorsal and ventral surface of thoracic horn. Metasternal plate sparsely hirsute; punctures thin and sparse homogeneously

covering the surface. Scutellar plate subtriangular, surface velutinous; moderately punctate, punctures thin. **Elytra:** Form 1.9 times longer than wide. Surface tomentose, thin punctures densely distributed on disc, rows of larger punctures near elytral suture; longitudinal striae on disc. Short bristles on elytral apex surrounding apical umbones. **Legs:** Protibia with 3 external teeth increasing in size distally, and 1 short internal tooth near protibial spur. Apical tooth almost straight compared to medial tooth; spine-like setae on protibial apex, near spur. Ventral surface of protibia with a thin velutinous stripe medially, sides smooth; punctures thin and dense. Distal tarsomere of protarsi strongly curved internally, basal portion covered by thickened setae and surface wrinkled; tarsal claws asymmetric, inferior claw simply curved, superior claw sinuous with a short round tooth basally and a round protuberance medially. Metacoxae with outer edges round, surface densely covered by long thin setae. Metatibiae dilated concave on outer edge apically. **Abdomen:** Tergite VIII convex, 2.6 times wider than long; surface with greyish tomentum, densely covered by thin punctures and short thin setae. Tergite VII slightly overlapping tergite VIII. Sternites IV–VIII velutinous, densely hirsute, covered by short thin setae; punctures thin and moderately dense. **Aedeagus:** Parameres symmetric. In caudal view, paddle-shaped, with distal half widening progressively to apex, internal edges concave (Fig. 15D). In lateral view, parameres almost 2 times longer than posterior phallobase, with short carina basally, ventrolateral portion slightly depressed, tips hook-shaped; posterior phallobase short and round (Fig. 15E). In ventral view, basal half subrectangular longer than wide; ventrolateral carinae ending smoothly before reaching internal edge of parameres; external edges of basal half round (Fig. 15F).

Measurements of holotype. Body length: 29.4 mm. Cephalic horn length: 11.7 mm. Elytral length: 17.7 mm. Elytral width: 9.2 mm. Pronotal width: 10.7 mm. Protibial length: 9.2 mm. Thoracic horn length: 14.4 mm.

Male variation. Major males with frontal protuberance of thoracic horn keel-shaped extending almost to the middle of horn; cephalic horns more curved upward apically, protuberance of horn either sharp and distinctive in some specimens or round and inconspicuous; apical umbones of elytra sharp, almost crossing apical edge of elytra in lateral view. Minor males (Fig. 20A, B) with cephalic horns shorter than head, slightly curved; smaller specimens with a slight protuberance on vertex but protuberance absent on horn, some specimens with an inconspicuous protuberance basally on horn; bifurcation of cephalic horn not as deep as in major males;

protuberance of thoracic horn absent. Body length: 24.2–35.1 mm. Cephalic horn length: 2.7–13.1 mm. Elytral length: 15.7–21.7 mm. Elytral width: 8.1–11 mm. Pronotal width: 8.9–13.5 mm. Protibial length: 7.7–11.6 mm. Thoracic horn length: 3.5–19.5 mm.

Females. Body oblong, pronotum wider than in males (Fig. 19A). **Head:** Cephalic horns absent. Frons with two strong triangular tubercles near ocular canthi (Fig. 16B), tomentum covering most part of tubercles except near vertex; surface of frons deeply depressed and covered by tomentum, punctures large and dense reaching the inner edge of tubercles. Clypeus trapezoidal elongate, apex with two teeth at corners, surface excavated, edges strongly deflected, 1.3 times wider than transverse eye diameter (Fig. 16B); punctures large and dense. Ocular canthi subrectangular, anterior margin oblique, tip truncate, surface almost bare. **Mouthparts:** Labrum as in the males, acuminate with sides acute, but more hirsute with long thin setae almost reaching posterior edge medially. Mandibles with apical corner more protruded than in males, outer edge slightly oblique, mesal brush not reaching internal lobe base on ventral side (Fig. 8E). Maxillae with teeth slender than in males, maxillary palpomere II shorter than in males; sensorial area striate, more elongate than round. Mentum with same shape and pattern as in males, but densely hirsute apically and ventrally (Fig. 7D). **Thorax:** Pronotum convex, thoracic horn absent, anterior margin slightly elongate, crossing the middle line of eye in lateral view; surface rugose, covered by tomentose punctures of large size and densely distributed on sides and posterior corners, smaller punctures medially on disc and near anterior margin. Scutellum densely covered by tomentum on apex and lateral edges, forming a V-shaped zone, disc bare, base with large tomentous punctures. Metasternal plate densely hirsute, setae long. **Elytra:** Shape more elongate than in males, surface more rugose near external edges. **Abdomen:** Tergite VIII almost straight in lateral view, completely velutinous; punctures coalescent and thin punctures mixed near sides, disc and anterior margin with thin and moderately dense punctures, posterior margin with large and moderately dense punctures; surface with white microsetae moderately distributed.

Measurements of females. Body length: 26.7–28.6 mm. Elytral length: 16.8–17.3 mm. Elytral width: 9–9.7 mm. Head length: 4.7–4.9 mm. Pronotal width: 11.8–12.7 mm. Protibial length: 7.1–8.1 mm.

Geographic distribution. Costa Rica: Alajuela, Guanacaste, Puntarenas. Panama: Chiriqui. Mexico: local data unknown (Fig. 30A).

Material examined. **Type** male (NHM) labeled: a) “Type”, b) “B.C.A. col. II (2)”, c) “V. de Chiriqui./ 4000-6000 ft./ Champion”, d) “*Lycomedes/ mniszechii*/ Thoms. m#”, e) “*Spodistes/ batesi* Arrow/ Type m#”. **Allotype** (NHM) labeled as the holotype. **Other specimens:** 1 male (NHM) labeled: a) “58204”, b) “Panama/ Chiriqui”, c) “Fry Coll./ 1905-100”; 3 males and 5 females (NHM): a) “V. de Chiriqui./ 4000-6000 ft./ Champion”, b) “B.C.A. col. II (2)/ *Lycomedes mniszechi*”; 1 male (NHM): a) “Batesi/ Arr.”, b) “Nevinson Coll./ 1918–14”; 1 female (NHM): a) “Chiriqui”, b) “Nevinson Coll./ 1918–14”, c) “*Lycomedes/ mniszechi*”; 2 males (NHM): a) “Brit. Mus./ 1950-6”, b) “COSTA RICA:/ C.H.Lankester”, c) “Poza Azul. Ap. 1915”, d) “*Spodistes/ batesi* Arrow/ R.-P. Dechambre det. 1974”; 2 males and 4 females (ZMNB) labeled: a) “Chiriqui”, b) “*Batesi/ Arrow*”, c) “*S./ batesi* Arr./ det. Dr. Endrödi 1968”; 1 male (ZMNB) labeled: a) “Chiriqui”, b) “Coll./ Jul. Moser”, c) “*S./ batesi* Arr./ det. Dr. Endrödi 1968”; 1 male (ZMNB) labeled: a) “Costa Rica/ (A. Bau)”, b) “*Spodistes/ batesi* Arrow”, c) “*Spodistes/ batesi* Arr./ det. Dr. Endrödi 1968”; 1 male (ZMNB) labeled: a) “Mexico”, b) “*Batesi/ Arrow*”, c) “*Spodistes/ batesi* Arr./ det. Dr. Endrödi 1968”; 1 male (ZMNB) labeled: a) “*Lycomedes/ Mniszechi* M# 20m/ Mexico Thoms.”, b) “*Batesi/ Arrow*”, c) “*Spodistes/ batesi* Arr./ det. Dr. Endrödi 1968”; 2 males and 1 female (ZMNB) with no data, just labeled: “*Spodistes/ batesi* Arr./ det. Dr. Endrödi 1968”; 1 female (ZMNB) labeled: a) “*Lycomedes mniszechi/ Chiriqui/ Pan. 760 m*”, b) “*S./ batesi* Arr./ det. Dr. Endrödi 1968”; 1 female (ZMNB) labeled: a) “PANAMA”, b) “Coll. Le Moul/ Naturaliste Paris”, c) “Coll. R”, d) “*Spodistes/ sp. F#*/ det. J. Schulze”; 1 male and 1 female (NHMB): a) “Panama”, b) “COLL LE MOULT/ Naturaliste, Paris”, c) “Coll. R”, d) “*Spodistes/ mniszechi/ Thoms.*”; 1 male (NHMB): a) “PANAMA/ V. DE CHIRIQUI”, b) “Arrow determ./ *Spodistes/ batesi* Arr.”; 1 male (OUMNH): a) “*Spodistes batesi/ Arrow/ det. D. Curoe*”, b) “PANAMA: Chiriqui/ Boquete, 750m elv./ iv.2006/ coll. D. Curoe/ OUMNH-2012-042”.

Remarks. *Spodistes batesi* has been historically recorded to Mexico since Endrödi (1970) based on specimens that he identified in ZMNB, but no other author since then was able to collect or to examine specimens of this species from Mexico. There are two male specimens in ZMNB with labels indicating Mexico as their local, and both of them were identified by Dr. Sebö Endrödi in 1968, having his identification label. However, none of them has further details about the collector, province or city, and the date of collect. One of them has an indication of being collected at 20m of elevation, but that is all. Therefore, we opt to keep the record to Mexico but it is

noteworthy that the majority of specimens of *S. batesi* was only confirmed to Panama and Costa Rica. In these two countries, the species can be found in the Puntarenas-Chiriquí province, occurring in areas of Isthmian-Pacific moist forests – an extremely wet zone in lowlands, with vegetation adapted to seasonal and permanently flooded areas – and Costa Rican seasonal moist forests on the Pacific coast – an intermediate habitat between the dry and moist forests (Powell *et al.* 2021). *S. batesi* has also a wide distribution along the Talamancan montane forests at higher elevations (600-1800m). Apparently, the mountain ranges of Panama and Costa Rica hinder the distribution of *S. batesi* to moist forests of Caribbean coast.

***Spodistes monzoni* Warner, 1992**

(Figs. 4, 7–8, 15–16, 21–22, 27, 29–30)

Spodistes monzoni Warner 1992: 378 (original description); Krajcik 2005: 5 (checklist); Ratcliffe & Cave 2006: 349 (catalogue to Honduras, Nicaragua and El Salvador).

Diagnosis. Males: pronotal disc not tomentose medially, presence of tomentose punctures large and dense (Fig. 21A); mandibles with outer edge almost subtrapezoidal, apical corner oblique, middle protruded and truncate, basally oblique (Fig. 4E); parameres in caudal view with apical region slender, outer edge smoothly round towards basal region (Fig. 15G); in ventral view, basal half of parameres subquadrangular wider than long (Fig. 15I). This species differs from the other *Spodistes* (except *S. batesi* and *S. mniszewski*) by the cephalic horn of males bifurcate apically, without a tooth near the bifurcation (Fig. 21A, B). For comparisons with *S. batesi* and *S. mniszewski* see the Diagnosis section of the two species.

Females: ocular canthi subrectangular, transverse, anterior corner round, posterior corner slightly angulate with tip truncate (Fig.); frontal surface with a shallow concavity (Fig. 22B); clypeal apex more than 1.5 times narrower than transverse eye diameter, and 2 times narrower than the space between tips of cephalic tubercles (Fig. 16C); tergite VIII in lateral view straight (Fig. 16F); mandibles with outer edge evenly round apically, straight medially and basally (Fig. 8D); galea with base slightly convex (Fig. 16I); mentum with apex distinctly acute (Fig. 7E). For comparisons with females of *S. batesi* and *S. mniszewski* see the Diagnosis section of the two species.

Redescription. Paratype. Male. **Color:** Head, anterolateral regions of pronotum, elytra, abdominal sternites and the main part of the legs tomentose, color light gray; dorsal region of pronotum non-tomentose, black and lustrous; medial and apical regions of cephalic horn, thoracic sternites, parts of the legs and tarsi black (Fig. 21A, B). **Head:** Vertex sparsely punctate, punctures thin, presence of a black thin stripe from vertex to the middle of horn dorsally; frons and base of horn with thin and moderately dense punctures. Cephalic horn projected forward, slightly longer than head, curving upwards medially; apex strongly bifurcate (Fig. 21A, B); tomentum only on basal region, medial and apical region bare, punctures thin and moderately dense on bare region. Clypeus acuminate, sides and apex round; clypeal punctures thin and moderately dense, bare apically and tomentose laterally. Ocular canthi transverse, anterior edge sinuous, ending apically with a short protuberance, tip acute, posterior edge almost straight and oblique; carinae crossing anterior margin basally, tomentum only on a subtrapezoidal area near anterior margin, punctures thin and sparse. **Mouthparts:** Labrum strongly arched, sinuous laterally, apically protruded, lateral corners oblique and straight, posterior edge concave. Mandible oblong with two long and strong teeth apically, outer edge with oblique apical corner, medially truncate, basally oblique with a tomentose region medially (Fig. 4E); presence of two ventral carinae, one apical on inner tooth finishing before the middle of mandible, and one more strong and prominent near outer edge reaching the base of mandible. In lateral view, mesal brush densely hirsute, covering internal lobe laterally reaching the base. In ventral view, mesal brush expanding medially almost reaching mandibular half; presence of a slight furrow running together with outer edge of mesal brush. Maxillae with galea subtriangular, elongate, apex twisted towards inner edge with two strong parallel teeth, dorsal surface densely hirsute; galea as long as stipe; maxillary palpomere II dilated apically; maxillary palpomere IV narrow basally and apically acuminate blunt, sensorial area drop-shaped, densely striate, almost reaching palpomere basally. Mentum pear-shaped, sides round, apex acuminate and blunt. **Thorax:** Pronotum convex and transverse, sides acute, strong thoracic horn projecting forward, tip slightly downward. Thoracic horn conical, not crossing clypeal apex (Fig. 21B), tomentum covering anterior and lateral region of pronotum; surface bare dorsally, in some straight zones laterally, and on ventrofrontal surface of horn, reaching anterior edge. Pronotal punctures tomentose large and dense near posterior edge and on ventrofrontal surface of horn, punctures thin and dense on disc, punctures non-tomentose thin and dense on horn dorsally (Fig. 21A). Prosternal process pointed,

with a short tomentose area basally, disc bare. Metepisternum tomentose except for a narrow stripe on inner edge, punctures moderately dense, short thin setae on punctures. Metasternal plate covered by long thin setae moderately dense, with some short thin setae near metasternal suture, punctures thin and moderately dense, rugose area on metasternal suture anteriorly. Scutellar plate subtriangular, apex acute; surface tomentose apically and laterally, bare on disc medially and basally, tomentose punctures near tomentose areas laterally. **Elytra:** Form 1.9 times longer than wide. Surface velutinous with two darker longitudinal stripes from humeral umbone to elytral disc; annular punctures large and dense weakly carved, surrounded by thin and dense punctures, humeral and apical umbones covered by thin and dense punctures. **Legs:** Protibia with 3 external teeth increasing in size distally, and 1 short internal tooth near protibial spur. Protibia dorsally with a tomentose area from base almost reaching middle tooth, punctures on tomentose area thin and moderately dense, punctures thin and large densely distributed on medial and apical teeth, C-punctures near inner edge, two rows of short thin setae, outer row on tomentose sockets, inner row on bare sockets. Metacoxae with outer edges angulate, surface moderately covered by long thin setae. Metatibiae dilated to apex, apical outer edge straight. Mesotarsi with basal tarsomere spur almost reaching the apex of tarsomere IV. Distal protarsal tarsomere strongly curved internally, tarsal claws asymmetric, inferior claw curved, superior claw with a short round tooth basally and a strong protuberance medially. **Abdomen:** Tergite VIII short and transverse, tomentose; punctures thin and dense, short thin setae densely distributed on surface, but barely visible in lateral view. Sternites IV–VI tomentose, punctures thin and dense uniformly distributed on surface, presence of a dark region medially to posterior edge, microsetae on surface. Sternite VII tomentose, punctures thin and moderately dense medially to anterior edge, punctures thin and dense on posterior edge, microsetae mainly on sides. Sternite VIII only laterally tomentose, punctures thin and dense, larger towards middle. **Aedeagus:** Parameres symmetric. In caudal view, apical region slender, inner edge strongly concave, outer edge smoothly round towards basal region, sclerite basal lateral round (Fig. 15G). In lateral view, phallobase smoothly convex, phallobase corners not prominent, carinae inconspicuous basally (Fig. 15H). In ventral view, basal sclerite trapezoidal short, posterior corners reaching phallobase laterally, anterior corners pointed and angulate; inferior edge of parameres with ventral carinae continuous with outer edge of parameres, carinae oblique and straight (Fig. 15I).

Measurements of paratype. Body length: 29.9 mm. Cephalic horn length: 5.7 mm. Elytral length: 19.2 mm. Elytral width: 9.9 mm. Pronotal width: 13.3 mm. Protibial length: 8.9 mm. Thoracic horn length: 6.5 mm.

Male variation. Males with bifurcation of cephalic horn asymmetric, with one corner upward and the other corner more lateral; absence of tomentum on some frontal areas near cephalic horn; males with short thoracic horn as a small triangular horn not crossing anterior margin in lateral view; ocular canthi with apical protuberance slightly short, tip in some minor males more round than acute; pronotum only tomentose on small areas near lateral margins and posterior corners; absence of tomentum on basal areas of anterior margins of meso- and metafemora. Body length: 24.3–28.4 mm. Cephalic horn length: 4.1–5.8 mm. Elytral length: 16.9–19 mm. Elytral width: 9.4–9.9 mm. Pronotal width: 11.9–12.7 mm. Protibial length: 6.9–9.1 mm. Thoracic horn length: 2.1–6.8 mm.

Females. Body oblong, pronotum wider than in males (Fig. 22A). **Head:** Cephalic horns absent. Frons with two strong triangular tubercles near ocular canthi, tomentum on tubercles surface, not reaching vertex, forming two stripes (Fig. 16C); punctures thin and moderately dense on vertex, punctures large and dense on frons, becoming coalescent near tubercles. Clypeus trapezoidal with two teeth at apical corners, strongly deflected upwards, punctures large and dense, thinner towards apex. Ocular canthi subretangular, transverse, anterior corner round, posterior corner slightly angulate, tomentose punctures large and dense on a short area anteriorly (Fig. 16C). **Mouthparts:** Labrum arched, sides blunt, shorter than in males. Mandibles shorter than in males, outer edge strongly protruded on apical corner, non-tomentose, inner ventral carina reaching mandibular base (Fig. 8D); in lateral view, mesal brush reaching the base of internal lobe as in males, but ventral side more membranous, dorsal side more hirsute. Maxillae with galea shorter than stipes, maxillary palpomere II less dilated apically than in males, sensorial area of palpomere IV ellipsoid and striate not reaching the narrow portion of palpomere. Mentum thinner than in males, apex more acute, long thick setae denser than in males (Fig. 7E). **Thorax:** Pronotum convex, thoracic horn absent, anterior margin slightly prominent forward medially. Punctures tomentose on disc, large and dense punctures, becoming larger near corners and thinner towards middle; borders densely covered by tomentose punctures forming a stripe from anterior margin to posterior corners, not reaching posterior edge medially (Fig. 22A). Metepisternum with few tomentose stripes, punctures large and dense, wrinkled near

inner edge, short thin setae moderately dense and whitish. Scutellum with a tomentose area apically and laterally, not reaching sides basally; tomentose punctures thin and dense on disc medially and basally; setae absent on disc. **Legs:** Protibia with tomentose area on outer edge, almost reaching basal tooth; punctures large and dense mixed with few thin punctures externally, outer row of setae with long thick setae intercalated with short thick setae. Metafemora smooth, weakly hirsute, only with two rows of long thin setae sparsely; punctures thin and moderately dense; tomentose area as a thin stripe from apex to posterior edge, almost reaching the base. **Elytra:** Surface tomentose; punctures thin and dense on disc, less carved than in males, thinner punctures on humeral umbones. In ventral view, epipleura non-tomentose with a longitudinal furrow medially. **Abdomen:** Tergite VIII slightly concave on disc, surface tomentose; punctures thin and dense on disc and sides, becoming sparser posteriorly; microsetae on punctures. Sternites IV–V tomentose on sides, punctures thin and moderately dense, microsetae denser on sides, almost absent medially. Sternites VI–VII completely tomentose, punctures thin and moderately dense, punctures denser on sternite VII than on sternite VI; sternite VII with short thin setae sparse on posterior edges. Sternite VIII non-tomentose, punctures large and dense on disc, wrinkles on corners and anterior edge, short thin setae densely distributed on posterior margin.

Measurements of females. Body length: 27.2–32.4 mm. Elytral length: 17.7–21.9 mm. Elytral width: 8.6–9.4 mm. Head length: 3.1–4.6 mm. Pronotal width: 12.8–14.3 mm. Protibial length: 6.4–6.6 mm.

Geographic distribution. El Salvador: La Unión, Morazán, San Salvador, Santa Ana. Guatemala: Jalapa, Santa Rosa, Sololá. Mexico: Chiapas, Guerrero, Oaxaca (Fig. 30A).

Material examined. Paratypes 1 male (CMNC) labeled: a) “GUAT {EMALA}: El Progreso/ 12km N Estancia de Is Virgen/ 15°01'N 69°55'W/ 7.vi.91 B.D. Gill”, b) “H.&A. Howden/ collectors”, c) “Paratype/ *Spodistes/ monzoni*/ Warner”, d) “CMNEN/ 2002-0249”, e) “Ratcliffe & Cave/ db Dynastine/ Mexico, Belize/ & Guatemala”; 2 females (CMNC) with same data as previous specimen except: d) “MIMSY: Data/ ENTERED”; 1 male (CMNC): a) “Paratype/ *Spodistes/ monzoni*/ Warner”, b) “San Salvador/ El Salvador/ IV.25.1960/ Virkki.No.757”, c) “CMNEN/ 2002-0247”; 1 male (CMNC): a) “2800m. Monte Cristo/ 23km. N. Metapan/ El Salvador, V.8-10/ 1971 H.F. Howden”, b) “Paratype/ *Spodistes/ monzoni*/ Warner”, c) “CMNEN/ 2002-0248”.

Other specimens: 1 male (CMNC) labeled: a) “EL SALVADOR/ San Salvador/ J.

Bechyné leg./ Coll. Martinez/ 27.iv.1960”, b) “H. & A. HOWDEN/ COLLECTION/ ex. A. Martinez coll.”, c) “*Spodistes m# / mniszzechi* (Thoms.)/ A. Martinez det. 1993”; 1 female (CMNC) labeled: a) “Los Planes/ San Salvador/ 19-v-82/ Asúa leg.”, b) “H. & A. HOWDEN/ COLLECTION/ ex. A. Martinez coll.”, c) “*Spodistes f# / mniszzechi* (Thoms.)/ A. Martinez det. 1993”; 1 female (CMNC): a) “MEXICO, Chiapas,/ Pq. Laguna Belgica,/ 16kmNW Ocozocoautla/ 25.vi.1989. H. Howden”, b) “at light”, c) “Ratcliffe & Cave/ db Dynastine Mexico, Belize & Guatemala”; 3 males and 4 females (RBINS) labeled: a) “Coll. R. I. Sc. N. B./ El Salvador/ San Salvador/ 23-v-1960/ Réc.: J. Bechyné”, b) “*Spodistes monzoni*/ Warner/ Det. Y. Ponchel, 2004”; 1 male and 1 female (RBINS) with same data as previous specimens except by: a) “Coll. R. I. Sc. N. B./ El Salvador/ San Salvador/ 19/23-v-1960/ Réc.: J. Bechyné”; 1 male (RBINS) with same data as previous specimens except by: a) “Coll. R. I. Sc. N. B./ El Salvador/ San Salvador/ 1-v-1960/ Réc.: J. Bechyné”; 2 females (RBINS) with same data as previous specimens except by: a) “Coll. R. I. Sc. N. B./ El Salvador/ San Salvador/ 19-21-vi-1960/ Réc.: J. Bechyné”; 1 female (RBINS) with same data as previous specimens except by: a) “Coll. R. I. Sc. N. B./ El Salvador/ San Salvador/ 2-v-1960/ Réc.: J. Bechyné”; 1 male (RBINS): a) “*Mniszzechi*/ Th./ Guar.”, b) “Guatemala”, c) “Collection/ E. Candéze”, d) “*Lycomedes mniszzechi* Thoms./ det. L. Candeze”; 3 males and 3 females (NHMB): “Mexico-Chiapas/ leg. Hartlg, 1953”; 1 male and 1 female (NHMB): a) “Guatemala/ V. de Atitlán/ Olas de Mocá”, a_verso) “G. Brückner S./ Juli-August/ Aus licht”, b) “Arrow determ./ *Spodistes mniszzechi*/ f# Thoms.”; 1 male (NHMB): “S. Antonio/ Guatemala/ iv-1929”.

Remarks. *Spodistes monzoni* has records from western portion of southern Mexico, southern Guatemala and El Salvador, occurring through the Sierra Madre del Sur province, Chiapas Highlands province, and in the Pacific Lowlands province. The presence of *S. monzoni* along the Pacific lowlands may indicate that the species did not find difficulties to spread in that province, perhaps due to the similarity among the vegetation of that region – mainly tropical and subtropical dry broadleaf forests –, a pattern that was seen for other scarabs (Mora-Aguilar *et al.* 2018). However, there are no records of *S. monzoni* in the lowlands of provinces near Caribbean coast, which may indicate that the mountain ranges of Mexican transition zone act as a barrier to the Veracruz province and Mosquito province (where *Spodistes mniszzechi* is widespread). In lowlands, *S. monzoni* can be found in southern pacific dry forests and Central American dry forests, areas ranging from 0-800m of altitude, with 4-7 months

of a dry season and a rainy season as wet as in a rainforest (Janzen, 1988). There are also specimens of *S. monzoni* in the Sierra Madre de Chiapas moist forest, a transitional area between the lowlands and highlands. In highlands, the species can be found in Sierra Madre del Sur and Central American pine-oak forests, ecoregions characterized mainly by the high diversity of *Pinus* spp. and *Quercus* spp. on landscapes shaped by volcanic activity (Almazán-Núñez *et al.* 2016).

***Spodistes beltianus* (Bates, 1888)**

(Figs. 6–8, 23–25, 27, 29–30)

Spodistes beltianus Arrow 1902: 143 (new combination); Sternberg 1903: 301 (key to species); Blackwelder 1944: 260 (checklist); Endrödi 1970: 87 (revision); Endrödi 1985: 227 (catalogue, key to species); Lachaume 1992: 25 (catalogue); Warner 1992: 382 (key to species); Dechambre 1994: 150 (citation); Ratcliffe 2003: 423 (catalogue to Costa Rica and Panama); Krajcik 2005: 5 (checklist); Ratcliffe & Cave 2006: 350 (catalogue to Honduras, Nicaragua and El Salvador); *Lycomedes beltianus* Bates 1888: 338 (original combination).

Diagnosis. *Spodistes beltianus* differs from other species by the cephalic horn projected forward with a simple apex acute followed posteriorly by a dorsal tooth (Fig. 23B). This previous trait is shared only with *Spodistes armstrongi*. However, males of *S. beltianus* differ from *S. armstrongi* by cephalic horn with a dorsal tooth near base bigger than apical tooth (Fig. 23B); thoracic horn with a distinct tooth ventrally not reaching frontal surface of pronotum (Fig. 23B); ocular canthi elongate with apical protuberance short, tip acute (Fig. 24F); parameres in caudal view with apex thin, tip round (Fig. 24A); parameres in lateral view with apical concavity more abrupt, posterior phallobase with corners almost round (Fig. 24B). In *S. armstrongi* cephalic horn with no tooth basally or with an inconspicuous protuberance near base (Fig. 26B); thoracic horn with a distinct tooth ventrally reaching frontal surface of pronotum (Fig. 26B); ocular canthi elongate with apical protuberance strong (Fig. 24G); parameres in caudal view with apex wider than in *S. beltianus*, tip oblique (Fig. 24D); parameres in lateral view with apical concavity smooth, posterior phallobase with corners distinctly acute (Fig. 24E).

Females: ocular canthi subrectangular, anterior margin slightly concave, apex truncate, tip slightly oblique (Fig. 6F); eye diameter less than 2.2 times the distance between cephalic tubercles (Fig. 6F); clypeal apex 1.8 times narrower than distance

between cephalic tubercles (Fig. 6F); mandibles with outer edge straight (Fig. 8F); mentum with basal half almost circular (Fig. 7F).

Redescription. Holotype. Male. **Color:** Head, pronotum, elytra, abdominal sternites and the main part of the legs tomentose, color darkish gray; frontal surface of cephalic horn, ventrolateral region of thoracic horn, tarsi and regions of legs non-tomentose, brown (Fig. 23A, B). **Head:** Frons and vertex weakly punctate, surface densely wrinkled and tomentose. Cephalic horn strong and projected forward obliquely, apical portion slightly upward; apex sharp with a short dorsal tooth posteriorly, presence of a protuberance on mesobasal region of horn (Fig. 23B), tomentum ending slightly after basal protuberance, not reaching dorsal tooth, punctures thin and moderately dense on frontal and lateral surface of horn. Clypeus acuminate, sides slightly sinuous, apex convex, corners slightly round, sides covered by tomentum, apex bare, punctures thin and moderately dense on apex. Ocular canthi elongate, anterior margin sinuous, slightly protruded medially, tip sharp, posterior margin almost straight, surface basally and medially covered by tomentum, tomentum not reaching tip nor posterior margin (Fig. 24F); canthi carinae curved and strong, prominent. **Mouthparts:** Mentum pear-shaped, apex slightly concave; sides densely covered by tomentum. Mandibles with two strong teeth, outer edge round from apical corner to base; surface on outer edge covered by an oblong area tomentose. Maxilla with two strong teeth parallel, maxillary palpomere III pedicelate, maxillary palpomere IV almost 2.5 times longer than palpomere I. **Thorax:** Pronotum short with same width as the distance between humeral umbones, sides round narrowing towards apex. Thoracic horn strong and slender, triangular in cross-section, directed forward, crossing the line of clypeus, apex acute; presence of a tooth basally on ventral side (Fig. 23B), tomentum dorsally ending in the middle, laterally ending after horn tooth, punctures thin and moderately dense. Pronotal disc tomentose, punctures thin and dense medially becoming moderately dense laterally, anterior margin border more than 2 times thicker than lateral borders. Prosternal process acute medially, tomentum on basal surface and almost all apical surface, except by small zones on apical corners. Metepisternum mainly wrinkled, completely tomentosum, few thin and sparse punctures posteriorly, densely covered by long thin setae. Metasternal plate densely punctate and hirsute, punctures large and dense. **Legs:** Protibia with 3 external teeth increasing in size distally, and 1 short internal tooth near protibial spur. Protibia dorsally mainly covered by tomentum, surface wrinkled on outer edge, except by large

and moderately dense punctures on teeth; ventrally as tomentose as dorsally, outer edge bare near teeth. Profemora tomentose with strong transversal carinae medially almost reaching profemoral apex. Distal protarsomere strongly curved internally; thickened setae basally on inner edge; tarsal claws asymmetric, inferior claw curved, superior claw with a short round tooth basally and a strong protuberance medially. Metafemora completely tomentose, surface wrinkled, with few thin and moderately dense punctures; surface covered by short thin setae, with two rows of short thick setae not reaching metafemoral apex. **Elytra:** Shape 1.9 times longer than wide, sides flattened, surface completely tomentose and punctate, punctures thin and dense irregularly distributed, absence of a row of punctures parallel with elytral suture. Punctures on apical umbones larger than on disc, short thin setae densely distributed on apical region of elytra.

Abdomen: Tergite VIII slightly convex, surface covered by short thin setae moderately dense. Sternites II–VI tomentose, on sternite VI only a small area of apical region bare; sternites II–V densely covered by short thin setae, with longer setae on posterior edges not reaching the middle; sternite VI with short thin setae only on sides, longer setae on posterior margin than on disc. **Aedeagus:** Parameres symmetric; in caudal view, apical half slender as long as basal half, apex round and flat, inner edge strongly concave, outer edge strongly prominent medially (Fig. 24A). In lateral view, apex of phallobase short and round, almost as long as basal portion of phallobase; parameres slightly concave dorsally near apex, tip hooked downward, presence of a basal longitudinal carinae sinuous and short (Fig. 24B). In ventral view, ventral carinae continuous with outer edge of parameres, resembling a boomerang (Fig. 24C).

Measurements of holotype. Body length: 29.4 mm. Cephalic horn length: 11.7 mm. Elytral length: 17.7 mm. Elytral width: 9.2 mm. Pronotal width: 10.7 mm. Protibial length: 9.2 mm. Thoracic horn length: 14.4 mm.

Female. Body oblong, pronotum wider than in males (Fig. 25A). **Head:** Cephalic horns absent. Frons with two strong triangular tubercles near ocular canthi, completely covered by tomentum from apex to vertex (Fig. 6F); frons covered by C-punctures large and dense, tubercles with annular punctures thin and moderately dense. Clypeus trapezoidal with two teeth at apical corners, edges strongly deflected upward, surface of clypeus and frons strongly concave (Fig. 25B); clypeal surface covered by C-punctures large and dense. Ocular canthi short, subtrapezoidal, anterior margin sinuous, anterior corner round, posterior margin concave, posterior corner acute, tip straight and oblique (Fig. 6F), tomentum only present on anterior half. **Mouthparts:** Mentum pear-

shaped with apex round, apical half 1.7 times shorter than basal half (Fig. 7F). Mandibles with outer edge strongly protruded apically, straight medially and basally; tomentum absent. **Thorax:** Pronotum weakly convex, thoracic horn absent, anterior margin weakly prominent medially, sides slightly acuminate; pronotum wider than distance between humeral umbones. Pronotal punctures tomentose, large and dense punctures on disc, becoming more coalescent laterally and smaller medially, borders almost completely covered by continuous punctures, only the middle of anterior and posterior margins not bordered (Fig. 25A). Metepisternum non-tomentose basally and on inner edge, in these areas covered by large and dense punctures; setae thin and long, but shorter than in males. Scutellum with a V-shaped tomentose area apically and laterally, punctures tomentose large and dense on disc, setae absent. **Legs:** Protibia mainly non-tomentose, in dorsal view, only with a small area of tomentum posteriorly to basal tooth; tomentose punctures near tomentose area, C-punctures on teeth and near apex. Profemoral carinae inconspicuous. Metafemora strongly punctate, punctures moderate and moderately dense mixed with thin tomentose punctures on apex. Metafemora and metatibiae thicker and less tomentose than in males. **Elytra:** Surface tomentose, as flattened as in males. Punctures thin and dense on disc, more carved than in males. Epipleura non-tomentose basally, with a thin stripe of tomentum apically; presence of a longitudinal furrow medially on epipleura. **Abdomen:** Tergite VIII evenly round in lateral view, apex acuminate, surface tomentose; punctures thin and dense on disc becoming denser on sides, presence of microsetae on disc. Sternites IV–V less tomentose than VI–VII, short thin setae on surface of sternites, only sternite VII with longer setae on posterior margin than on disc. Sternite VIII with a transversal stripe of tomentum, punctures thin and moderately dense on disc, large and dense punctures on posterior margin, C-punctures on anterior margin; short thin setae on posterior margin.

Measurements of female. Body length: 28.4 mm. Elytral length: 17.5 mm. Elytral width: 8.8 mm. Head length: 3.4 mm. Pronotal width: 13.1 mm. Protibial length: 7.9 mm.

Geographic distribution. Costa Rica: Alajuela, Guacanaste, Heredia. Nicaragua: Chontales (Fig. 30A).

Material examined. **Type** male (NHM) labeled: a) “Lectotype”, b) “Syntype”, c) “Type”, d) “B.C.A. col. II (2)/ *Lycomedes/ beltianus*”, e) “Chontales/ Nicaragua/ T. Belt”, f) “*Lycomedes/ beltianus/ Bates*”, g) “Lectotypus/ *Spodistes/ beltianus/ Bates/ America*”. **Allotype** (NHM) labeled: a) “Syntype”, b) “Type”, c) “B.C.A. col. II (2)/

Lycomedes/ beltianus”, d) “Chontales/ Nicaragua/ T. Belt”, e) “*Lycomedes/ beltianus/* Bates f#”.

Remarks. *Spodistes beltianus* is one of the rarest species in this genus. Ratcliffe (2003) collected three specimens in premontane areas (400-700m height) throughout the Guanacaste Cordillera and Central Cordillera, Costa Rica. Besides those records, I only have access to the couple of type-specimens described by Bates (1888), which were collected in Chontales, Nicaragua, by T. Belt. As we do not know where exactly in Chontales Belt collected those specimens, we only can hypothesize that was in an area of Isthmian-Atlantic moist forest, because in Costa Rica *S. beltianus* occurs in that ecoregion. It appears that the mountain ranges of Costa Rica separates *S. beltianus* from *S. batesi*, with the first species distributed on the eastern side and the late species occurring on western side.

***Spodistes armstrongi* Dechambre, 1994**

(Figs. 24, 26, 29–30)

Spodistes armstrongi Dechambre 1994: 149 (original description); Ratcliffe 2002: 36 (checklist to Panama); Ratcliffe 2003: 419 (catalogue to Costa Rica and Panama).

Diagnosis. *Spodistes armstrongi* differs from other species (except *S. beltianus*) by the cephalic horn projected forward with a simple apex acute followed posteriorly by a dorsal tooth (Fig. 26B). In *S. armstrongi* males have cephalic horn with no tooth basally or with an inconspicuous protuberance near base (Fig. 26B); thoracic horn with a distinct tooth ventrally reaching frontal surface of pronotum (Fig. 26B); ocular canthi elongate with apical protuberance strong (Fig. 24G); parameres in dorsal view with apex wider than in *S. beltianus*, tip oblique (Fig. 24D); parameres in lateral view with apical concavity smooth, posterior phallobase with corners distinctly acute (Fig. 24E). For comparisons with *S. beltianus* see the Diagnosis section of that species.

Redescription. Holotype. Male. **Color:** Head, pronotum, elytra, abdominal sternites and the main part of the legs tomentose, color light gray; ventral surface and medioapical portion of cephalic horn, medioapical portion of thoracic horn, and all the tarsi non tomentose (Fig. 26A, B). **Head:** Cephalic horn triangular in cross-section, 2.3 times longer than head, slightly curving upwards, base dorsally with a small bump at the end of tomentose area, apex acute, presence of a strong tooth dorsally near apex forming

an angle of almost 90° (Fig. 26B). Punctures thin and dense. Ocular canthi slender; anterior margin sinuous with base distinctly concave, medially convex, narrowing to a thin and acute apex (Fig. 24G). **Thorax:** Pronotum convex with a strong thoracic horn projecting forward, with apex diagonal towards cephalic horn apex; ventral surface of horn with strong round protuberance basally (Fig. 26B); in dorsal view, pronotal sides almost straight posteriorly, slightly oblique anteriorly; punctures on pronotal disc thin and dense. Scutellar plate acuminate, apex round, surface tomentose except by a thin U-shaped area apically and laterally. **Elytra:** Form 2.1 times longer than wide, with round aspect. Presence of thin and dense punctures, denser near elytral outer edges. Apical umbones round and distinctly protuberant in lateral view. **Legs:** Protibia tridentate, with teeth increasing in size distally. Distal tarsomere of protarsi as long as protarsomeres I-IV together, inner edge with a small tooth basally, concave medially, widening apically; presence of long and thick setae near basal tooth of distal protarsi. Claws of protarsi asymmetric, superior claw with short acuminate tooth basally and a round protuberance medially, inferior claw curved and acute, shorter than superior claw. Pro-, meso-, and metafemora covered by tomentum ventrally. Meso- and metatarsi with almost same length, but tarsomere V of metatarsi thicker than in mesotarsi. **Abdomen:** Tergite VIII transverse, round in lateral view, inferior edge with a small concavity medially; surface completely tomentose. Sternite VIII tomentose posteriorly, bare anteriorly; presence of thin setae on posterior margin. **Aedeagus:** Parameres symmetric. In caudal view, apical half longer and slender than basal half, outer margins angulate medially, presence of a strong carina on inner side reaching the middle portion of parameres (Fig. 24D). In lateral view, posterior phallobase shorter than parameres. Parameres subtriangular with apical half distinctly slender, tip of parameres slightly downwards, ventral edge almost straight (Fig. 24E).

Measurements of holotype. Body length: 29.4 mm. Cephalic horn length: 13.8 mm. Elytral length: 18.6 mm. Elytral width: 8.5 mm. Pronotal width: 11.3 mm. Protibial length: 7.6 mm. Thoracic horn length: 14.9 mm.

Geographic distribution. Panama: Provincia de Panama (Fig. 30B).

Material examined. Holotype male (MNHN) labeled: a) “Cerro Azul – Cerro Jefe/ PANAMA 3000 ft/ vi.1992 L. Armstrong”, b) “*Spodistes* m#/ *armstrongi* n. sp./ HOLOTYPE/ R.-P. DECHAMBRE det. 1994”, c) “MUSÉUM PARIS/ coll. GÉNÉRALE”, d) “HOLOTYPE”, e) “MNHN/ EC2470”.

Remarks. *Spodistes armstrongi* shares with *S. beltianus* not only the distinct type of cephalic horn in males, but also the status of the rarest species in the genus. Up until now, this species was only found in Panama, on areas of Isthmian-Atlantic moist forests and on patches of Eastern Panamanian montane forests (near Cerro Azul), apparently not crossing the isthmus of Panama. According to Ratcliffe (2003), one of the main spots to collect *S. armstrongi* was deforested in Cerro Azul. We could not have access to females of *S. armstrongi*, so they were not included in our proposed key to species of *Spodistes* below.

Key to species of *Spodistes* Burmeister, 1847

(Key modified from Ratcliffe 2003)

- 1. Head and pronotum with horns, both horns reduced in minor specimens (Figs. 1A–B, 9A–B, 12A–B, 13A–B, 18A–B, 20A–B, 21A–B, 23A–B, 26A–B). Mentum tomentose on sides ventrally (Fig. 4A–E) (males)..... 2
 - Head and pronotum without horns, presence of triangular tubercles near ocular canthi (Figs. 5A–B, 10A–B, 17A–B, 19A–B, 22A–B, 25A–B). Mentum with no tomentum ventrally (Fig. 7A–F) (females)..... 9
- 2. Cephalic horn apex acuminate (Fig. 23B, 26B)..... 3
 - Cephalic horn apex bifurcate (Fig. 1A, 9A, 12A, 13A, 18A, 21A)..... 4
- 3. Cephalic horn with a conspicuous tooth dorsally near base of horn (Fig. 23B). Thoracic horn with a conspicuous tooth ventrally, distant from frontal margin of pronotum (Fig. 23B). Parameres in caudal view with apex thin, tip round (Fig. 24A)..... ***S. beltianus* (Bates, 1888)**
 - Cephalic horn with no tooth dorsally near base of horn or with an inconspicuous protuberance (Fig. 26B). Thoracic horn with a conspicuous tooth ventrally near frontal margin of pronotum (Fig. 26B). Parameres in caudal view with apex subrectangular, tip oblique (Fig. 24D)..... ***S. armstrongi* Dechambre, 1994**
- 4. Presence of a conspicuous tooth near apical bifurcation of cephalic horn (Figs. 1B, 9B, 12B)..... 5
 - Absence of tooth near apical bifurcation of cephalic horn (Figs. 13B, 18B, 21B).....7
- 5. Clypeus with lateral margins oblique, apex bilobate (Fig. 2D). Presence of an inconspicuous or conspicuous protuberance near base of cephalic horn (Fig. 9B)..... ***S. grandis* Sternberg, 1903**

- Clypeus with lateral margins concave, apex round (Fig. 2C, E). Absence of protuberance near base of cephalic horn (Fig. 1B, 12B)..... 6
- 6. Pronotal lateral margin round (Fig. 1A). Elytral punctures almost inconspicuous (Fig. 1A). Lateral margins of clypeus strongly concave (Fig. 2E). Parameres with outer edge strongly angulate, like a boomerang (Fig. 3A)..... ***S. hopei* Arrow 1902**
- Pronotal lateral margin acute (Fig. 12A). Elytral punctures conspicuously visible (Fig. 12A). Lateral margins of clypeus slightly concave (Fig. 2C). Parameres with outer edge round (Fig. 3G)..... ***S. angulicollis* Dechambre, 1992**
- 7. Presence of conspicuous carinae reaching cephalic horn basally (Fig. 18B). Parameres in lateral view slightly concave medially and apically (Fig. 15E). Outer edge of mandibles truncate (Fig. 4D)..... ***S. batesi* Arrow, 1902**
- Absence of carinae reaching cephalic horn basally (Fig. 13B, 21B). Parameres in lateral view straight or round medially and apically (Fig. 15B, H). Outer edge of mandibles round or subtrapezoidal (Fig. 4C, E)..... 8
- 8. Pronotal disc completely tomentose (Fig. 13A). Lateral margins of pronotum round (Fig. 13A). Mandibles with outer edge conspicuously round (Fig. 4C). In caudal view apex of parameres almost touching each other, inner edge almost straight medially (Fig. 15A). Parameres in lateral view with ventral edge round near apex (Fig. 15B)..... ***S. mniszehi* (Thomson, 1860)**
- Pronotal disc not tomentose medially (Fig. 21A). Lateral margins of pronotum angulate (Fig. 21A). Mandibles with outer edge subtrapezoidal (Fig. 4E). In caudal view apex of parameres distant, inner edge concave (Fig. 15G). Parameres in lateral view with ventral edge straight near apex (Fig. 15H)..... ***S. monzoni* Warner, 1992**
- 9. Mandibles with conspicuous carina, in dorsal view (Fig. 8B). Abdomen almost semicircular, sternite VII width equivalent to more than 6.5 times the sternite VIII length (Fig. 6C). Distance between cephalic tubercles more than 3 times the width of clypeal apex (Fig. 6E)..... ***S. grandis* Sternberg, 1903**
- Mandibles with carina absent, in dorsal view (Fig. 8A, C–F). Abdomen acute, sternite VII equivalent to less than 6.5 times the sternite VIII length (Fig. 6D). Distance between cephalic tubercles less than 3 times the width of clypeal apex (Fig. 6F)..... 10
- 10. Apex of mentum distinctly acute, corners emarginate (Fig. 7E). Meso- and metatibial apex with thick setae round at outer edge (Fig. 27A). Mandibles with outer edge convex apically, oblique towards base (Fig. 8E)..... ***S. monzoni* Warner, 1992**

- Apex of mentum round, corners round (Fig. 7 A, C, D, F). Meso- and metatibial apex with thick setae acute at outer edge (Fig. 27B). Mandibles not as above (Figs. 8A, C, D, F)..... 11
- 11. Procoxae with punctures large and coalescent (Fig. 27C). Hypopygium with a distinct protuberance near anterior corners (Fig. 27C) Ventral carina on protibiae reaching medial tooth (Fig. 27E). Tergite VIII slightly concave near anterior margin, in lateral view (Fig. 16D)..... *S. mniszewski* (Thomson, 1860)
- Procoxae with punctures thin and not coalescent (Fig. 27D). Hypopygium with no protuberance near anterior corners (Fig. 27D) Ventral carina on protibiae not trespassing basal tooth (Fig. 27F). Tergite VIII completely round or evenly round, in lateral view (Fig. 16E)..... 12
- 12. Outer edge of mandibles straight (Fig. 8F). Clypeal apex less than 2 times wider than distance between cephalic tubercles (Fig. 6F)..... *S. beltianus* (Bates, 1888)
- Outer edge of mandibles with a slight emargination apically (Figs. 8A, D). Clypeal apex more than 2 times wider than distance between cephalic tubercles (Fig. 6A, 16B)..... 13
- 13. Mandibles elongate, protuberance of outer edge closer from second tooth (Fig. 8D). Mentum slightly elongate with basal half less than 1.2 times longer than apical half (Fig. 7D). Distance between cephalic tubercles less than 3 times wider than transverse eye diameter (Fig. 16B)..... *S. batesi* Arrow, 1902
- Mandibles short, protuberance of outer edge distant from second tooth (Fig. 8A). Mentum slightly short with basal half more than 1.2 times longer than apical half (Fig. 7A). Distance between cephalic tubercles more than 3 times wider than transverse eye diameter (Fig. 6A)..... 14
- 14. Clypeal base concave (Fig. 32A). Clypeal sculpture formed by thin and sparse punctures near apex (Fig. 32B). Tomentum on profemora shortly restricted to distal portion (Fig. 33B). Prosternal anterior portion short and slender (Fig. 33A)..... *S. hopei* Arrow, 1902
- Clypeal base convex (Fig. 32D). Clypeal sculpture formed by deep and large punctures from base to apex (Fig. 32E). Tomentum on profemora widely covering anterior portion in ventral view (Fig. 33E). Prosternal anterior portion slightly long and thick (Fig. 33D)..... *S. angulicollis* Dechambre, 1992

Acknowledgments

We thank all the curators from the cited collections for their contributions of material for this study. We thank Max Barclay, Michael Geiser and Keita Matsumoto for all the support to RS during his time in the Natural History Museum (London, United Kingdom) and for all the help with the photography of specimens. Also, we thank the owner of the YouTube Channel “AKIRA RISING” for the authorization to use his images in this work, and Dr. Diego Mendes for the photographs of specimens at the Instituto Nacional de Pesquisas da Amazônia (INPA). RS and JWM acknowledge the Instituto Nacional de Pesquisas da Amazônia for research support; the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for the PhD scholarship to RS (process number 006/2020) and for the PRONEX Project, edital 016/2006, 1437/2007, coordinated by Dr. José Albertino Rafael (INPA, Manaus, Amazonas, Brazil); and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Sandwich Doctorate scholarship to RS (process number 88881.362061/2019-01). PCG acknowledges the Universal Project, 449366/2014-6.

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Figures

FIGURE 1. Male of *Spodistes hopei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm. Photo by: Keita Matsumoto.

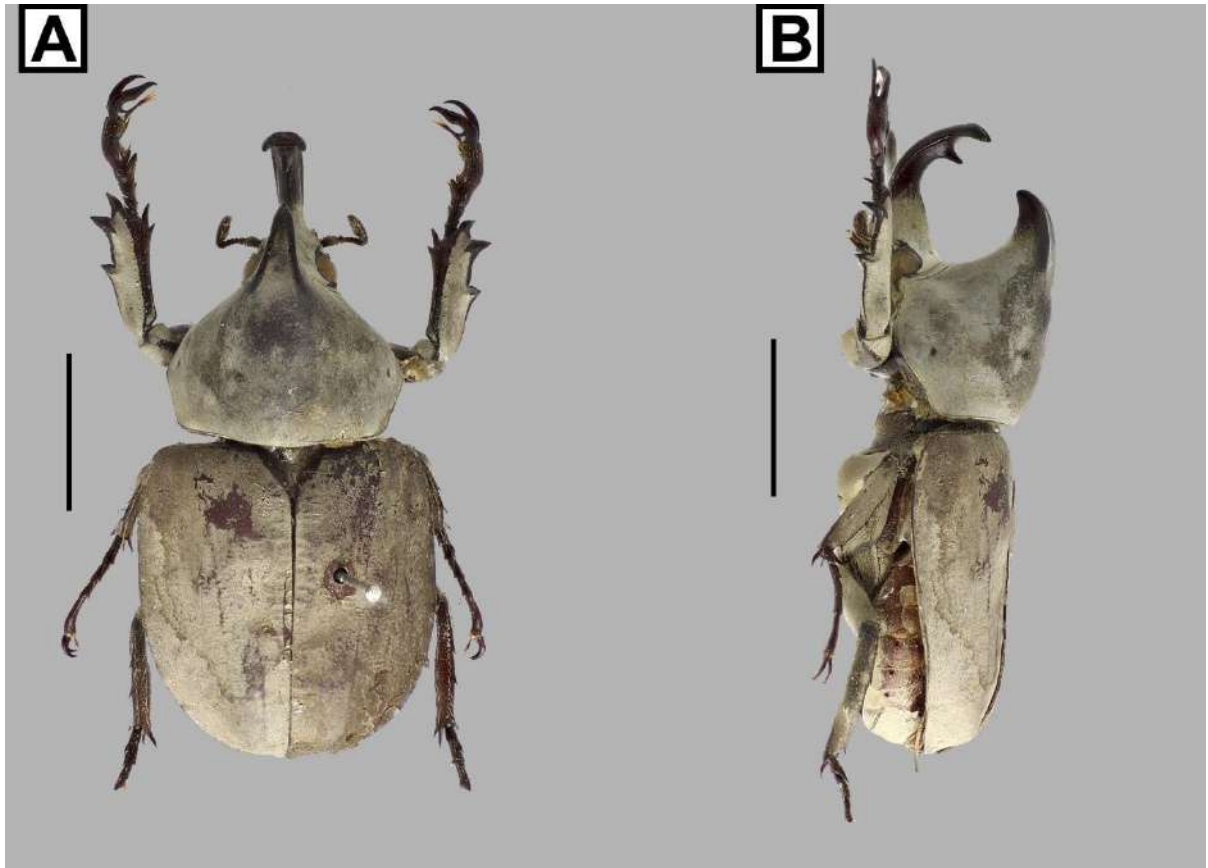


FIGURE 2. Head of *Spodistes hopei*, *Spodistes grandis*, *Spodistes angulicollis*. **A**, Ocular canthus of *S. grandis*; **B**, ocular canthus of *S. angulicollis*; **C**, head of *S. hopei* in frontal view; **D**, head of *S. grandis* in frontal view; **E**, head of *S. angulicollis* in frontal view; **F**, mouthparts of *S. angulicollis* in ventral view. White arrow pointing to outer edge of mandible. Scale bars: 1 mm.

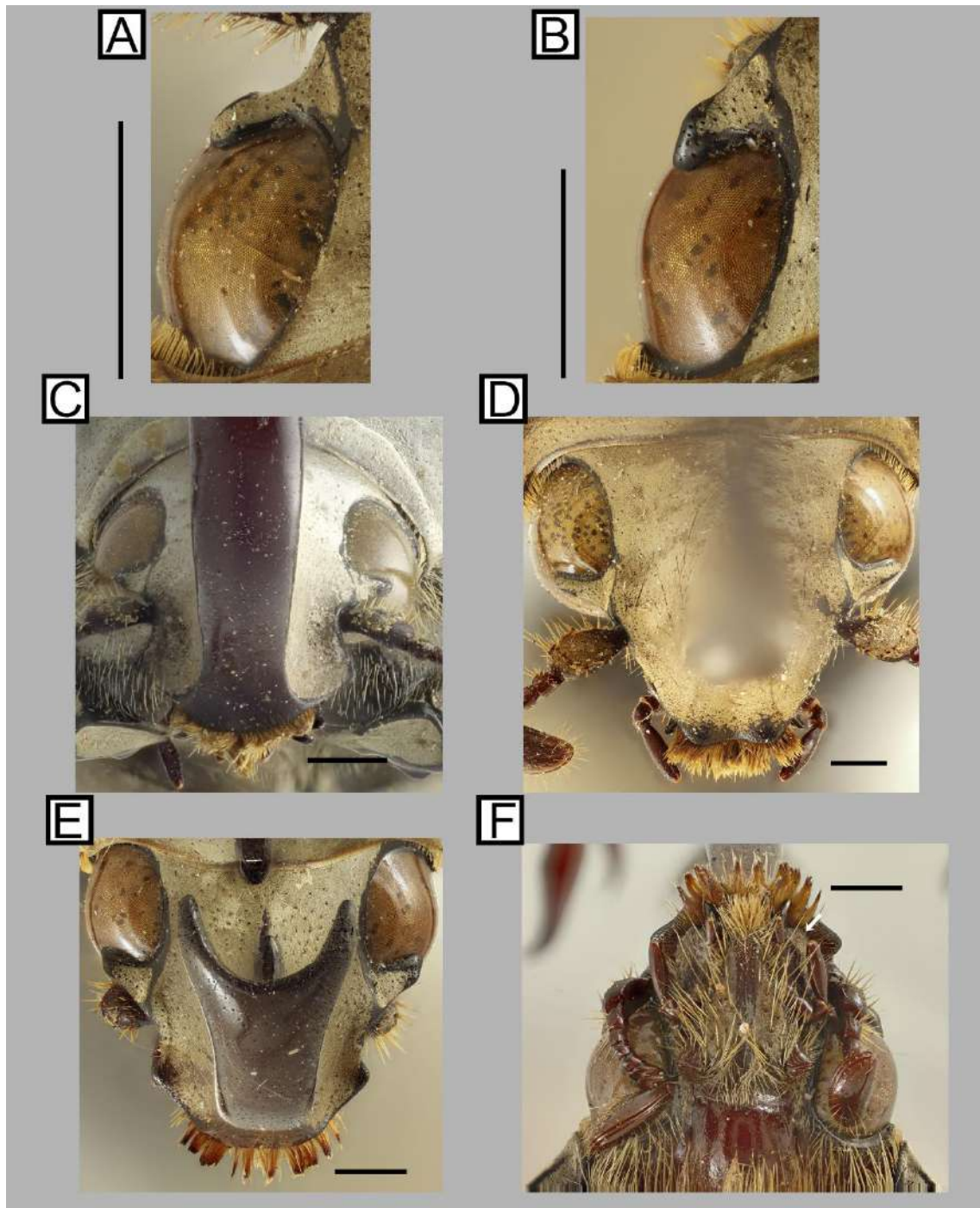


FIGURE 3. Aedeagus of *Spodistes hopei*, *Spodistes grandis*, *Spodistes angulicollis*. **A**, Parameres of *S. hopei* in caudal view; **B**, aedeagus of *S. hopei* in lateral view; **C**, parameres of *S. hopei* in ventral view; **D**, parameres of *S. grandis* in caudal view; **E**, aedeagus of *S. grandis* in lateral view; **F**, parameres of *S. grandis* in ventral view; **G**, parameres of *S. angulicollis* in caudal view; **H**, aedeagus of *S. angulicollis* in lateral view; **I**, parameres of *S. angulicollis* in ventral view. Scale bars: 1 mm.

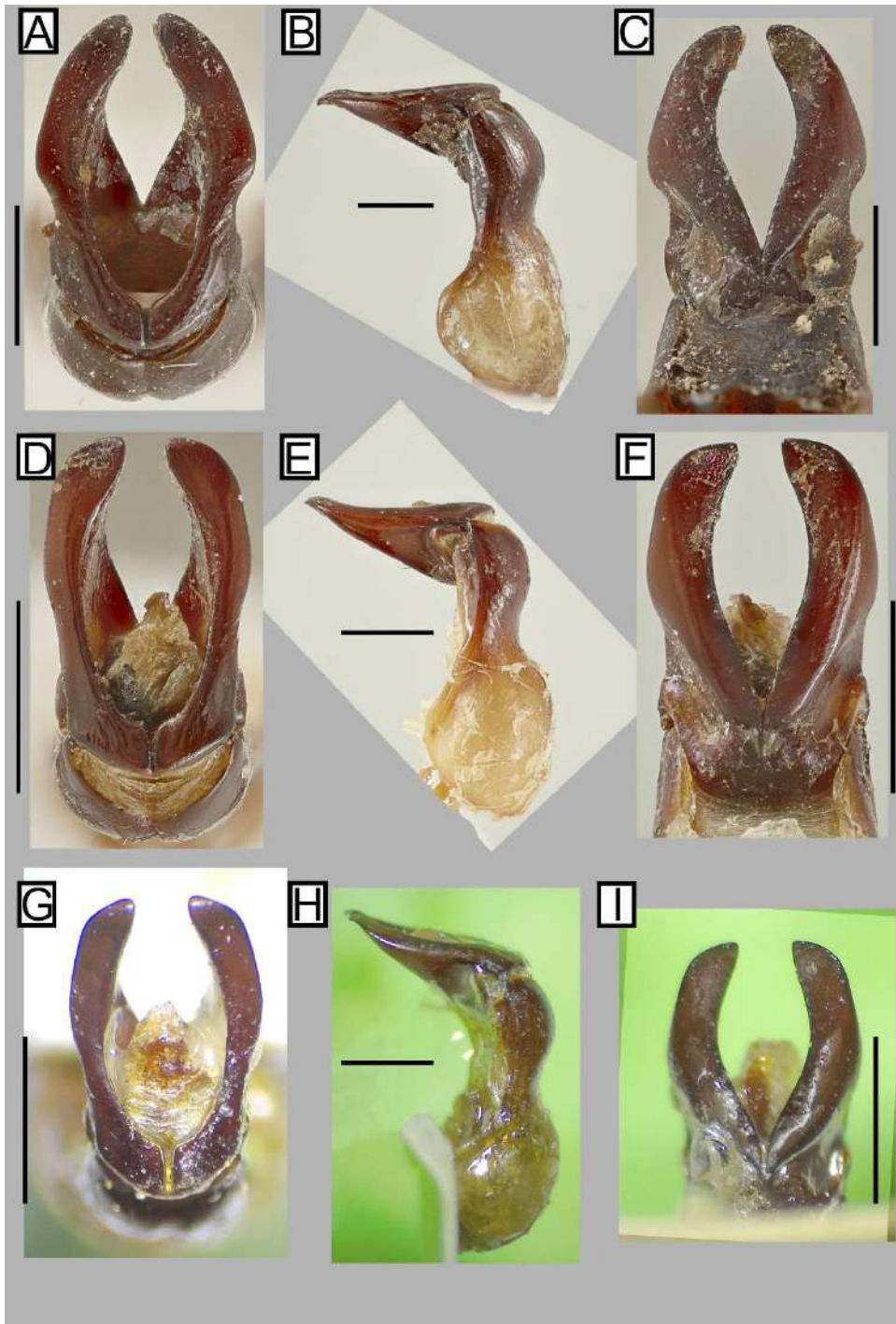


FIGURE 4. Mandibles of male *Spodistes* in ventral view. **A**, Mandible of *S. hopei*; **B**, mandible of *S. grandis*; **C**, mandible of *S. mniszehi*; **D**, mandible of *S. batesi*; **E**, mandible of *S. monzoni*. White arrows pointing to the apical corner of outer edge in D and E. Scale bars: 1 mm.

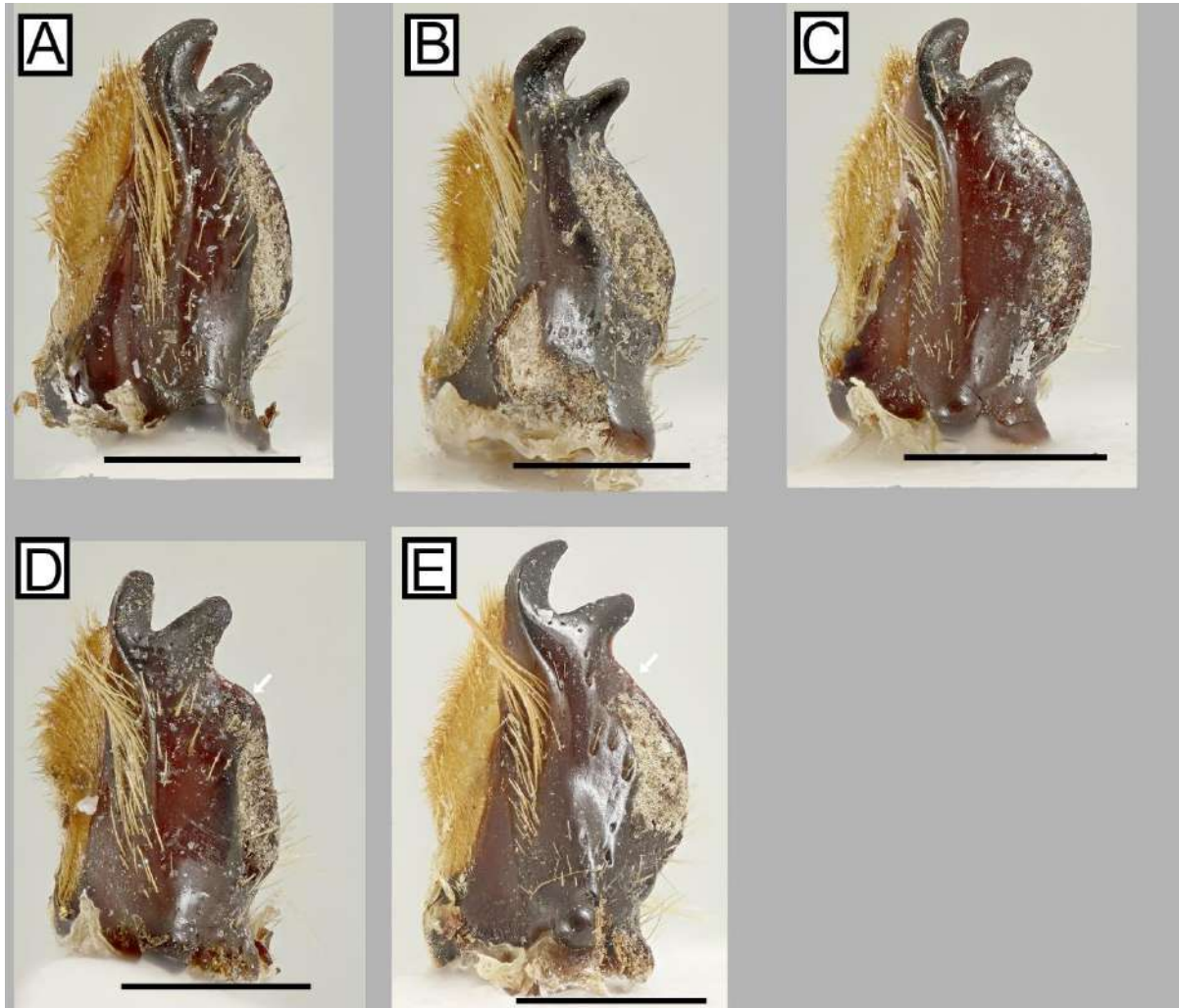


FIGURE 5. Female of *Spodistes hopei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

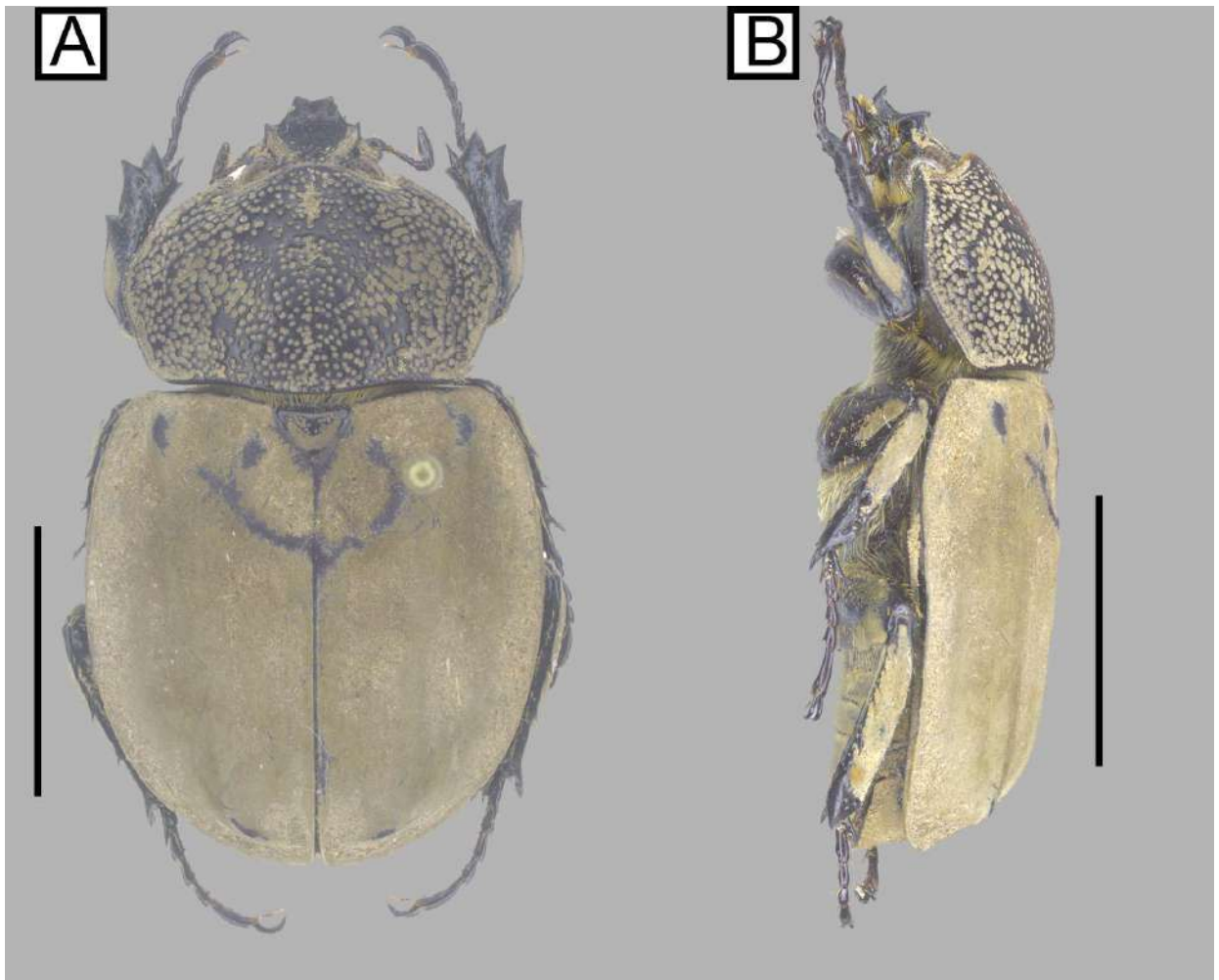


FIGURE 6. Females of *Spodistes hopei*, *Spodistes grandis* and *Spodistes beltianus*. **A**, Head of *S. hopei* in dorsal view; **B**, head of *S. grandis* in dorsal view; **C**, head of *S. beltianus* in dorsal view; **D**, abdomen of *S. grandis* in ventral view; **E**, abdomen of *S. beltianus* in ventral view. White arrows indicating for comparisons the width of clypeal apex, the distance between cephalic tubercles and diameter of the eye, in A–C; white arrows indicating the width of sternite VII related to the length of sternite VIII in D–E. Scale bars: A–C, 1 mm, D–E, 5 mm.



FIGURE 7. Mentum of female *Spodistes* in ventral view. **A**, Mentum of *S. hopei*; **B**, mentum of *S. grandis*; **C**, mentum of *S. mniszewski*; **D**, mentum of *S. batesi*; **E**, mentum of *S. monzoni*; **F**, mentum of *S. beltianus*. Pair of white arrows indicating the length of apical half and basal half of mentum in A and D; white arrows pointing to the apical region of mentum in C and E. Scale bars: 1 mm.

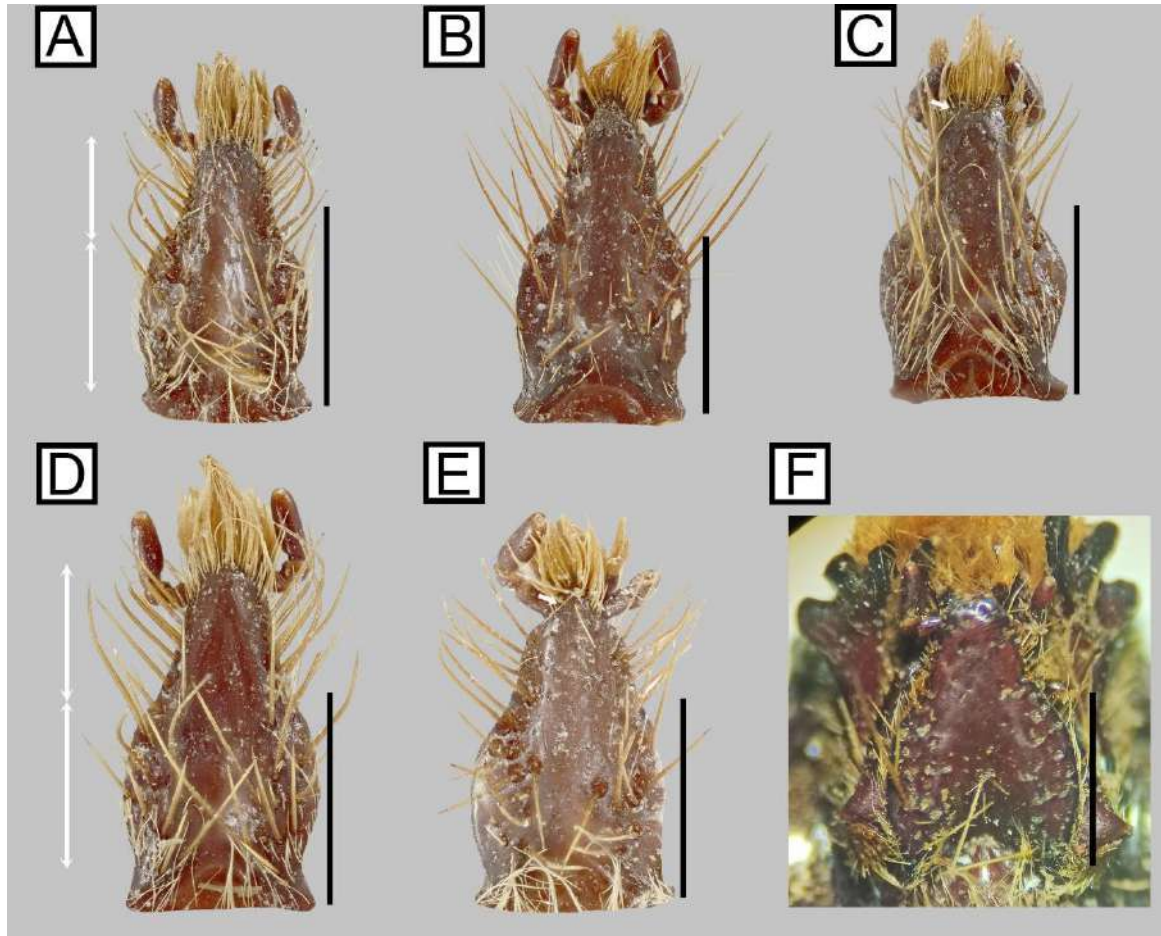


FIGURE 8. Mandibles of female *Spodistes*. **A**, Mandible of *S. hopei* in dorsal view; **B**, mandible of *S. grandis* in dorsal view; **C**, mandible of *S. mniszehi* in dorsal view; **D**, mandible of *S. batesi* in dorsal view; **E**, mandible of *S. monzoni* in dorsal view; **F**, mandible of *S. beltianus* in ventral view. White arrows pointing to indentation of outer edge in A and D; white arrow pointing to carina of apical tooth in B; black arrows pointing to apical corner of outer edge in A and D. Scale bars: 1 mm.

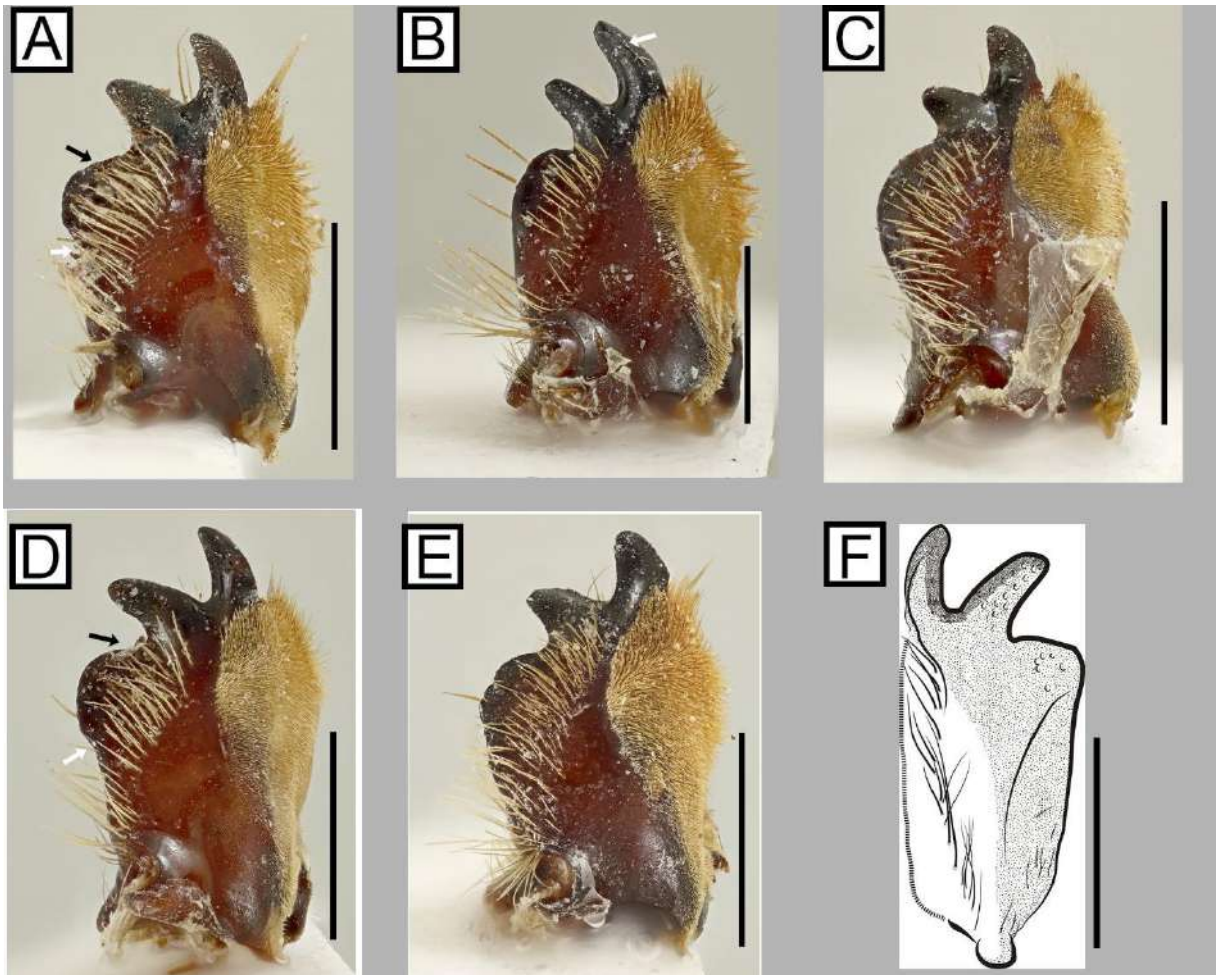


FIGURE 9. Male of *Spodistes grandis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

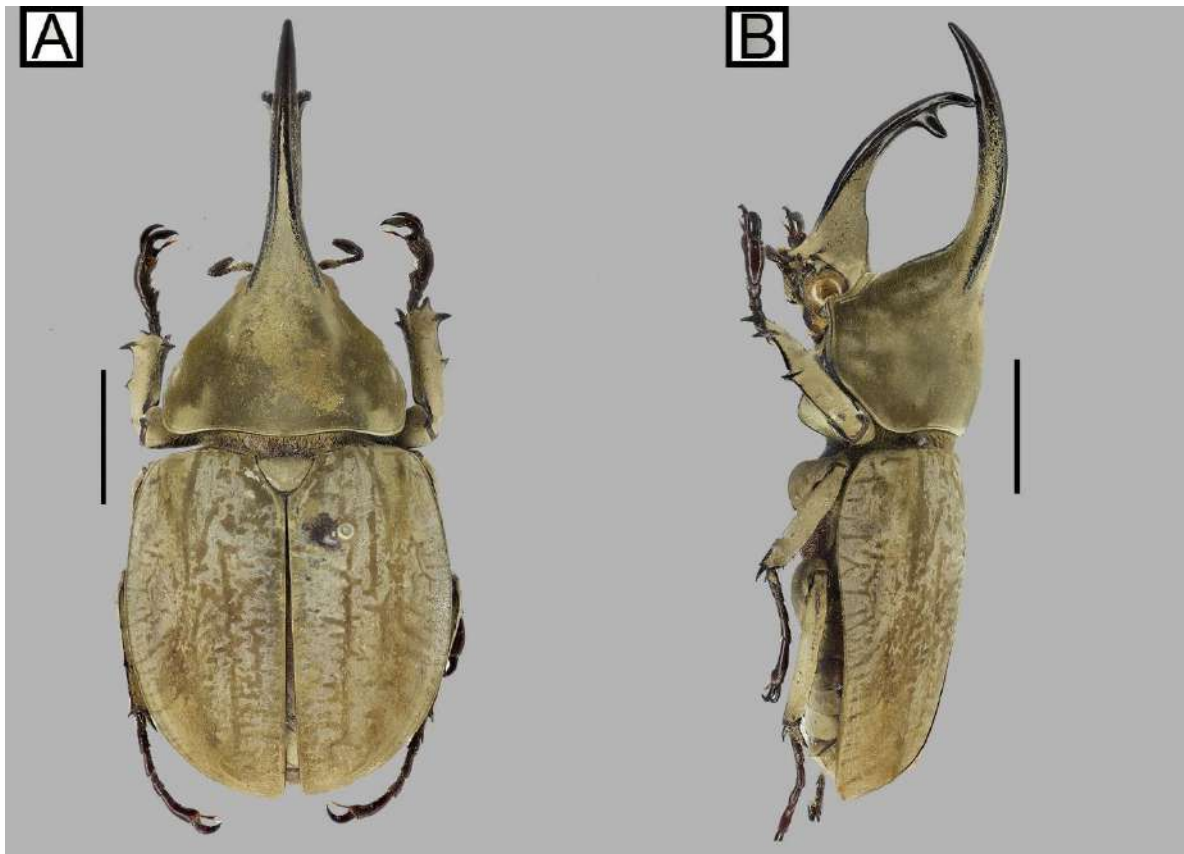


FIGURE 10. Female of *Spodistes grandis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.



FIGURE 11. Mating of *Spodistes grandis*. Image by: YouTube Channel “AKIRA RISING”.



FIGURE 12. Male of *Spodistes angulicollis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

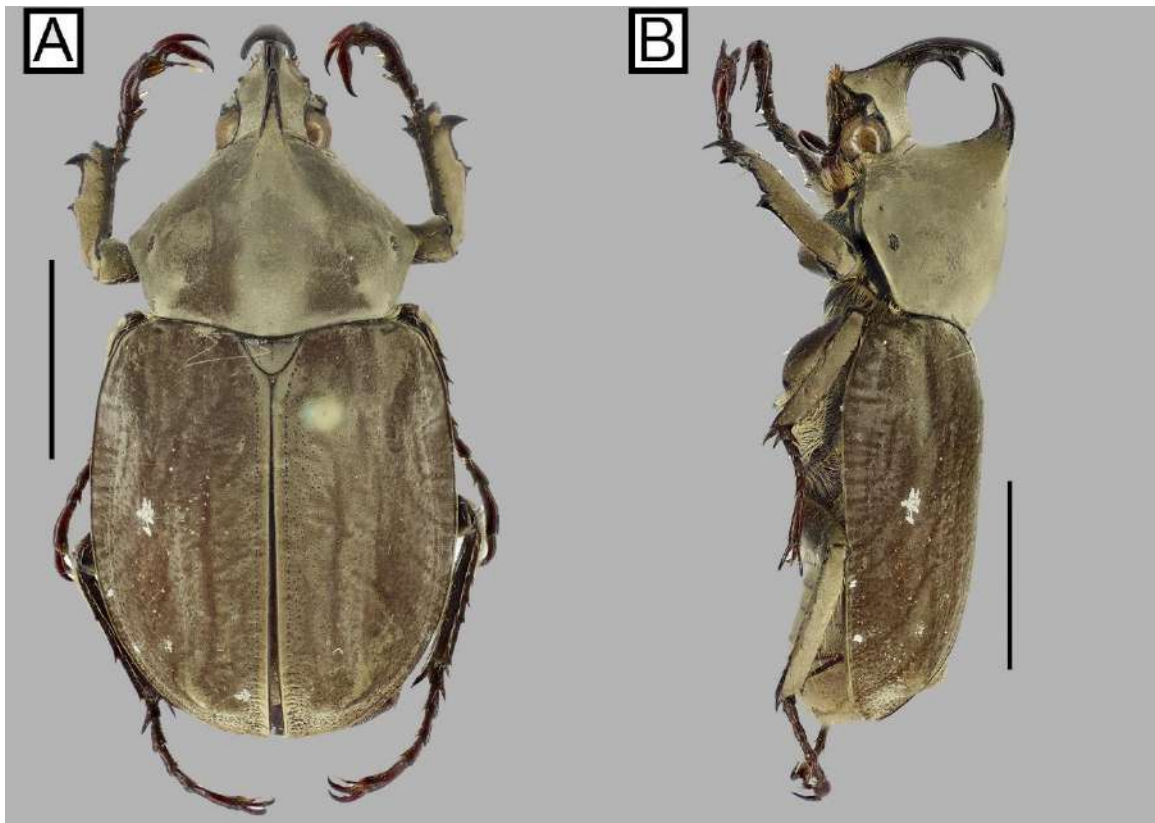


FIGURE 13. Male of *Spodistes mniszewi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

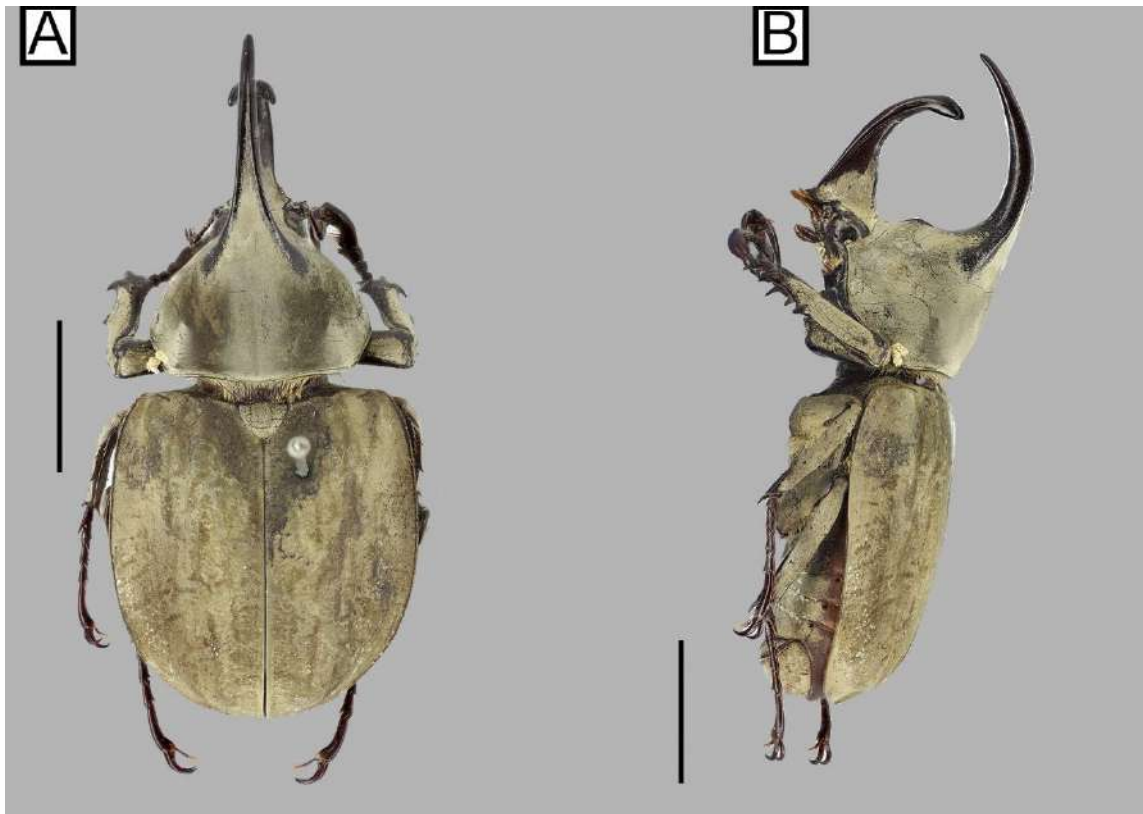


FIGURE 14. **A**, Labrum of *S. mniszewski* male in dorsal view; **B**, labrum of *S. batesi* male in dorsal view; **C**, mentum of *S. batesi* male in ventral view; **D**, mentum of *S. mniszewski* male in ventral view. Scale bars: 1 mm.

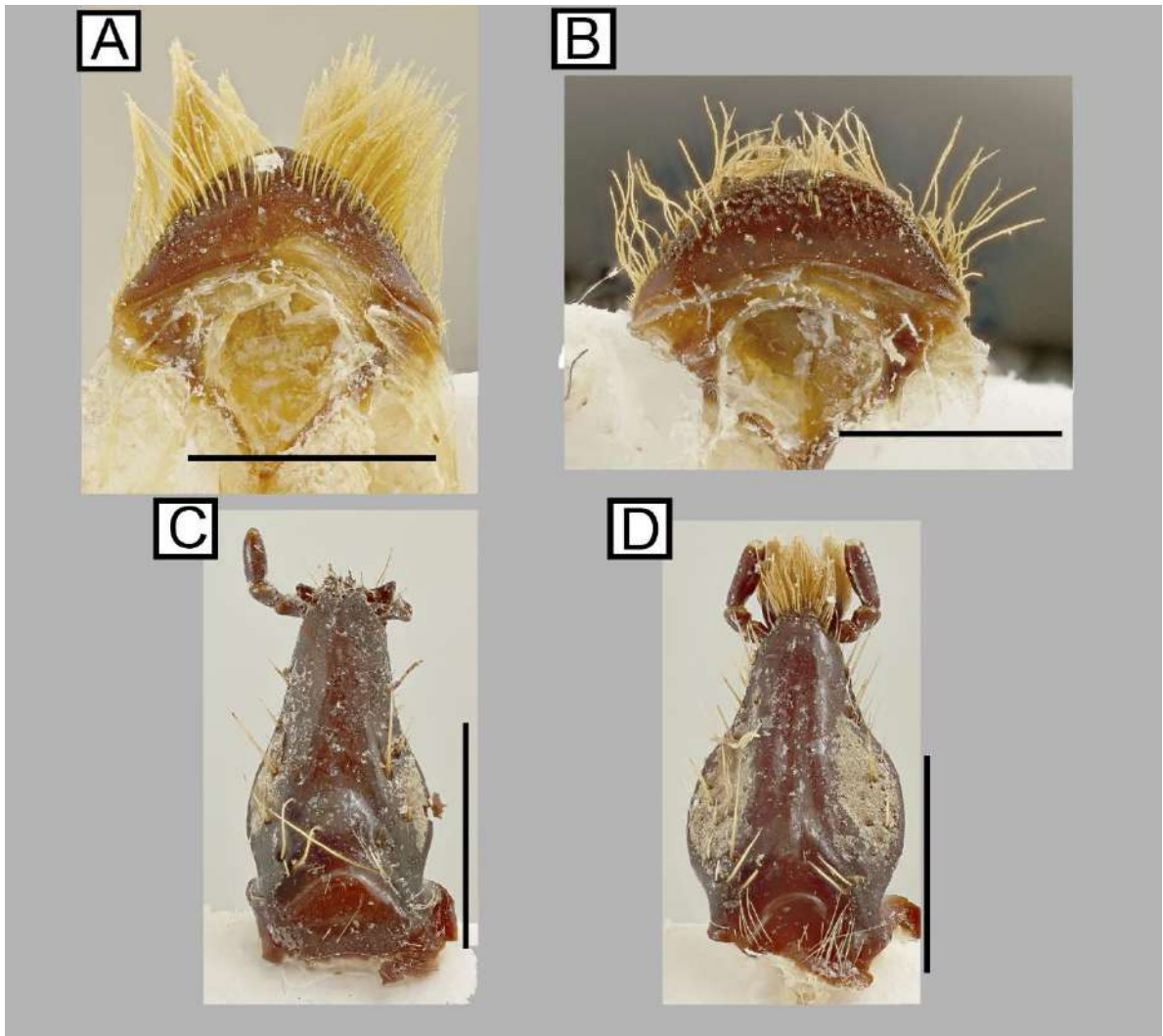


FIGURE 15. Aedeagus of *Spodistes mniszewi*, *Spodistes batesi*, *Spodistes monzoni*. **A**, Parameres of *S. mniszewi* in caudal view; **B**, aedeagus of *S. mniszewi* in lateral view; **C**, parameres of *S. mniszewi* in ventral view; **D**, parameres of *S. batesi* in caudal view; **E**, aedeagus of *S. batesi* in lateral view; **F**, parameres of *S. batesi* in ventral view; **G**, parameres of *S. monzoni* in caudal view; **H**, aedeagus of *S. monzoni* in lateral view; **I**, parameres of *S. monzoni* in ventral view. Black arrows pointing to basal protuberance at outer edge of parameres in F and I. Scale bars: 1 mm.

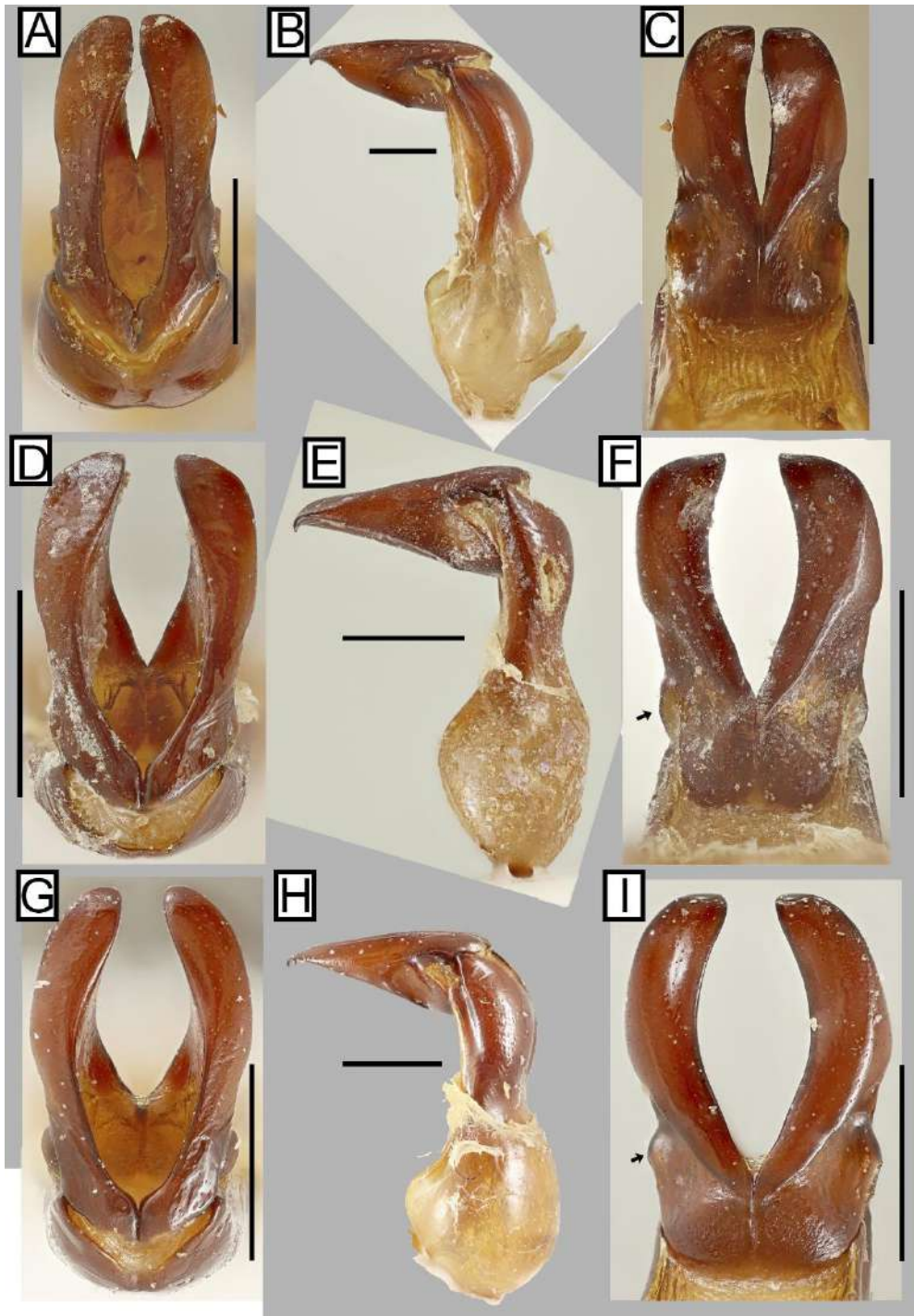


FIGURE 16. Head, abdomen and maxilla of female *Spodistes mniszewi*, *Spodistes batesi*, *Spodistes monzoni*. **A**, Head of *S. mniszewi* in dorsal view; **B**, head of *S. batesi* in dorsal view; **C**, head of *S. monzoni* in dorsal view; **D**, tergite VIII of *S. mniszewi* in lateral view; **E**, tergite VIII of *S. batesi* in lateral view; **F**, tergite VIII of *S. monzoni* in lateral view; **G**, maxilla of *S. mniszewi* in ventral view; **H**, maxilla of *S. batesi* in ventral view; **I**, maxilla of *S. monzoni* in ventral view. White arrows indicating for comparisons the width of clypeal apex, the distance between cephalic tubercles and diameter of the eye, in A–C; black arrows indicating the anterior margin of tergite VIII in D–E; white lines contouring base of galea in G–I. Scale bars: 1 mm.

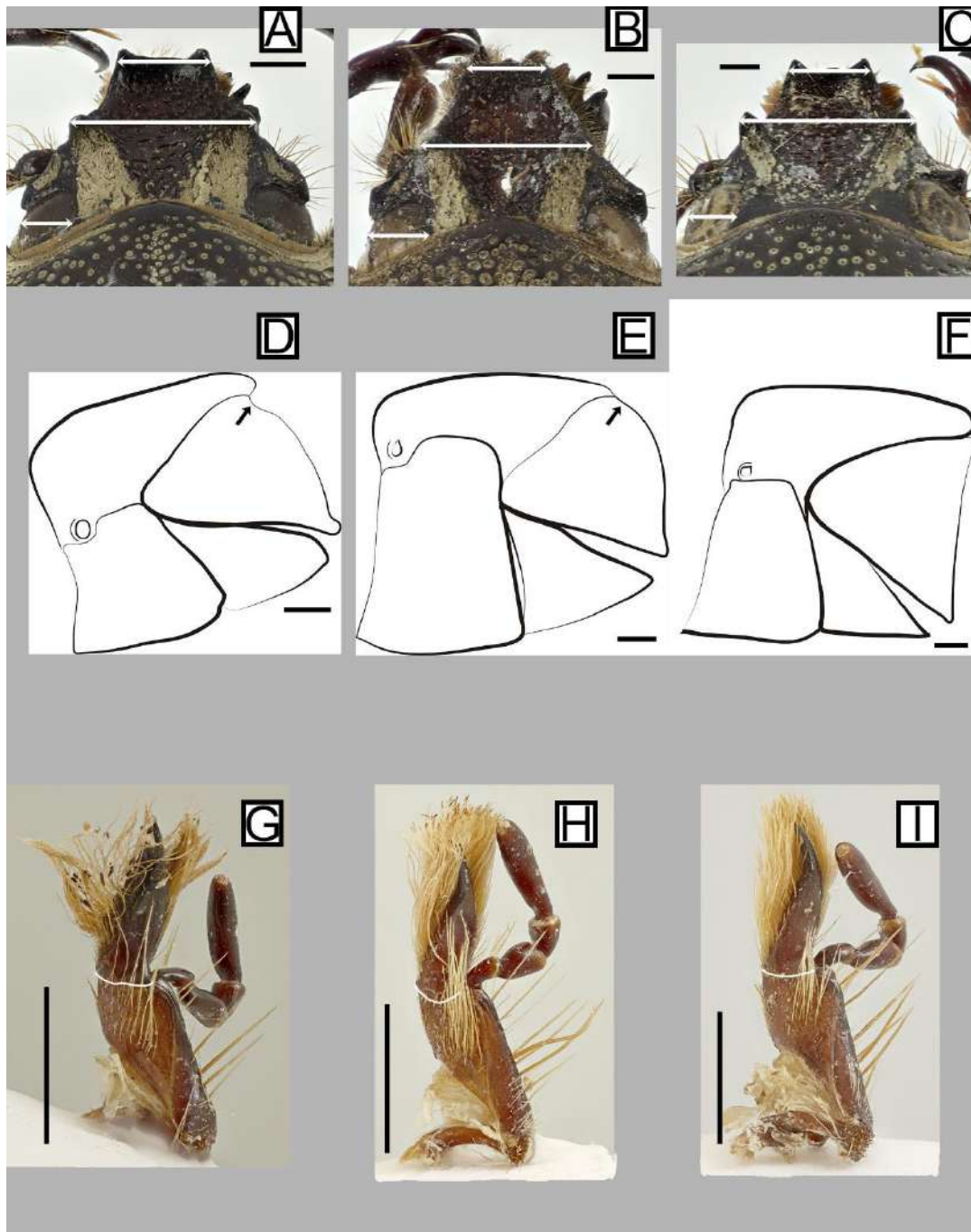


FIGURE 17. Female of *Spodistes mniszечи*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

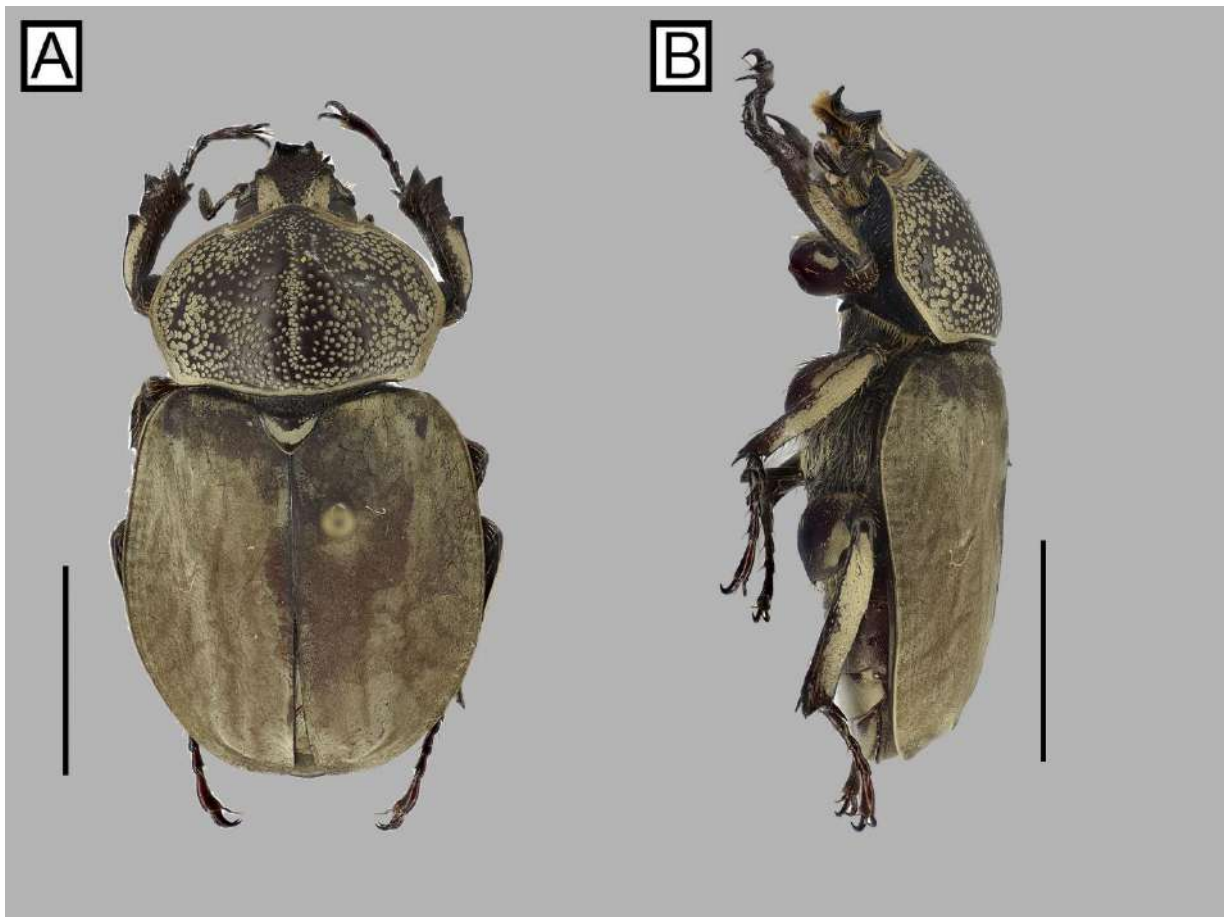


FIGURE 18. Male of *Spodistes batesi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

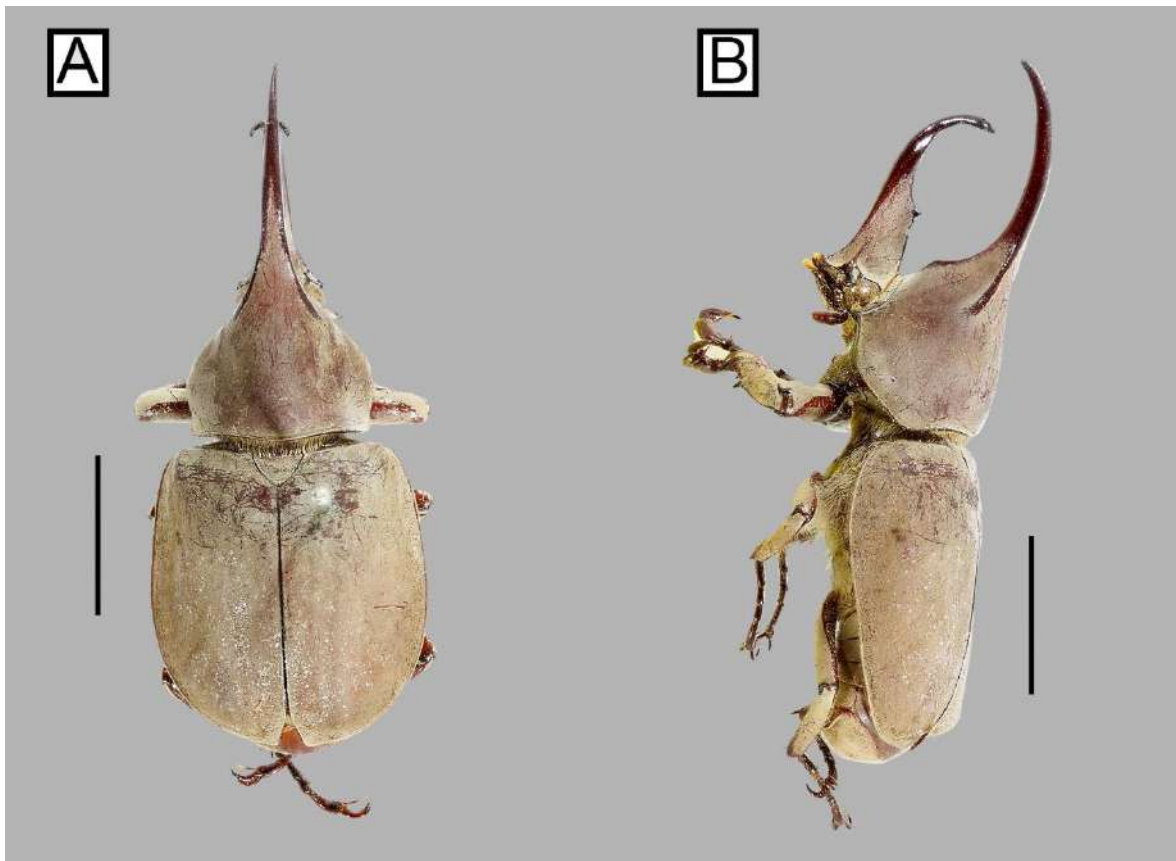


FIGURE 19. Feale of *Spodistes batesi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

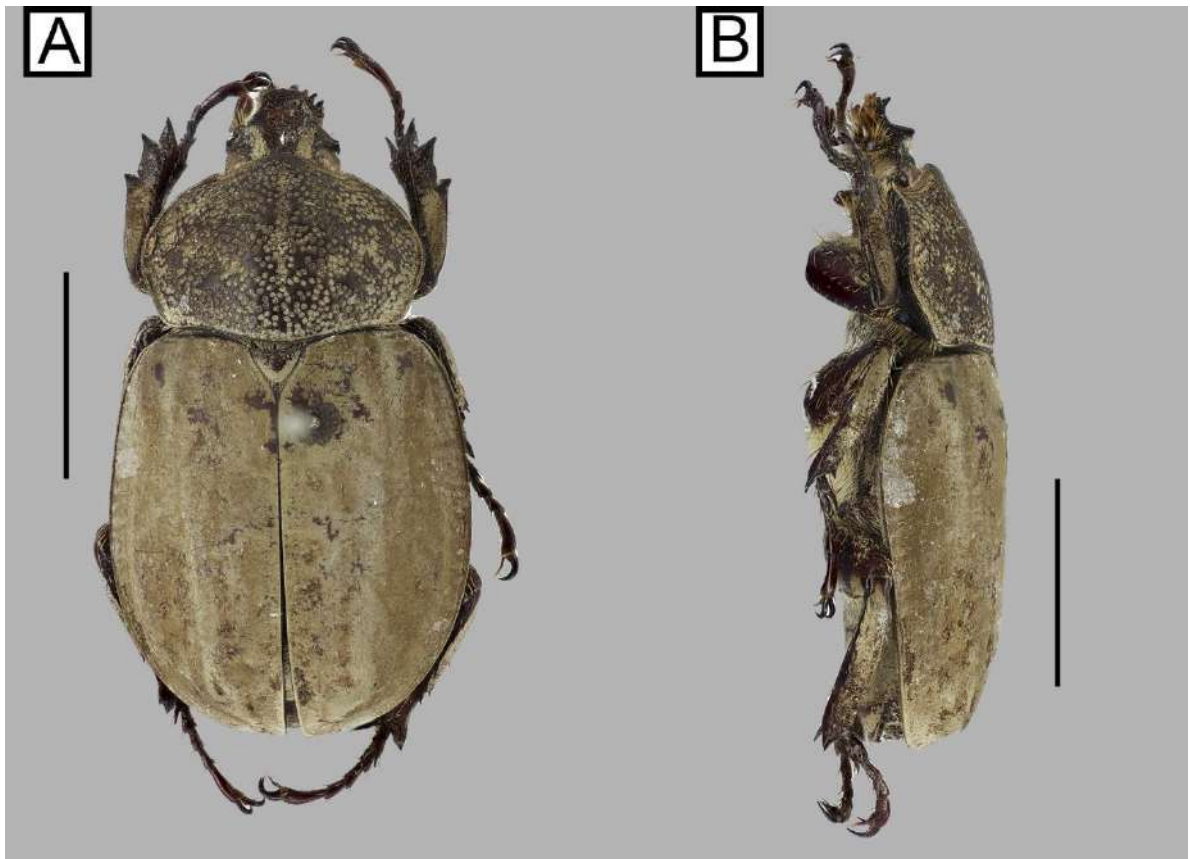


FIGURE 20. Minor male of *Spodistes batesi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

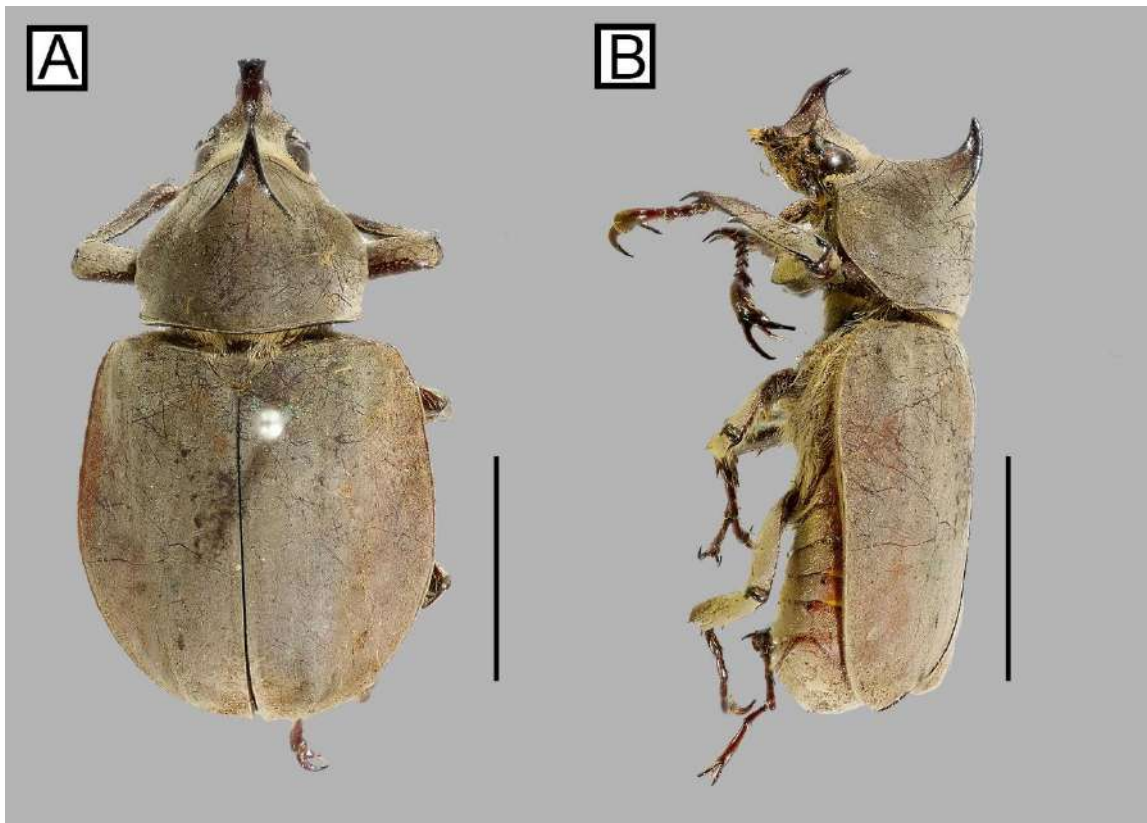


FIGURE 21. Male of *Spodistes monzoni*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

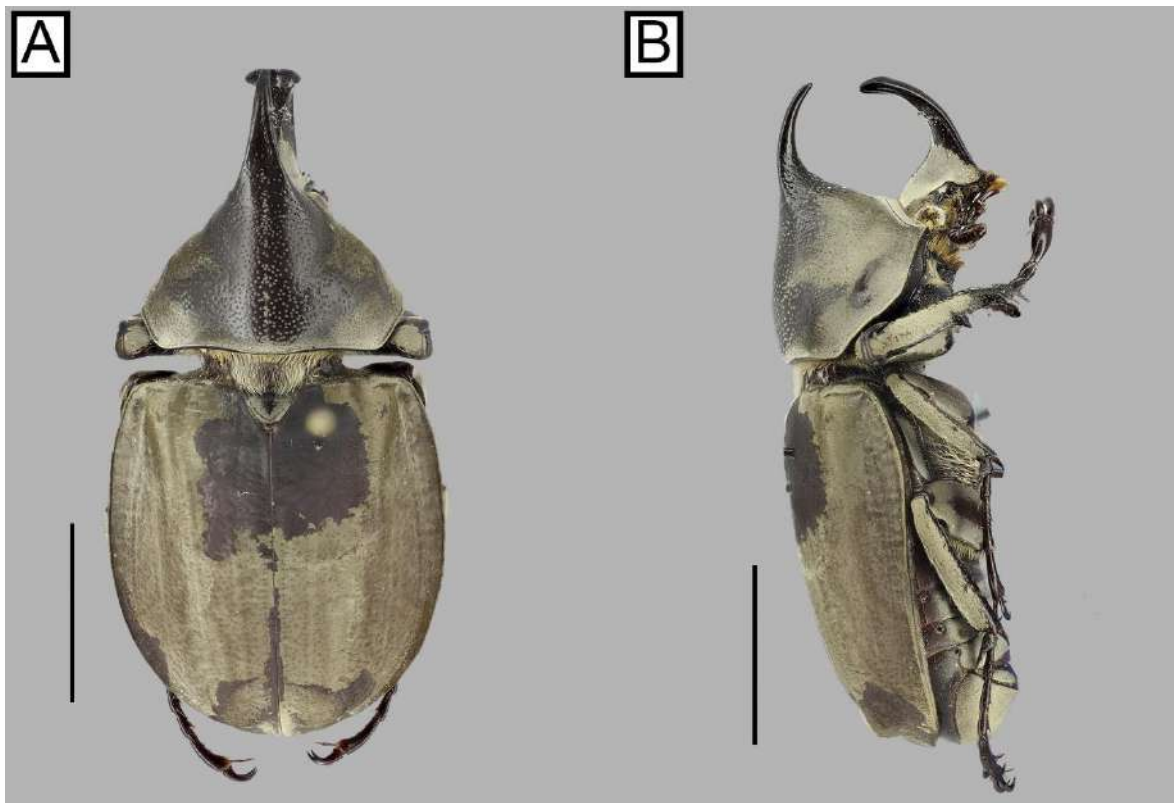


FIGURE 22. Female of *Spodistes monzoni*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

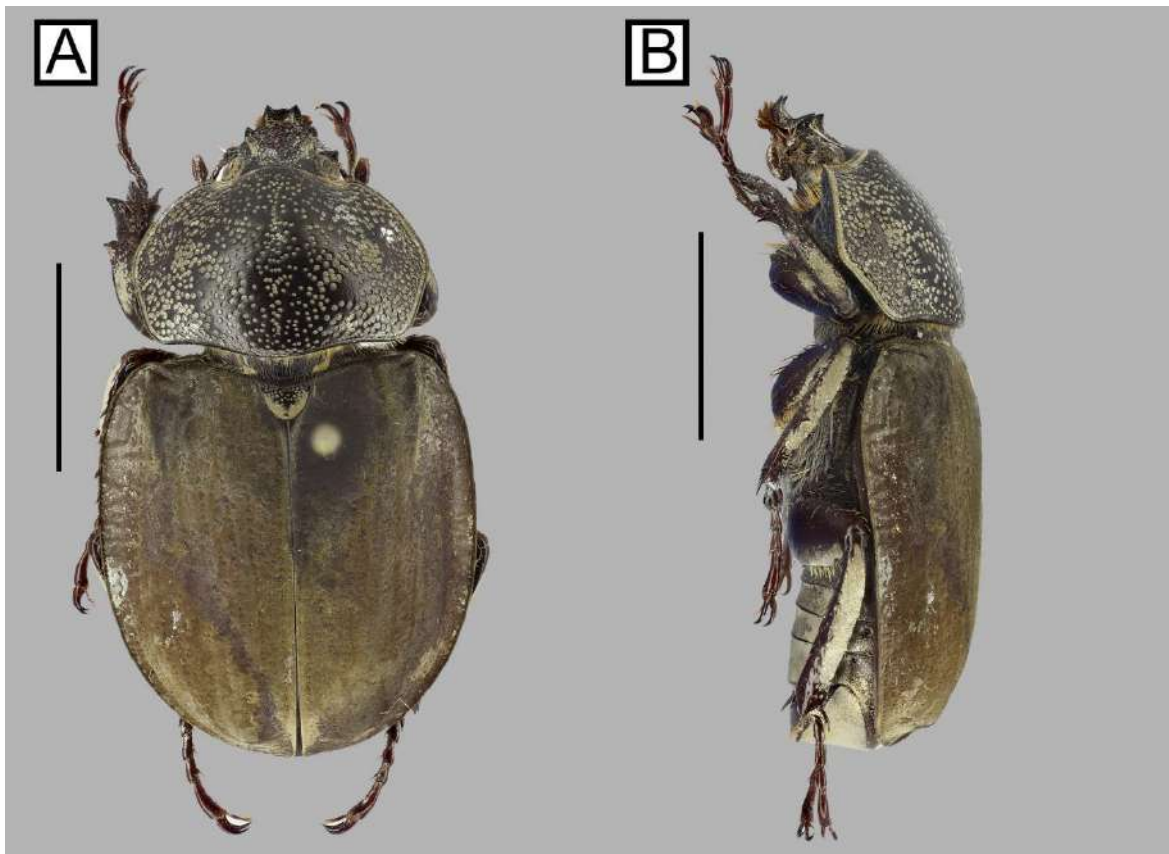


FIGURE 23. Male of *Spodistes beltianus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

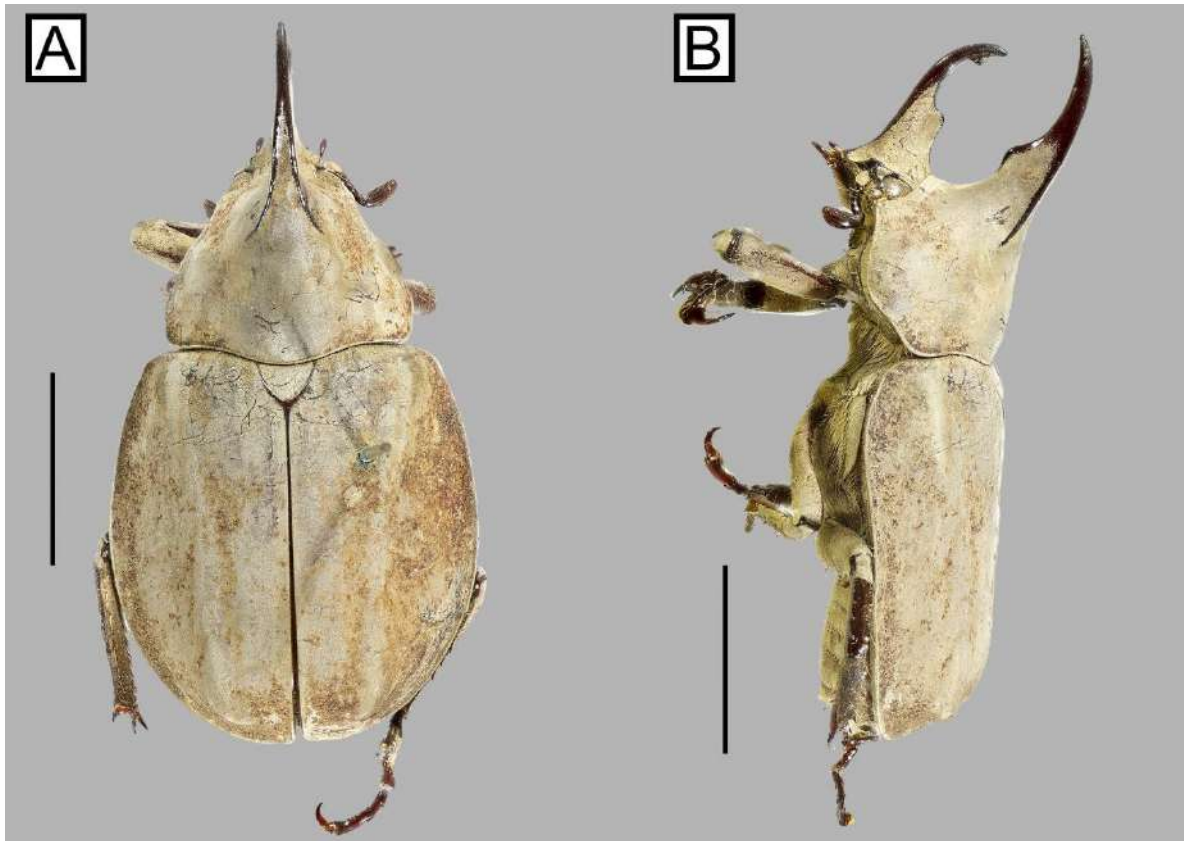


FIGURE 24. Aedeagus and ocular canthus of *Spodistes beltianus*, *Spodistes armstrongi*. **A**, Parameres of *S. beltianus* in caudal view; **B**, aedeagus of *S. beltianus* in lateral view; **C**, parameres of *S. beltianus* in ventral view; **D**, parameres of *S. armstrongi* in caudal view; **E**, aedeagus of *S. armstrongi* in lateral view; **F**, ocular canthus of *S. beltianus* in dorsal view; **G**, ocular canthus of *S. armstrongi* in dorsal view. Scale bars: 1 mm.

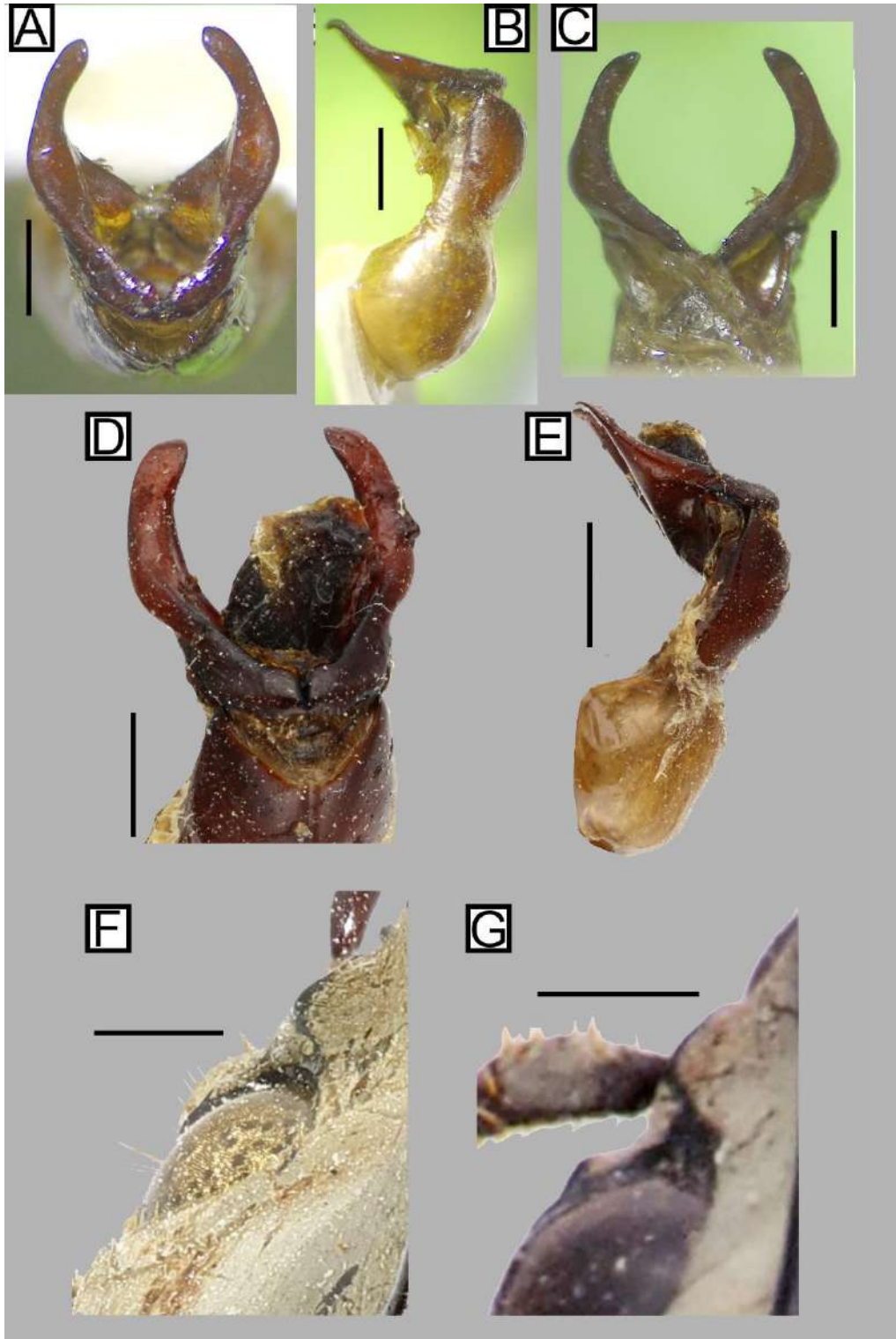


FIGURE 25. Female of *Spodistes belianus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

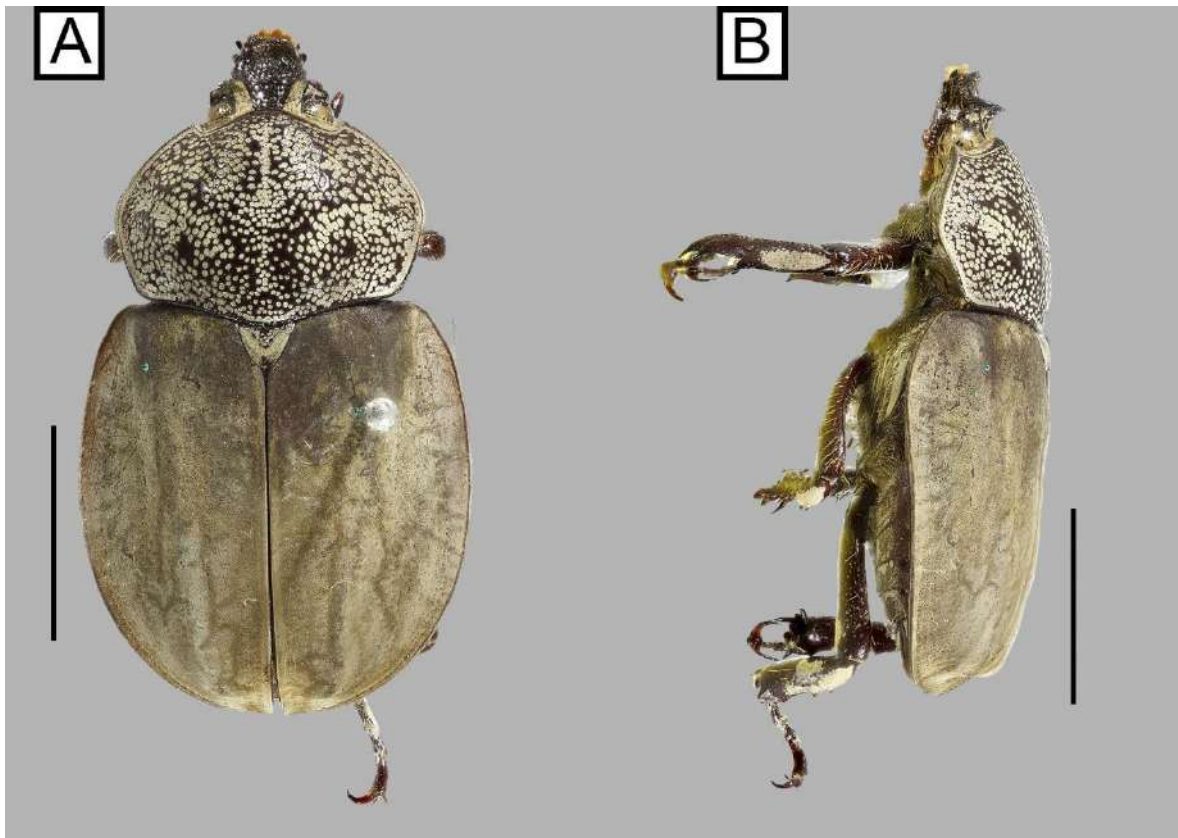


FIGURE 26. Male of *Spodistes armstrongi*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm. Photo by: Antoine Mantilleri.

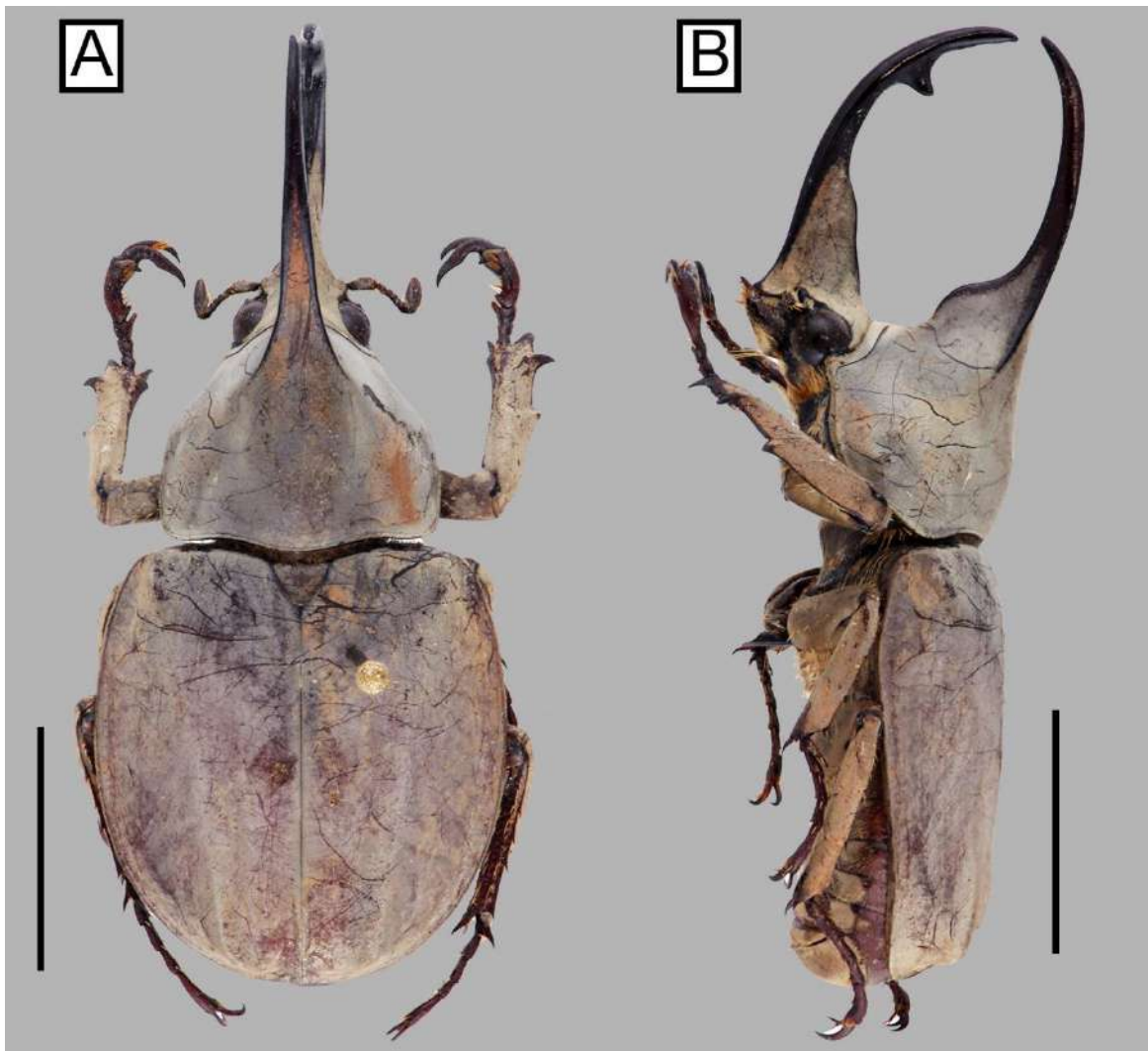


FIGURE 27. **A**, Metatibial apex of female *S. monzoni* in ventral view; **B**, metatibial apex of female *S. mniszewi* in ventral view; **C**, hypopygium and procoxa of female *S. mniszewi* in ventral view; **D**, hypopygium and procoxa of female *S. belianus* in ventral view; **E**, protibia of female *S. mniszewi* in ventral view; **F**, protibia of female *S. hopei* in ventral view. Black arrows pointing to thick setae on metatibial apex in A–B; white arrows pointing to the hypopygial protuberance and to punctures on procoxa in C–D; white arrows pointing to apex of protibial carina in E–F. Scale bars: 1 mm.

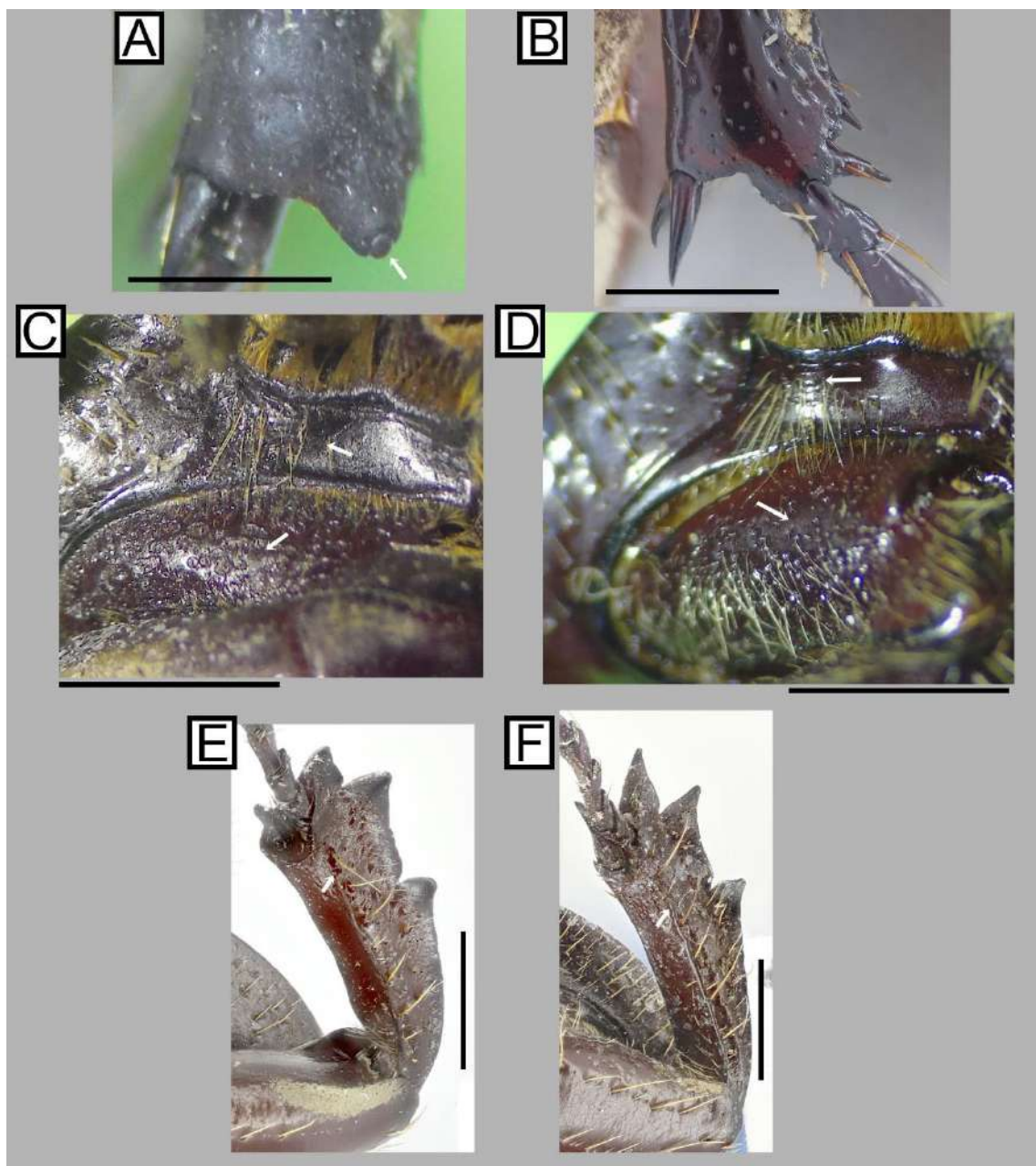


FIGURE 28. *Lycomedes buckleyi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view; **E**, mentum in ventral view. Scale bars A–D: 10 mm; scale bar E: 1 mm.

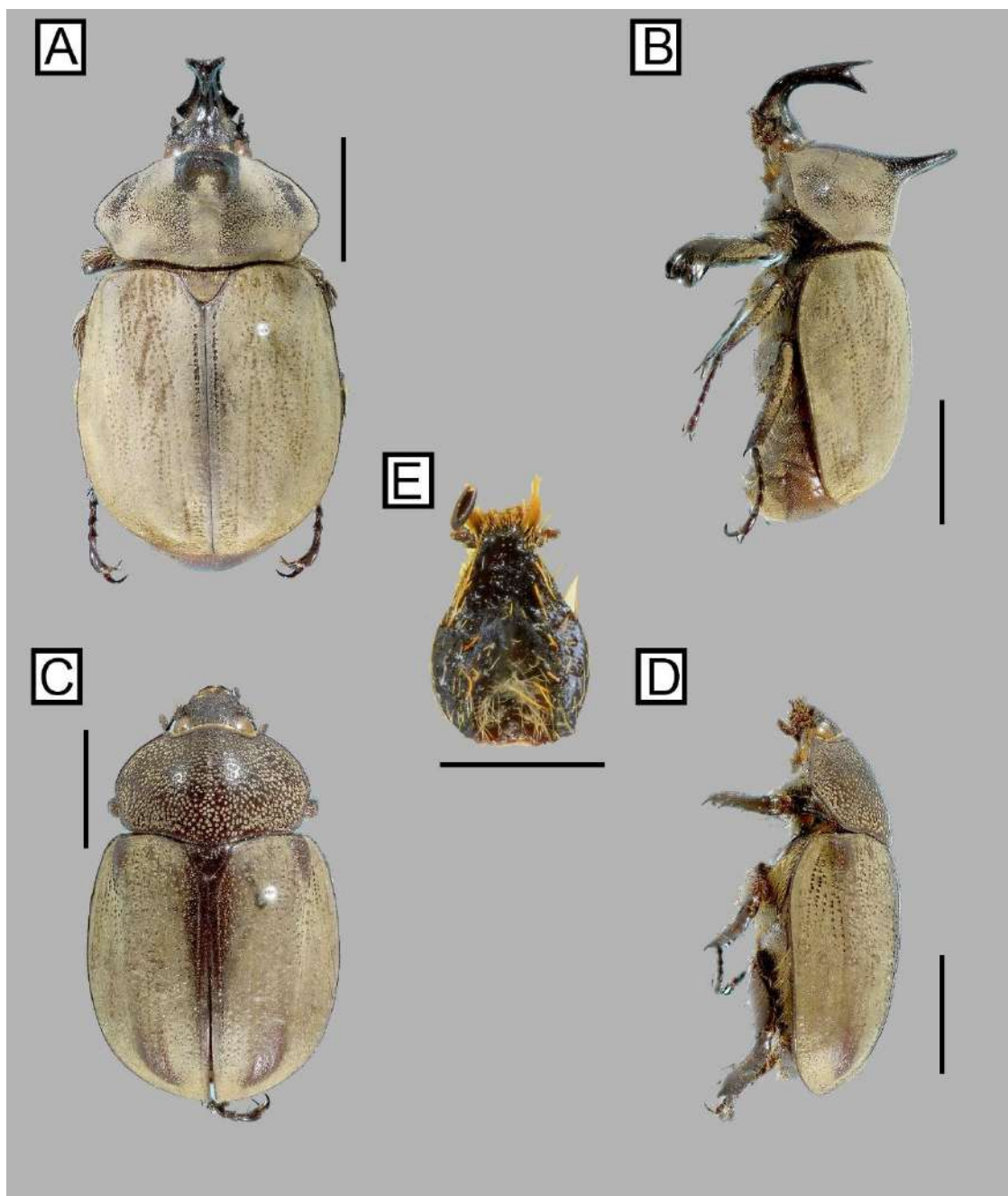


FIGURE 29. Distribution map of the species of *Spodistes*.

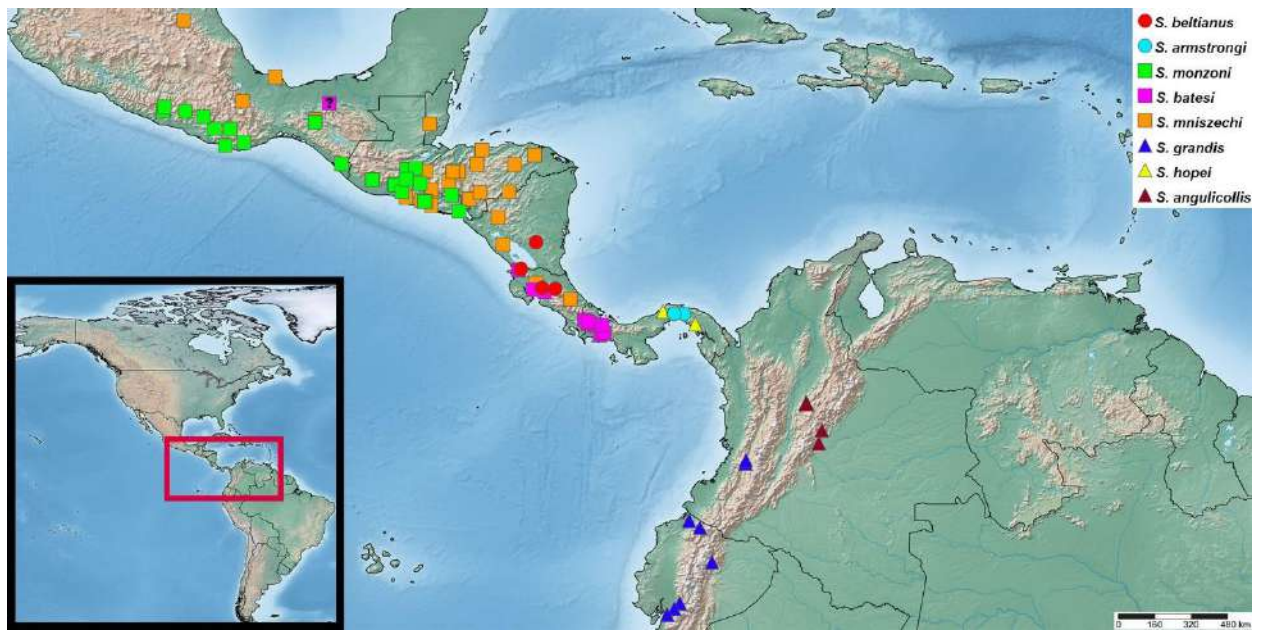


FIGURE 30. Zoomed distribution of *Spodistes*. **A**, Species from Southern Mexico to Costa Rica; **B**, species from Panama to southern Ecuador. Question mark referring to a dubious distribution in A; black ellipsis zomming the distribution in western Panama in B.

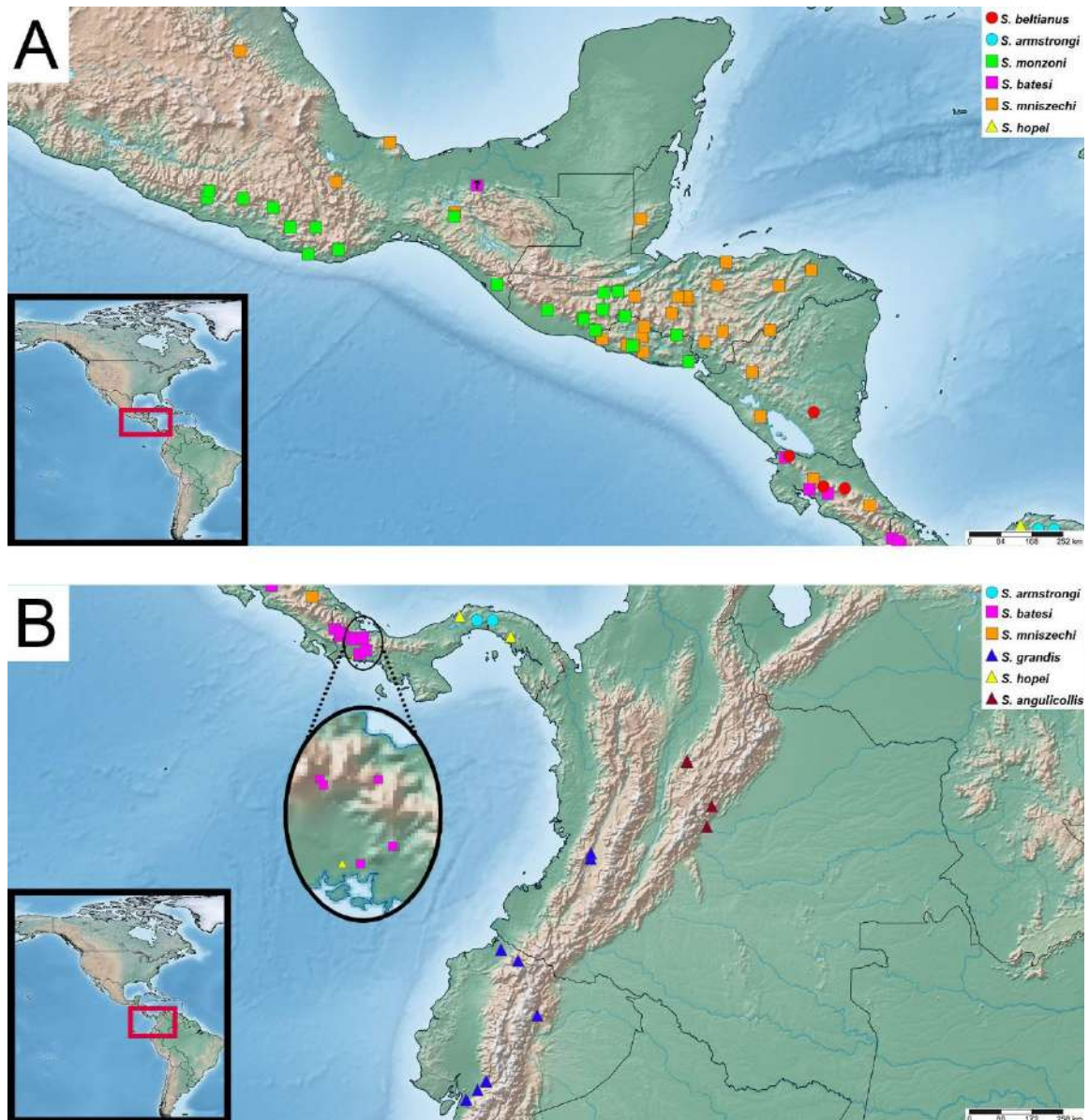


FIGURE 31. Female of *Spodistes angulicollis*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

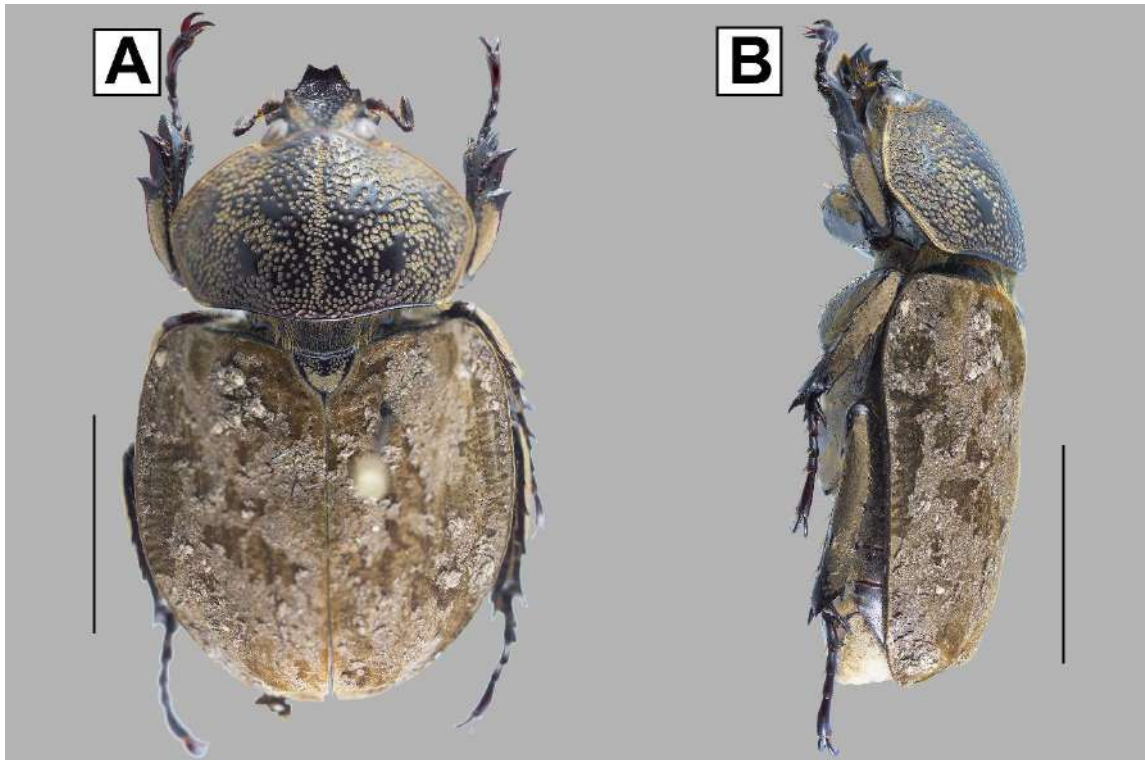


FIGURE 32. Head of *Spodistes hopei* and *Spodistes angulicollis*. **A**, Head of *S. hopei* in dorsal view; **B**, head of *S. hopei* in frontal view; **C**, head of *S. hopei* in lateral view; **D**, head of *S. angulicollis* in dorsal view; **E**, head of *S. angulicollis* in frontal view; **F**, head of *S. angulicollis* in lateral view. Scale bars: 1 mm.

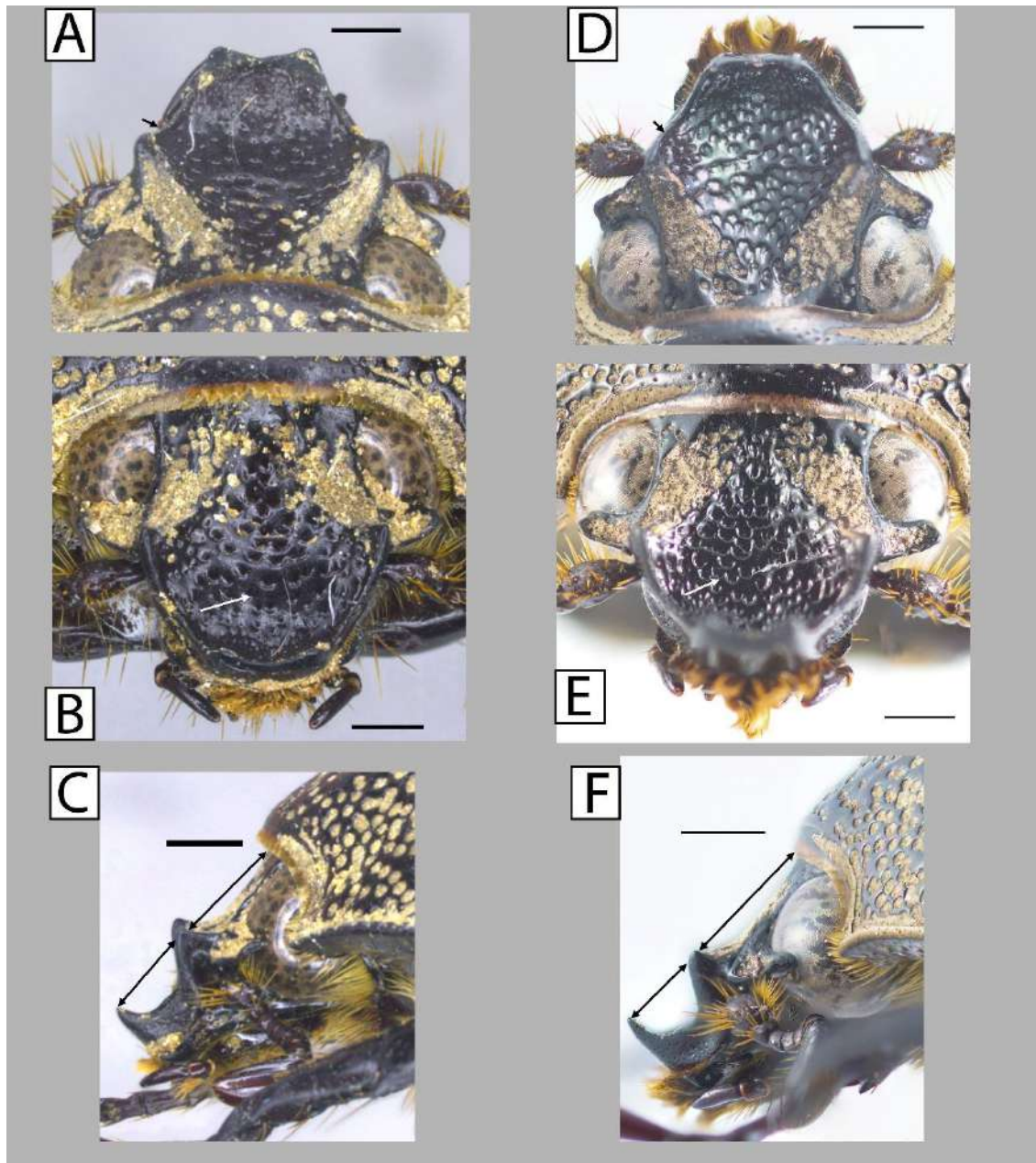
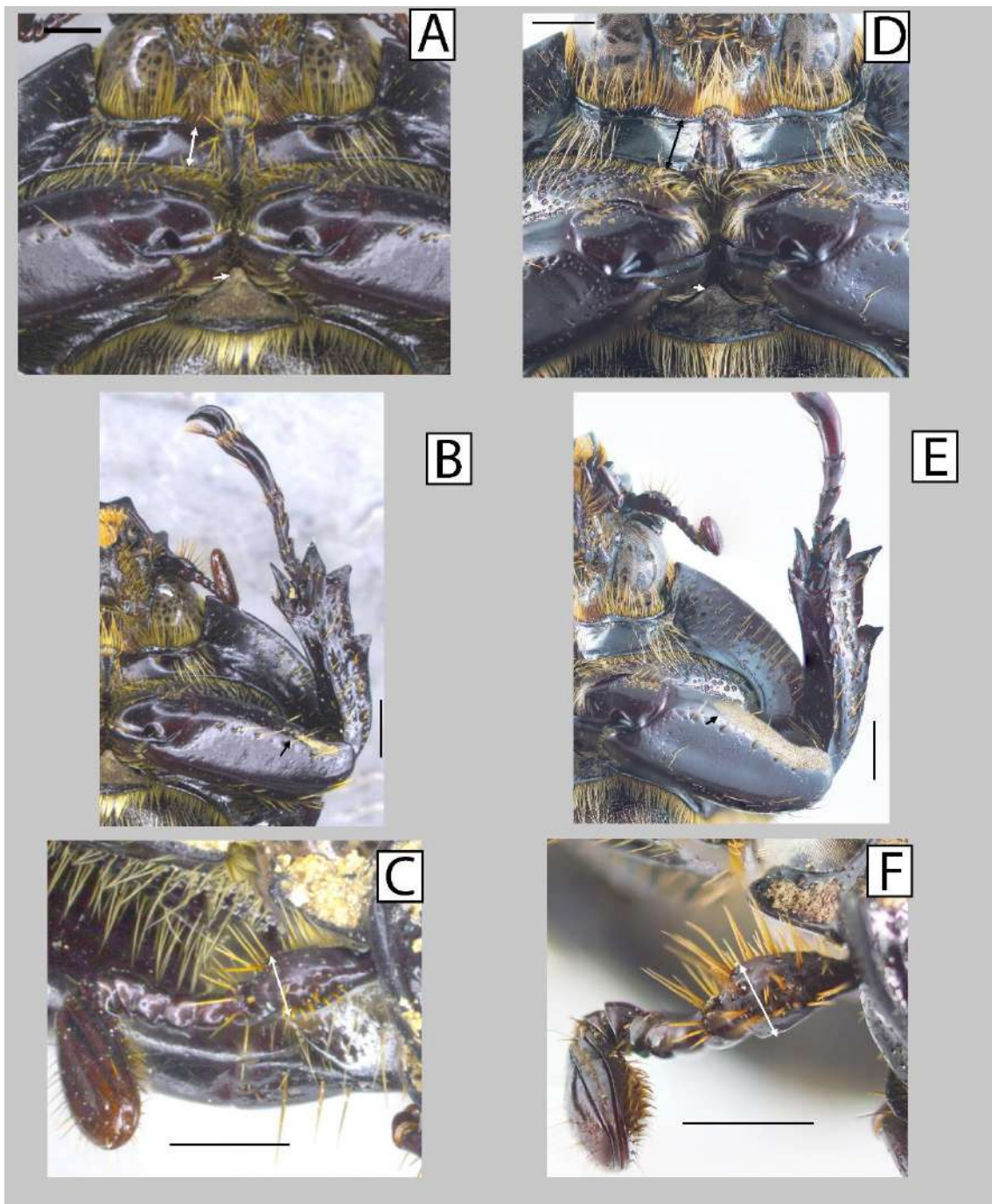


FIGURE 33. Thorax, leg and antenna of *Spodistes hopei* and *Spodistes angulicollis*. **A**, Prosternum of *S. hopei* in ventral view; **B**, proleg of *S. hopei* in ventral view; **C**, antenna of *S. hopei* in frontal view; **D**, prosternum of *S. angulicollis* in ventral view; **E**, proleg of *S. angulicollis* in ventral view; **F**, antenna of *S. angulicollis* in frontal view. Scale bars: 1 mm.



CAPÍTULO V

Sobral, R., Morais, J.W. de & Grossi, P.C. Review of *Lycomedes* de Brême (Coleoptera, Scarabaeoidea, Dynastinae), with notes on *Horridocalia* Endrödi. Manuscrito em preparação para submeter à revista *Zootaxa*.

Review of *Lycomedes* de Brême (Coleoptera, Scarabaeoidea, Dynastinae), with notes on *Horridocalia* Endrödi

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Abstract

The majority of species of *Lycomedes* is reviewed, with new characters proposed to their diagnosis, including traits of mouthparts. Females are given detailed description focusing on diagnostic characters to distinguish them even when collected alone, with no related male specimen. A new distribution map is provided as well as a key to species. Here we describe for the first time a major male of *Lycomedes enigmaticus* Neita-Moreno & Ratcliffe, 2019, a species that was once believed to be composed by minor specimens only. A new species of *Horridocalia* is described to Peru, which is a new country record to the genus.

Key words: Agaoccephalini, Andes, Melolonthidae, new species, rhinoceros beetles.

Introduction

Lycomedes De Brême, 1844 (Coleoptera: Melolonthidae: Dynastinae: Agaoccephalini) is a Neotropical genus of rhinoceros beetles distributed along the northwestern Andes from western Colombia to northern Peru. It is a distinctive genus within the Agaoccephalini, resembling *Spodistes* due to the tomentose body and the fancy cephalic and thoracic horns of males, but being unique in the shape of thoracic horn directed upward, the yellowish color of tomentum, and the presence of prosternal process elongated or short. *Lycomedes* is also characterized by the strong sexual dimorphism: male adults have distal protarsomere long and thick with asymmetrical claws, presence of horns on head and pronotum, and tomentum on pronotal surface, whereas female adults have distal protarsomere thinner than in male with symmetrical claws, absence of

horns on head and pronotum, and pronotal surface bare densely covered by tomentose punctures (Endrödi 1985; Milani 2017; Ratcliffe, Cave & Paucar-Cabrera, 2020). Currently there are 10 known species in the genus: *L. reichei* De Brême, 1844, *L. burmeisteri* Waterhouse, 1879, *L. buckleyi* Waterhouse, 1880, *L. hirtipes* Arrow, 1902, *L. velutipes* Arrow, 1902, *L. ramosus* Arrow, 1902, *L. ohausi* Arrow, 1908, *L. salazari* Pardo-Locarno, Villalobos-Moreno & Stechauner, 2015, *L. bubeniki* Milani, 2017, and *L. enigmaticus* Neita-Moreno & Ratcliffe, 2019 (Milani 2017; Ratcliffe, Cave & Paucar-Cabrera, 2020).

The taxonomic history of *Lycomedes* begins with the Marquis de Breme who described the genus and its first species, *L. reichei*, based on a female specimen from his own collection and a male specimen from Louis Reiche's collection (De Breme 1844). In 1847, Burmeister published his *Handbuch der Entomologie*, in which he redescribed *Lycomedes reichei* (misspelled as "*Lycomedes reichii*") including a new morphologic variation of this species based on specimens from Hope's and Dupont's collection. It turned out that this "variation" was actually a distinct genus (*Spodistes* Burmeister, 1847) that would only be considered as one by Arrow (1902) (for more details about that story see the Remarks section of *Spodistes* in Sobral et al.). In 1879 and 1880, Waterhouse was responsible for the description of two new species: *L. burmeisteri*, of which he described the first minor male to the genus, and *L. buckleyi*, the first species from Ecuador. The first and last novelties to *Lycomedes* in the XX century were provided by Arrow with the description of *L. hirtipes*, *L. ramosus*, *L. velutipes* (Arrow 1902) and *L. ohausi* (Arrow 1908). After that, it took a hundred years for a new species of *Lycomedes* to be discovered. Arnaud (2012) analyzed specimens similar to *L. reichei* but with differences in the shape of cephalic horn, of which he considered as a new species: *L. lydiae*. Posteriorly, Pardo-Locarno *et al.* (2015) described *L. salazari* based on specimens collected in areas of Colombian montane grasslands and shrublands in Eastern Cordillera of Andes at high altitudes, above 2300 m. Milani (2017) provided the description of *L. bubeniki* and the redescription of *L. ohausi*, including a new record to Peru. Then, Neita-Moreno & Ratcliffe (2019) published a work about the Agaocephalini of Colombia in which they described the most recent species of *Lycomedes*, *L. enigmaticus*, based on a minor male. Also, in the same work the authors decided to synonymize *L. lydiae* to *L. reichei* based on the similarity of diagnostic traits and the fact that both species are sympatric.

Biological data of *Lycomedes* is still scarce for the majority of species and its specimens are rare to find in the nature (Ratcliffe, Cave & Paucar-Cabrera, 2020). *Lycomedes hirtipes* is the only species of the genus with immature stages described, both larvae and pupa (Pardo-Locarno & Morón, 2006). Species of *Lycomedes* can be found in elevated areas, ranging from 1000 to almost 2800m of altitude throughout a wide variety of ecoregions in the Andes from Colombia to Peru (Milani 2017). Most species of *Lycomedes* are sympatric and, despite the male characters – especially the horns and genitalia – being useful to identify them, the females are difficult to identify when not associated with males from the same collecting. Females of *Lycomedes* can also be misidentified with females of *Horridocalia* Endrödi, 1974, sharing the same clypeal shape and general patterns of pronotal punctuation and distribution of tomentum on body. Also, the resemblance of the male of *Horridocalia* with males of *Lycomedes* is noticeable. Few morphological traits are used in the diagnosis of *Horridocalia* proposed by Endrödi (1974) and, considering the morphological plasticity existent in *Lycomedes*, it lead us to think about the possibility of these two genus being actually only one.

The last revision of the genus was made by Endrödi (1970) and some other works previously mentioned also brought novelties to the original descriptions of some species of *Lycomedes* described before the XXI century. Female descriptions of *Lycomedes* were not sufficient to help in their diagnosis, being restricted to few lines. In this work, we review most species of *Lycomedes*, proposing differential diagnosis for males and females with remarks about their distribution along their respective ecoregions. We describe a new species of *Horridocalia* to Peru. We also provide an identification key to male and female species modified from Ratcliffe, Cave & Paucar-Cabrera (2020), and a distribution map of these species.

Materials and methods

More than a hundred specimens were studied from the following collections (acronyms according Evenhuis (2022) when available).

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

CMNC Canadian Museum of Nature, Ottawa, Canada (François Génier)

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

HNHM Hungarian Natural History Museum (Otto Merkel)

MNHN Muséum National d'Histoire Naturelle, Paris, France (Antoine Mantillieri)
MSUC Michigan State University Albert J. Cook Arthropod Research Collection
(Anthony Cognato, Gary Parsons)
NHM Natural History Museum, London, United Kingdom (Max Barclay)
NHMB Naturhistorisches Museum Basel, Basel, Switzerland (Cristoph Germann)

The male genitalia was dissected through an aperture between tergite VI and tergite VII with forceps, and the aedeagi were then glued onto a paper point and pinned below the specimen. The mouthparts were dissected with an entomological stylet adapted with a sharp hypodermic needle on tip, and then glued on a small card according to Ohaus (1934) and pinned below the specimen. Terminology follows in part Endrödi (1985) and Ratcliffe (2003) for general aspects of the body, Nel & Scholtz (1990) for mouthparts, and Cristóvão & Vaz-de-Mello (2020) for genitalia. The nomenclature for biogeographic regionalisation follows Morrone (2014) and for ecoregions follows Dinnerstein (2017). The occurrence records were based on the labels of the specimens examined by the authors, and on literature records. The distribution map of the species was made using SimpleMappr (Shorthouse 2010).

Results

Taxonomy

Lycomedes de Brême, 1844

(Figs. 1–28, 35)

Lycomedes de Brême 1844: 299 (original description); Burmeister 1847: 245 (cited); Waterhouse 1879: 422 (description of new species); Waterhouse 1880: 288 (description of new species); Arrow 1902: 142 (description of new species); Sternberg 1903: 301 (cited); Arrow 1908: 354 (description of new species); Blackwelder 1944: 260 (checklist); Endrödi 1970: 72 (revision); Endrödi 1985: 221 (catalogue, characters in key); Lachaume 1992: 26 (catalogue); Restrepo-Giraldo *et al.* 2003: 262 (checklist to Colombia); Pardo-Locarno & Morón 2006: 661 (description of larva and pupa, notes on biology); Arnaud 2012: 2 (description of new species); Pardo-Locarno, Grossi & Rohringer 2014: 166 (cited); López-García, García-Atencia & Amat-García 2015: 327 (checklist to Colombia); Pardo-Locarno *et al.* 2015: 1 (description of new species); Milani 2017: 755 (description of new species, description of female of *L. ohausi*); Neita-Moreno & Ratcliffe 2019: 1049 (description of new species); Pardo-Locarno, Villalobos-Moreno & Ruiz 2020: 83 (checklist); Ratcliffe, Cave & Paucar-Cabrera 2020: 464 (catalogue of species from Ecuador)

Type species: *Lycomedes reichei* de Brême, 1844: 299.

Diagnosis. *Lycomedes* differs from other genera of Agaoccephalini by the combination of the following characters. **Males:** body mainly tomentose, head and legs partially tomentose, pronotum and elytra completely tomentose, abdomen completely or not tomentose; tomentum yellowish to darkish yellow, sometimes elytra and pronotum brindled (Figs. 1A-B, 6A-B, 7A-B, 16A-B, 17A-B, 18A-B, 27A-B, 28A-B). Cephalic horn distinct and elongated with apex bifid generally without posterior tooth (Figs. 8G, 8K) (except in *Lycomedes buckleyi* (Fig. 8C)), base of horn elevated or flat, horn split into anterior and posterior branches in *Lycomedes reichei* and *Lycomedes ramosus* (Figs. 2D, 2H). Clypeal corners angulated or round, directly connected with base of horn (Fig. 2F). Mandibles with two apical teeth and one molar protuberance on outer apical corner (Fig. 9A), some species without the protuberance or with protuberance short (Figs. 9E, 9I); in ventral view, presence of two or three oblique carina, reaching inner margin, inner tooth and other reaching outer corner. Protarsi compact, shorter than protibiae, protarsomeres I-IV wider than long, protarsomere IV with inner corner obliquely elongated with two teeth on tip (Fig. 4C, 4G, 11C, 11G, 11K, 22C, 22G, 22K). Protarsomere V distinctly dilated, inner edge strongly emarginated, presence of one basal and one mesal teeth, protarsal claws asymmetric, superior claw pincer-like shaped with a basal elongated tooth, superior claw longer and thicker than inferior claw, presence of a smooth or distinct protuberance at middle on superior claw (Fig. 4C, 4G, 11C, 11G, 11K, 22C, 22G, 22K). Pronotum broad and slightly flat on sides, lateral margins distinctly prominent at middle; pronotal disc with or without punctures conspicuous, with thoracic horn distinct and elongated, directed upward, slightly or strongly concave on anterior surface, depressed on posterior surface reaching posterior portion of pronotal disc (Figs. 3C, 3E, 10C, 10F, 10I, 21C, 21F, 21I). Elytra generally irregularly punctate (Fig. 7A) (except in *L. velutipes* (Fig. 17A)), apical umbones sharp or round. Prosternal process present (Figs. 4A, 4E, 11A, 11E, 11I, 22A, 22E, 22I).

Females: Head with clypeal base, on junction with frons, prominently acute or round (Figs. 13C, 13F, 13I, 24C, 24F), clypeus campaniform with two teeth on apex, surface punctate but not tomentose (Figs. Figs. 13B, 13E, 13H, 24B, 24E). Mandibles shorter and broader than in males, with two apical teeth and one distinct protuberance on outer apical corner, oblique or perpendicularly projected (Figs. 14A, 14E, 14I, 25A). Maxillae with three apical teeth at galea, two teeth longer and more external, one tooth shorter

and internal; galea elongated and curved outwards (Fig. 14C, 14G, 14K, 25C). Mentum drop-shaped or slightly pear-shaped, tomentum absent in ventral view, apex not covering base of labial palpi; in dorsal view, apex with two short and broad teeth on corners. Pronotum round, horn absent, lateral margins not as prominent as in males, pronotal disc densely punctate, punctures tomentose, anterior margin of pronotum not thickened (Fig. 15A, 15D, 15G, 26A, 26D). Elytral punctures conspicuous, punctures stronger near elytral suture (Figs. 7C-D, 16C-D, 17C-D, 18C-D, 28C-D). Prosternal process variable, projected in some species and bloated in others (Figs. 15B, 15E, 15H, 26E). Protibiae tridentate as in males, but with an indentation distinct between medial and basal teeth. Protarsi thin, protarsomeres I-IV longer than wide, protarsomere V simply curved, protarsal claws symmetric and simple.

Male description. Color: Body tomentose, covered by yellowish to dark yellowish tomentum on parts of head, pronotum, elytra and parts of legs, abdomen completely or not tomentose; elytra and pronotum brindled or not. **Head:** Shape elongate, ocular canthi with acute projections like teeth (Fig. 8E) or round on outer corner of anterior margin (Fig. 8I) or acute projections on base of anterior margin (Fig. 8A). Cephalic horn distinct and elongated with apex bifid, generally without posterior tooth (Figs. 8G, 8K) (except in *Lycomedes buckleyi* (Fig. 8C)), base of horn elevated or flat, horn split into anterior and posterior branches in *Lycomedes reichei* and *Lycomedes ramosus* (Figs. 2D, 2H). Clypeus sinuous laterally, apex round, truncate or slightly emarginated, continuous with cephalic horn; clypeal anterior corners protruded acute (Fig. 8B, F) or round (Fig. 19J), presence of pair of carinae reaching cephalic horn. Antennae 10-segmented. **Mouthparts:** Mandibles with two apical teeth and one round protuberance on outer apical corner; in ventral view, presence of two oblique carina, one reaching inner tooth and other reaching outer corner (Figs.). Maxillae with three teeth on galea, galea similar to isosceles triangle curved at apical outer edge (Figs.). Mentum drop-shaped or pear-shaped, apex in dorsal view with two short and broad teeth, tomentum absent in ventral view (Fig.). **Legs:** Protibiae tridentate on outer edge, inner apical corner slightly prominent, presence of one apical protibial spur (Figs. 4B, 4F, 11B, 11F, 11J, 22B, 22F, 22J). **Thorax:** Pronotum broad, transverse and slightly flat on sides, lateral margins distinctly prominent at middle; pronotal disc with or without punctures conspicuous, with thoracic horn distinct and elongated, directed upward, slightly or strongly concave on anterior surface, depressed on posterior surface reaching posterior portion of pronotal disc. Elytra generally irregularly punctate (except in *L. velutipes*),

apical umbones sharp or round. Prosternal process present, elongated in some species (Figs. 4A) or bloated (Figs. 22A, 22I). **Abdomen:** Tergite VII with no signs of stridulatory apparatus. Tergite VIII round and mainly tomentose with or without short setae on surface, posterior margin generally with agglomerated setae.

Female description. Body partially tomentose, elytra, and parts of legs with tomentum, head, pronotum and venter not tomentose. **Head:** Absence of horn. Surface distinctly punctate, vertex flat or with shallow fovea, frons flat or slightly depressed, tomentum absent. Clypeus campaniform with base more elevated than apex; clypeal base, on junction with frons, with sides prominently acute or round; clypeal apex with two teeth at middle or at corners. Ocular canthi transverse or oblique; projections on anterior margin, when present, round or weakly acute. **Thorax:** Pronotum convex with margins round, horn absent, lateral margins not as prominent as in males, pronotal disc densely punctate, punctures tomentose, anterior margin of pronotum not thickened. Elytral punctures conspicuous, irregularly distributed on disc, punctures stronger near elytral suture. Prosternal process variable, projected in some species and bloated in others. **Legs:** Protibiae tridentate as in males, but with an indentation distinct between medial and basal teeth. Protarsi thin, protarsomeres I-IV longer than wide, protarsomere V simply curved, protarsal claws symmetric and simple. Metatibiae with apical outer corner projected, surface distinctly punctate, tomentum present or not on outer edge. **Abdomen:** Tergite VIII more depressed on sides than in males.

Geographical distribution. South America, directly linked to the Andes, recorded to the following countries: Colombia, Ecuador and Peru (Fig.). Regarding the biogeographical regions (Morrone 2014), the distribution of *Lycomedes* occur in the Pacific dominion (provinces of Chocó-Darién, Western Ecuador, Cauca, Ecuadorian and Magdalena) and part of South American transition zone (Paramo province) (Fig. 35).

Remarks. *Lycomedes* is closely similar with two other genera in Agaoccephalini: *Spodistes* Burmeister, 1847 and *Horridocalia* Endrödi, 1874. Both genera share the presence of tomentum on the body and the strong sexual dimorphism regarding more than one trait as presence of cephalic and thoracic horns in males, absence in females; protarsi dilated with asymmetrical claws in males, protarsi slender with symmetric claws in females, etc. This similarity have proportioned some misidentification along the History. The first species of *Spodistes* were described as *Lycomedes* before Arrow (1902) realize they belonged actually to a new different genus, and it is not uncommon

in the entomological collections to see some *Horridocalia* labeled as *Lycomedes* sp. as we saw in HNMB.

The differences between *Spodistes* and *Lycomedes* are more discernible (as we can see in the Remarks of *Spodistes* in the “Review of *Spodistes* with notes on mating behavior of *Spodistes grandis*” by Sobral *et al.*), but the diagnosis of *Horridocalia* put some issues in our minds. The main reason for this is that Endrödi (1974) used only male traits as diagnostic to *Horridocalia* (which is reasonable since he did not have a female for comparison), and, when we compare with all species of *Lycomedes*, some of those traits are questionable as we can discuss sequentially. First, prosternal process dilated on apex and elongated can be seen in *L. velutipes* even that it is less dilated than in *Horridocalia*, but it still is dilated; elytra with regular rows of punctures can be seen in *L. velutipes*, but the punctures are not as large as in *Horridocalia*. The surface of pronotum and shape of cephalic horn are truly unique to *Horridocalia*, but it is noteworthy that *Lycomedes* have a wide plasticity in horn shapes among species, so: would be the *Horridocalia* actually *Lycomedes* with distinct shape of horn and pronotal surface? We believe that despite that similarity, they are in fact two distinct genera because of the differences in mouthparts of males and females combined with elytral pattern and tomentose pattern on head in females. We discuss more about the similarities of these genera in the Remarks of the new species of *Horridocalia* from Peru, described further in this paper.

With that said, *Lycomedes* differs from *Horridocalia* by the pronotal surface tomentose with punctures inconspicuous (Fig. 21A) [not tomentose with tomentose punctures conspicuous in *Horridocalia* (Fig.)]; elytral punctuation generally irregularly distributed (Fig. 1A) but, when regularly distributed (in *L. velutipes*), absence of irregular row between first and second regular rows near elytral suture (Figs. 17A) [in *Horridocalia*, elytral punctuation distributed regularly in rows, presence of irregular row between first and second regular rows near elytral suture]; mandibles with tomentum absent (Fig. 14A) [in *Horridocalia*, mandibles with tomentose stripe on outer edge in ventral view (Fig. 31A)]; maxilla with two apical teeth paired and one small tooth near them (Fig. 14C) [in *Horridocalia*, maxilla with one tooth (Fig. 31C)]; tergite VII with stridulatory apparatus absent [in *Horridocalia*, stridulatory apparatus present]. Female of *Lycomedes* differs by absence of tomentose stripe on frons and vertex (Fig. 13A) [in *Horridocalia*, presence of tomentose stripe on frons and vertex (Fig. 33A)], galea with three or two teeth on apex (Fig. 14C) [in *Horridocalia*, galea with one slim

apical tooth (Fig. 31G)], mentum with apical portion wide [in *Horridocalia*, mentum with apical portion distinctly narrow].

***Lycomedes reichei* de Brême, 1844**

(Figs. 1–5, 35)

Lycomedes reichei de Brême 1844: 299 (original description); Waterhouse 1879: 423 (cited); Arrow 1902: 143 (cited); Sternberg 1903: 300 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 77 (revision); Endrödi 1985: 223 (catalogue, characters in key); Lachaume 1992: 26 (catalogue); Restrepo-Giraldo *et al.* 2003: 262 (checklist to Colombia); Arnaud 2012: 3 (cited);); López-García, García-Atencia & Amat-García 2015: 327 (checklist to Colombia); Pardo-Locarno *et al.* 2015: 1 (cited); Milani 2017: 758 (cited); Neita-Moreno & Ratcliffe 2019: 1062 (cited); Pardo-Locarno, Villalobos-Moreno & Ruiz 2020: 83 (checklist)

Lycomedes reichii de Brême 1847: 285 (cited)

syn. *Lycomedes lydiae* Arnaud 2012: 2 (original description); Neita-Moreno & Ratcliffe 2019: 1062 (synonymization)

Diagnosis. *Lycomedes reichei* differs from other species of *Lycomedes* by the presence of a posterior portion of cephalic horn projected and slightly excavated dorsally (Fig. 2A), and presence of keel connecting anterior and posterior portions of horn (Fig. 2B). Base of cephalic horn can be elongated (as in the holotype) (Fig. 2D) or short (as in minor males and major males previously described as *L. lydiae*). The only species of *Lycomedes* that has a projected posterior portion of cephalic horn is *Lycomedes ramosus*, but in this species the posterior portion of horn is distinctly elongated and branched, with apex bifid and directed forward (Fig. 2H). Also, males of *L. reichei* differ from *L. ramosus* by the shape of ocular canthi subquadrate (Fig. 2A), pronotal disc on sides convex (Fig. 3A), parameres, in dorsal view, with pair of keels from base barely reaching medial portion forming a subtriangular depression near inner margin (Fig. 5A), whereas in *L. ramosus*, ocular canthi is transverse with anterior margin concave (Fig. 2E), pronotal disc on sides depressed near anterior corners (Fig. 3D) and parameres, in dorsal view, with ellipsoid fovea on base, keels absent (Fig. 5E).

Redescription. Holotype. Male. **Color:** Body weakly tomentose, tomentum gray, surface reddish brown and dull (Fig. 1A-B). **Head:** Cephalic horn projected upward, perpendicular to frons, base longitudinal and elevated with medial keel connecting

anterior and posterior portions; anterior portion elongate, more than 3 times longer than base length, apex transversally flat, tip bifid (Fig. 2C); posterior portion with basal projection slightly excavated dorsally, with minute margins oblique and tooth-like (Fig. 2A). Tomentum on sides basally, not crossing the line of medial keel; frontal and posterior sides of anterior portion of horn not tomentose (Fig. 2B). Horn and frons shagrinated, portions of vertex not covered by tomentum with punctures large and dense. Clypeus bell-like shaped, lateral margins elongate and narrowing to apical third, apex slightly round, sides slightly concave, anterior portion of clypeus continuous upward to horn (Fig. 2B); sides tomentose with some scattered long thin setae on dorsal surface. Ocular canthi square-like, presence of distinct tooth prominent on anterior corners, surface slightly excavated on posterior margin near eyes, presence of thin recurved carina from base of anterior margin to frons (Fig. 2A). **Thorax:** Pronotum transverse, lateral margins sinuous with posterior corners divergent to mesolateral portions projected to sides, mesolateral portions converging to acute anterior corners; lateral surface with few bumps and depressions (Fig. 3A). Pronotal disc weakly tomentose, with prominent horn directed upward, slightly widening from base to apex (Fig. 3B); presence of pair of basal carina frontally, horn apex distinctly bilobated and abruptly directed forward, perpendicular to base of horn (Fig. 3C). Frontal portion of pronotum near anterior margin with few thin setae sparsely distributed, frontal surface of horn densely punctate with large and thin punctures intertwined (Fig. 3B). Prosternum with mesal portion at anterior margin campaniform, surface with transversal slight depression almost reaching medial elevation; presence of prosternal process spoon-like shaped, glabrous, ventral surface distinctly excavated and shagrinated, margins thick (Fig. 4A). Metasternum hirsute, metepisternum with posterior margins thick, surface sparsely hirsute. Scutellum parabolic, dorsal surface shagrinated with a V-shaped zone of tomentum near margins, punctures moderate and sparse basally. **Elytra:** Form 2.4 times longer than wide. Surface weakly tomentose and rugose, disc covered by moderate and sparse punctures, becoming denser near lateral margins. Apical and humeral umbones with thin dense punctures, apical umbones distinctly acute and prominent (Fig. 1B). **Legs:** Protibia with three distinct external teeth, medial tooth bigger than apical and basal teeth, basal teeth shorter than others, tomentum absent. In dorsal view, surface shagrinated, punctures moderate and C-punctures near teeth on outer edge, thinner punctures near inner edge, micropunctures covering entire surface, presence of elongate thin setae on longitudinal rows and scattered near apex (Fig. 4B).

Protarsomeres I–IV short, wider than long; protarsomere IV with anterior inner corner projected with two spaced teeth. Protarsomere V strongly curved internally, with one basal tooth on ventral side and one medial tooth on dorsal side; protarsal claws asymmetric, inferior claw thin and curved, superior claw with acuminate tooth basally and weak protuberance medially near tip (Fig. 4C). Meso- and metacoxae with a weak stripe of tomentum on distal posterior corners. Metatibia with one tooth on outer edge near apex, surface wrinkled and punctate; metatibial apex sinuous, convex near inner edge and concave near outer edge. **Abdomen:** Tergite VIII round and projected posteriorly (Fig. 4D); surface distinctly covered by C-punctures on sides, disc with thin and dense punctures, sides and margins covered by microsetae; posterior margin with a dense group of long thin setae (Fig. 4D). Sternite IV with distinct round projection of posterior margin over sternite V and part of sternite VI (Fig. 4D). Sternite VI tomentose on posterior half, sternite VII tomentose on anterior half; sternites VI–VII with short thin setae on sides, with longer setae on posterior margins. Sternite VIII bilobated, with short area weakly tomentose near corners, surface densely covered by thin punctures, presence of short thin setae densely distributed on posterior margin. **Aedeagus:** Parameres symmetric and elongate. In dorsal view, mesoapical portion almost 2 times longer than basal portion, a pair of keels from base barely reaching medial portion forming a subtriangular depression near inner margin; apex with inner margin deflected laterally forming a slight depression on apical surface (Fig. 5A). In lateral view, anterior phallobase 2 times shorter than posterior phallobase, posterior phallobase slightly angulate (not round) on caudal surface (Fig. 5D); parameres with apical portion oblique with caudal surface completely visible in lateral view, presence of short carina near apex (Fig. 5B). In ventral view, ventral sclerites not emarginated, basal portion slightly depressed, mesoapical portion flat, sides sinuous narrowing to apex (Fig. 5C).

Measurements of holotype. Body length: 31.6 mm. Cephalic horn length: 7.8 mm. Elytral length: 17.9 mm. Elytral width: 9 mm. Pronotal width: 12.5 mm. Protibial length: 7.2 mm. Thoracic horn length: 8.8 mm.

Females. Not examined.

Geographic distribution. Colombia: Boyacá, Santander (Fig. 35).

Material examined. Holotype male (NHM): a) “Type”, b) “67 45”, c) “*Lycomedes* de Brême/ Ann{ales}. {de la} Soc{iété}. Ent{omologique} {de France}. 1844{year of description} – 299{page of description}/ *Reichei* de Br. ibid/ Nov{a}. Granata”, d) “So named/ in Reiche’s/ Collection/ C.W.”.

Remarks. In the original description, De Breme mentioned that the male specimen of *L. reichei* was collected on a tree trunk – of an unknown plant species – in Chucuri, a city in the province of Soccora (a misspelled form of Socorro), New Granada. In 1844, when this species was described, the Republic of New Granada included the territory of what we know today as Colombia, Panama and smaller areas of Costa Rica, Ecuador, Venezuela and Peru. Therefore, some names of provinces and municipalities have changed along the time. Nowadays, the type locality of *L. reichei* is known as San Vicente de Chucurí, in the province of Santander, Colombia. The specific epithet of this species is a homage to Louis Jérôme Reiche, a French entomologist who had the male specimen of *L. reichei* (which became the holotype) in his collection.

Recently, Neita-Moreno & Ratcliffe (2019) considered *Lycomedes lydiae* Arnaud, 2012 as junior synonym of *L. reichei*. Both species are sympatric with records of *L. lydiae* to Santander, Colombia as well as *L. reichei*. Also, the authors examined other specimens collected in Boyacá and Santander and realized that the diagnostic traits of *L. lydiae*, i.e. the shape of posterior protuberance of cephalic horn, are variations of the traits of *L. reichei*. As we did not have access to females of the former *L. lydiae*, we did not redescribe the female of *L. reichei*.

Lycomedes reichei is found in the Cordillera Oriental, the easternmost branch of the Colombian Andes, in elevations of 1965m to 2150m (López-García *et al.* 2015; Neita-Moreno & Ratcliffe 2019). The species occurs in the Magdalena Valley montane forests, an ecoregion with a unique kind of tropical moist forest composed by some endemic plant species as *Pithecellobium bogotense*, *Steriphoma colombiana* and other trees not higher than 15 meters (Constantino, WWF 2021). *L. reichei* shares this environment with *L. ramosus*, despite not being collected in nearby areas, once *L. reichei* is distributed to the north of the Cordillera Oriental whereas *L. ramosus* is more central.

***Lycomedes buckleyi* Waterhouse, 1880**

(Figs. 7–15, 35)

Lycomedes buckleyi Waterhouse 1880: 288 (original description); Arrow 1902: 143 (cited); Sternberg 1903: 300 (cited); Arrow 1908: 355 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 74 (revision); Endrödi 1985: 222 (catalogue, characters in key); Lachaume 1992: 26 (catalogue); Pardo-Locarno *et al.* 2015: 4 (cited); Milani 2017: 758 (cited); Ratcliffe, Cave & Paucar-Cabrera 2020: 467 (catalogue)

Diagnosis. *Lycomedes buckleyi* is a unique species within *Lycomedes*, differing from other species of the genus by the male with cephalic horn apex bifid with presence of long thick tooth posteriorly to apex, pointing backward (Fig. 8A). Also, other diagnostic traits of males of this species are: clypeal apical corners distinctly acute, pointing to sides (Fig. 8C), ocular canthi transverse with basal portion distinctly projected (Fig. 8A), pronotal disc not completely covered by tomentum, with tomentose punctures conspicuous on sides and pronotal anterior portion (Fig. 10B), anterior phallobase bigger than posterior phallobase, posterior phallobase with short corners (Fig. 12D).

Females of *L. buckleyi* can be characterized by: ocular canthi with distinct tooth basally on anterior margin (Fig. 13A), frons and vertex flat (Fig. 13C), clypeal apex slightly widened, 1.5 times narrower than clypeal base (Fig. 13B), labrum subtrapezoidal, sides acute and anterior margin truncate (Fig. 14D), elytral punctures thin between first row of punctures and elytral suture (Fig. 7C), elytral disc with big and thin shallow punctures intertwined and irregularly distributed (Fig. 7D), prosternal process short, like a bulb (Fig. 15B).

Redescription. Male. Color: Body tomentose on head, pronotum, elytra and parts of legs, tomentum greyish yellow, surface dark brown and dull (Fig. 7A-B). **Head:** Cephalic horn projected upward with a slight basal curvature, horn thick, apex bifid with tips anteriorly pointing upward with presence of long tooth posteriorly pointing backward (Fig. 8D). Tomentum absent on horn and middle of frons and vertex, sides of frons and vertex tomentose (Fig. 8A). Punctures coalescent on frons and vertex. Presence of a frontal shallow depression with shape subtriangular (Fig. 8B). Clypeus contiguous with cephalic horn, clypeal lateral margins sinuous almost parallel, apex slightly convex, apical corners distinctly acute pointing laterally (Fig. 8C), lateral surface excavated and tomentose (Fig. 8B). Clypeal punctures thin and sparse frontally. Ocular canthi transverse with posterior portion projected to eye and anterior portion as a distinct oblique tooth on basal corner pointing forward, presence of thin carina from tooth to frons, base weakly tomentose (Fig. 8A). **Mouthparts:** Labrum with sides widened, almost 5 times wider than medial length, anterior margin truncate (Fig. 9D). Mandibles robust, with two apical teeth and one lateral molar protuberance, in ventral view molar protuberance round, inner and medial carina covered by long thin setae, setae touching mesal brush apically (Fig. 9A); in dorsal view, row of setae on outer

margin not reaching inner tooth, mesal brush slightly thick at apex and weakly covering lateral molar area at base (Fig. 9B). Maxilla with medial tooth elongated and sharp; lateral borders of stipes with outer margin oblique; ventral stipes with short thin setae densely distributed on outer margin, oblique row of long thin setae medially (Fig. 9C).

Thorax: Pronotum transverse, lateral margins anteriorly strongly oblique to round tips medially and concave to posterior corners, lateral margins with borders thicker medially than anteriorly and posteriorly (Fig. 10A). Pronotal disc tomentose except frontally on a longitudinal stripe not tomentose from anterior margin medially to thoracic horn but with tomentose punctures sparse, area near anterior corners with tomentose punctures (Fig. 10B). Thoracic horn present and directed upward, length shorter than cephalic horn, posterior side of thoracic horn slightly excavated, anterior side with two discrete carina, apex of horn slightly emarginated and thin (Fig. 10C); anterior side of horn roughly punctate, punctures thin and moderate densely distributed (Fig. 10B).

Prosternum with mesal portion at anterior margin parabolic, surface not excavated; presence of prosternal process short and convex, not crossing posterior margin of prosternum (Fig. 11A). Metasternum hirsute, metepisternum with posterior margins thin, punctures thin and sparse. Scutellum subtriangular, surface covered by tomentum, punctures undistinguishable, presence of thin and sparse setae basally and medially.

Elytra: Form 2.2 times longer than wide. Surface tomentose, disc covered by dense tomentose punctures becoming sparser towards lateral margins, presence of microsetae sparse and abundant on disc and denser on apex. Apical and humeral umbones with thin tomentose punctures, apical umbones smoothly round (Fig. 7B). **Legs:** Protibia with three distinct external teeth, medial tooth bigger than apical and basal teeth, basal teeth shorter than others, presence of short tomentose area on base near outer edge. In dorsal view, protibia with tomentose punctures on basal half near outer edge, not crossing basal tooth; surface with moderate and thin punctures intertwined on apical half with some transverse punctures on teeth, bigger punctures basally (Fig. 11B). Protarsomeres I–IV short, wider than long; protarsomere IV with anterior inner corner projected with two spaced teeth. Protarsomere V strongly curved internally, with one basal tooth distinctly acuminate and one short medial protuberance; protarsal claws asymmetric, inferior claw thin and curved, superior claw with short tooth basally and medial protuberance inconspicuous near tip, surface of claw wrinkled (Fig. 11C). Protocantheri with oblique carina (Fig. 11A). Meso- and metafemora with no traces of tomentum, mesofemora more hirsute than metafemora. Metafemora with thin and sparse punctures

on disc, thinner punctures near junction with metatibia. Metatibial apex with a V-shaped emargination medially, outer margin apically angulated, metatibial surface with tomentose punctures on outer edge, elongate C-punctures medially, thinner punctures basally, carinae discrete. **Abdomen:** Tergite VIII round and transverse, surface completely tomentose with microsetae densely distributed on entire surface. Sternites IV–VI with thin and sparse punctures on disc, sides with long thin setae sparsely distributed not reaching middle. Sternite VII with almost same pattern as previous sternites, but with a dense conglomerate of thin punctures near posterior margin medially (Fig. 11D). Sternite VIII transverse and shorter than sternite VII, posterior margins with long thin setae, surface covered by thin punctures. **Aedeagus:** Parameres symmetric and elongate. In caudal view, basal portion sinuous on outer edge narrowing at portion near posterior phallobase, mesoapical surface slightly excavated, mesoapical portion diverging basally and then converging toward apex (Fig. 12A). In lateral view, anterior phallobase bigger than posterior phallobase, posterior phallobase smooth dorsally with corners short (Fig. 12D), parameres with dorsolateral oblique carina, ventral portion of parameres slightly convex (Fig. 12B). In ventral view, mesoapical surface excavated, inner margins thick and elevated (Fig. 12C).

Measurements of holotype. Body length: 30.3–34.1 mm. Cephalic horn length: 8.4–9.6 mm. Elytral length: 18.9–21.3 mm. Elytral width: 10.4–12 mm. Pronotal width: 14.8–15.9 mm. Protibial length: 8.2–8.5 mm. Thoracic horn length: 5–5.4 mm.

Females. Body oblong, head and pronotum not tomentose as in males (Fig. 7C–D). **Head:** Cephalic horns absent. Vertex with punctures thinner and sparser than on frons, with some areas not punctate (Fig. 13B). Frons almost flat, densely punctate, punctures larger and coalescent toward clypeus (Fig. 13A, 13C). Clypeal base, on junction with frons, prominently upward and elevated compared to clypeal apex (Fig. 13C); clypeus campaniform with two teeth on apex, surface excavated medially and on sides, punctures large and dense (Fig. 13B). Ocular canthi similar to males, anterior margin contiguous between basal tooth and canthi apex, tooth not sharp as in males, canthi apex more oblique than transverse, punctures large and dense (Fig. 13A).

Mouthparts: Labrum subtrapezoidal, sides acute, posterior margin distinctly concave, anterior margin truncate (Fig. 14D). Mandibles with two apical teeth and one molar protuberance on apical outer corner (Fig. 14A), presence of short truncate protuberance on outer side near base (Fig. 14A); in dorsal view, internal lobe excavated, outer row of setae not crossing outer tooth (Fig. 14B). Maxilla with galea with three elongate teeth,

two teeth dorsoventrally parallel and one tooth more close to outer edge of galea, outer edge of galea slightly concave (Fig. 14C), presence of apical short tooth at inner edge of galea. Mentum subtriangular, sides round, apex acute; in dorsal view, presence of short protuberance apically. **Thorax:** Pronotum convex but slightly flat to sides, lateral margins of pronotum parabolic, thoracic horn absent. Pronotal disc with tomentose punctures, punctures bigger and denser on lateral margins, smaller and sparser punctures near anterior margin (Fig. 15A). Scutellum punctate, punctures not tomentose moderate and dense on sides. Prosternum with mesal portion at anterior margin parabolic and distinctly prominent, surface slightly excavated on sides, medial portion of prosternum with a longitudinal keel from anterior margin to the junction of legs (Fig. 15B); prosternal posterior margin medially round, presence of prosternal process short, like a bulb (Fig. 15B). Metasternum hirsute, more hirsute on sides than medially, presence of two parallel excavated areas near metasternal suture, ending as a round posterior margin. **Elytra:** As broad as in males, tip slightly acute than in males. Disc tomentose; apical and humeral umbones and elytral suture not tomentose (Fig. 7C). Elytral punctures tomentose; punctures deeper on basal half of elytra and along elytral suture, punctures on apical half of elytra shallow or barely not excavated, apical and humeral umbones with thin and dense tomentose punctures (Fig. 7D). **Legs:** Protibia tridentate as in males, medial tooth more prominent than others with an indentation near basal tooth, surface with punctures large and dense surrounding medial row of setae. Protarsi simple, protarsomere V slightly concave medially, protarsal claws simple. Procoxal insertion on prosternum transverse. Tomentum absent on meso- and metafemora. Metafemora with circa of 10 long thin setae sparse at posterior row, metatibial apex projected on outer edge with 3 round thick setae on tip, metatibial surface with moderate punctures intertwined with thinner punctures. **Abdomen:** Tergite VIII acute, slightly flat near posterior margin medially; surface not tomentose, punctures thin and dense on corners and near anterior margin, thin and sparser on disc (Fig. 15C). Tomentum absent on sternites. Sternite III with posterior margin distinctly concave (Fig. 15C). Sternites IV–VI with thin and sparse punctures on disc, presence of short thin setae on sides only reaching medial portion in sternite IV. Sternite VII with short thin setae only on posterior margin, disc sparsely punctate, punctures thin, punctures on disc more abundant than on previous sternites. Sternite VIII finely punctate, short thin setae on posterior margin with shorter setae on tip.

Measurements of females. Body length: 27.5–31.3 mm. Elytral length: 18.8–

21.1 mm. Elytral width: 10.4–11.9 mm. Head length: 4.1–5.6 mm. Pronotal width: 13.3–15.4 mm. Protibial length: 6.7–8.1 mm.

Geographic distribution. Ecuador: Azuay, Cañar, Loja, Morona Santiago, Napo, Pastaza, Sucumbíos, Tungurahua, Zamora Chinchipe. Peru: unknown locality (Fig. 35).

Material examined. Syntype. 1 male (NHM): a) “Type”, b) “Chiquin/da/ 80.14”, c) “*Lycomedes/ buckleyi* (Type) Waterh{ouse}.”; 1 female (NHM): a) “Type”, b) “Chiquin/da/ 80.14”, c) “*Lycomedes/ buckleyi* (Type) Waterh{ouse}.”. **Other specimens:** 1 male and 1 female (NHM): a) “Nevinson coll./ 1918 – 14”, b) “*Lycomedes/ buckleyi* Peru”; 1 male and 1 female (NHM): a) “*Lycomedes/ buckleyi* Waterhouse/ R.-P. Dechambre det. 1976”; 1 male (NHM): a) “Levick Bequest/ B.M. 1941-83”; 1 female (NHM): a) “Buckley”, b) “Equador”, c) “Fry Coll./ 1905-100”; 1 male (RBINS): a) “*Lycomedes/ buckleyi* Ecuador”, b) “Le Moulte vend.”; 1 male and 1 female (NMPC): a) “Ecuador, 2 {II}. {19}90./ Azuay prov. 1800m/ P. Arnaud leg.”, b) “ex coll. S. Pokorný/ National Museum/ Prague, Czech Republic”, c) “*Lycomedes/ buckleyi* Waterh./ ing. S.Pokorný det. {19}95”; 1 female (CERPE): a) “PERU/ Apurimac, Abancay/ 13°42.6’S, 73°00’W/ 9-10.XII.2010, H=3632m”.

Remarks. *Lycomedes buckleyi* is recorded to Ecuador, occurring along the Ecuadorian Andes and adjacencies, a territory seismically active and characterized by its volcanic activity. The main distribution of *L. buckleyi* is through the Eastern Cordillera Real montane forests, an ecoregion characterized by the high forests at lower elevations and cloud forests, with its trees short and crooked, at higher elevations (Schipper, WWF 2020). However, the species is not restricted to this ecoregion having few records in the Napo moist forests, Western Ecuador moist forests and the Tumbes-Piura dry forests. Specimens of *L. buckleyi* have been collected in a wide range of altitude, from 500m to 2600m (Ratcliffe, Cave & Paucar-Cabrera, 2020). *L. buckleyi* is sympatric with *L. ohausi* and *L. bubeniki* at the southern and central areas of Eastern Cordillera and with *L. velutipes* at foothills of Western Cordillera (Fig. 35). However, *L. buckleyi* is one of the species with a unique type of cephalic horn in the genus. The males of *L. buckleyi* are the only species of *Lycomedes* with a long thick tooth behind the apical bifurcation of cephalic horn, whereas in the others the tooth is absent. The females are also easily distinguished by the shape of ocular canthi with distinct tooth basally on anterior margin, and the prosternal process short like a bulb.

A curious fact about *L. buckleyi* is its social relevance to traditional indigenous

population who lives near the city of San Juan de Ambato, practically at the middle of Central Cordillera. In the tradition, the prothorax of *L. buckleyi* is macerated and mixed with paste of *Aloe vera* (L.) to create an ointment used to treat back pain (Naranjo & Escaleras, 1995). According to Milani (2017), the specific use of the prothorax is due to the relative similarity with human thoracic vertebrae, separated from the head and abdomen.

***Lycomedes burmeisteri* Waterhouse, 1879**

(Figs. 19–24, 26, 28, 35)

Lycomedes burmeisteri Waterhouse 1879: 422 (original description); Waterhouse 1880: 288 (cited); Arrow 1902: 143 (cited); Sternberg 1903: 300 (cited); Arrow 1908: 355 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 79 (revision); Endrödi 1985: 223 (catalogue, characters in key); Lachaume 1992: 27 (catalogue); Restrepo-Giraldo *et al.* 2003: 262 (checklist to Colombia); Pardo-Locarno *et al.* 2015: 1 (cited); Milani 2017: 758 (cited); Neita-Moreno & Ratcliffe 2019: 1062 (cited); Pardo-Locarno, Villalobos-Moreno & Ruiz 2020: 86 (checklist); Ratcliffe, Cave & Paucar-Cabrera 2020: 469 (catalogue)

Diagnosis. *Lycomedes burmeisteri* can be distinguished from other species of *Lycomedes* (except *L. ohausi* and *L. bubeniki*) by the cephalic horn of males flat anteroposteriorly and bifid on apex, without a posterior projection, tooth or fovea (Fig. 19L). Males of *L. burmeisteri* differ from *L. ohausi* by the base of cephalic horn near frons not depressed (Fig. 19J), thoracic horn with basal carina slightly convex in lateral view (Fig. 19H-I), posterior depression on pronotal disc elongate, almost reaching pronotal posterior margin (Fig. 19I), clypeal anterior corners round (Fig. 19K), mandibles with molar protuberance absent (Fig. 20I), whereas in *L. ohausi*, base of cephalic horn near frons with shallow depression (Fig. 19B), thoracic horn with basal carina straight (Fig. 21B-C), posterior depression on pronotal disc short (Fig. 21C), clypeal anterior corners acute (Fig. 19C), mandibles with molar protuberance short but distinct (Fig. 20A).

Females of *L. burmeisteri* are very similar to females of *L. ohausi* but can be separated by clypeal base, on junction with frons, distinctly acute (Fig. 24F), presence of tomentose punctures on clypeal base (Fig. 24D), metatibia with insertion of setae short near inner margin (Fig. 26F), ocular canthi with anterior corner distinctly projected and round (Fig. 24E), and in *L. ohausi*, clypeal base, on junction with frons,

round and short (Fig. 24C), tomentose punctures absent on clypeal base (Fig. 24A), metatibia with insertion of setae big near inner margin (Fig. 26C), ocular canthi with anterior corner smooth (Fig. 24B).

Redescription. Male. **Color:** Body tomentose on head, pronotum, elytra and parts of legs, tomentum greyish yellow, surface dark brown and dull (Fig. 28A-B). **Head:** Cephalic horn projected upward, curved basally, apex bifid with tips slightly backward, surface flat, horn smoothly connected to frons (Fig. 19L); in dorsal view, lateral edges of cephalic horn like flaps. Tomentum on sides of vertex, frons and base of horn, medial area from vertex to horn not tomentose. Presence of few punctures tomentose on vertex and frons, C-punctures on vertex and frons near tomentose area, punctures thin and dense medially on vertex and basal part of frons, punctures sparse on apical portion of frons and horn. Clypeus campaniform, contiguous with cephalic horn, lateral margins sinuous, apical margin completely covered by dense bristles, apical corners simply round, punctures tomentose on sides (Fig. 19K). Ocular canthi transverse, anterior margin concave, canthi base with inconspicuous protuberance, outer corner of anterior margin with acute distinct tooth, lateral margin straight with slight angulation basally, surface punctate, punctures thin and sparse, tomentum on anterior margin, presence of transverse carina from canthi to frons (Fig. 19I). **Mouthparts:** Labrum with anterior margin slightly round medially, densely covered by setae (Fig. 20L). Mandibles with two distinct teeth, molar protuberance not projected in ventral view, inner margin near mesal brush distinctly oblique (Fig. 20I); in dorsal view, row of setae dense on outer margin reaching mesal brush near inner tooth, molar area distinctly elongated (Fig. 20J). Maxilla with galea with three apical teeth, presence of short protuberances on outer margin; stipes with shape robust, long thin setae only medially, outer margin with short thin setae; lateral border of stipes distinctly convex medially and narrowing to cardo (Fig. 20K). **Thorax:** Pronotum transverse, lateral margins more prominent at middle, anterior portion of lateral margins slightly oblique to anterior corners, posterior portion of lateral margins concave to a round posterior corner (Fig. 21G). Pronotal disc tomentose, tomentum denser on sides and anterior and posterior margins than on disc, tomentose punctures dense; presence of thoracic horn elongated directed upward, apex slightly emarginated abruptly directed forward, basal carina of horn slightly convex in lateral view, frontal and posterior sides of horn excavated with presence of dark yellow tomentum on both depressions (Fig. 21G-H). Prosternum with mesal portion at anterior

margin angulated, medial area near junction with procoxae thick and wide (Fig. 22I). Prosternal process not prominent, but as a globose mass. Metasternum hirsute, sides of metasternal suture with surface striated. Scutellum densely covered by tomentose punctures, punctures coalescent laterally and less dense basally. **Elytra:** Form 2.1 times longer than wide. Surface tomentose, disc covered by tomentose punctures, punctures parallel with elytral suture larger and more conspicuous than those on disc, presence of thin and sparse punctures between big punctures and elytral suture (Fig. 28A). Apical and humeral umbones with thin and sparse punctures, apical umbones with sparse microsetae on surface, apical umbones round and almost indistinct in lateral view (Fig. 18B). **Legs:** Protibia with three distinct external teeth, medial tooth bigger than other teeth, presence of an indentation between medial and basal teeth. Protibia in dorsal view completely covered by tomentose punctures from base to apex, punctures large and dense basally on outer edge, becoming smaller but still dense apically (Fig. 22J). Protarsomeres I–IV short, protarsomere IV with anterior inner corner elongate with two spaced teeth, protarsomere V strongly curved internally, with one short basal tooth and one acute medial protuberance; protarsal claws asymmetric, inferior claw thin and curved, superior claw with long and protuberant tooth basally and thick protuberance medially near tip (Fig. 22K). Meso- and metafemora half-covered by tomentum, denser on posterior margin. Metafemora with thin punctures with distinct range of sizes near base. Metatibial apex with outer edge projected with short thick setae on it, apical margin crenulated; metatibial surface tomentose, apex with tomentose punctures thin and moderate densely distributed. **Abdomen:** Tergite VIII round, not projected, surface tomentose. Sternites IV with tomentum only on anterior corners, surface with thin and sparse punctures, short thin setae more abundant on anterior margin than on posterior margin. Sternite V with tomentum on anterior corners and part of anterior margin, anterior half covered by thin and dense tomentose punctures, posterior half with thin and sparse tomentose punctures. Sternite VI tomentose on sides and anterior margin, tomentose punctures thin and dense on anterior half, presence of short thin setae on sides on posterior margin. Sternite VII–VIII with anterior half almost completely tomentose, posterior half with thin and dense tomentose punctures (Fig. 22L). **Aedeagus:** Parameres symmetric and elongate. Parameres in caudal view with apical portion longer than basal portion and oblique, basal portion slightly angulated, almost L-shaped, inner margin curved basally and oblique apically (Fig. 23I); in lateral view, anterior phallobase bigger than posterior phallobase, posterior phallobase with apical

corners sharp and short, outer margin round (Fig. 23L), parameres with lateral carina almost indistinct, apical depression distinct (Fig. 23J); in ventral view, inner margin V-shaped basally, outer margin distinctly sinuous, medial portion concave and apical portion strongly oblique (Fig. 23K).

Male variation. Minor males with cephalic horns almost with same length than head from vertex to clypeal apex; curvature of cephalic horn near apex; thoracic horn shorter than head, lateral carinae inconspicuous, apex of horn with tomentose punctures bigger than in major males. Ocular canthi with outer corner less prominent than on major males.

Measurements. Body length: 27.6–31.4 mm. Cephalic horn length: 5–11.9 mm. Elytral length: 18.7–20.3 mm. Elytral width: 10.1–11.5 mm. Pronotal width: 12.7–14.1 mm. Protibial length: 6.3–7.5 mm. Thoracic horn length: 4–8.7 mm.

Female. Body oblong, head and pronotum not tomentose as in males (Fig. 28C-D). **Head:** Cephalic horns absent. Vertex flat, frons slightly excavated, better visible in lateral view. Vertex with minute punctures medially, punctures moderate and tomentose laterally. Frons with punctures large and dense, tomentose punctures near clypeal base (Fig. 24D). Clypeal base, on junction with frons, distinctly acute, punctures tomentose and dense (Fig. 24F); clypeus campaniform, clypeal apex with two distinct teeth upward, space between teeth concave, surface with slight depressed borders near lateral margins, punctures on clypeal surface large and dense (Fig. 24E). Ocular canthi subquadrate, anterior margin slightly concave, outer corners of anterior margin acuminate, lateral margin of canthi almost straight, surface finely punctate, tomentose area near anterior margin (Fig. 24D). **Thorax:** Pronotum convex, 4 times wider than head, lateral margins round with anterior portion round and posterior portion almost straight to posterior corners, disc with thoracic horn absent (Fig. 26D). Pronotal disc with tomentose punctures on entire surface, punctures moderate and sparser medially than laterally, punctures on sides bigger and few coalescent, lateral margins with thick tomentose border reaching anterior and posterior corners (Fig. 26D). Scutellum not tomentose but with tomentose punctures dense laterally and apically, sparse medially and basally. Prosternum with mesal portion at anterior margin acute, surface with row of setae from corners ending on posterior margin before middle, medial area near junction with procoxae thick. Prosternal process distinctly short (Fig. 26E). Metepisternum with a thick area between it and elytral epipleura. **Elytra:** Elytral disc tomentose, punctures on disc mainly concealed by tomentum; elytral suture with

mesobasal area not tomentose, punctures tomentose and large near elytral suture, presence of micropunctures dense on thin space between tomentose punctures and elytral suture (Fig. 28C). Humeral umbones with tomentose punctures thin and moderate densely distributed, apical umbones evenly round (Fig. 28D). **Legs:** Protibia with three external teeth as in males, space between medial and basal tooth with an indentation, tomentum absent on dorsal surface; protarsi simple, with protarsomeres longer than wide and claws symmetric. Meso- and metafemora not tomentose. Metafemoral punctures tomentose, punctures moderate and sparse on disc intertwined by thinner punctures, punctures thin and agglomerated near posterior margins. Metatibiae with tomentose punctures on outer edge mesobasally, weakly tomentose apically, metatibial surface micropunctate with bigger punctures near row of setae, metatibial apex with projection half as long as spur, inner margin with insertion of setae short (Fig. 26F). **Abdomen:** Tergite VIII acute, weakly tomentose on sides, punctures moderate and dense on disc. Sternites IV-VI with thin tomentose stripe on anterior margins, punctures thin and sparse on disc, presence of short thin setae sparsely distributed near posterior margin. Sternite VII with thin tomentose stripe on anterior margin but extending laterally to disc, punctures thin and sparse becoming thinner and denser on middle of posterior margin. Sternite VIII not tomentose, densely punctate on corners, disc slightly sparsely punctate.

Measurements of females. Body length: 25.5 mm. Elytral length: 16.4 mm. Elytral width: 8.9 mm. Head length: 3.9 mm. Pronotal width: 12.1 mm. Protibial length: 6 mm.

Geographic distribution. Colombia: Antioquia. Ecuador: Carchi (Fig. 35).

Material examined. Lectotype male (NHM): a) "Lectotype", b) "Syntype", c) "Type", d) "Medellin/ 78.39", e) "*Lycomedes/ Burmeisteri/ M# Type C*{ollection}. Waterhouse, f) "Lectoypus/ *Lycomedes/ burmeisteri/ Waterh.*"; **Paralectotypes** 2 females (NHM): a) "PARA-/LECTO-/TYPE", b) "SYN-/TYPE", c) "Medellin/ 78-37". **Other specimens:** 2 males (NHM): a) "Medellin/ 1878", b) "G. Lewis./ 1915-38".

Remarks. *Lycomedes burmeisteri* is considered one of the rarest species of the genus (Milani 2017). The species is presumably distributed along the Western Cordillera from Colombian Andes to Ecuadorian Andes, but it only has records to Medellin, Colombia (in the literature and specimens housed in NHM), and Carchi, Ecuador (specimens from the Leonello Milani private collection). In Colombia, the species is found in the Magdalena Valley Montane Forests, whereas in Ecuador it is

found in the Northwest Andean Montane Forests.

***Lycomedes enigmaticus* Neita-Moreno & Ratcliffe, 2019**

(Figs. 19–23, 27, 35)

Neita-Moreno & Ratcliffe 2019: 1051 (original description); Pardo-Locarno, Villalobos-Moreno & Ruiz 2020: 83 (checklist)

Diagnosis. *Lycomedes enigmaticus* is characterized by the cephalic horn elongated with drop-like depression at base (Fig. 19F), borders slightly elevated connected with posterior face of horn as carinae (Fig. 19F); clypeal apical corners distinctly acute and oblique (Fig. 19G); ocular canthi thin and transverse, outer corner of anterior margin projected and acute (Fig. 19E); thoracic horn strong and transverse, apex wider than base (Fig. 21E), tip abruptly deflected frontwards and slightly bilobated (Fig. 21D); prosternal process elongated, depression ellipsoid (Fig. 22E); posterior phallobase more than 2 times longer than anterior phallobase (Fig. 23H), parameres elongated, in caudal view with basal portion with pair of round carinae (Fig. 23E).

Description. Male. **Color:** Body destitute of tomentum, surface weakly reddish brown, some signs of tomentum on posterior surface of pronotum, near thoracic horn, and on elytral apex (Fig. 27A-B). **Head:** Cephalic horn curved basally at clypeus, apex bifid, surface flat with two distinct carinae parallel becoming more elevated at base (Fig. 19H), base of horn with distinct drop-like deep depression dorsally near frons (Fig. 19F); punctures thin and sparse on horn. Clypeus elongated, sides sinuous, apical corners distinctly acute and oblique with paired carinae obliquely connecting with cephalic horn (Fig. 19G), clypeal apex weakly convex (Fig. 19F). Ocular canthi transverse and thin, outer corner of anterior margin projected and acute, anterior margin slightly concave, presence of oblique carina reaching frons (Fig. 19E). **Mouthparts:** Labrum parabolic, medial portion of anterior margin distinctly more projected than sides (Fig. 20H). Mandibles slender, with two apical teeth and one molar protuberance angulated, pointing laterally in ventral view (Fig. 20E); in dorsal view mandibular outer margin distinctly concave medially (Fig. 20F). Maxilla slender, galea with three apical teeth, lateral border of stipes with outer margin oblique (Fig. 20G). Mentum pear-shaped, apex distinctly acute in ventral view. **Thorax:** Pronotum transverse; pronotal lateral margin distinctly sinuous, middle portion round, anterior portion concave toward

acute anterior corners, posterior portion distinctly concave to round posterior corners (Fig. 21D). Pronotal disc with traits of tomentum on posterior half, punctures large and dense conspicuous on middle and posterior half, anterior half with punctures indistinct. Thoracic horn strong and transverse, apex wider than base, tip abruptly deflected frontwards and slightly bilobed (Fig. 21E); anterior and posterior surfaces of horn slightly excavated (Fig. 21F), anterior surface with a medial line distinctly marked from anterior margin to horn apex, sculpture shagrinated (Fig. 21E). Prosternum with mesal portion at anterior margin parabolic and elongated, corners distinctly hirsute, setae sparse on disc reaching medial protuberance (Fig. 22E). Prosternal process present, elongated, apex acute, ventral surface with ellipsoid depression (Fig. 22E). Metasternum and metepisternum distinctly hirsute. Scutellum with weak signs of tomentum, surface transversely with shallow depression. **Elytra:** Shape 2.2 times longer than wide. Surface tomentose only on elytral apex. Punctures irregular, thin and ocellate, elytral surface rugose. Apical and humeral umbones with punctures shorter than punctures on disc, apical umbones distinctly angulated in lateral view (Fig. 27B). **Legs:** Protibia with three distinct external teeth, increasing in size anteriorly, medial and apical teeth closer than medial and basal teeth. Protibia in dorsal view with base slightly tomentose, presence of tomentose punctures reaching basal tooth and almost reaching medial tooth, apical punctuation coalescent and mixed of thin and moderate punctures (Fig. 22F). Protarsomeres I–IV short, protarsomere IV with anterior inner corner elongate with two spaced teeth, protarsomere V strongly curved internally, with one elongated basal tooth and one acute and short medial protuberance; protarsal claws asymmetric, inferior claw thin and curved, superior claw with long and protuberant tooth basally and distinct medial protuberance near tip (Fig. 22G). Meso- and metafemora with a weak trait of tomentum obliquely near apex, surface distinctly hirsute. Metatibial apex smoothly concave near spur, outer edge smoothly angulated, surface distinctly wrinkled, outer edge tomentose, presence of distinct carina near apex with long thin setae. **Abdomen:** Tergite VIII round, distinctly punctate on sides and posterior margin. Sternite IV distinctly projected toward sternite V medially (Fig. 22H). Sternite VI two times shorter than sternite VII, surface weakly tomentose, short thin setae on sides not reaching middle. Sternite VII weakly tomentose on anterior half, punctures thin and dense on posterior half, punctures larger and denser on sides at anterior half not reaching middle. Sternite VIII with two weak tomentose stripes oblique on corners, disc densely punctate. **Aedeagus:** Parameres symmetric and elongated. In

caudal view basal portion with pair of round carinae, inner margin straight medially and becoming concave near apical portion (Fig. 23E); in lateral view posterior phallobase more than 2 times longer than anterior phallobase, apical corners of posterior phallobase elongated, anterior margin distinctly emarginated (Fig. 23H), parameres with apical tips round, ventrolateral carina angulated near base, basal portion round (Fig. 23F); in ventral view lateral margin of basal portion truncated, ventral portion of parameres distinctly wrinkled (Fig. 23G).

Measurements. Body length: 26 mm. Cephalic horn length: 6.7 mm. Elytral length: 16.7 mm. Elytral width: 8.9 mm. Pronotal width: 11.6 mm. Protibial length: 6.2 mm. Thoracic horn length: 5.6 mm.

Geographic distribution. Colombia: Tolima (Fig. 35).

Material examined. 1 male (HNHM): a) “Coll. Nonfried/ Columbia”, b) “*Lycomedes/ burmeisteri/* det. Nádai, 1991”, c) “m# {male}”.

Remarks. This mysterious major specimen of *Lycomedes* was misidentified as *L. burmeisteri* for many years due to the general similarity between the species. However, the mysterious specimen is completely different from *L. burmeisteri* and from any other *Lycomedes* species already described. It is almost like a chimaera, the mythological Greek beast, having mixed characters of other species, as the drop-like depression on horn base similar to *L. enigmaticus*, the thoracic horn abruptly deflected forward with tip bilobated similar to *L. ohausi*, and the ocular canthi thin with outer corner projected like *L. hirtipes*.

It is certain to us that this specimen is not from any other species that have major males known. As we don't have the details about the locality in Colombia where it was collected, we have two hypothesis: 1. The specimen is a major male of *Lycomedes enigmaticus*, based on the shape of ocular canthi, horn depression semicircular and prosternal process with apex acute; or 2. The specimen is a new species. We opted to consider that this specimen is a major male of *L. enigmaticus* due to the quantity of similar diagnostic traits. Therefore, here we describe for the first time the major male of *L. enigmaticus*.

***Lycomedes hirtipes* Arrow, 1902**

(Figs. 8–16, 35)

Lycomedes hirtipes Arrow 1902: 144 (original description); *Lycomedes hirtipes* Arrow 1902: 144 (original description); Sternberg 1903: 300 (cited); Blackwelder 1944: 260 (checklist);

Endrödi 1970: 81 (revision); Endrödi 1985: 224 (catalogue, characters in key); Lachaume 1992: 27 (catalogue); Restrepo-Giraldo *et al.* 2003: 262 (checklist to Colombia); Pardo-Locarno & Morón 2006: 661 (description of larva and pupa, notes on biology); Pardo-Locarno 2013: 1 (cited); Pardo-Locarno *et al.* 2015: 1 (cited); Milani 2017: 758 (cited); Neita-Moreno & Ratcliffe 2019: 1062 (cited); Pardo-Locarno, Villalobos-Moreno & Ruiz 2020: 86 (checklist)

Diagnosis. *Lycomedes hirtipes* is the shortest species of the genus differing from other species of *Lycomedes* by the distinct closed fovea posteriorly to cephalic horn (Fig. 8F), ocular canthi transverse and thin with anterior margin distinctly concave (Fig. 8E), thoracic horn short with shallow depression behind it (Fig. 10F). Males can also be distinguished from *L. enigmaticus* by anterior corners of clypeus not projected laterally (Fig. 8G); prosternal process with apex round (Fig. 11E); parameres with apex slightly truncate and setose (Fig. 12E), whereas in *L. enigmaticus* anterior corners of clypeus projected laterally (Fig. 19G); prosternal process with apex parabolic (Fig. 22E); parameres with apex acuminate and bare (Fig. 22E) [images of minor males of *L. enigmaticus* in Neita-Moreno & Ratcliffe (2019)].

Females of *L. hirtipes* are very similar to *L. burmeisteri* but can be distinguished from it by clypeal base round (Fig. 13F), clypeus distinctly elongated (Fig. 13D), ocular canthi transverse (Fig. 13D), frons and vertex distinctly excavated (Fig. 13E), prosternal process projected and acuminate (Fig. 15E), whereas in *L. burmeisteri* clypeal base acuminate (Fig. 24F), clypeus broad (Fig. 24D), ocular canthi subquadrate (Fig. 24D), frons and vertex flat (Fig. 24E), prosternal process not projected (Fig. 26E).

Redescription. Male. **Color:** Body tomentose on head, pronotum, elytra and parts of legs, tomentum greyish yellow, surface dark brown and dull (Fig. 16A-B). **Head:** Cephalic horn projected forward, apex distinctly curved backwards, tip bifid (Fig. 8G), horn base with pair of carina elevated and convergent to frons, basal area of horn excavated between carina (Fig. 8F). Presence of tomentum on sides not crossing carina apically, medial area of frons and vertex not tomentose. Punctures moderate and sparse on vertex, thinner and sparser on frons. Clypeus campaniform, contiguous with cephalic horn, lateral margins sinuous, apex slightly round, apical corners discretely acute and oblique (Fig. 8G) with pair of carinae rising to frontal side of horn, frontal side of clypeus and horn slightly depressed (Fig. 8H). Punctures on lateral sides of clypeus thin and sparse as well as on apex, presence of few setae on sides. Ocular canthi transverse,

tip with short distinct lateral projection, anterior margin distinctly concave, basal portion of anterior margin prominent, outer corner of anterior margin with short distinct tooth, punctures thin and sparse (Fig. 8E). **Mouthparts:** Labrum with anterior margin round, sides oblique (Fig. 9H). Mandibles slender and with two apical teeth, in ventral view with molar protuberance absent, presence of medial carina slightly curved proximally, setae not crossing medial carina (Fig. 9E); in dorsal view, inner tooth distinctly upturned, row of setae from base of outer margin to inner tooth (Fig. 9F). Maxilla with galea with three teeth, medial tooth short and round; lateral border of stipes with outer margin strongly concave; stipes slender, with outer margin oblique, ventrally covered by long thin setae on apical portion (Fig. 9G). **Thorax:** Pronotum transverse, lateral margins more prominent at middle, anterior portion of lateral margins slightly curved to anterior corners, posterior portion of lateral margins concave to a round posterior corner (Fig. 10D). Pronotal disc mainly tomentose with some areas weakly tomentose on sides and near posterior margin, presence of tomentose punctures large and dense, thinner punctures near corners and horn (Fig. 10E); presence of thoracic horn directed upward, apex emarginated, base of horn slightly excavated posteriorly, tomentum absent on apical portion of horn (Fig. 10F). Prosternum with mesal portion at anterior margin acuminate, medial area near junction with procoxae thickened. Prosternal process present and big, spoon-like shaped, ventral surface distinctly excavated (Fig. 11E). Metasternum with two protuberant areas, metasternal suture with two parallel thin depressions medially. Scutellum tomentose on apex and sides, mesobasal area not tomentose with moderate and thin tomentose punctures. **Elytra:** form 2.3 times longer than wide. Surface tomentose, disc covered by moderate and sparse punctures, punctures near elytral suture bigger and denser than on disc, surface distinctly rugose near elytral suture. Apical and humeral umbones covered by thin punctures, apical umbones slightly projected (Fig. 16B). **Legs:** Protibia with three distinct external teeth, increasing in size anteriorly with medial and apical teeth with similar sizes. Protibia in dorsal view with tomentose punctures basally on outer and inner edge, not crossing basal tooth, punctures bigger basally than apically, apical punctures thinner and entangled (Fig. 11F). Protarsomeres I–IV short, protarsomere IV with anterior inner corner elongate with two spaced teeth, protarsomere V strongly curved internally, with one short basal tooth and one acute medial protuberance; protarsal claws asymmetric, inferior claw thin and curved, superior claw with long and protuberant tooth basally and short medial protuberance near tip (Fig. 11G). Meso- and

metafemora with diagonal stripe distally on posterior margin. Metafemora with apex of posterior margin distinctly concave, surface with long thin setae on anterior and posterior margins with shorter setae sparser and irregularly distributed on disc. Metatibial apex emarginated near spur, distinctly angulate on apical outer edge, outer apical protuberance prominent; metatibial surface with tomentose punctures on outer edge, punctures medially not tomentose with distinct sizes coalescent. **Abdomen:** Tergite VIII round, slightly projected, surface tomentose with microsetae sparse on entire surface, long thin setae agglomerated medially on posterior margin (Fig. 11H). Sternites IV-V with posterior margin distinctly elevated over posterior sternite; sternite IV with surface slightly excavated medially. Sternites IV-VI with same pattern of punctuation, punctures thin and sparse; setae long and thin near posterior margin, setae shorter on disc and near anterior margin. Sternite VII weakly tomentose, setae more abundant on sides and posterior margin. Sternite VIII with two oblique and short tomentose stripes laterally on posterior margin, short thin setae on posterior margin and long thin setae near corners, disc shagrinated (Fig. 11H). **Aedeagus:** Parameres symmetric, in caudal view elongated with basal portion longer than apical portion, apex slightly truncate and setose (Fig. 12E); in lateral view, posterior phallobase more than 2 times longer than anterior phallobase, apical corners projected and long (Fig. 12H), outer margin of parameres shortly marked on apical portion, dorsal surface distinctly depressed on apical portion (Fig. 12F); in ventral view, outer margin sinuous, ventral portion of parameres flat (Fig. 12G).

Measurements of holotype. Body length: 22.2–23.4 mm. Cephalic horn length: 2.5–2.7 mm. Elytral length: 15.2–15.4 mm. Elytral width: 7.7–7.8 mm. Pronotal width: 9.8–10.5 mm. Protibial length: 5–5.5 mm. Thoracic horn length: 0.6–0.8 mm.

Females. Body oblong, head and pronotum not tomentose as in males (Fig. 16C-D). **Head:** Cephalic horns absent. Frons and vertex with distinct shallow V-shaped depression (Fig. 13E). Vertex and frons with punctures moderate and dense, punctures coalescent on depression and thinner near clypeal base. Clypeal base, on junction with frons, evenly round (Fig. 13F); clypeus elongate and narrow, clypeal apex 2.6 times narrower than clypeal base, apex with two teeth on corners, space between teeth truncate, surface slightly depressed posteriorly to clypeal apex, punctures on clypeus coalescent; clypeal lateral borders thick, apex with almost same thickness as base (Fig. 13E). Ocular canthi similar to males but with no tooth, transverse with anterior margin distinctly concave, basal portion of anterior margin evenly round, outer corner of

anterior margin slightly prominent, punctures thin and sparse (Fig. 13D). **Mouthparts:** Labrum with anterior margin round, anterior corners evenly round to anterior margin (Fig. 14H). Mandibles in ventral view with two outer teeth and one molar protuberance, inner carina basally close to lateral portion of molar area, outer margin of mandible straight (Fig. 14E); in dorsal view, outer tooth equidistant to inner tooth and molar protuberance, basal lateral margin near molar area not distinctly projected (Fig. 14F). Maxilla with galea with two teeth paired and one short tooth below them, lateral border of stipes distinctly thick, ventral sclerite with inner margin almost oblique (Fig. 14G).

Thorax: Pronotum convex, lateral margins parabolic with anterior portion almost oblique and posterior portion slightly concave to posterior corners, disc with thoracic horn absent. Pronotal disc with tomentose punctures except on small medial area near anterior margin, punctures irregularly distributed with some central areas sparsely punctate and areas densely punctate toward margins, tomentose punctures moderate sized becoming bigger laterally and smaller on corners, lateral margins with a thin tomentose border barely reaching posterior corners and not reaching anterior corners (Fig. 15D). Scutellum not tomentose, punctures on basal corners, apex not punctate. Prosternum with mesal portion at anterior margin parabolic, surface with setae reaching medial elevation, medial area near junction with procoxae with short longitudinal area elevated and narrow (Fig. 15E). Prosternal process acute and prominent (Fig. 15E). Metepisternum with just a thin stripe between it and the elytral epipleura. **Elytra:** Elytral disc weakly tomentose; punctures thin and sparse on disc and mesoapical portion of elytral suture, punctures bigger on basal portion of elytral suture near scutellum (Fig. 16C). Humeral umbones with thin and tomentose punctures, apical umbones not protuberant (Fig. 16D). **Legs:** Protibia with three external teeth as in males, space between medial and basal tooth with an indentation, tomentum absent on dorsal surface; protarsi simple, with protarsomeres longer than wide and claws symmetric. Meso- and metafemora with no tomentum, metafemoral punctures thin and sparse with small area of agglomerated punctures distally. Metatibiae with tomentose punctures only basally near junction with metafemora, surface densely punctate, punctures large coalescent and intertwined with micropunctures apically. **Abdomen:** Tergite VIII acute, surface with no tomentum, punctures thin and coalescent on corners, thin and sparse on disc (Fig. 15F). Sternite III with posterior margin medially distinctly emarginated (Fig. 15F). Sternites IV-VI finely and sparsely punctate; presence of short thin setae on entire surface, setae near posterior margins bigger than setae on disc and

anterior margins. Sternite V with posterior margin medially distinctly concave. Sternite VII almost two times longer than sternite VI, setae on posterior margin and disc longer than on previous sternites, medial portion on disc with micropunctures agglomerated. Sternite VIII densely micropunctate, posterior margins with short thin setae becoming longer toward corners.

Measurements of females. Body length: 24.4–25.1 mm. Elytral length: 15.6–15.9 mm. Elytral width: 8.2–8.8 mm. Head length: 3.6–3.8 mm. Pronotal width: 10.8–10.9 mm. Protibial length: 5.2–5.8 mm.

Geographic distribution. Colombia: Boyacá, Caldas, Cauca, Huila, Tolima and Valle del Cauca (Fig. 35).

Material examined. Syntypes 1 male and 1 female (NHM): a) “Co-/type”, b, frente) “COLOMBIA”, b, verso) “1902 - 302”; 1 male and 1 female (NHM) with same data as previous specimens but with label a) “Co-type” absent. **Other specimens:** 2 males (HNHM): a) “S{an}. Antonio/ Columbia”, b) “*Lycomedes/ Reichei* Brem{e}./ v. Steinwehr. Koln.”, c) “*L. Arr./ hirtipes/ det. Dr. Endrödi 1968*”; 1 female (HNHM): a) “Collumbia/ Villa Elvira”, b) “Coll./ Jul. Moser”, c) “*L. Arr./ hirtipes/ det. Dr. Endrödi 1968*”.

Remarks. *Lycomedes hirtipes* can be found in the Cauca Valley, at foothills of eastern side of Western Cordillera, and in the Central Cordillera of Colombian Andes. In the Cauca Valley, *L. hirtipes* is recorded to areas of tropical dry forests and gallery forests near Cauca river, and to humid montane forests on higher elevations. The Cauca Valley Dry Forests is an ecoregion originally characterized by the combination of deciduous dry forests with evergreen dry forests and arid scrubland, having biannual rainy seasons in March-May and October-December separated by dry seasons. The Cauca Valley Montane Forests is an intermediary habitat between the dry forests of Andes foothills and the alpine moist forests, with annual precipitation ranging from 1000mm near western ridges and 3000mm near Central Cordillera. The knowledge about the fauna and flora of the Cauca Valley forests is still incipient and these forests are highly threatened due to the anthropic deforestation for agriculture, especially for monocultures like sugar cane (Berrío *et al.* 2002; Schipper WWF 2020). Pardo-Locarno (2013), in a recent study of Melolonthidae beetles in Agroecosystems of Cauca Valley, suggests that the population of *L. hirtipes* in the gallery forests of the alluvial plains of Cauca river may be facing a local extinction due to the decreasing numbers of specimens in recent collecting.

L. hirtipes is one of the few Agaoccephalini with the immatures described. The third-instar larva and the pupa of this species was described by Pardo-Locarno & Morón (2006), based on specimens collected by the first author under the litter in coffee plantations. For more details about the original description of the immatures see Pardo-Locarno & Morón (2006), and for an identification key to all the known Agaoccephalini larvae, see Neita-Moreno *et al.* (2014). The larvae of *L. hirtipes* presents slow movements, tending to retract the body, when disturbed, and are found in litter of forested or shadowed areas (Pardo-Locarno & Morón 2006). The adults are active flyers at dawn and can feed on mature fruits, being attracted by lights and fruit baited traps, occurring in abundance during the rainy season in the Cauca Valley, Colombia (Pardo-Locarno & Morón 2006).

Along the Central Cordillera, *L. hirtipes* can be found in the Magdalena Valley Montane Forests, the same ecoregion as *Lycomedes enigmaticus* (but not in the same locality). *L. hirtipes* is one of the shortest species of *Lycomedes* and there are no records of major males in this species. It can be misidentified with minor males of other Colombian species, like *L. burmeisteri* and *L. enigmaticus*, but the characters of genitalia, ocular canthi, and cephalic horn fovea are assertive to distinguish them (see the Diagnosis of *L. hirtipes*).

***Lycomedes ohausi* Arrow, 1908**

(Figs. 18–26, 35)

Lycomedes ohausi Arrow 1908: 354 (original description); Blackwelder 1944: 260 (checklist); Endrödi 1970: 78 (revision); Endrödi 1985: 223 (catalogue, characters in key); Lachaume 1992: 27 (catalogue); Pardo-Locarno *et al.* 2015: 4 (cited); Milani 2017: 758 (cited); Ratcliffe, Cave & Paucar-Cabrera 2020: 471 (catalogue)

Diagnosis. *Lycomedes ohausi* differ from other species by the cephalic horn with apex bifurcate (Fig. 19A) and absence of teeth or additional protuberances near horn (Fig. 19D). This trait is also shared with *Lycomedes bubeniki* and *Lycomedes salazari*. However, males of *L. ohausi* differ from *L. bubeniki* by the apex of thoracic horn dilated and bilobated with tip abruptly directed forward (Fig. 21C); cephalic horn more elongate than thoracic horn in major males (Fig. 18B); mentum in ventral view more excavated basally; tergite VIII with short setae distinct on disc, group of setae on medial portion of posterior margin. In *L. bubeniki*, apex of thoracic horn not dilated with tip

upward; cephalic horn shorter than thoracic horn in major males; mentum in ventral view less excavated basally with sides more depressed than middle; tergite VIII with microsetae inconspicuous, medial portion of posterior margin bare (images of *L. bubeniki* in Milani 2017). Also, males of *L. ohausi* differ from *L. salazari* by the shape of ocular canthi almost subrectangular (Fig. 19A), pronotum completely tomentose with punctures sparse (Fig. 21A), parameres, in dorsal view, with apical portion as narrow as basal portion (Fig. 23A), while in *L. salazari*, the shape of ocular canthi is transverse with tooth basally, pronotum with tomentose punctures large and coarse, parameres, in dorsal view, with apical portion wider than basal portion (images of *L. salazari* in Pardo-Locarno *et al.* (2015)).

Females of *L. ohausi* can be sympatric with *L. buckleyi*, *L. velutipes* and *L. bubeniki* in some areas along the Andes in Ecuador, being more similar to *L. bubeniki* but differing by clypeal sculpture densely rugose, clypeal apex with pair of sharp protuberances, ocular canthi with anterior corners sharp and pronotal punctures distinctly coalescent on lateral portion of disc, whereas in *L. bubeniki* clypeal sculpture is sparse and weakly marked, clypeal apex with pair of round protuberances, ocular canthi with anterior corners round, pronotal punctures distinctly sparse on lateral portion of disc (images of these characters can be seen in Milani (2017)). Also, it differs from *L. buckleyi* by clypeal shape narrowing to apex (Fig. 24B), ocular canthi transverse with anterior margin concave (Fig. 24A) and mandibles with molar protuberance sharp (Fig. 25A), prosternum with anterior margin medially short with protuberance not as elevated as in *L. buckleyi* (Fig. 26B) whereas in *L. buckleyi*, clypeal apex not as narrow as base compared to *L. ohausi* (Fig. 13B), ocular canthi distinctly acute on anterior margin (Fig. 13A), mandibles with molar protuberance truncate (Fig. 14A) and anterior margin slightly projected medially with protuberance elevated and thicker than in *L. ohausi* (Fig. 15B). *L. ohausi* also can be distinguished from *L. velutipes* by vertex smooth and flat (Fig. 24B), clypeal anterior corners angulated (Fig. 24A) and elytral punctures shallow and irregularly distributed on disc (Fig. 18C), while in *L. velutipes* vertex with V-shaped fovea with borders elevated like keels (Fig. 13H), clypeal anterior corners straight (Fig. 13G) and elytral punctures deep and distributed as regular rows on disc (Fig. 17C).

Redescription. Male. **Color:** Body tomentose on head, pronotum, elytra and parts of legs, tomentum greyish yellow, surface dark brown and dull (Fig. 18A-B). **Head:**

Cephalic horn projected upward, slightly curved in lateral view, horn flat, apex bifid (Fig. 19D), presence of mesobasal carina longitudinal on horn. Tomentum only at basal portion of horn on sides and dorsally near frons, frons and vertex tomentose. Punctures thin and sparse on vertex, frons and horn. Frons with a longitudinal shallow depression near horn (Fig. 19B). Clypeus campaniform, contiguous with cephalic horn, clypeal lateral margins angulate basally and oblique to apex, apex truncate as wide as eye, apical corners distinctly acute and oblique with two diagonal carinae connecting to horn (Fig. 19C). Clypeal punctures on corners large and dense, apically thin and sparse. Ocular canthi almost subrectangular, tip not projecting towards eye, anterior margin with acute oblique tooth on outer corner, outer margin of canthi slightly emarginated, punctures moderate and sparse, presence of tomentum basally (Fig. 19A). **Mouthparts:** Labrum with anterior margin irregularly convex, sides oblique, setae almost reaching medial line in dorsal view (Fig. 20D). Mandibles with two apical teeth elongated, in ventral view molar protuberance angulated with slight depressed area, not tomentose, presence of distinct carina on inner tooth (Fig. 20A); in dorsal view, mesal brush almost reaching outer setae on apex, molar area partially covered by mesal brush basally (Fig. 20B). Maxillae with galea tridentate, two transversal parallel teeth and one outer tooth bigger than others, stipes densely hirsute on middle, lateral border distinctly hirsute, covered by short and long thin setae (Fig. 20C). Mentum pear-shaped with apical narrow half almost two times longer than wide half, apex truncate; in dorsal view apex with two broad teeth. **Thorax:** Pronotum transverse, lateral margins with tip round, oblique to posterior corners and round to anterior corners (Fig. 21A). Pronotal disc completely tomentose with tomentose punctures conspicuous and dense; presence of thoracic horn directed upward, apex dilated and bilobated with tip abruptly directed forward (Fig. 21C), frontal and posterior faces of horn distinctly excavated, horn with tomentum absent laterally and apically but covered with dense tomentose punctures (Fig. 21B). Prosternum with mesal portion at anterior margin round, medial area near junction with procoxae not thickened, presence of setae diagonally grouped on prosternal anterior corners (Fig. 22A). Prosternal process present and short, not reaching middle of prosternal posterior margin (Fig. 22A). Metasternum hirsute, setae slightly dense, metepisternum hirsute. Scutellum completely tomentose, presence of moderate and sparse punctures basally and laterally. **Elytra:** Form 2.3 times longer than wide. Surface tomentose, disc covered by thin and sparse punctures, bigger punctures parallel to elytral suture and on outer side of elytra after humeral umbone, presence of

micropunctures between normal punctures. Apical and humeral umbones covered by thin punctures, apical umbones smoothly round (Fig. 18D). **Legs:** Protibia with three distinct external teeth, medial and apical tooth distinctly connected basally, presence of indentation anteriorly to basal tooth (Fig. 22B). Protibia, in dorsal view, with basal tomentose area on outer edge not crossing basal tooth, tomentose punctures longitudinal near row of setae, punctures on teeth thin and dense. Protarsomeres I–IV short, wider than long; protarsomere IV with anterior inner corner projected with two spaced teeth. Protarsomere V strongly curved internally, with one parabolic basal tooth and one oblique medial protuberance; protarsal claws asymmetric, inferior claw thin and curved, superior claw with long and protuberant tooth basally and short medial protuberance near tip (Fig. 22C). Mesofemora with diagonal tomentose stripe distally on anterior and posterior margin, metafemora half-tomentose and densely punctate on base. Metatibia tomentose on outer side with tomentose punctures medially, metatibial apex with outer margin projected and with a short tooth near inner margin, surface with large ellipsoid punctures medially and thinner punctures apically. **Abdomen:** Tergite VIII round, not projected, surface completely tomentose with microsetae sparse distributed on entire surface. Sternite IV not tomentose, covered by short thin setae and thin sparse punctures. Sternite V with tomentose stripe on sides and anterior margin, posterior margin medially not tomentose, punctures thin and dense near posterior margin. Sternites VI–VII completely tomentose, presence of short thin setae on posterior margins. Sternite VIII with two paired tomentose stripes on posterior corners extending posteriorly but not reaching middle, surface finely punctate, posterior margin with short thin setae bigger than setae on sternite VII (Fig. 22D). **Aedeagus:** Parameres symmetric. In dorsal view, base with lateral protuberances, base smoothly connected to apex, apex wide and acute, tips convergent (Fig. 23A). In lateral view, posterior phallobase almost 3 times shorter than anterior phallobase, junction of anterior and posterior phallobase distinctly depressed, posterior phallobase with corners short (Fig. 23D), parameres with ventrolateral carina inconspicuous, apex thickened (Fig. 23B). In ventral view, base of parameres connected with suture conspicuous, ventral carina inconspicuous (Fig. 23C).

Measurements of males. Body length: 24.9–31.2 mm. Cephalic horn length: 3.7–11.7 mm. Elytral length: 16.6–19.3 mm. Elytral width: 9.2–10.7 mm. Pronotal width: 11.7–14.3 mm. Protibial length: 6.8–8.1 mm. Thoracic horn length: 2.8–9.4 mm.

Females. Body oblong, head and pronotum not tomentose as in males (Fig. 18C-

D). **Head:** Cephalic horns absent. Vertex not punctate medially. Frons and vertex almost flat, punctures moderate and dense, punctures coalescent near clypeus (Fig. 24B). Clypeal base, on junction with frons, discretely upward and less projected than clypeal apex (Fig. 24C); clypeus campaniform with two acute teeth upward on apex, space between teeth distinctly concave (Fig. 24B), punctures large and dense basally and medially, sides with punctures coalescent, apex with thin punctures barely conspicuous. Ocular canthi with anterior margin concave, surface anteriorly depressed, lateral margin oblique, punctures moderate and dense posteriorly (Fig. 24A), thinner anteriorly, presence of anterior curved carina near base of clypeus. **Mouthparts:** Labrum with anterior margin straight becoming round laterally, sides acute near posterior margin (Fig. 25D). Mandibles with two moderate teeth apically, in ventral view outer edge on molar protuberance protuberant with apex sharp, space between outer tooth and apical protuberance more than 1 time wider than outer tooth, presence of distinct carina on inner tooth (Fig. 25A); in dorsal view, teeth slightly curved upward, apical corner not curved, mesal brush not covering basal portion of inner tooth, base of mandibles elongated on outer edge (Fig. 25B). Maxillae with galea with two teeth and one medial tooth not projected on outer edge; lateral border of stipes almost hairless, with few short setae in ventral view (Fig. 25C). Mentum subtriangular, apical corners oblique, base distinctly depressed; in dorsal view, two parallel broad teeth on apex. **Thorax:** Pronotum convex, slightly irregular near anterior margin, lateral margins parabolic with anterior portion almost oblique, thoracic horn absent (Fig. 26A). Pronotal anterior margin with borders absent at middle (Fig. 26A). Pronotal disc with tomentose punctures, punctures moderate and dense becoming shorter anteriorly and denser posteriorly, lateral margins completely bordered by tomentose lines reaching part of posterior margin. Scutellum with tomentose punctures on basal corners becoming bigger medially, apex with thin punctures. Prosternum similar to males, with medial area near junction with procoxae flat, presence of setae diagonally grouped on prosternal anterior corners, prosternal posterior margin medially with acute projection, prosternal process short and round (Fig. 26B). Metasternum hirsute with two oblique bumps on each side. **Elytra:** Surface broader than in males. Disc tomentose; punctures on disc mainly inconspicuous, punctures near elytral suture moderate and tomentose with thinner punctures almost reaching elytral suture, punctures on outer margin of elytra moderate and sparse (Fig. 18C). **Legs:** Protibia tridentate as in males, protibial teeth slender and sharper, indentation between medial and basal tooth more

conspicuous, tomentum absent on dorsal surface. Meso- and metafemora with short tomentose stripe diagonal on posterior margin distally (Fig. 26C). Metatibial apex projected on outer edge with 3 short teeth, apical margin with spur insertion triangular, spurs thick, metatibial surface with moderate sparse punctures almost reaching apical portion, apical portion with thinner punctures, tomentum present only at outer portion basally. **Abdomen:** Tergite VIII acute, surface completely tomentose, microsetae on entire surface. Sternites IV-V with pattern similar to males, but in females sternite V less tomentose on sides. Sternite VI almost completely tomentose except by a straight area near posterior margin, bare area covered by tomentose punctures thin and sparse. Sternite VII as in males. Sternite VIII with short tomentose area near corners, surface wrinkled on disc and anterior margin, punctate near apical margin (Fig. 26C).

Measurements of females. Body length: 28.1–28.5 mm. Head length: 4.3–4.7 mm. Elytral length: 18.5–19.5 mm. Elytral width: 9.6–10.2 mm. Pronotal width: 12.7–13.5 mm. Protibial length: 6.4–7.3 mm.

Geographic distribution. Ecuador: El Oro, Loja, Los Rios, Napo, Pichincha, Santo Domingo de Los Tsáchilas. Peru: Piura (Fig. 35).

Material examined. Holotype male (NHM): a) “Type”, b) “Holotype”, c) “1908.15a”, d) “*Lycomedes/ Ohausi* Arrow/ type M#”; **Allotype** female (NHM): a) “Type”, b) “Allotype”, c) “S.ECUADOR/ Rio Casanga”, d) “*Lycomedes/ Ohausi* Arrow/ type F#”. **Other specimens:** 1 male (NHM): a, frente) “S. Ecuador/ Rio Casanga”, a, verso) “1908 15”; 1 male and 1 female (NHM) with same data as previous specimen, except: b) “Nevinson coll./ 1918-14”; 1 male and 1 female (RBINS): a) “Dr. V. ALLARD/ Quito/ 3{III}-{19}80/ Ecuador”, b) “LYCOMEDES/ ohausi/ Arrow/ Dr. V. ALLARD det. 1987”, c) “Photo sur le Site de/ A. GALANT/ Coll. R.I.Sc.N.B.”; 2 males (HNHM): a) “S. ECUADOR/ Rio Casanga”; 1 male (NHMB): a) “*Lycomedes/ ohausi/ ECUADOR*”; 1 female (NHMB): a) “Cotypus”, b) “S. ECUADOR/ Casanga/ E. Witt S.”, c) “Arrow determ./ *Lycomedes/ ohausi* Arr.”.

Remarks. *L. ohausi* occurs mainly in the Ecuadorian Andes and in the northern Peruvian Andes. The species is distributed in areas ranging from 40m to almost 2000m of altitude, not being found in areas of higher altitudes (Ratcliffe, Cave & Paucar-Cabrera, 2020). Apparently, the Andes does not limit the distribution of *L. ohausi* in both sides of the Cordillera, but the majority of records in the literature and collections are from the Western Cordillera and western lowlands. In both sides of the Andes, the species is sympatric with *L. bubeniki*, *L. buckleyi* and *L. velutipes*. Of these species,

only the males of *L. bubeniki* are more similar to *L. ohausi* due to the horn flat and bifid with no tooth nor keels on base of horn. For the differences between *L. ohausi* and the other sympatric species see the Diagnosis section of this species. The species occurs in three different ecoregions: Western Ecuador moist forests, in areas with semi-deciduous vegetation under annual rainfall ranging 1300-2000mm (Kvist *et al.* 2004); Northwest Andean montane forests, in premontane vegetation reaching heights of 20m or more (Schipper WWF 2020); and Eastern Cordillera Real montane forests.

Adults of *L. ohausi* are attracted to lights but no further detail about the biology and habits of the species is known (Ratcliffe, Cave & Paucar-Cabrera, 2020). In the original description, Arrow (1908) mentioned that a correspondent of Mr. Friedrich Ohaus collected some specimens of *L. ohausi* on a flowering “*Schling*” plant. It is unknown to us if Arrow knew the meaning of “*Schling*” as he wrote it in italic and with quote marks. We found that “*Schling*”, like in *Schlingpflanzen*, is a German word used to refer to epiphytes or lianas. Probably these specimens were just using the epiphytes or lianas to climb the tree, as the correspondent of Ohaus did not mention about feeding activity.

***Lycomedes ramosus* Arrow, 1902**

(Figs. 2–6, 35)

Lycomedes ramosus Arrow 1902: 143 (original description); Sternberg 1903: 301 (cited); Endrödi 1970: 75 (revision); Endrödi 1985: 223 (catalogue, characters in key); Lachaume 1992: 26 (catalogue); Restrepo-Giraldo *et al.* 2003: 262 (checklist to Colombia); Pardo-Locarno *et al.* 2015: 1 (cited); Milani 2017: 758 (cited); Neita-Moreno & Ratcliffe 2019: 1062 (cited); Pardo-Locarno, Villalobos-Moreno & Ruiz 2020: 87 (checklist)
Lycomedes ramosa Blackwelder 1944: 260 (checklist, misspelled)

Diagnosis. Males of *Lycomedes ramosus* can be distinguished from other species of *Lycomedes* by: cephalic horn elevated and branched, divided into an anterior and posterior portion, posterior portion elongated with apex bifid and directed forward (Fig. 2H); in lateral view, the connection between clypeus and cephalic horn distinctly curved (Fig. 2H); ocular canthi transverse, posterior margin longer than anterior margin, lateral margin emarginated (Fig. 2E); pronotal disc with pair of depressions near anterior corners (Fig. 3D); prosternal process distinctly prominent, spoon-like shaped, posterior borders densely hirsute (Fig. 4E); parameres, in caudal view, with basal portion wider than apical portion, apical portion excavated with inner edge more elevated than outer

edge, inner edge touching on apex (Fig. 5E); parameres, in lateral view, with anterior phallobase almost 3 times shorter than posterior phallobase (Fig. 5H), apex of parameres distinctly emarginated (Fig. 5F). Comparisons with *L. reichei* are in the diagnosis section of that species.

Redescription. Male. **Color:** Body tomentose on head, pronotum, elytra and parts of legs, tomentum greyish yellow, surface dark brown and dull (Fig. 6A-B). **Head:** Cephalic horn elevated and branched, with base peduncle-like; anterior branch directed forward with slight curvature near apex (Fig. 2E); posterior branch directed upward, apex bifid and obliquely directed forward (Fig. 2H). Tomentum on sides of horn reaching middle of posterior branch of horn and base of anterior branch. Vertex only not tomentose medially, presence of thin and sparse punctures. Frons completely tomentose and covered by horn base. Clypeus campaniform, contiguous with cephalic horn, lateral margins sinuous, apical margin round (Fig. 2G), apical corners acute and upward, tomentum on sides barely reaching apical corners, medial area of clypeus slightly excavated apically with presence of thin and sparse punctures (Fig. 2F); in lateral view, the connection between clypeus and cephalic horn distinctly curved (Fig. 2H). Ocular canthi transverse, anterior margin obliquely concave with outer corners distinctly acuminate like teeth, lateral margin emarginated, posterior portion of canthi longer than anterior portion, surface tomentose with few punctures (Fig. 2E), presence of sinuous carina longitudinally extending from canthi base to frons (Fig. 2F). **Thorax:** Pronotum transverse, lateral margins distinctly prominent medially, anterior portion slightly sinuous to anterior corners, posterior portions of lateral margins distinctly emarginated to posterior corners (Fig. 3D). Pronotal disc tomentose with two big depressions laterally reaching anterior corners, punctures inconspicuous, presence of microsetae sparse on surface. Pronotal disc with presence of thoracic horn shorter than cephalic horn, shape simple and acuminate, apex emarginated dorsally (Fig. 3D), anterior surface of horn flat, posterior surface slightly depressed with fovea between base of horn and posterior half of pronotum, punctures thin and sparse on frontal non-tomentose area of horn (Fig. 3E). Prosternum with mesal portion at anterior margin elongate and acuminate (Fig. 4E), surface with area near anterior corners distinctly thick and covered by setae. Prosternal process distinctly prominent, spoon-like shaped, posterior borders densely hirsute (Fig. 4E). Metasternum hirsute and sparsely punctate on posterior margins. Scutellum tomentose on apical and lateral portions, basal portion

non-tomentose with tomentose punctures dense. **Elytra:** Form 2.1 times longer than wide. Surface irregularly covered by thin and moderate deep punctures, punctures deeper parallel to elytral suture, punctures on disc shallow and more conspicuous near lateral margins (Fig. 6B). Apical and humeral umbones with punctures thin and sparse, microsetae densely distributed near apical umbones, apical umbones distinctly acute. **Legs:** Protibia with three distinct external teeth, medial tooth longer than other teeth. Protibia in dorsal view tomentose on outer area below basal tooth with tomentose punctures disperse basally and medially, punctures non-tomentose thin and dense medially, punctures slightly sparser and transverse near medial and apical teeth (Fig. 4F). Protarsomeres I–IV short, protarsomere IV with anterior inner corner elongate with two spaced teeth, protarsomere V strongly curved internally, with basal tooth and medial protuberance almost with same size and distinctly acute; protarsal claws asymmetric, inferior claw thin and curved, superior claw with elongate with round tip tooth basally and thick protuberance medially near tip (Fig. 4G). Meso- and metafemora densely hirsute with tomentose stripes distally on posterior margins. Metatibial apex with outer corner distinctly projected with a long thick setae on it, apical margin slightly concave to spur, metatibial surface densely punctate, punctures thin and coalescent from base to apex, outer edge with tomentum. **Abdomen:** Tergite VIII round, slightly projected, surface tomentose with short setae densely distributed on entire surface (Fig. 4H). Sternites IV–VI distinctly narrowed medially compared to sides. Sternites IV–V barely weakly tomentose on sides, surface densely covered by short thin setae, thin and dense punctures near posterior margins. Sternite VI similar to sternites IV–V regarding setae and punctures but with a tomentose stripe on anterior half. Sternite VII with tomentum on entire surface except medial portion near posterior margin, presence of short thin setae on entire surface, triple row of thin and dense punctures on medial portion of posterior margin. Sternite VIII with two tomentose stripes from corners to posterior margins laterally not reaching middle (Fig. 4H), disc densely punctate, C-punctures on anterior margin and regular round punctures near posterior margin and middle. **Aedeagus:** Parameres symmetric and elongate. In caudal view, basal portion wider than apical portion, basal surface with ellipsoid fovea, apical portion excavated with inner edge more elevated than outer edge, inner edge touching on apex (Fig. 5E). In lateral view, anterior phallobase almost 3 times shorter than posterior phallobase, posterior phallobase with corners elongate and posterior margin distinctly concave, presence of lateral depression on posterior phallobase (Fig. 5H), parameres with outer

edge deflected upward near apex (Fig. 5F). In ventral view, parameres with outer edge straight, connected basally and apically; ventral sclerite distinctly punctate, flat medially and basally, slightly concave apically (Fig. 5G).

Measurements. Body length: 29.8 mm. Cephalic horn length: 8.9 mm. Elytral length: 17.6 mm. Elytral width: 9.7 mm. Pronotal width: 13.3 mm. Protibial length: 6.7 mm. Thoracic horn length: 3.5 mm.

Females. Unknown.

Geographic distribution. Colombia: Cundinamarca (Fig. 35).

Material examined. Holotype male (NHM): a) “*Lycomedes/ ramosus*, Arrow/ type m#”, b) “Type”, c) “Bogotá”, d) “Crowley/ Bequest/ 1901-78”.

Remarks. *Lycomedes ramosus* is, perhaps, the rarest species of the genus. The species was described based only on the type specimen (a male) and we could not find other specimens in the examined collections. The holotype was collected in the Eastern Cordillera, in Bogotá, and there is no other *Lycomedes* species occurring in the same locality. Another record of *L. ramosus* can be found on the website *iNaturalist.org*: the user “sandragean” found a live specimen in Otanche, Boyacá, a city at foothills of Eastern Cordillera located more to the north compared to the type locality of *L. ramosus*. With these data, it is possible to infer that the distribution of this species occurs in the Magdalena Valley Montane Forests between the Central and Eastern Cordilleras. This ecoregion is shared with *L. reichei*, the only species in the genus with a little resemblance with *L. ramosus*, as both species have posterior projection at cephalic horn base, but in *L. reichei* it is simple whereas in *L. ramosus* it is branched.

***Lycomedes velutipes* Arrow, 1902**

(Figs. 8–15, 17, 35)

Lycomedes velutipes Arrow 1902: 144 (original description); Sternberg 1903: 300 (cited); Blackwelder 1944: 260 (checklist); Endrödi 1970: 82 (revision); Endrödi 1985: 224 (catalogue, characters in key); Lachaume 1992: 26 (catalogue); Pardo-Locarno *et al.* 2015: 6 (cited); Milani 2017: 758 (cited); Ratcliffe, Cave & Paucar-Cabrera 2020: 474 (catalogue)

Diagnosis. Males of *Lycomedes velutipes* can be distinguished from other species of the genus by: base of cephalic horn with two parallel round or oblique keels (Fig. 8I); vertex with shallow and semicircular fovea (Fig. 8J); ocular canthi transverse with tip globose and semicircular protuberance on outer corner (Fig. 8I); elytra with regular

rows of deep punctures on disc (Fig. 17A); prosternal process distinctly prominent, ventrally excavated with posterior corners slightly acuminate (Fig. 11I); protarsus with basal tooth elongated and round, distal protuberance distinctly projected (Fig. 11K).

Females: vertex with V-shaped fovea (Fig. 13I), borders elevated like keels (Fig. 13H); frons slightly excavated and densely wrinkled (Fig. 13G); clypeal apex distinctly narrow and elongate (Fig. 13H); ocular canthi transverse, outer corner and tip round (Fig. 13G); elytral disc with regular rows of deep punctures (Fig. 17C); mandibular outer carina distinctly projected over outer margin in ventral view (Fig. 14I); mandibular molar protuberance round (Fig. 14J). For comparisons with *L. ohausi* see the Diagnosis section of that species.

Redescription. Male. **Color:** Body tomentose on head, pronotum, elytra and parts of legs, tomentum greyish yellow, surface dark brown and dull (Fig. 17A-B). **Head:** Cephalic horn projected upward, slightly curved only near clypeus, apex bifid with apical surface flat (Fig. 8K), base of horn with two parallel round keels, space between keels deeply excavated (Fig. 8I). Tomentum on sides of horn and ending at the end of keels apically. Vertex with semicircular fovea, surface shallow (Fig. 8J). Punctures not visible on neither vertex nor frons, surface completely tomentose. Clypeus campaniform, contiguous with cephalic horn, lateral margins sinuous, apical margin acute, apical corners oblique and acute with distinct carinae connecting to cephalic horn, punctures thin and sparse, base of clypeus completely tomentose (Fig. 8K). Ocular canthi transverse, tip globose, anterior margin with short concavity basally and semicircular protuberance on outer corner, surface of canthi completely tomentose, presence of longitudinal carinae basally (Fig. 8I). **Mouthparts:** Labrum with anterior margins continuously round (Fig. 9L). Mandibles with two strong teeth and one short molar protuberance; in ventral view, outer carina strongly projected over outer margin, medial carina distinctly concave (Fig. 9I); in dorsal view, molar protuberance short and almost inconspicuous, mesal brush distinctly robust on apical portion (Fig. 9J). Maxilla with galea with basal portion round and projected (Fig. 9K), ventral portion of stipes with long thin setae sparse and intertwined by few short setae. **Thorax:** Pronotum transverse, lateral margins more prominent at middle, anterior and posterior portions of lateral margins slightly oblique to respective corners (Fig. 10G). Pronotal disc tomentose, tomentose punctures on entire surface, punctures medially on posterior half more conspicuous than punctures on sides and on anterior half, anterior margin with a

short carina medially (Fig. 10H). Pronotal disc with presence of thoracic horn shorter than cephalic horn and obliquely directed upward, apex emarginated, posterior depression of horn deeper than frontal depression, punctures thin and dense on horn, some tomentose thin punctures laterally (Fig. 10I). Prosternum with mesal portion at anterior margin semicircular, posterior corners distinctly spreading laterally to proepisternum, medial area near junction with procoxae with distinct keel connected with prosternal process (Fig. 11I). Prosternal process distinctly prominent, spoon-like shaped but with posterior corners slightly acuminate, ventral surface concave completely covered by tomentum (Fig. 11I). Metasternum hirsute, mesal area near metasternal suture bare, presence of shallow fissure continuous to metasternal posterior margin. Metepisternum densely tomentose. Scutellum tomentose, densely punctate, tomentum on sides thicker than on disc, lateral punctures coalescent. **Elytra:** Form 2.2 times longer than wide. Surface tomentose, disc covered by deep punctures, punctures parallel to elytral suture bigger than punctures on disc, some bigger punctures coalescent near elytral suture, row of punctures near outer margins closer to each other than rows on disc (Fig. 17A). Apical and humeral umbones with punctures shallow thin and sparse. **Legs:** Protibia with three distinct external teeth, increasing in size distally. Protibia in dorsal view almost completely tomentose, punctures basally inconspicuous, punctures apically tomentose and sparse becoming smaller towards teeth (Fig. 11J). Protarsomeres I–IV short, protarsomere IV with anterior inner corner elongate with two spaced teeth, protarsomere V strongly curved internally, with basal tooth and medial protuberance almost with same size; protarsal claws asymmetric, inferior claw thin and curved, superior claw with short and protuberant tooth basally and thick protuberance medially near tip (Fig. 11K). Meso- and metafemora completely tomentose, presence of two parallel rows of thin setae near anterior and posterior margins. Metatibial apex with outer corner distinctly elongate and projected with no setae on it, apical margin slightly concave to spur, apical socket of thick setae on outer edge distinctly angulate. **Abdomen:** Tergite VIII round, not projected, surface tomentose, short setae on posterior margin medially. Sternites IV–VII completely tomentose, punctures thin and sparse on disc, setae thin and short on sides and posterior margins not reaching middle. Sternite VIII distinctly thin, almost 3 times shorter than sternite VII, disc tomentose, punctures denser medially than laterally, posterior margin with long and short setae intertwined (Fig. 11L). **Aedeagus:** Parameres symmetric. In caudal view, parameres with basal portion bigger than apical portion, outer margin oblique medially and

widening apically to apex, apical portion elongated and ellipsoid (Fig. 12I); in lateral view, anterior phallobase bigger than posterior phallobase, posterior phallobase with corners short and apex not excavated (Fig. 12L), parameres with apex slightly hook-shaped, presence of basal carina not reaching lateral surface medially (Fig. 12J), short ventrolateral carina projected to lateral margin (Fig. 12J); in ventral view, base distinctly projected, outer margin oblique, widening to apical portion, presence of curved carina basally on ventral surface (Fig. 12K).

Male variation. Minor males with cephalic and thoracic horns distinctly shorter than major males. Ocular canthi with outer corner of anterior margin more projected but always round. Punctures on posterior half of pronotum inconspicuous in some specimens. In major males, keels of cephalic horn more semicircular. One major male found with teratology only on thoracic horn, horn short and distinctly asymmetric on left side, apex on left side slightly twisted forward.

Measurements. Body length: 30.2–32.4 mm. Cephalic horn length: 7.1–10.2 mm. Elytral length: 18.4–20.7 mm. Elytral width: 10.1–10.7 mm. Pronotal width: 14.6–16.7 mm. Protibial length: 8–9.3 mm. Thoracic horn length: 4.3–6.9 mm.

Females. Body oblong, head and pronotum not tomentose as in males (Fig. 17C-D). **Head:** Cephalic horns absent. Vertex with V-shaped fovea (Fig. 13H), borders elevated like keels (Fig. 13I), punctures thin and sparse laterally, wrinkles on fovea. Frons slightly excavated, densely wrinkled. Clypeal base, on junction with frons, distinctly acute, punctures coalescent; clypeus campaniform elongated toward apex, clypeal apex 2.3 times narrower than base, apical corners with two distinct teeth acute upward, clypeal surface with middle more depressed than sides, punctuation on middle transversely wrinkled and on sides longitudinally wrinkled (Fig. 13G). Ocular canthi transverse, outer corner round, tip round, anterior margin inconspicuously concave near base, surface densely punctate, presence of short carinae on canthi base (Fig. 13G).

Mouthparts: Labrum with anterior margin slightly truncate, anterior corners round and densely covered by setae (Fig. 14L). Mandible with two strong teeth and one distinct molar protuberance; in ventral view, outer carina distinctly projected over outer margin, area between inner and medial carina depressed, medial carina distinctly concave near tooth (Fig. 14I), distance between inner carina and basal lateral margin of molar area almost 3 times longer than distance between inner carina and medial carina (Fig. 14I); in dorsal view, mesal brush with outer portion almost touching outer row of setae (Fig. 14J). Maxilla with galea with basal outer margin round and projected, apex with two

distinct teeth paired, lateral border of stipes thick with ventral portion covered by short thin setae, inner portion with long thick setae (Fig. 14K), cardo with projection slightly curved at distal portion. **Thorax:** Pronotum convex, lateral margins round and not projected laterally, anterior portion slightly oblique and posterior portion almost straight to posterior corners, disc with thoracic horn absent, anterior margin with border complete and straight medially (Fig. 15G). Pronotal disc with tomentose punctures sparser medially and denser laterally and near margins, punctures coalescent near posterior corners, lateral margins with tomentose border on lateral and posterior margins not reaching anterior margin (Fig. 15G). Scutellum parabolic, sides and apex densely tomentose, base not tomentose but with dense tomentose punctures. Prosternum with mesal portion at anterior margin semicircular not projected, surface slightly depressed near posterior margins (Fig. 15H). Prosternal process acuminate and narrow, ventral surface slightly excavated (Fig. 15H). Metasternum hirsute laterally, bare medially near metasternal suture, punctures on sides bigger than medially. **Elytra:** Elytral disc tomentose, punctures tomentose and deep regularly distributed in rows, punctures near elytral suture bigger than others, row parallel to elytral suture with few punctures coalescent, row of punctures near outer margin of elytra with gaps non punctate (Fig. 17C). Humeral umbones with tomentose punctures thinner than on disc reaching them basally, tomentose punctures not reaching area near apical umbones (Fig. 17D). **Legs:** Protibia with three external teeth as in males, presence of indentation at space between apical and medial teeth and between medial and basal teeth, short tomentose stripe present on outer edge basally, punctures moderate and sparse, thin punctures near row of setae; protarsi simple, with protarsomeres longer than wide and claws symmetric. Mesofemora with tomentose stripe on posterior margin, stripe thicker distally than medially, tomentum scattered near base. Metafemora with tomentose stripes on anterior and posterior margins not reaching base, metafemoral disc with thin and sparse punctures, thin tomentose punctures distally. Metatibiae tomentose only on outer edge, metatibial surface with moderate punctures sparse, thin punctures basally dense, metatibial apical margin slightly concave with outer corner projected and acute, spur insertion concave, spur thin. **Abdomen:** Tergite VIII acute, completely tomentose, presence of short setae denser on sides. Sternites IV-VII with surface completely tomentose, presence of short thin setae on posterior margins. Sternite VII with setae on posterior margin bigger than on previous sternites, disc with sparse setae shorter than those on posterior margin. Sternite VIII tomentose on posterior half, anterior half with

narrow stripe non-tomentose and wrinkled, short thin setae on posterior margin, microsetae on disc (Fig. 15I).

Measurements of females. Body length: 28.4–28.8 mm. Elytral length: 17.8–18.1 mm. Elytral width: 9.6–10.2 mm. Head length: 4.2–4.7 mm. Pronotal width: 13.1–13.5 mm. Protibial length: 6.6–6.7 mm.

Geographic distribution. Colombia: Nariño. Ecuador: Cañar, Esmeraldas, Guayas, Imbabura, Loja, Napo, Pichincha, Santo Domingo de Los Tsáchilas (Fig. 35).

Material examined. Lectotype male (NHM): a) “Lectotype”, b) “Syntype”, c) “Type”, d) “Chimbo/ Equateur/ M. de Mathan/ 1891”, e) “*Lycomedes/ velutipes* Arrow/ type M#”, f) “Lectotypus/ *Lycomedes/ velutipes* Arrow”; **Paralectotype** female (NHM): a) “Paralectotype”, b) “Syntype”, c) “Type”, d) “Equateur/ La Chima/ M. de Mathan/ 1er{first} Semestre 1893”, e) “*Lycomedes/ velutipes* Arrow/ type F#”. **Other specimens:** 1 male and 1 female (NHM): a) “COLOMBIA: Narino,/ Barbacoas 40m{of altitude}/ 6.x.1990/ M. Cooper”, b{in male}) “Cooper coll./ BMNH-ENT-2018-128/ NHMUK013741592”, b{in female}) “Cooper coll./ BMNH-ENT-2018-128/ NHMUK013741593”; 1 male (NHM): a) “ECUADOR, Pichincha/ Nanegal 4200m {of altitude}/ II{2}.vii.1984/ M. Cooper”, b) “Cooper coll./ BMNH-ENT-2018-128/ NHMUK013741591”, c) “*LYCOMEDES/ VELUTIPES/ ARROW/* det. B.C. Ratcliffe 2019”; 1 male (NHMB): a) “Chimbo/ Equateur/ M. de Mathan/ 1891”, b) “Type”, c) “*Lycomedes/ velutinus* {*velutipes*} Arrow/ type”.

Remarks. The type series of *Lycomedes velutipes* was collected by Marc de Mathan, during his field trips in the western Ecuador, and posteriorly incorporated to the collection of René Oberthür. It was Oberthür, then, who showed the specimens to Arrow, giving him some of the specimens to his own collection (Arrow 1902). Hitherto, *L. velutipes* was only known to Ecuador, but after examining specimens housed in NHM, London, we found a couple collected in the 1990’s by Martin Cooper in Barbacoas, Colombia at 40m of elevation. This is the first record of this species to Colombia.

L. velutipes occurs mainly in the Western Cordillera along the Ecuadorian Andes and southern portion of Colombian Andes, with few records to the Eastern Cordillera in Ecuador. The species is sympatric with *L. bubeniki* and *L. ohausi* in the Northwest Andean montane forests and in the Western Ecuador moist forests, and it is sympatric with *L. buckleyi* in the Eastern Cordillera Real montane forests. *L. velutipes* is really unique in the genus, the males distinguish from the other sympatric species by the

cephalic horn with two parallel keels at base, elytral disc with regular rows of deep punctures and metatibial apex with outer corner distinctly elongate and projected (those two last traits very similar to *Horridocalia delislei*), and the females can also be distinguished by the vertex with V-shaped fovea and borders keel-like (Fig.).

Notes on *Horridocalia* Endrödi, 1974

Horridocalia was up until now a monotypic genus described by Endrödi (1974) base on one male specimen. The genus resemble *Lycomedes* due to the color of elytral tomentum and the shape of thoracic horn, both genera share the distribution on Colombian Andes. Pardo-Locarno *et al.* (2014) did the first review of the genus, redescribing it, describing new variations of male specimens of *Horridocalia delislei* Endrödi, 1974 and adding new records to Colombia. Also, Pardo-Locarno *et al.* (2014) did the first description of the female of this genus. While reviewing material housed in NHMB, we found a couple of *Horridocalia* specimens, but from Peru, a distinct locality than the current records of *H. delislei*. After examining the specimens, we realized that they are in fact a distinct species and we are describing it below.

***Horridocalia* Endrödi, 1974**

(Figs. 29–34, 36)

***Horridocalia peruviana* Sobral & Grossi, new species**

(Figs. 29–33, 36)

Diagnosis. Male of *Horridocalia peruviana* can be characterized by parameres, in lateral view, with slight ventral protuberance near apex (Fig. 32B), anterior phallobase bigger than posterior phallobase (Fig. 32D), parameres in caudal view wider on apex, left and right sides of parameres distinctly separated (Fig. 32A), in ventral view with ventral carina round, apical portion slightly emarginated (Fig. 32C). The new species differ from *H. delislei* by cephalic horn with small fovea near frons (Fig. 30D), pronotal horn short and not projected to anterior margin (Fig. 30E), pronotum with carina absent on sides near horn, tomentose punctures densely aggregated near horn (Fig. 30F), prosternal process moderate and with tip straight (Fig. 30F) whereas in *H. delislei*, cephalic horn elongated with longitudinal keel medially (Fig. 30A), pronotal horn longer than in *H. peruviana*, projecting to anterior margin (Fig. 30B), pronotum with

carina present on sides of horn, tomentose punctures sparser on horn (Fig. 30C) and prosternal process long and with tip projected posteriorly (Fig. 30C). Females of *Horridocalia peruviana* are characterized by the following characters: distance between clypeal teeth 4 times narrower than distance between basal protuberances (Fig. 33A), clypeal apical corner strongly angulated (Fig. 33A), frons with transversal tomentose stripe (Fig. 33B), mandible with outer protuberance more prominent (Fig.), ocular canthi with anterior margin slightly concave basally and outer corner distinctly round (Fig. 33A).

Redescription. Male. **Color:** Body tomentose with tomentum greyish yellow on head, legs and abdomen, tomentum dark yellow on elytra, surface black to dark brown, dull (Fig. 29A-B). **Head:** Cephalic horn elongated and bifid (Fig. 30F), base of horn with elongate depression subrectangular narrowing near vertex, presence of two parallel carinae reaching posterior surface of cephalic horn (Fig. 30D). Tomentum covering vertex, frons and basal portion of cephalic horn, horn apex not tomentose, punctures thin and sparse on cephalic horn. Clypeus campaniform, contiguous with cephalic horn, lateral margin sinuous, apical margin acuminate, apical corners angulated, tomentum not reaching apical corners. Ocular canthi transverse and oblique with outer corner prominent and round, boot-shaped (Fig. 30D); anterior margin slightly concave and covered by tomentum. **Mouthparts:** Labrum subtrapezoidal, sides oblique, posterior margin distinctly concave, anterior margin slightly acuminate (Fig. 31D). Mandibles with two apical teeth thick and long, in ventral view outer edge round with tomentum, presence of distinct carina on inner tooth (Fig. 31A); in dorsal view, teeth distinctly curved upward, mesal brush covering inner edge completely, molar protuberance absent, outer edge curved on apical corner (Fig. 31B). Maxillae with galea shape like isosceles triangle, apex curved inward with just one tooth, presence of longitudinal carina on inner side of galea (Fig. 31C). Mentum pear-shaped distinctly narrow on apex, almost 4 times narrower than base, apex with two teeth in dorsal view, tip in ventral view distinctly parabolic. **Thorax:** Pronotum transverse, lateral margins parabolic. Pronotal disc with thoracic horn short, like a transverse robust protuberance with apex slightly emarginated (Fig. 30E); tomentose punctures densely distributed uniformly on entire pronotum, presence of tomentose borders surrounding pronotal margins completely, punctures denser near horn (Fig. 30F). Prosternum with distinct keel near junction with procoxae. Prosternal process distinctly prominent, apical corners slightly angulated,

ventral surface depressed and covered by tomentum. Metasternum with punctures large and dense near outer margin, punctures thinner and sparser on disc towards metasternal suture. Metaepisternum with longitudinal carina splitting surface in outer depressed area and inner flat area. Scutellum completely tomentose except medially on base, non-tomentose area covered by tomentose punctures dense and moderate. **Elytra:** Form 2.1 times longer than wide. Surface covered by deep and large punctures, punctures distributed in 10-11 regular rows with at least 3 irregular rows between some of the rows, one irregular row always between first and second regular row, from right to left (Fig. 29A). Apical and humeral umbones with punctures shallow, thin and sparse. **Legs:** Protibia with three distinct external teeth, medial tooth longer than other teeth. Protibial surface in dorsal view tomentose on outer edge and medially near middle tooth, presence of punctures moderate and sparse longitudinally at middle, punctures thin and sparse on teeth, some tomentose punctures near basal tooth. Protarsomeres I–IV short, protarsomere IV with anterior inner corner elongate with two spaced teeth, protarsomere V strongly curved internally, with basal tooth distinctly longer than medial protuberance; protarsal claws asymmetric, inferior claw thin and curved, superior claw with elongated tooth with round tip basally and discrete protuberance medially near tip. Mesofemora completely tomentose, metafemora tomentose on anterior and posterior margins, with a non-tomentose longitudinal area with thin and sparse tomentose punctures from base to first third of femora, not reaching apex. Metatibia with 6 protuberances with thick setae, protuberances I-IV and VI on outer margin, protuberance V slightly medial, distance from protuberance VI to protuberance IV bigger than distance from protuberance IV to protuberance I; metatibial apex with outer corner distinctly elongate and projected with no setae on it. Metatarsi with thin tomentose punctures on tarsomeres I-V, metatarsomere I with tomentum on outer edge. **Abdomen:** Tergite VIII round, surface tomentose with microsetae sparsely distributed on surface, presence of long thin setae coarse at middle on posterior margin. Sternites IV-V less tomentose than other sternites. Sternite VI-VII completely tomentose, with long thin setae on posterior margins decreasing in size medially, punctures thin and sparse more conspicuous near posterior margins. Sternite VIII completely tomentose, wrinkled on anterior margin and punctate on disc and posterior margin, long thin setae on sides of posterior margin, short setae at middle and on disc. **Aedeagus:** Parameres symmetric and elongate. In caudal view, basal portion slightly wider than apical portion, base with lateral carinae bilobated, apex paddle-like shaped slightly emarginated near

tip (Fig. 32A). In lateral view, anterior phallobase bigger than posterior phallobase, posterior phallobase with apical corners short (Fig. 32D), parameres with basal lateral carina ending medially, ventral surface of parameres slightly prominent near apex, apical tip hook-shaped (Fig. 32B). In ventral view, lateral portion of ventral sclerite roundly protruded near inferior edge, inferior edge narrowing basally (Fig. 32C).

Measurements. Body length: 35.5 mm. Cephalic horn length: 6.6 mm. Elytral length: 23.1 mm. Elytral width: 12.5 mm. Pronotal width: 18 mm. Protibial length: 9.2 mm. Thoracic horn length: 1.1 mm.

Females. Body oblong, as broad as in males, head not tomentose as in males, pronotum less punctate than in males (Fig. 29C-D). **Head:** Cephalic horns absent. Vertex barely punctate, presence of pair of tomentose stripes oblique from vertex to clypeal base (Fig. 33B). Frons densely punctate, punctures large and dense, punctures coalescent towards clypeus, presence of transverse tomentose stripe on junction with clypeus (Fig. 33B). Clypeal base, on junction with frons, distinctly prominent and sharp (Fig. 33C), punctures tomentose thinner than on frons; clypeus campaniform, clypeal apex less than 1.5 times narrower than base, apical corners angulated, clypeal apex medially with two slightly oblique teeth, clypeal surface slightly depressed near apex, clypeal punctures large and dense, punctures coalescent near clypeal base. Ocular canthi transverse, outer corners round and not as protuberant as in males, anterior margin slightly concave, surface of anterior margin tomentose, posterior margin shagrinated (Fig. 33A). **Mouthparts:** Labrum subtrapezoidal, sides oblique, posterior margin concave, anterior margin almost straight (Fig. 31H). Mandibles with two apical teeth thick and long, in ventral view molar protuberance elongated and truncate, tomentum absent, presence of short depression basally near inner margin with dense row of setae (Fig. 31E); in dorsal view, teeth and protuberance of corner curved upward, presence of carina between outer and inner teeth (Fig. 31F). Maxillae with galea longer than stipes, apex with one elongate tooth longer than in male (Fig. 31G). Mentum slightly less narrow on apex than in male, surface not tomentose, apical teeth parallel. **Thorax:** Pronotum broad and convex, lateral margins round, thoracic horn absent (Fig. 33D). Pronotal disc with tomentose punctures bigger and denser on sides than medially, pronotal margins completely surrounded by tomentose borders (Fig. 33D). Prosternum with mesal portion at anterior margin round not projected, prosternal process acuminate and short, not conspicuous as in male (Fig. 33E). Metasternum with punctures thin and sparse, setae shorter on sides than medially. Metepisternum as in males. Scutellum

acuminate, apex and sides tomentose, middle and base with tomentose punctures thin and dense. **Elytra:** Elytral disc tomentose, punctures tomentose and deep distributed in rows as in males, with 10-11 regular rows and 3-4 irregular rows, space between first regular row and second regular row always with one irregular row (Fig. 29C). Humeral and apical umbones with thin and sparse normal punctures, apical umbones with few deep punctures reaching them basally (Fig. 29D). **Legs:** Protibia with three external teeth as in males, indentation at space between apical and medial teeth and between medial and basal teeth, short tomentose area on outer edge basally not reaching basal tooth, punctures thin and sparse; protarsi simple, with protarsomeres longer than wide and claws symmetric. Meso- and metafemora with thin tomentose stripe on posterior margins not reaching metafemoral apex, surface with punctures thin and sparse abundant (Fig. 33F). Metatibiae with 5 outer protuberances with thick setae, outer edge of metatibiae tomentose; metatibial apex with outer corner distinctly elongate and projected with no setae on it; apical margin straight from spur to metatibial projection. **Abdomen:** Tergite VIII slightly acute, surface tomentose with microsetae. Sternites IV-VI with surface almost completely tomentose except by a thin stripe on posterior margins, non-tomentose stripe covered by thin and sparse punctures, short thin setae on sides and posterior margins but not reaching middle. Sternite VII completely tomentose, punctures tomentose moderate and sparse near anterior margin, posterior margin with short thin setae not reaching middle, disc with microsetae. Sternite VIII tomentose on sides and posterior half of disc, anterior margin distinctly wrinkled, disc punctate and with sparse microsetae, posterior margin with short thin setae shorter medially than on sides (Fig. 33F).

Measurements of female. Body length: 33.7 mm. Elytral length: 21.8 mm. Elytral width: 12.4 mm. Head length: 5.6 mm. Pronotal width: 16 mm. Protibial length: 7.9 mm.

Geographic distribution. Peru: unknown locality (Fig. 36).

Material examined. 1 male and female (NHMB): a) “Pérou/ ex {illegible, probably a name of the former collection}”, b) “*Lycomedes*/ sp./ Pérou”.

Remarks. *Horridocalia peruviana* is known to Peru, but the precise locality is still unknown as there is no further information in the labels. The type specimens was housed in NHMB and it is unknown to us who was the collector. We hypothesized that this species occurs in the Western Cordillera of Peruvian Andes, because *Horridocalia delislei*, the other species in the genus, is distributed only along the Western Cordillera

of Colombian and Ecuadorian Andes.

Horridocalia is the closest genus to *Lycomedes*, regarding the similarity in morphology and distribution. Both genera have species occurring in the Andes and adjacencies from Colombia to Peru. Also, both genera share males with body covered by yellowish tomentum on head, elytra, legs and some ventral areas (as the abdomen); strong sexual dimorphism, with males having elongated cephalic horns bifid on apex, that could be shorter in minor males, and strong protarsi dilated on apex, with protarsal claws asymmetric. Females are more similar than males: both share pair of teeth on clypeal apex, clypeal base on junction with frons with two lateral protuberances (that could be acute or round), pronotum with no sign of horn nor protuberance, densely covered by tomentose punctures. However, there are some diagnostic traits that are used to distinguish those two genera, especially comparing the males: in *Horridocalia*, elytra nebulously tomentose with punctures arranged in rows (elytra irregularly punctate in *Lycomedes*), prosternal process strongly round at tip (prosternal process reduced in *Lycomedes*) and tergite VII with distinct stridulatory area (tergite VII without stridulatory area in *Lycomedes*) (Endrödi 1974). Pardo-Locarno *et al.* (2014) did the first description of a female of *Horridocalia* and commented about the sexual dimorphism within the genus, but did not compare the new female with females of *Lycomedes*.

Therefore, we propose here a diagnosis to distinguish females of *Horridocalia* sympatric with females of *Lycomedes velutipes*. Females of *Horridocalia* can be distinguished by vertex flat (Fig. 33B-C), frons with transverse tomentose stripe reaching clypeal base (Fig. 33A), clypeal apical corners angulated with teeth oblique and at middle (Fig.), ocular canthi transverse with outer corners round (Fig. 33A), elytral punctures tomentose and ocellate (Fig. 29C), elytra with space between first regular row of punctures and second regular row always with one irregular row (Fig. 29C). In *L. velutipes*, vertex with V-shaped fovea with borders elevated (Fig. 13H-I), frons not tomentose (Fig. 13G), clypeal apical corners continuous with teeth (Fig. 13G), elytral punctures tomentose not ocellate (Fig. 17C), elytra with space between first regular row of punctures and second regular row not completely punctate (Fig. 17C).

Key to species of *Lycomedes* de Brême, 1844 (except for *L. salazari* and *L. bubeniki*)

1. Presence of horn on head and pronotum, pronotal horn directed upward (Fig. 1B).

Protarsomere V distinctly dilated, protarsi with inner claw pincer-like shaped (Fig. 4C) (males).....	2
- Head with horn absent (Fig. 7D). Protarsomere V thin, protarsi with claws symmetric and simply curved (females).....	9
2. Cephalic horn with basal posterior branching (Figs. 2D, 2H).....	3
- Cephalic horn with base not branched.....	4
3. Posterior branch of cephalic horn elongated and with apex bifid directed forward.....	<i>L. ramosus</i> Arrow, 1902
- Posterior branch of cephalic horn short and slightly emarginated.....	<i>L. reichei</i> de Brême, 1844
4. Cephalic horn with presence of posterior long tooth behind apex (Fig. 8D). Clypeal anterior corners distinctly sharp and projected to sides (Fig. 8C).....	<i>L. buckleyi</i> Waterhouse, 1880
- Cephalic horn with apex bifid, posterior tooth absent. Clypeal anterior corners sharp or round but not projected to sides.....	5
5. Frons with deep fovea continuous to posterior portion of cephalic horn.....	6
- Frons with shallow depression or surface flat near cephalic horn.....	8
6. Head with dorsal fovea on vertex (Fig. 8J). Ocular canthi with anterior corners round (Fig. 8I).....	<i>L. velutipes</i> Arrow, 1902
- Head with dorsal fovea not reaching vertex (Figs. 8F, 19F). Ocular canthi with anterior corners acute and projected (Figs. 8E, 19E).....	7
7. Thoracic horn short, apex simple (Fig. 10F). Mandible with molar protuberance absent (Fig. 9E). Parameres with apex truncate and setose (Fig. 12E).....	<i>L. hirtipes</i> Arrow, 1902
- Thoracic horn elongated, apex bilobated (Fig. 21F). Mandible with molar protuberance distinct and sharp (Fig. 20E). Parameres with apex sharp and bare (Fig. 23E).....	<i>L. enigmaticus</i> Neita-Moreno & Ratcliffe, 2019
8. Frons with shallow depression near cephalic horn (Fig. 19B). Clypeal anterior corners sharp (Fig. 19C). Mandible with molar protuberance short (Fig. 20A). Parameres with apical portion thick in lateral view (Fig. 23B).....	<i>L. ohausi</i> Arrow, 1908
- Frons flat near cephalic horn (Fig. 19J). Clypeal anterior corners round (Fig. 19K). Mandible with molar protuberance absent (Fig. 20I). Parameres with apical portion slender in lateral view (Fig. 23J).....	<i>L. burmeisteri</i> Waterhouse, 1879

9. Vertex and frons distinctly depressed medially (Fig. 13D). Clypeal apex 2.5 to 3 times narrower than clypeal base (Fig. 13H)..... 10
- Vertex and frons flat medially (Fig. 13A). Clypeal apex around 2 times or less narrower than clypeal base (Fig. 13B)..... 11
10. Vertex protuberant (Fig. 13I). Clypeal base sharp and distinct (Fig. 13I). Ocular canthi with anterior margin straight medially (Fig. 13G). Mandibular outer carina projected over outer margin (Fig. 14I)..... ***L. velutipes* Arrow, 1902**
- Vertex flat (Fig. 13F). Clypeal base round and short (Fig. 13F). Ocular canthi with anterior margin concave medially (Fig. 13D). Mandibular outer carina oblique and not projected over outer margin (Fig. 14E)..... ***L. hirtipes* Arrow, 1902**
11. Presence of tomentum on clypeal base (Fig. 24D). Prosternal process globose, not projected (Fig. 26E)..... ***L. burmeisteri* Waterhouse, 1879**
- Tomentum absent on clypeal base (Fig. 13A). Prosternal process projected (Fig. 15B)..... 12
12. Ocular canthi with basal short protuberance (Fig. 13A). Latero-ventral margins of clypeus occluded in frontal view (Fig. 13B). Clypeal base sharp and projected (Fig. 13C). Mandible with molar protuberance truncate (Fig. 14A)..... ***L. buckleyi* Waterhouse, 1880**
- Ocular canthi with base of anterior margin not protruded (Fig. 24A). Latero-ventral margins of clypeus exposed in frontal view (Fig. 24B). Clypeal base short and round (Fig. 24C). Mandible with molar protuberance sharp apically (Fig. 25A)..... ***L. ohausi* Arrow, 1908**

Acknowledgments

We thank all the curators from the cited collections for their contributions of material for this study. We thank Max Barclay, Michael Geiser and Keita Matsumoto for all the support to RS during his time in the Natural History Museum (London, United Kingdom). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. RS acknowledge the Instituto Nacional de Pesquisas da Amazônia for research support; the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for the PhD scholarship to RS and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Sandwich Doctorate scholarship to RS. PCG acknowledges the Universal Project, 449366/2014-6.

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Figures

FIGURE 1. Male of *Lycomedes reichei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

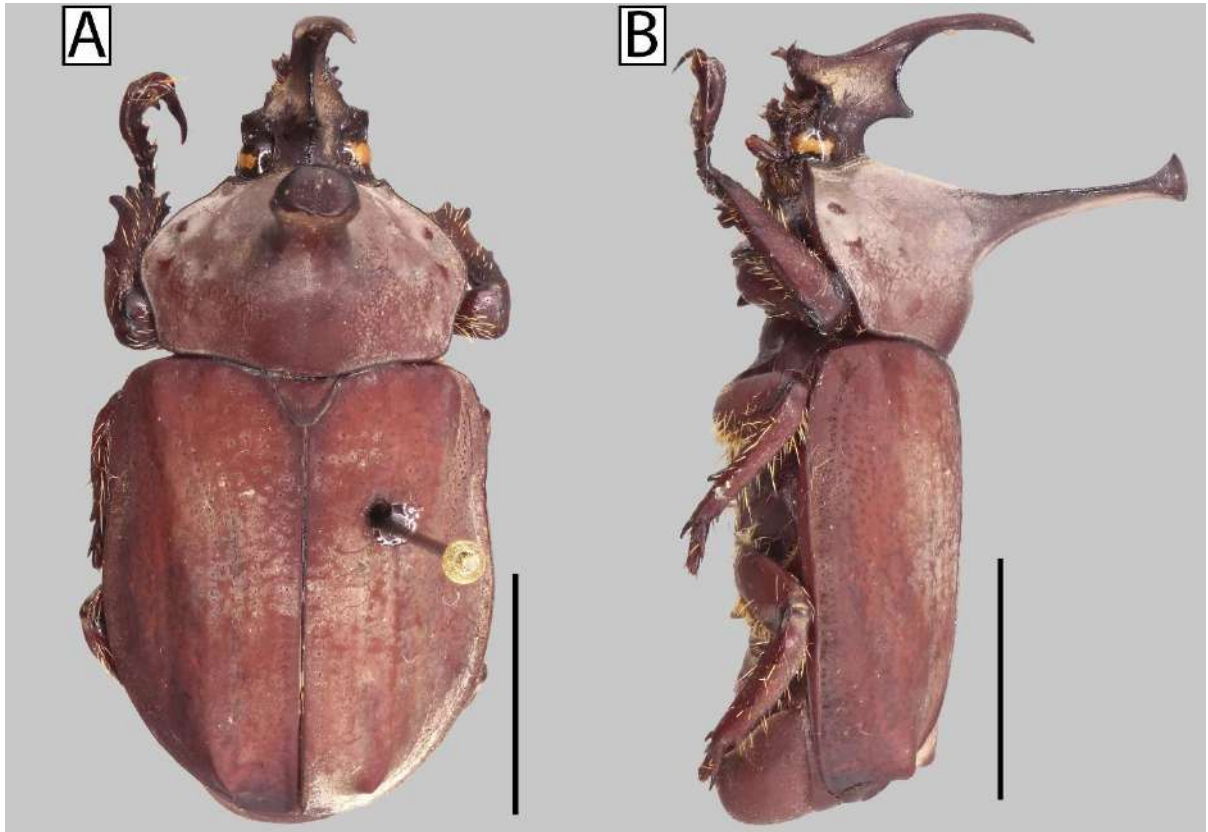


FIGURE 2. Male head of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Head of *L. reichei* in dorsal view. White arrow pointing to emargination of posterior branch of horn; black arrow pointing to ocular canthus. **B**, Head of *L. reichei* in dorsolateral view. White arrow pointing to keel between anterior and posterior branches of horn. **C**, Head of *L. reichei* in frontal view. **D**, Head of *L. reichei* in lateral view. **E**, Head of *L. ramosus* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **F**, Head of *L. ramosus* in dorsolateral view. Superior black arrows pointing to apical corners of clypeus; inferior black arrow pointing to carina of ocular canthus. **G**, Head of *L. ramosus* in lateral view. **H**, Head of *L. ramosus* in lateral view. Superior black arrow pointing to apex of posterior branch of cephalic horn; inferior black arrow pointing to frontal concavity of horn. Scale bars: 1 mm.

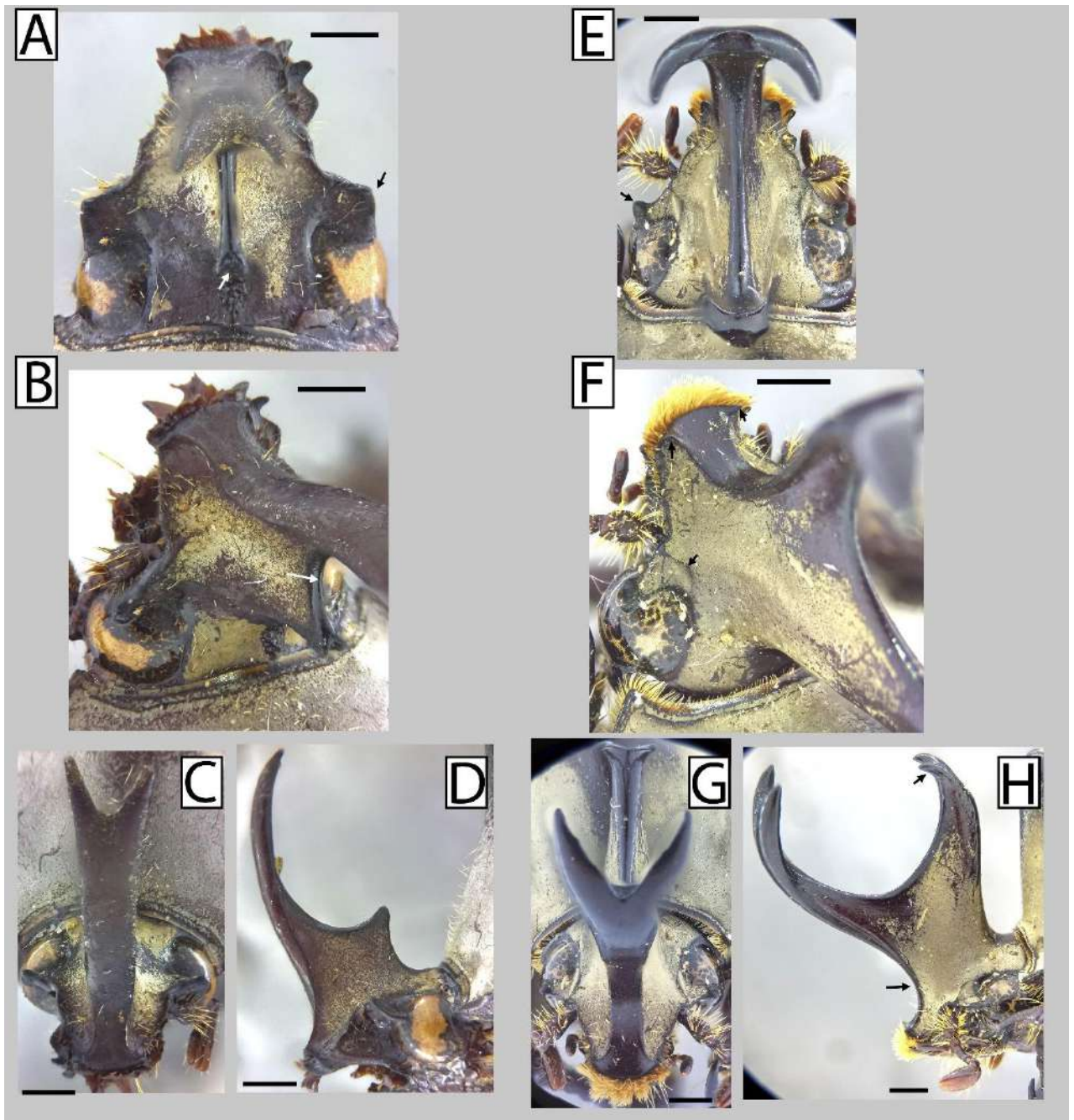


FIGURE 3. Male thorax of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Pronotum of *L. reichei* in dorsal view. **B**, Pronotum of *L. reichei* in frontolateral view. Black arrow pointing to emargination of horn. **C**, Pronotum of *L. reichei* in lateral view. Black arrows pointing to lateral carinae of thoracic horn. **D**, Pronotum of *L. ramosus* in dorsal view. Lateral black arrows pointing to pronotal depressions; central black arrow pointing to emargination of horn. **E**, Pronotum of *L. ramosus* in lateral view. Black arrow pointing to posterior depression. Scale bars: 1 mm.

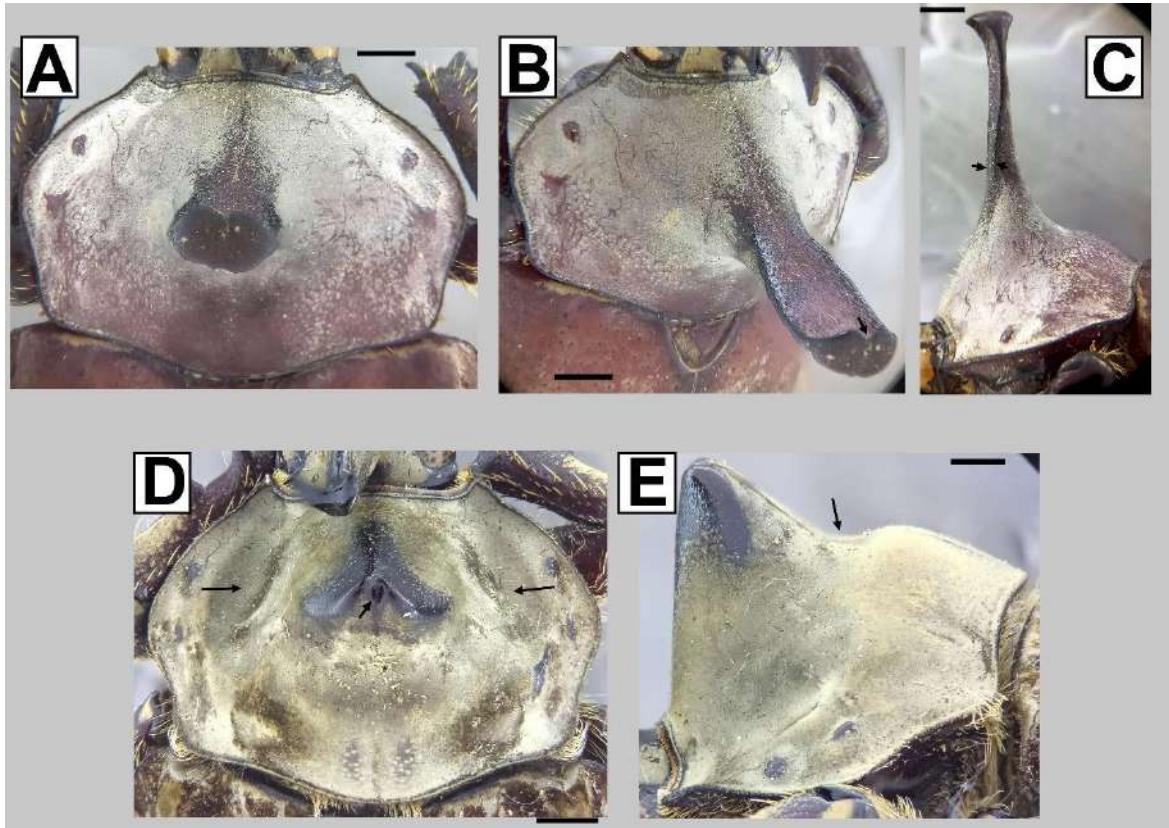


FIGURE 4. Male thorax, leg and abdomen of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Prosternum of *L. reichei* in ventral view. White arrow pointing to prosternal process. **B**, Protibia of *L. reichei* in dorsal view. **C**, Protarsus of *L. reichei* in dorsal view. **D**, Abdomen of *L. reichei* in ventral view. Superior white arrow pointing to medial projection of sternite III; inferior white arrow pointing to setae on posterior margin of tergite VIII. **E**, Prosternum of *L. ramosus* in ventral view. Superior white arrow pointing to medial projection of anterior margin; inferior white arrow pointing to prosternal process. **F**, Protibia of *L. ramosus* in dorsal view. **G**, Protarsus of *L. ramosus* in dorsal view. White arrow pointing to basal tooth of protarsal claw. **H**, Abdomen of *L. ramosus* in ventral view. Superior white arrow pointing to medial projection of sternite III. Scale bars: 1 mm.

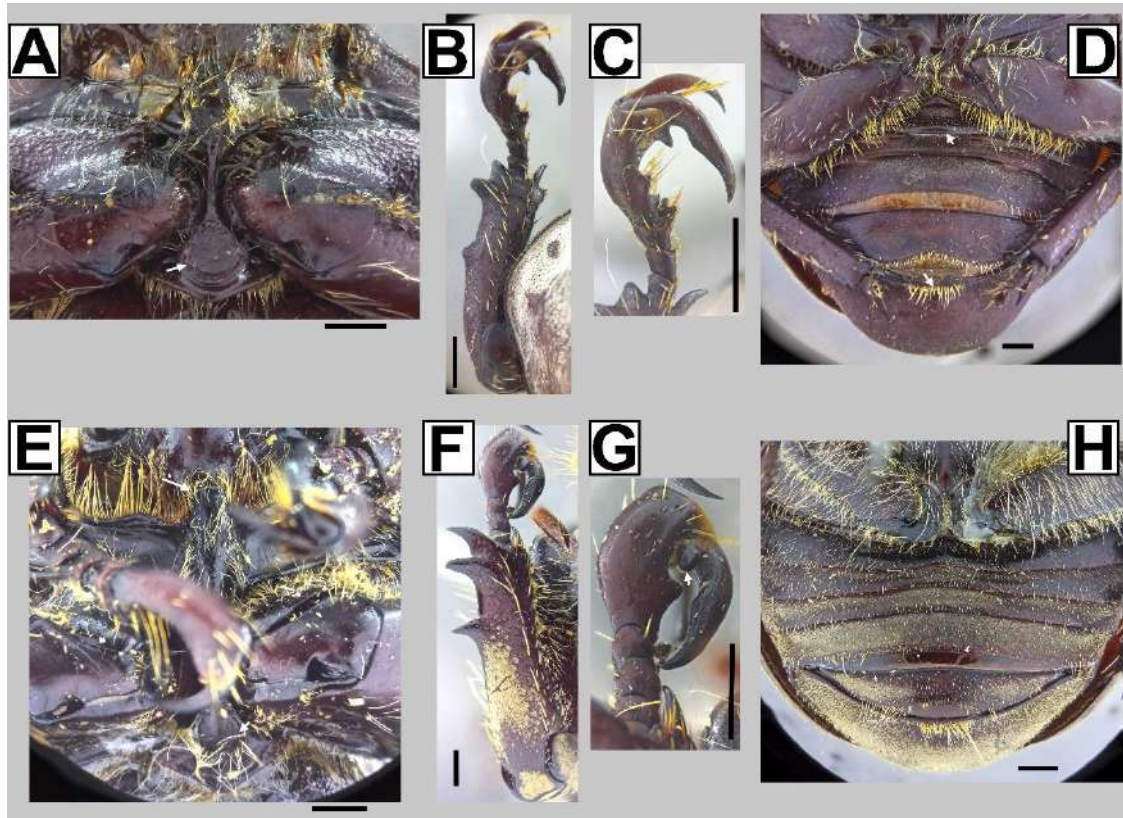


FIGURE 5. Male genitalia of *Lycomedes reichei* and *Lycomedes ramosus*. **A**, Parameres of *L. reichei* in caudal view. Black arrow pointing to basal carina. **B**, Parameres of *L. reichei* in lateral view. Black arrow pointing to lateral carina. **C**, Parameres of *L. reichei* in ventral view. **D**, Aedeagus of *L. reichei* in lateral view. Black arrow pointing to posterior phallobase. **E**, Parameres of *L. ramosus* in caudal view. **F**, Parameres of *L. ramosus* in lateral view. Black arrow pointing to apex of parameres. **G**, Parameres of *L. ramosus* in ventral view. **H**, Aedeagus of *L. ramosus* in lateral view. Scale bars: 1 mm.

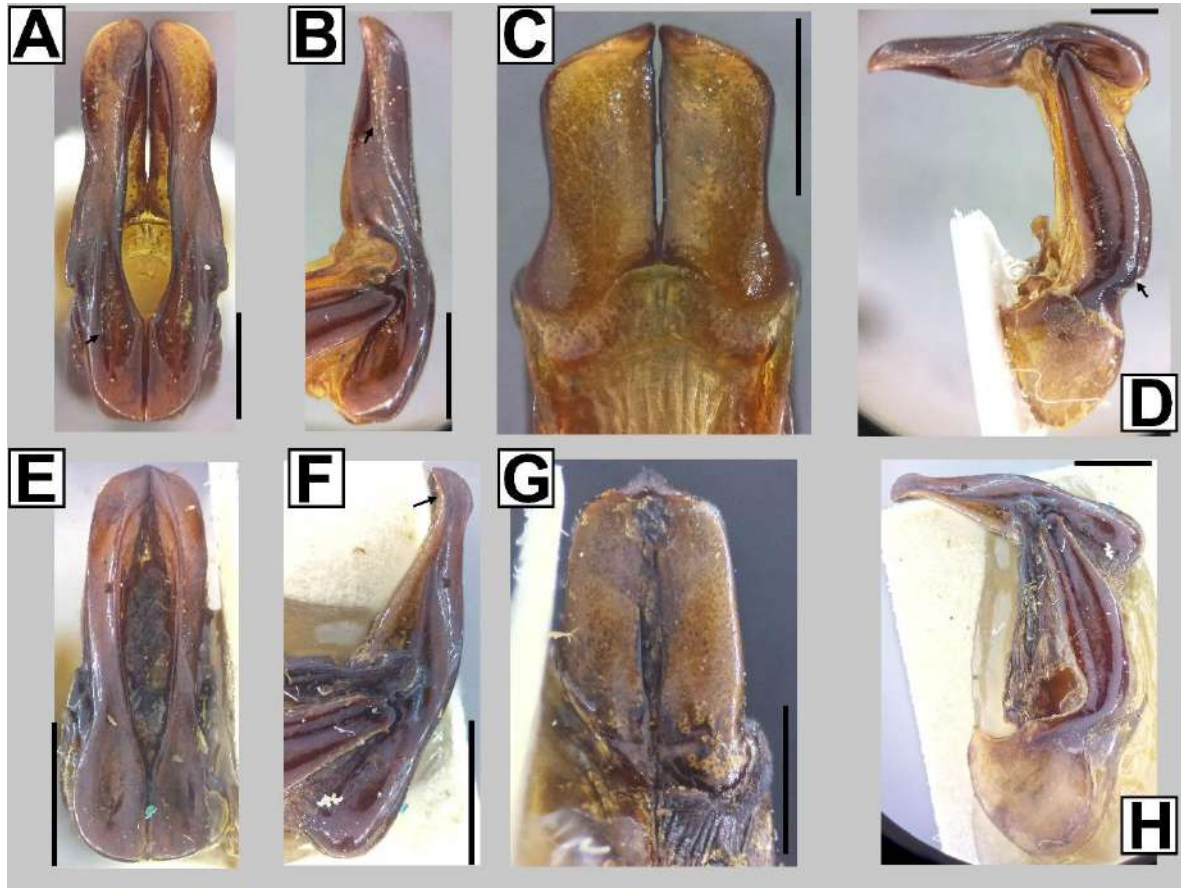


FIGURE 6. Male of *Lycomedes ramosus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

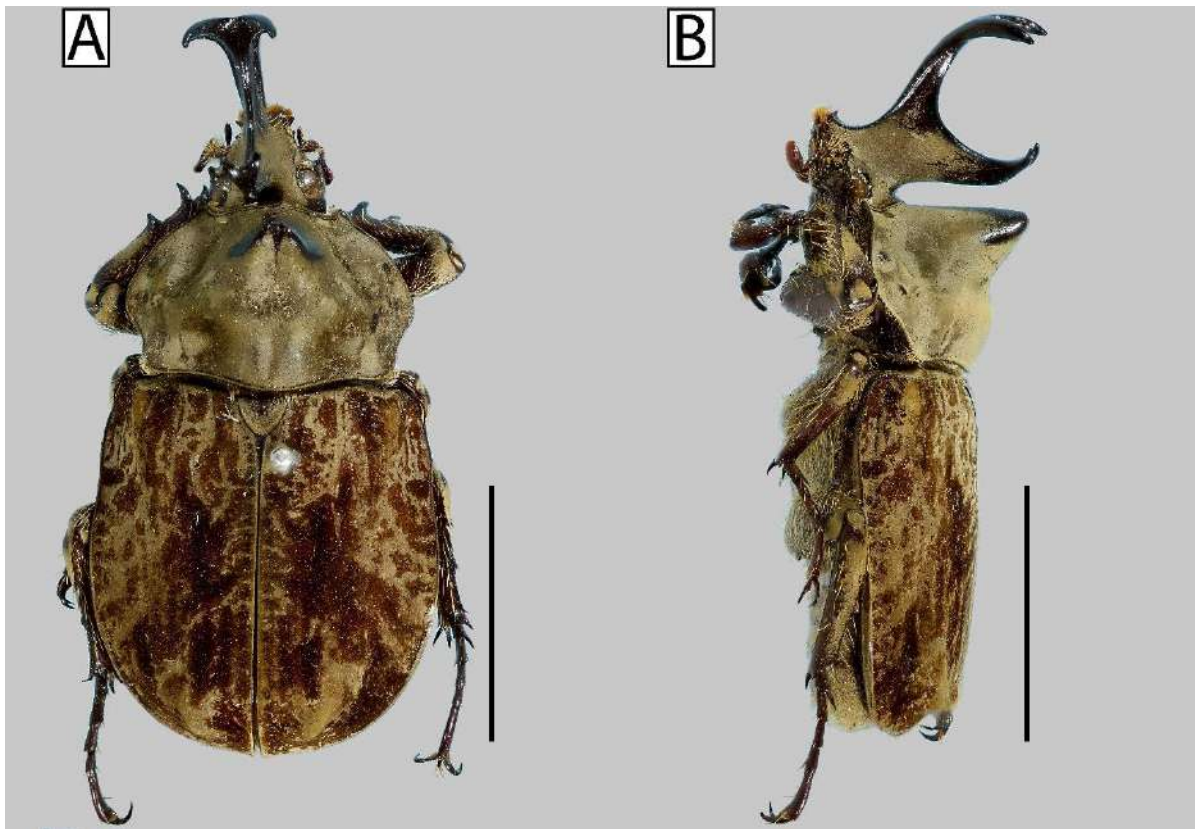


FIGURE 7. Male and female of *Lycomedes buckleyi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.

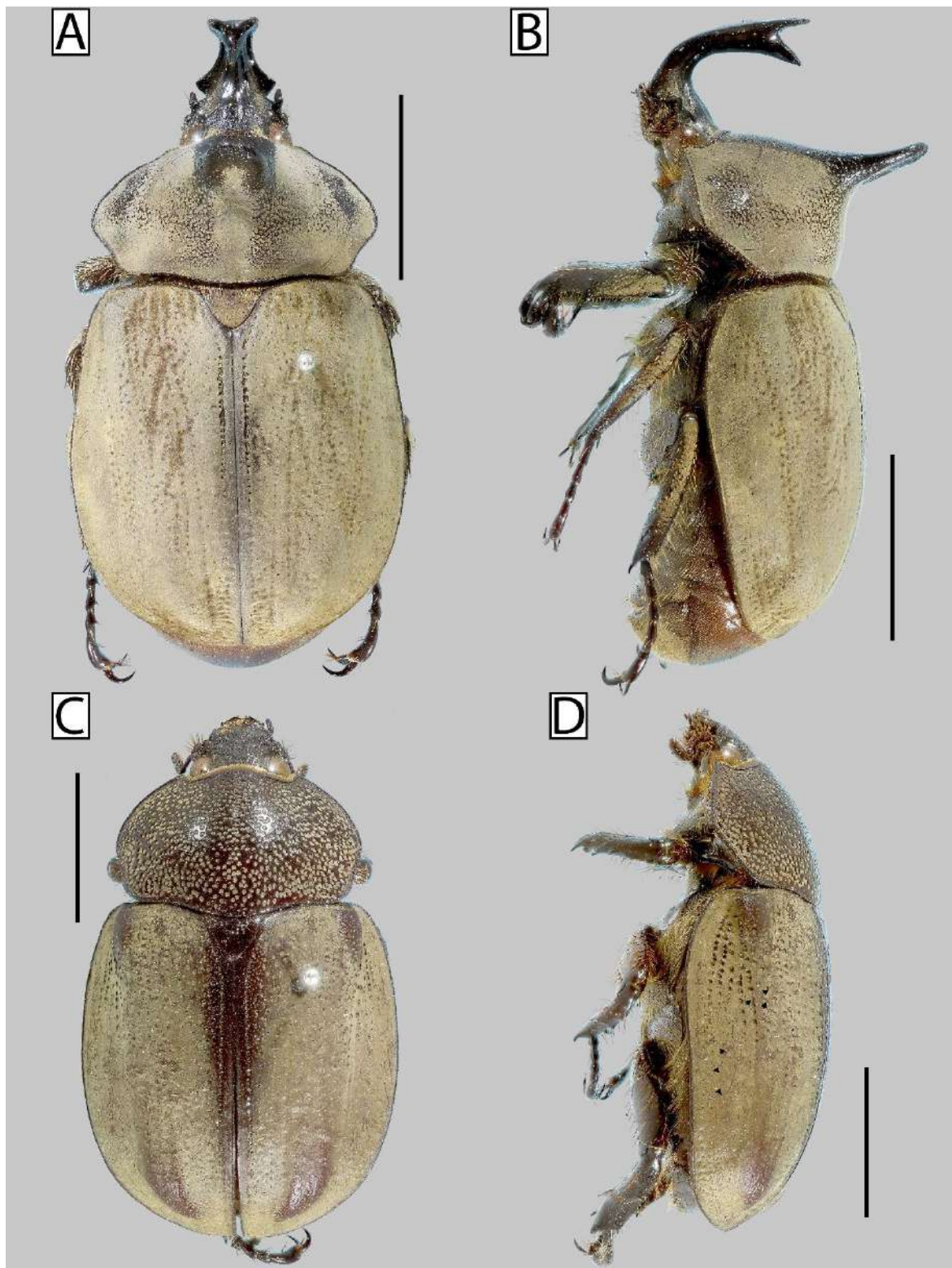


FIGURE 8. Male head of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Head of *L. buckleyi* in dorsal view. Superior white arrows pointing to apex of cephalic horn; inferior white arrow pointing to posterior tooth of horn; black arrow pointing to basal projection of ocular canthus. **B**, Head of *L. buckleyi* in dorsolateral view. Black arrow pointing to shallow depression of frons. **C**, Head of *L. buckleyi* in frontal view. Black arrows pointing to anterior corners of clypeus. **D**, Head of *L. buckleyi* in lateral view. **E**, Head of *L. hirtipes* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **F**, Head of *L. hirtipes* in dorsolateral view. Black arrow pointing to fovea. **G**, Head of *L. hirtipes* in frontal view. Superior white arrow pointing to apex of cephalic horn; inferior white arrows pointing to anterior corners of clypeus. **H**, Head of *L. hirtipes* in lateral view. Black arrow pointing to frontal portion of cephalic horn. **I**, Head of *L. velutipes* in dorsal view. Black arrows pointing to carinae; white arrow pointing to anterior margin of ocular canthus. **J**, Head of *L. velutipes* in dorsolateral view. Black arrow pointing to fovea. **K**, Head of *L. velutipes* in frontal view. Black arrow pointing to apex of cephalic horn; white arrows pointing to clypeal carinae. **L**, Head of *L. velutipes* in lateral view. Scale bars: 1 mm.

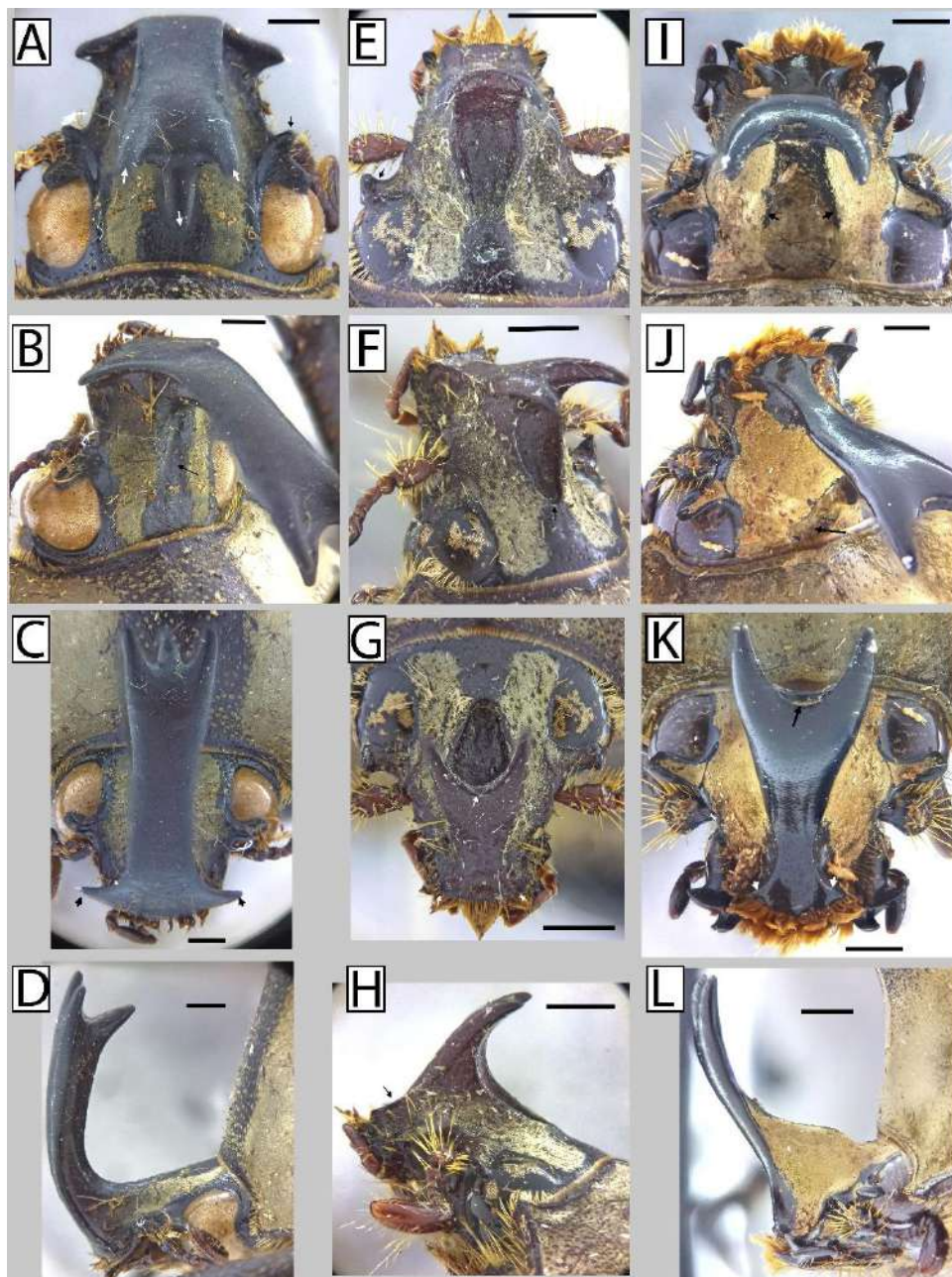


FIGURE 9. Male mouthparts of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Mandible of *L. buckleyi* in ventral view. Black arrows pointing to inner and medial carina respectively from left to right. **B**, Mandible of *L. buckleyi* in dorsal view. Double-headed black arrow showing width of mesal brush apically; simple black arrow pointing to base of inner margin laterally. **C**, Maxilla of *L. buckleyi* in ventral view. Superior black arrow pointing to medial tooth of galea; inferior black arrow pointing to outer margin of lateral border. **D**, Labrum of *L. buckleyi* in dorsal view. Double-headed arrows comparing medial length to lateral width. **E**, Mandible of *L. hirtipes* in ventral view. White arrow pointing to inner carina; black arrow pointing to apical outer margin. **F**, Mandible of *L. hirtipes* in dorsal view. Black arrow pointing to apex of inner tooth. **G**, Maxilla of *L. hirtipes* in ventral view. Superior black arrow pointing to medial tooth of galea; inferior black arrow pointing to outer margin of lateral border. **H**, Labrum of *L. hirtipes* in dorsal view. **I**, Mandible of *L. velutipes* in ventral view. Left black arrow pointing to medial carina; right black arrow pointing to outer carina. **J**, Mandible of *L. velutipes* in dorsal view. Simple black arrow pointing to molar protuberance area; double-headed black arrow showing width of mesal brush. **K**, Maxilla of *L. velutipes* in ventral view. Black arrow pointing to outer margin of galea base. **L**, Labrum of *L. velutipes* in dorsal view. Scale bars: 1 mm.

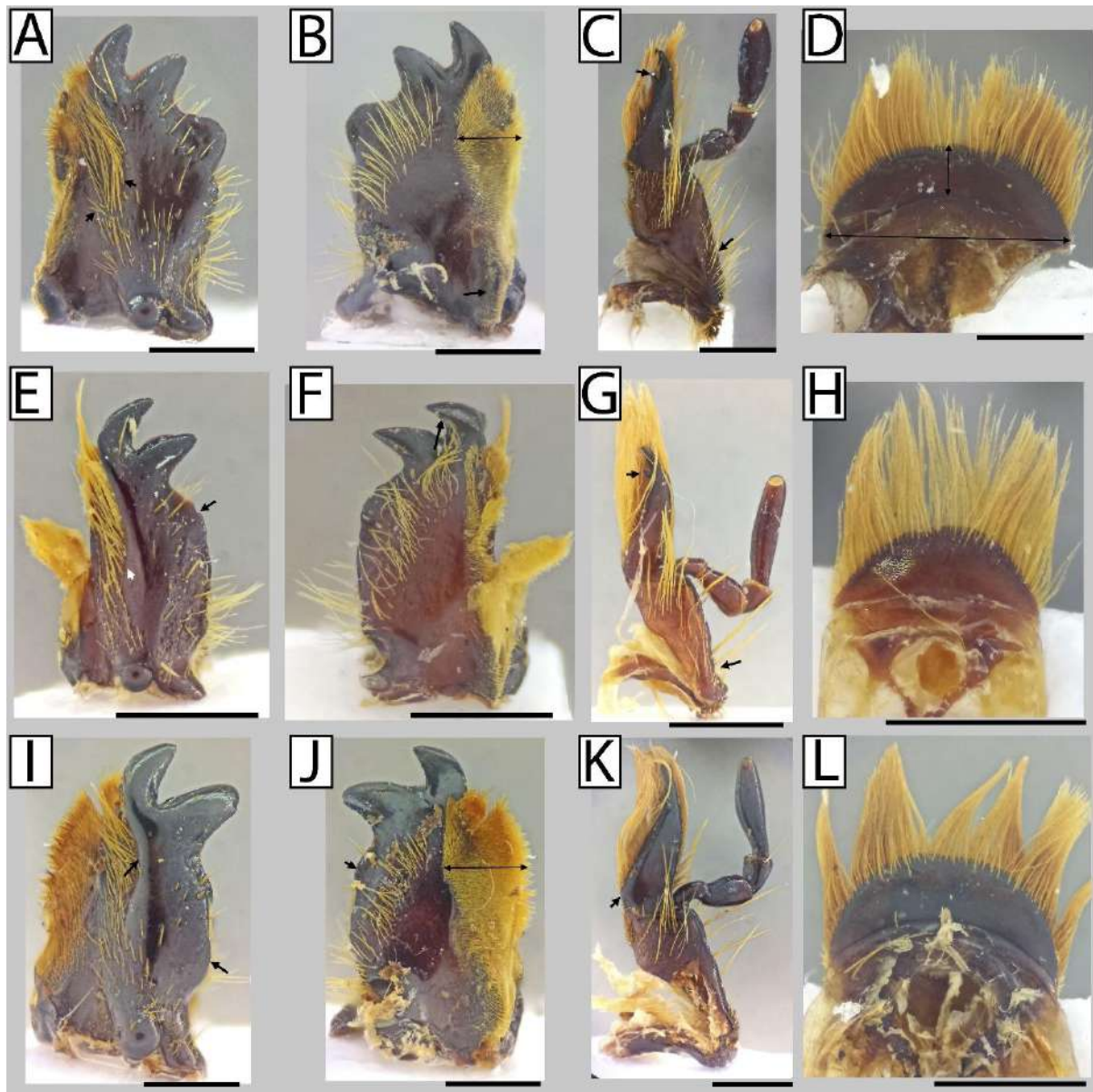


FIGURE 10. Male thorax of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Pronotum of *L. buckleyi* in dorsal view. **B**, Pronotum of *L. buckleyi* in frontolateral view. **C**, Pronotum of *L. buckleyi* in lateral view. Black arrow pointing to posterior depression. **D**, Pronotum of *L. hirtipes* in dorsal view. **E**, Pronotum of *L. hirtipes* in frontolateral view. **F**, Pronotum of *L. hirtipes* in lateral view. Black arrow pointing to posterior depression. **G**, Pronotum of *L. velutipes* in dorsal view. **H**, Pronotum of *L. velutipes* in frontolateral view. Black arrow pointing to medial carina. **I**, Pronotum of *L. velutipes* in lateral view. Scale bars: 5 mm.

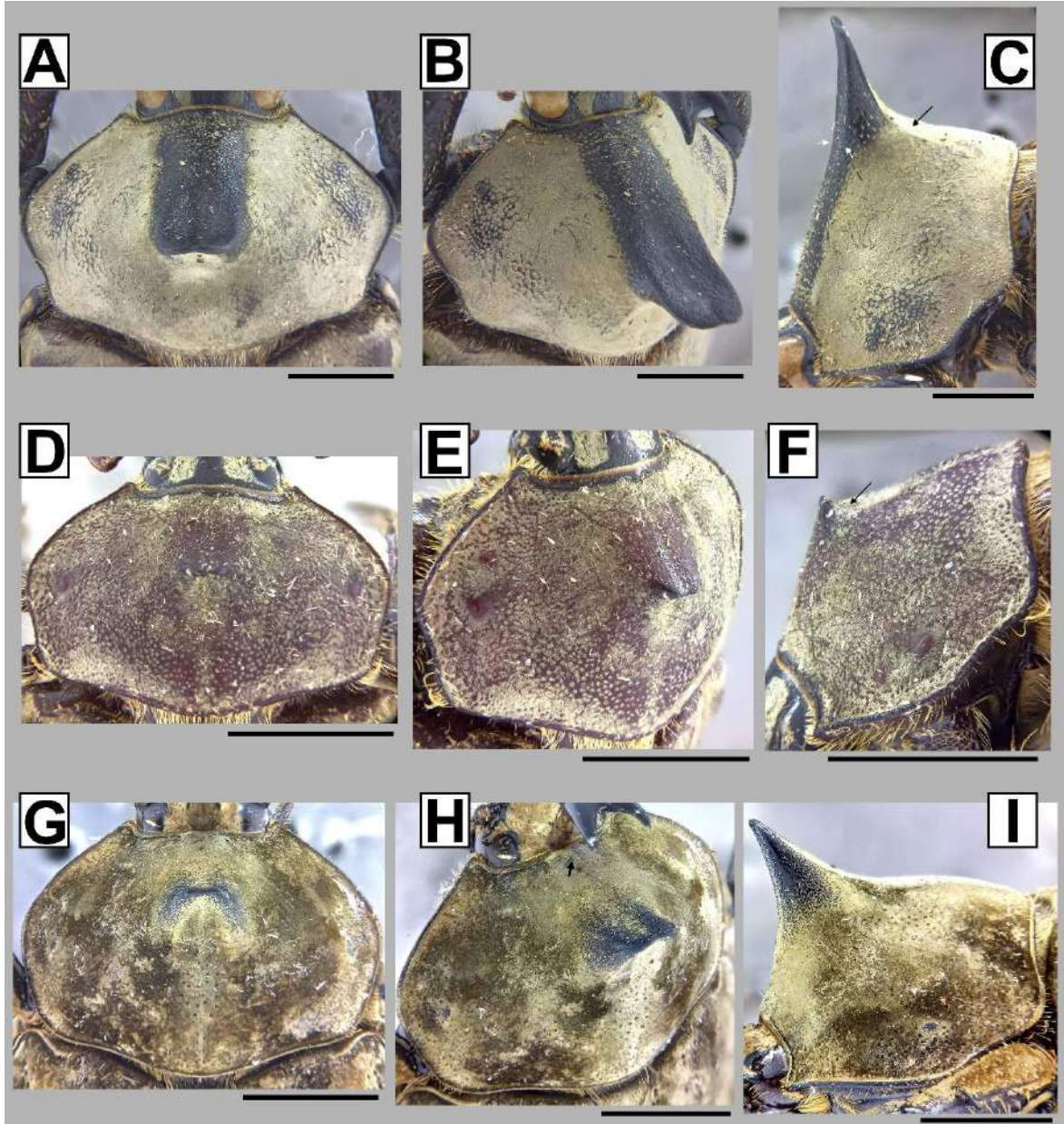


FIGURE 11. Male thorax, leg and abdomen of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Prosternum of *L. buckleyi* in ventral view. Black arrow pointing to carina; white arrow pointing to prosternal process. **B**, Protibia of *L. buckleyi* in dorsal view. **C**, Protarsus of *L. buckleyi* in dorsal view. Black arrow pointing to basal tooth of protarsal claw; white arrow pointing to mesobasal portion of claw. **D**, Abdomen of *L. buckleyi* in ventral view. **E**, Prosternum of *L. hirtipes* in ventral view. Black arrow pointing to prosternal process. **F**, Protibia of *L. hirtipes* in dorsal view. **G**, Protarsus of *L. hirtipes* in dorsal view. **H**, Abdomen of *L. hirtipes* in ventral view. Superior white arrow pointing to medial projection of sternite III. **I**, Prosternum of *L. velutipes* in ventral view. White arrow pointing to prosternal process. **J**, Protibia of *L. velutipes* in dorsal view. **K**, Protarsus of *L. velutipes* in dorsal view. White arrow pointing to mesobasal tooth of protarsal claw. **L**, Abdomen of *L. velutipes* in ventral view. Scale bars: C, G, K, 1 mm; A-B, D, E-F, H, I-J, L, 5 mm.

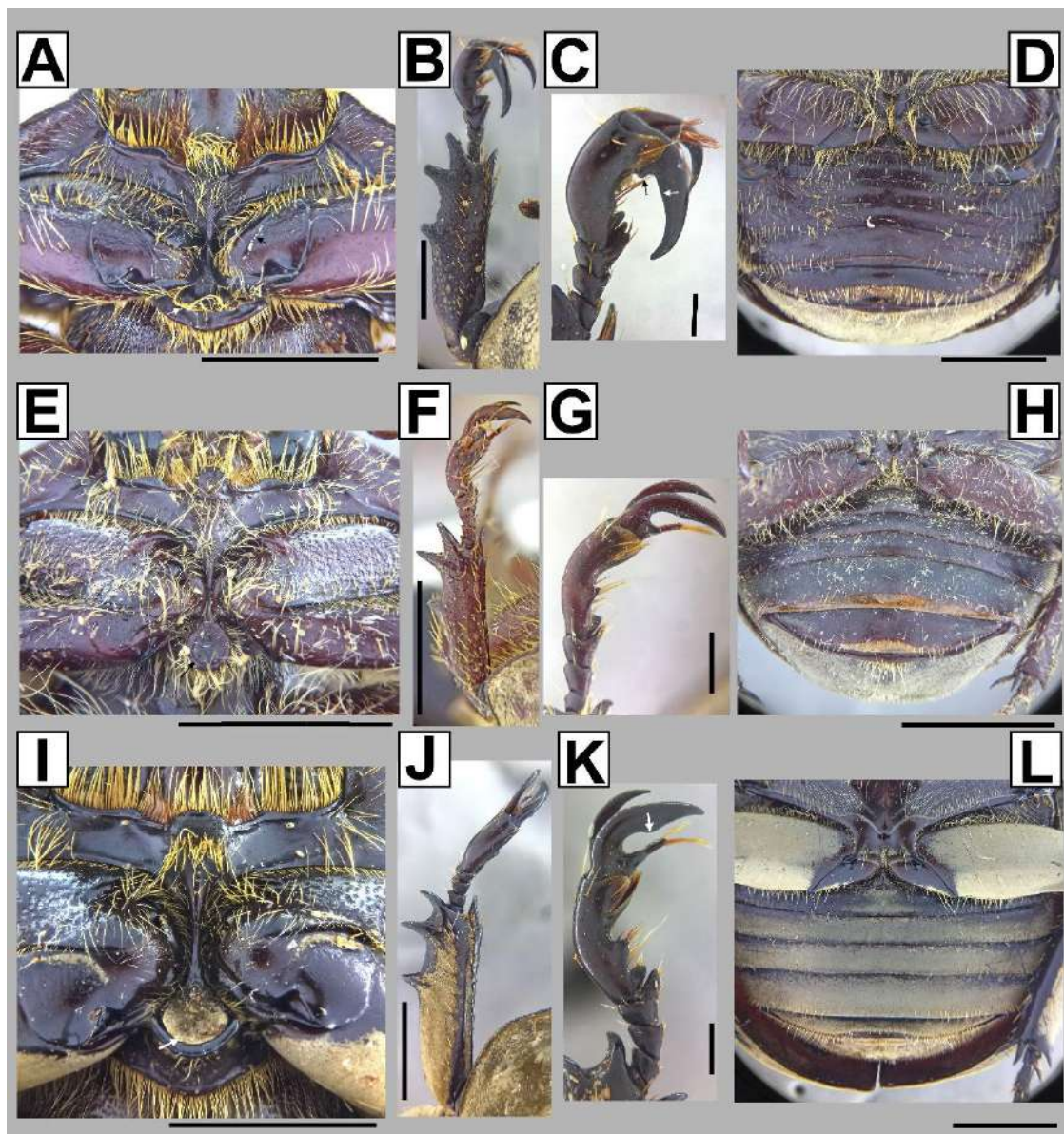


FIGURE 12. Male genitalia of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Parameres of *L. buckleyi* in caudal view. **B**, Parameres of *L. buckleyi* in lateral view. Left black arrow pointing to ventral margin; right black arrow pointing to lateral carina. **C**, Parameres of *L. buckleyi* in ventral view. **D**, Aedeagus of *L. buckleyi* in lateral view. Black arrow pointing to apical corner of posterior phallobase. **E**, Parameres of *L. hirtipes* in caudal view. Left black arrow pointing to setae; right black arrow pointing to apex of parameres. **F**, Parameres of *L. hirtipes* in lateral view. White arrow pointing to lateral carina; black arrow pointing to apical depression. **G**, Parameres of *L. hirtipes* in ventral view. **H**, Aedeagus of *L. hirtipes* in lateral view. White arrow pointing to apical corner of posterior phallobase. **I**, Parameres of *L. velutipes* in caudal view. Double-headed black arrows comparing width of apical and basal portions; simple black arrow pointing to outer margin medially. **J**, Parameres of *L. velutipes* in lateral view. Left black arrow pointing to ventral carina; right black arrow pointing to basal carina. **K**, Parameres of *L. velutipes* in ventral view. Left black arrow pointing to base of parameres; right black arrow pointing to ventral carina. **L**, Aedeagus of *L. velutipes* in lateral view. White arrow pointing to apical corner of posterior phallobase; black arrow pointing to apical margin of posterior phallobase. Scale bars: 1 mm.

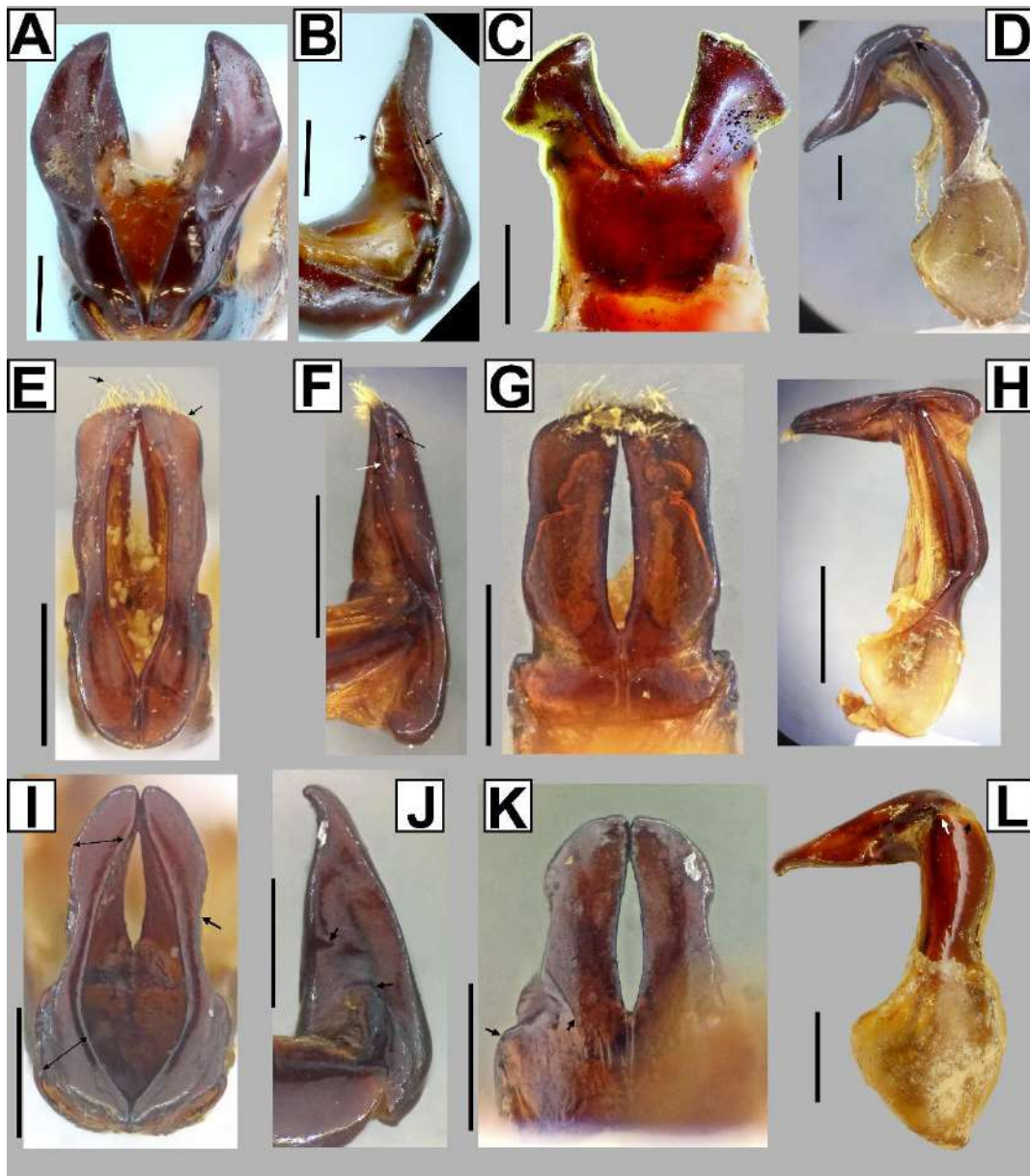


FIGURE 13. Female head of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Head of *L. buckleyi* in dorsal view. Black arrow pointing to basal protuberance of ocular canthus. **B**, Head of *L. buckleyi* in frontal view. Double-headed black arrows comparing clypeal apex with base. **C**, Head of *L. buckleyi* in lateral view. Black arrows pointing to clypeal apical horns and clypeal base projections. **D**, Head of *L. hirtipes* in dorsal view. Black arrow pointing to anterior margin of ocular canthus. **E**, Head of *L. hirtipes* in frontal view. White arrows pointing to depression on vertex; double-headed black arrows comparing clypeal apex with base; simple black arrow pointing to lateral margin of clypeus. **F**, Head of *L. hirtipes* in lateral view. Black arrows pointing to clypeal base. **G**, Head of *L. velutipes* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **H**, Head of *L. velutipes* in frontal view. White arrows pointing to depression on vertex; double-headed black arrows comparing clypeal apex with base. **I**, Head of *L. velutipes* in lateral view. Black arrows pointing to protuberance on vertex. Scale bars: 1 mm.

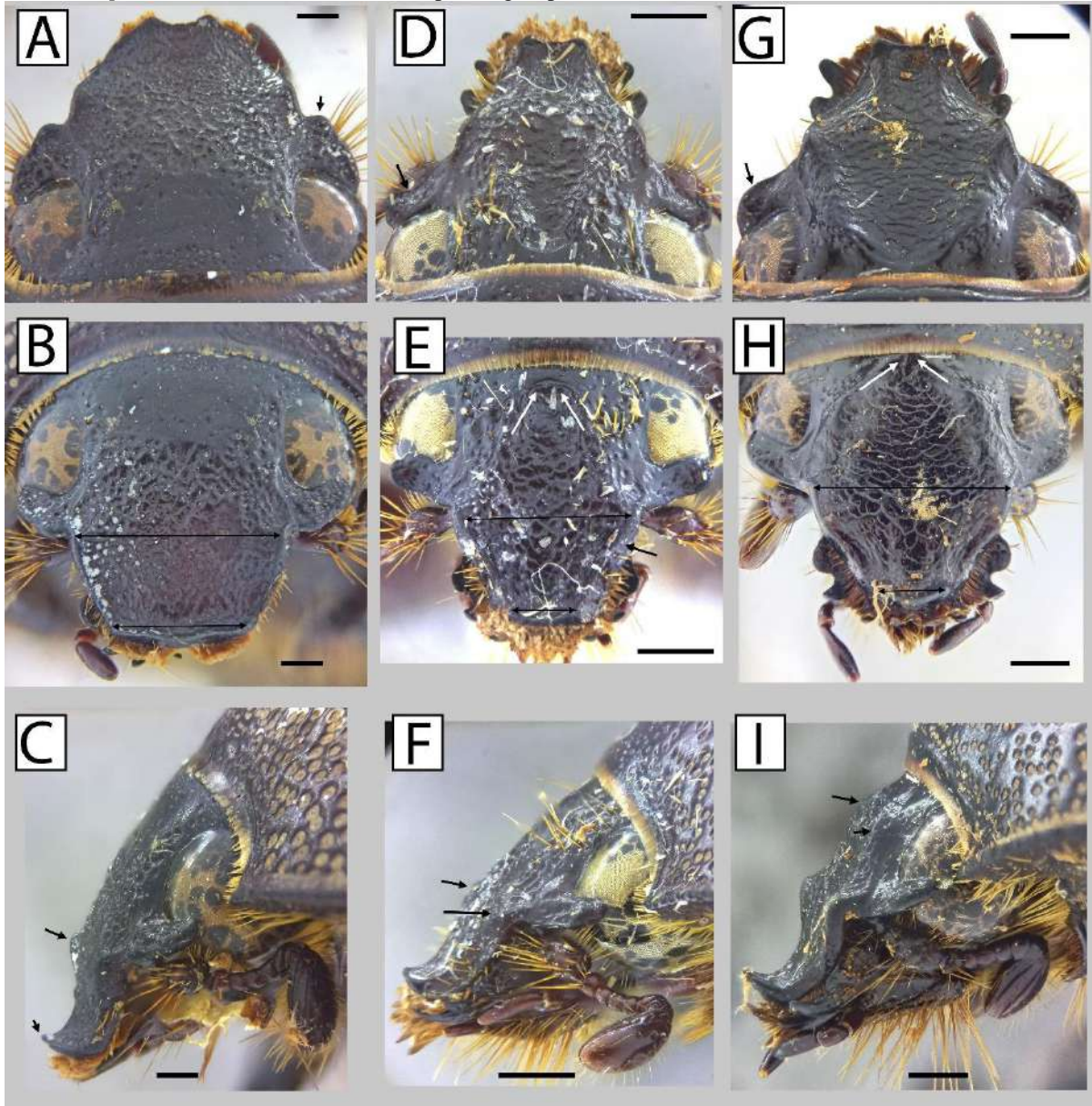


FIGURE 14. Female mouthparts of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Mandible of *L. buckleyi* in ventral view. Black arrow pointing to outer margin. **B**, Mandible of *L. buckleyi* in dorsal view. **C**, Maxilla of *L. buckleyi* in ventral view. Black arrows pointing to maxillar teeth. **D**, Labrum of *L. buckleyi* in dorsal view. Black arrow pointing to anterior margin. **E**, Mandible of *L. hirtipes* in ventral view. Double-headed black arrow showing distance from inner margin to inner carina; simple black arrow pointing to outer margin. **F**, Mandible of *L. hirtipes* in dorsal view. Double-headed black arrows showing distance between teeth; simple black arrow pointing to inner margin basally. **G**, Maxilla of *L. hirtipes* in ventral view. Simple black arrow pointing to tooth; double-headed black arrow showing thickness of lateral border. **H**, Labrum of *L. hirtipes* in dorsal view. **I**, Mandible of *L. velutipes* in ventral view. White arrow pointing to medial carina; simple black arrow pointing to outer carina; superior double-headed black arrow showing distance between inner and medial carina; inferior double-headed black arrow showing distance between inner margin and inner carina basally. **J**, Mandible of *L. velutipes* in dorsal view. Black arrow pointing to outermost portion of mesal brush. **K**, Maxilla of *L. velutipes* in ventral view. Simple black arrow pointing to base of galea; double-headed black arrow showing thickness of lateral border. **L**, Labrum of *L. velutipes* in dorsal view. Scale bars: 1 mm.

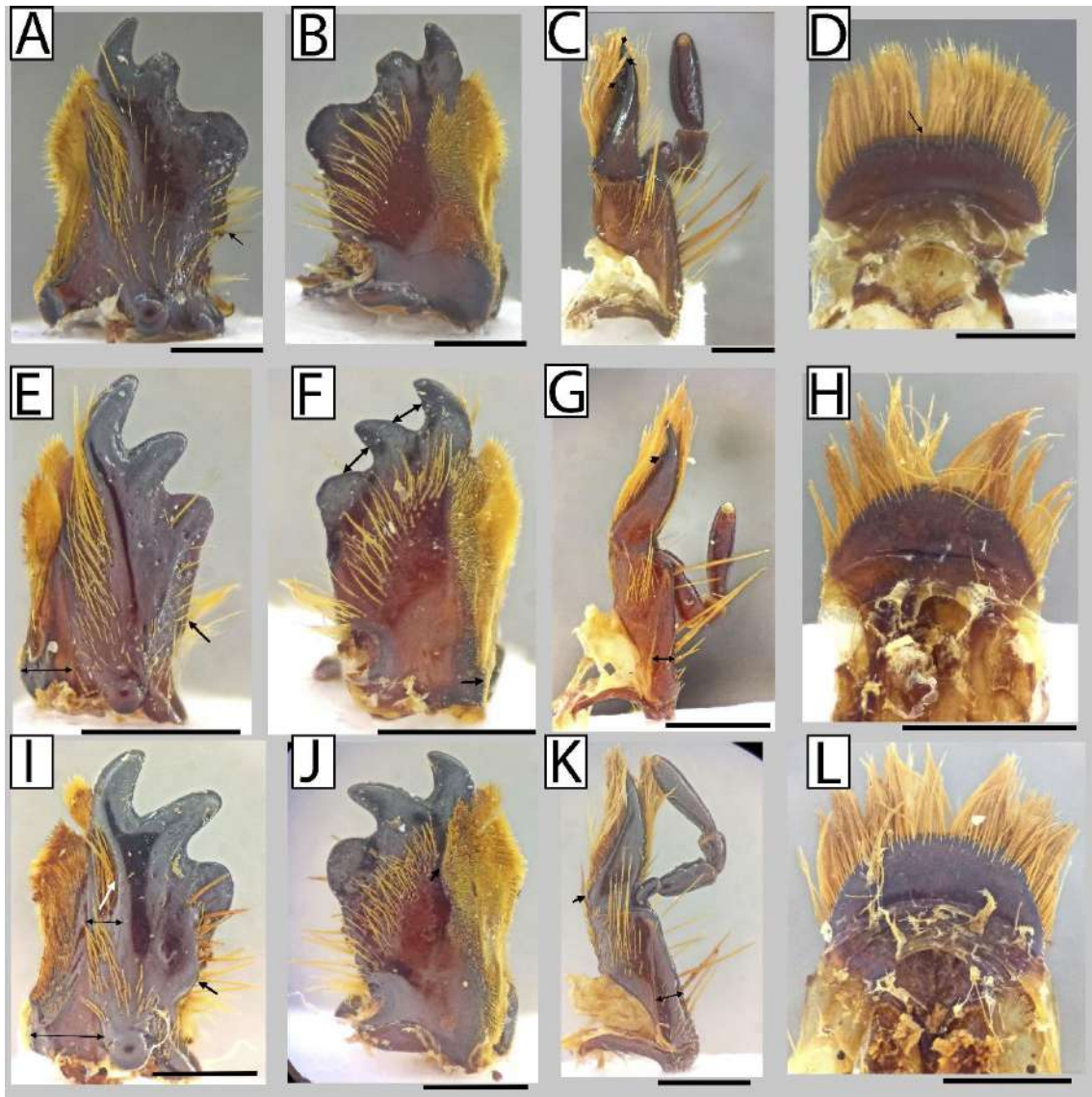


FIGURE 15. Female thorax and abdomen of *Lycomedes buckleyi*, *Lycomedes hirtipes* and *Lycomedes velutipes*. **A**, Pronotum of *L. buckleyi* in dorsal view. **B**, Prosternum of *L. buckleyi* in ventral view. Black arrow pointing to medial elevation of prosternum; superior white arrow pointing to medial keel; inferior white arrow pointing to prosternal process. **C**, Abdomen of *L. buckleyi* in ventral view. **D**, Pronotum of *L. hirtipes* in dorsal view. **E**, Prosternum of *L. hirtipes* in ventral view. Superior white arrow pointing to medial elevation; inferior white arrow pointing to prosternal process. **F**, Abdomen of *L. hirtipes* in ventral view. Black arrow pointing to tergite VIII. **G**, Pronotum of *L. velutipes* in dorsal view. **H**, Prosternum of *L. velutipes* in ventral view. Superior black arrows pointing to prosternal depression; inferior black arrow pointing to prosternal process. **I**, Abdomen of *L. velutipes* in ventral view. Scale bars: 5 mm.

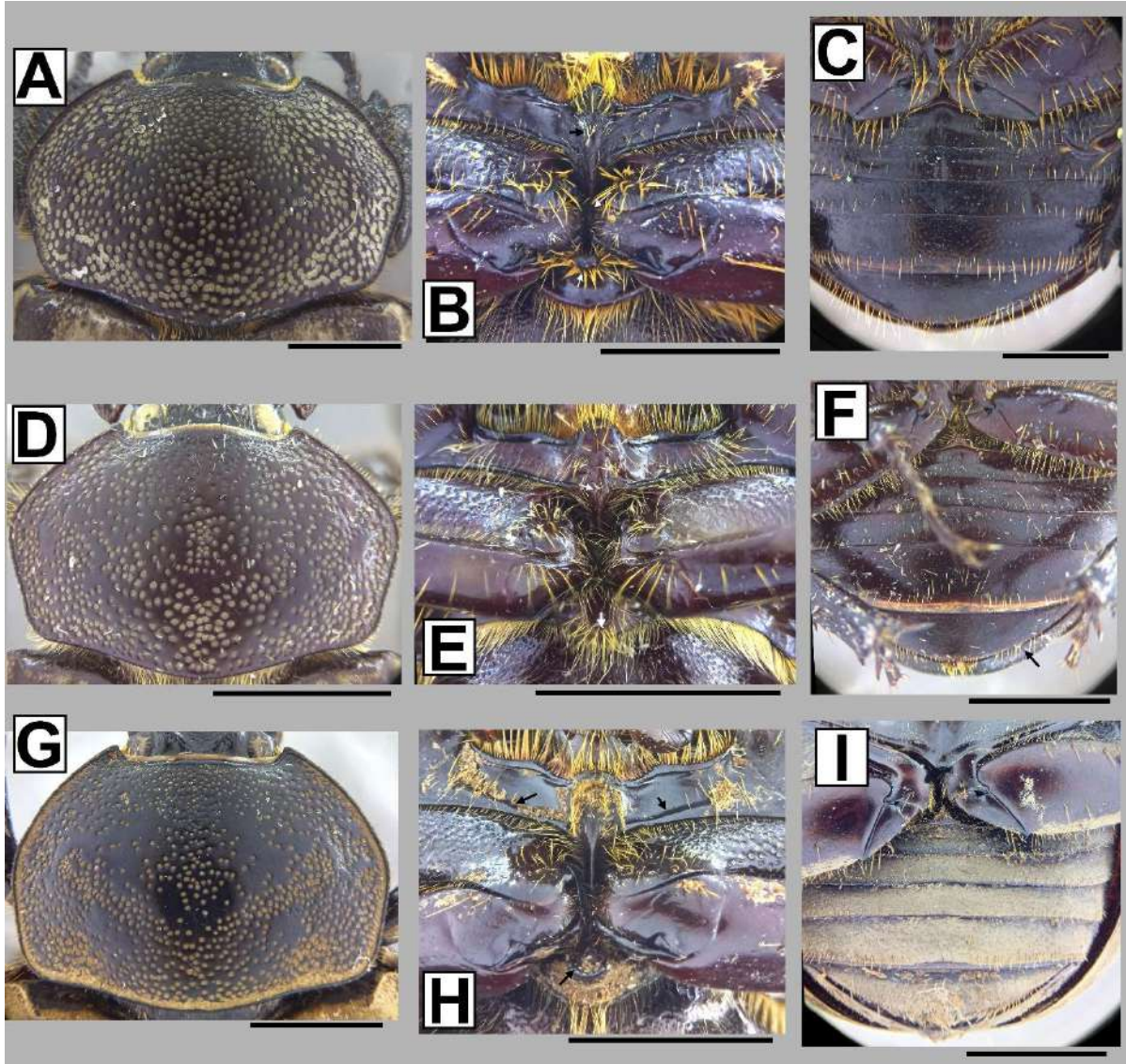


FIGURE 16. Male and female of *Lycomedes hirtipes*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.

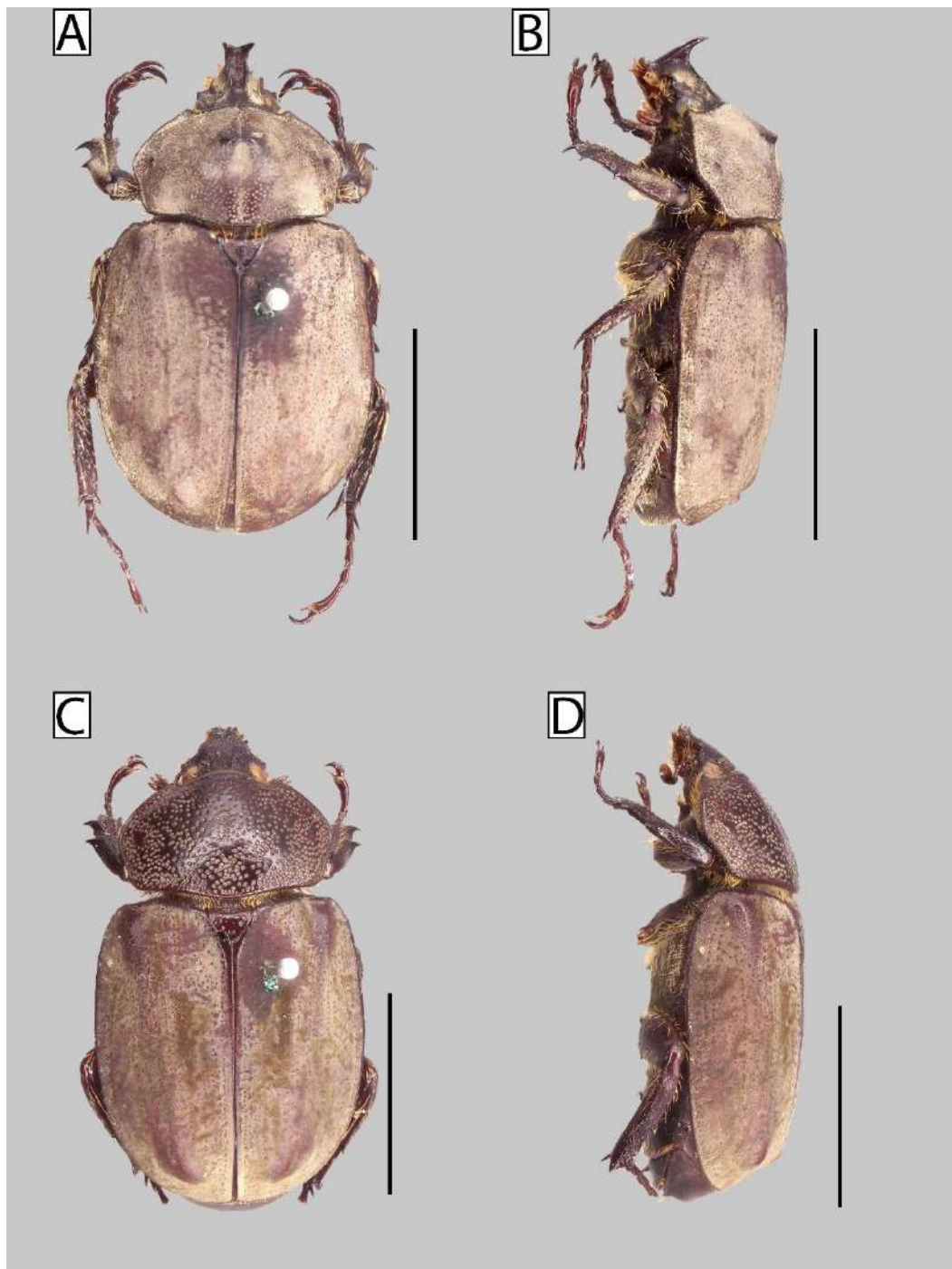


FIGURE 17. Male and female of *Lycomedes velutipes*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.

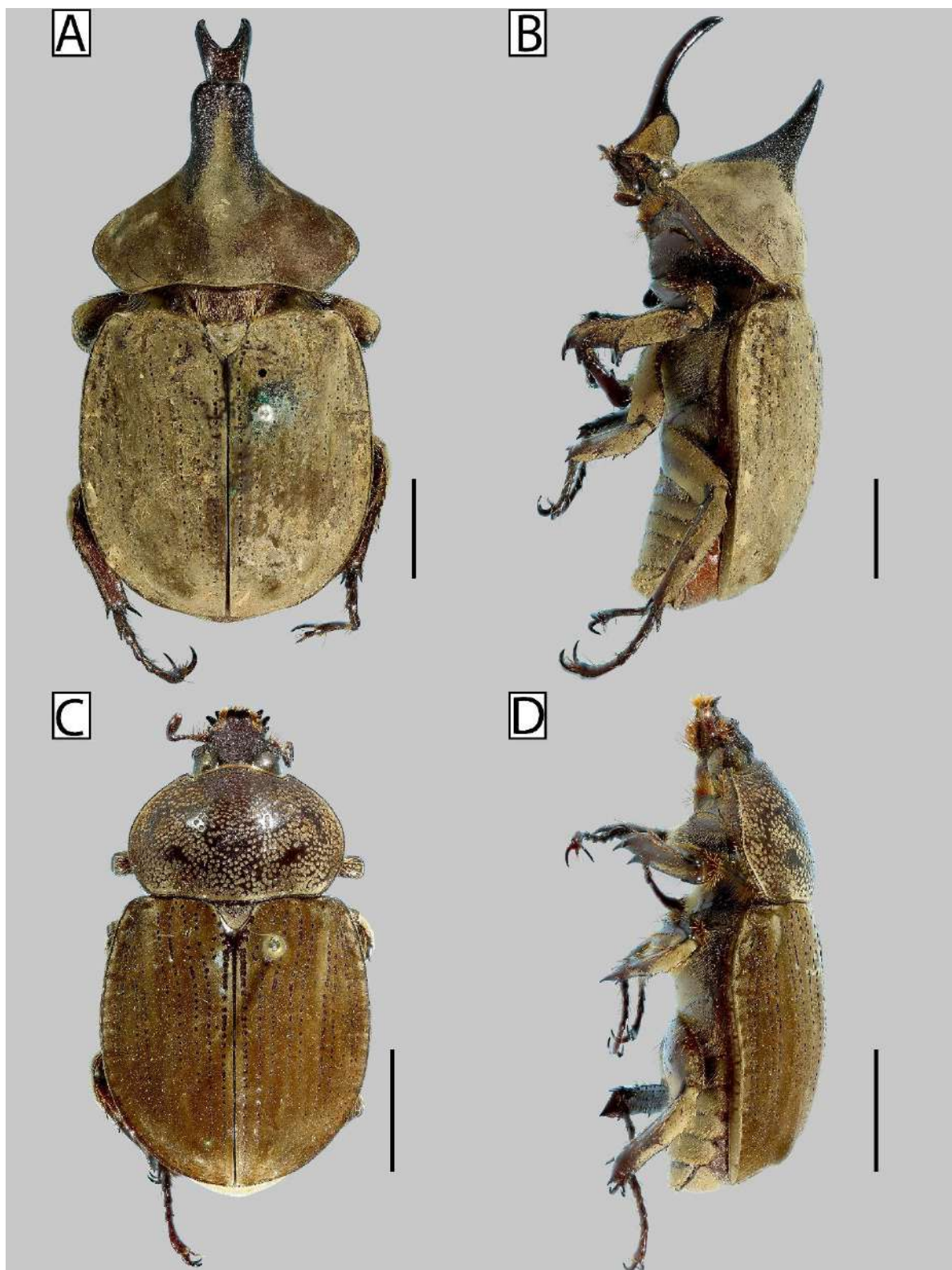


FIGURE 18. Male and female of *Lycomedes ohausi*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.

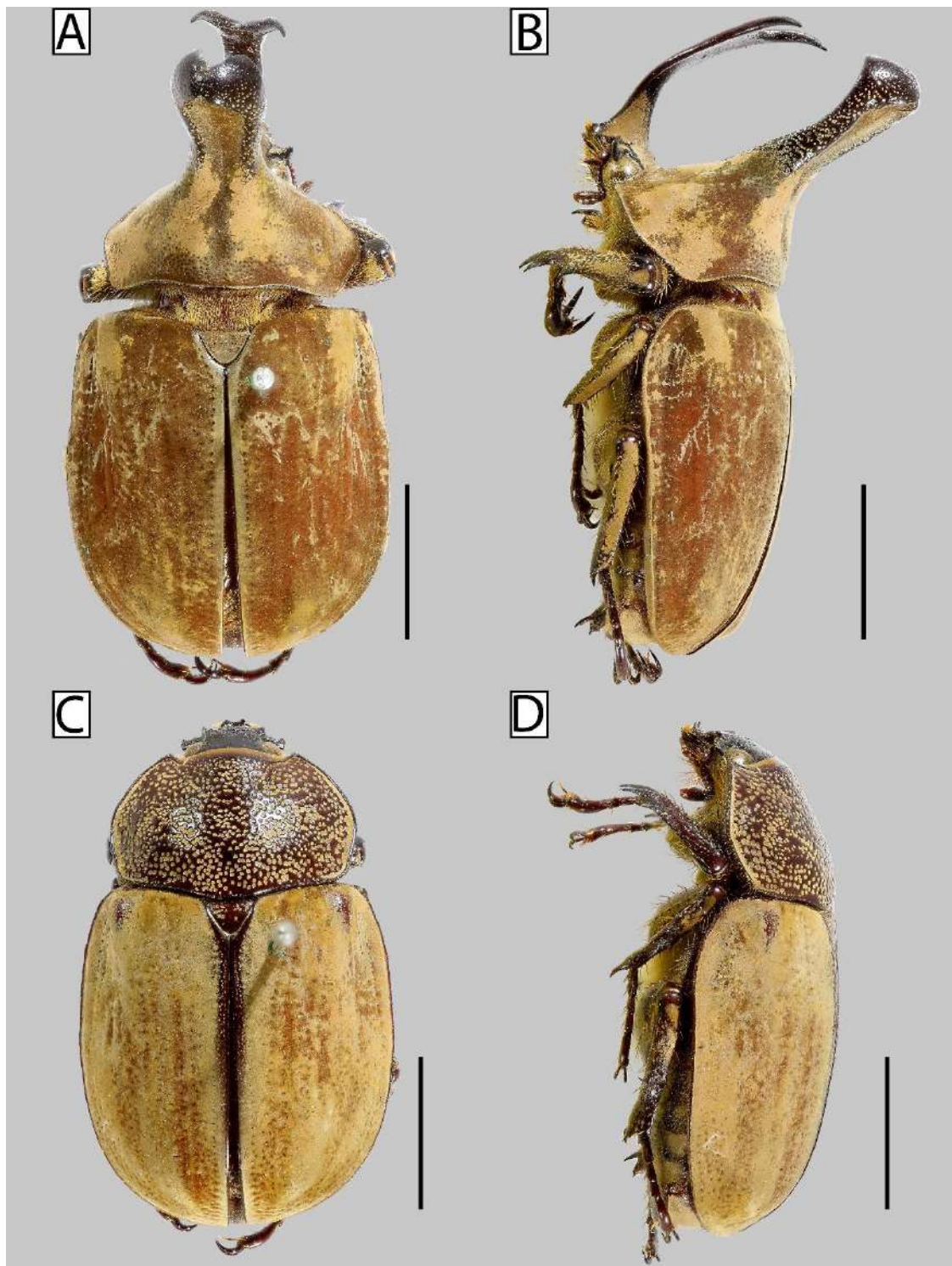


FIGURE 19. Male head of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Head of *L. ohausi* in dorsal view. Black arrow pointing to anterior margin of ocular canthus. **B**, Head of *L. ohausi* in dorsolateral view. Black arrow pointing to shallow depression of frons. **C**, Head of *L. ohausi* in frontal view. Black arrows pointing to anterior corners of clypeus. **D**, Head of *L. ohausi* in lateral view. **E**, Head of *L. enigmaticus* in dorsal view. Black arrow pointing to anterior corner of ocular canthus. **F**, Head of *L. enigmaticus* in dorsolateral view. Superior black arrow pointing to clypeal apex; inferior black arrow pointing to fovea. **G**, Head of *L. enigmaticus* in frontal view. Black arrows pointing to anterior corners of clypeus. **H**, Head of *L. enigmaticus* in lateral view. Black arrow pointing to frontal portion of cephalic horn. **I**, Head of *L. burmeisteri* in dorsal view. **J**, Head of *L. burmeisteri* in dorsolateral view. **K**, Head of *L. burmeisteri* in frontal view. Black arrows pointing to clypeal anterior corners. **L**, Head of *L. burmeisteri* in lateral view. Scale bars: 1 mm.

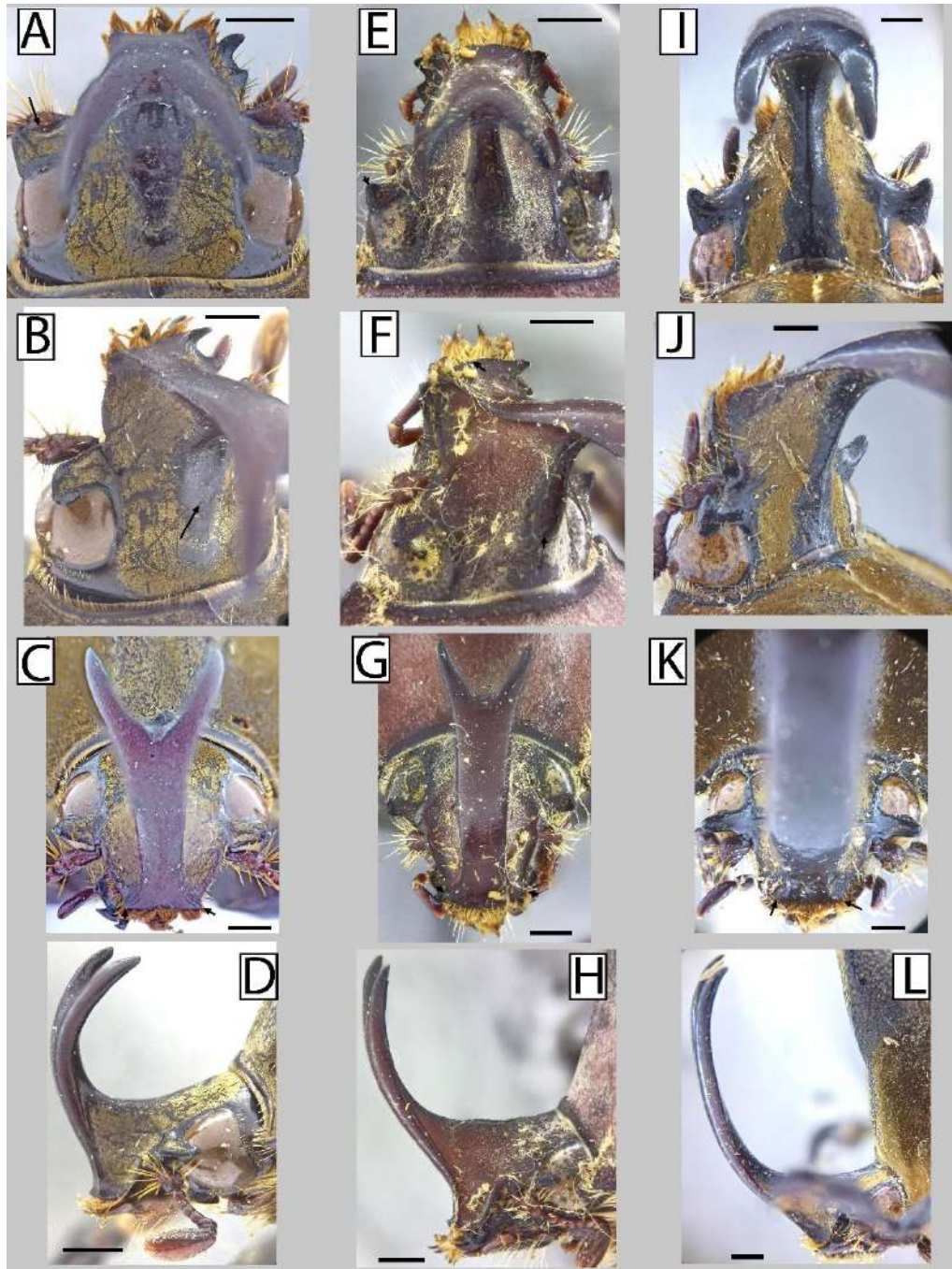


FIGURE 20. Male mouthparts of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Mandible of *L. ohausi* in ventral view. Left black arrow pointing to carina on tooth; right black arrow pointing to molar protuberance; white arrow pointing to ventral depression. **B**, Mandible of *L. ohausi* in dorsal view. White arrow pointing to outermost portion of mesal brush; black arrow pointing to base of inner margin. **C**, Maxilla of *L. ohausi* in ventral view. Black arrows pointing to maxillar teeth. **D**, Labrum of *L. ohausi* in dorsal view. Black arrow pointing to setae insertion. **E**, Mandible of *L. enigmaticus* in ventral view. Black arrow pointing to molar protuberance. **F**, Mandible of *L. enigmaticus* in dorsal view. Black arrow pointing to concavity on outer margin. **G**, Maxilla of *L. enigmaticus* in ventral view. Black arrows pointing to maxillar teeth; white arrow pointing to lateral border outer margin. **H**, Labrum of *L. enigmaticus* in dorsal view. **I**, Mandible of *L. burmeisteri* in ventral view. Left black arrow pointing to inner margin; right black arrow pointing to area of molar protuberance. **J**, Mandible of *L. burmeisteri* in dorsal view. Simple black arrow pointing to outermost portion of mesal brush; double-headed black arrow showing length of molar area. **K**, Maxilla of *L. burmeisteri* in ventral view. Black arrows pointing to maxillar teeth; red arrow pointing to outer margin of lateral border. **L**, Labrum of *L. burmeisteri* in dorsal view. Scale bars: 1 mm.

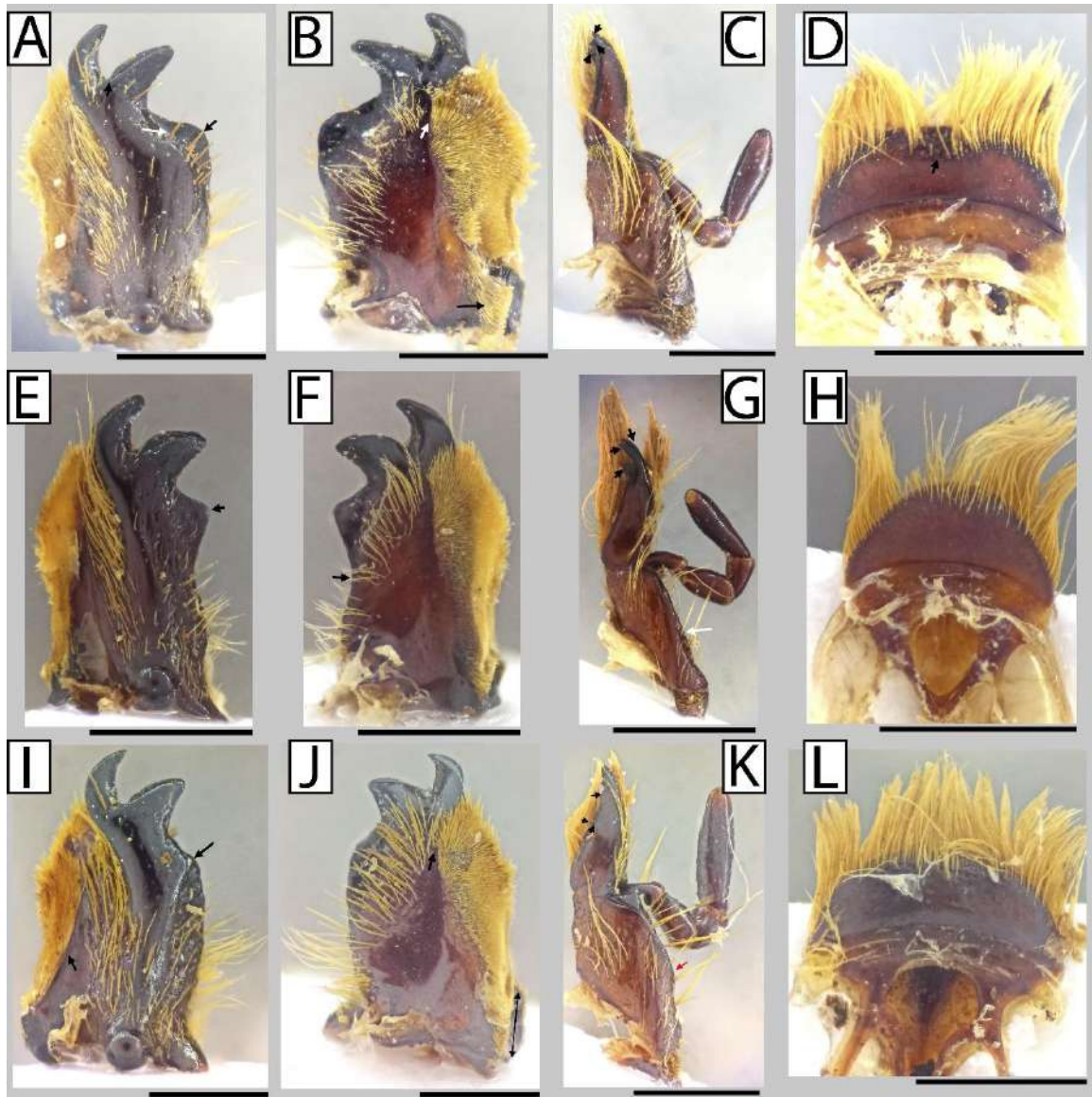


FIGURE 21. Male thorax of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Pronotum of *L. ohausi* in dorsal view. **B**, Pronotum of *L. ohausi* in frontolateral view. **C**, Pronotum of *L. ohausi* in lateral view. **D**, Pronotum of *L. enigmaticus* in dorsal view. Black arrow pointing to emargination of thoracic horn. **E**, Pronotum of *L. enigmaticus* in frontolateral view. Black arrow pointing to medial line of thoracic horn. **F**, Pronotum of *L. enigmaticus* in lateral view. Left black arrow pointing to anterior depression; right black arrow pointing to posterior depression. **G**, Pronotum of *L. burmeisteri* in dorsal view. Black arrow pointing to posterior depression of horn. **H**, Pronotum of *L. burmeisteri* in frontolateral view. Black arrow pointing to lateral carina; white arrow pointing to tomentum. **I**, Pronotum of *L. burmeisteri* in lateral view. Left black arrow pointing to lateral carina at base; right black arrow pointing to posterior depression. Scale bars: 1 mm.

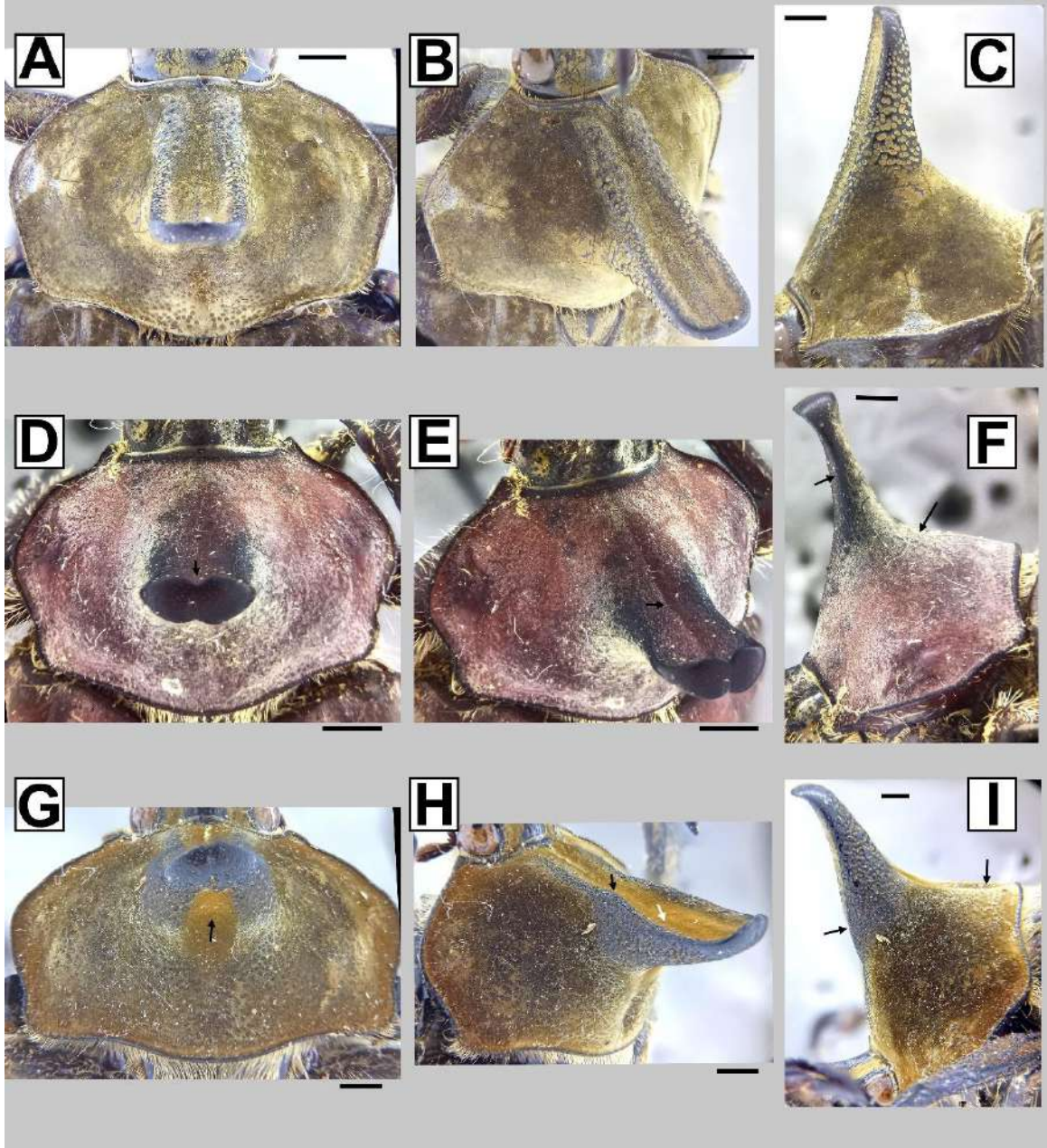


FIGURE 22. Male thorax, leg and abdomen of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Prosternum of *L. ohausi* in ventral view. White arrow pointing to keel; black arrow pointing to prosternal process. **B**, Protibia of *L. ohausi* in dorsal view. **C**, Protarsus of *L. ohausi* in dorsal view. Black arrow pointing to mesobasal protuberance of protarsal claw. **D**, Abdomen of *L. ohausi* in ventral view. **E**, Prosternum of *L. enigmaticus* in ventral view. Black arrow pointing to prosternal process. **F**, Protibia of *L. enigmaticus* in dorsal view. **G**, Protarsus of *L. enigmaticus* in dorsal view. White arrow pointing to basal tooth of protarsus; black arrow pointing to mesobasal protuberance of protarsal claw. **H**, Abdomen of *L. enigmaticus* in ventral view. Superior white arrow pointing to medial projection of sternite III. **I**, Prosternum of *L. burmeisteri* in ventral view. Black arrow pointing to medial elevation. **J**, Protibia of *L. burmeisteri* in dorsal view. **K**, Protarsus of *L. burmeisteri* in dorsal view. Black arrow pointing to basal tooth of protarsal claw; white arrow pointing to mesobasal protuberance of protarsal claw. **L**, Abdomen of *L. burmeisteri* in ventral view. Scale bars: C, G, K, 1 mm; A-B, D, E-F, H, I-J, L, 5 mm.

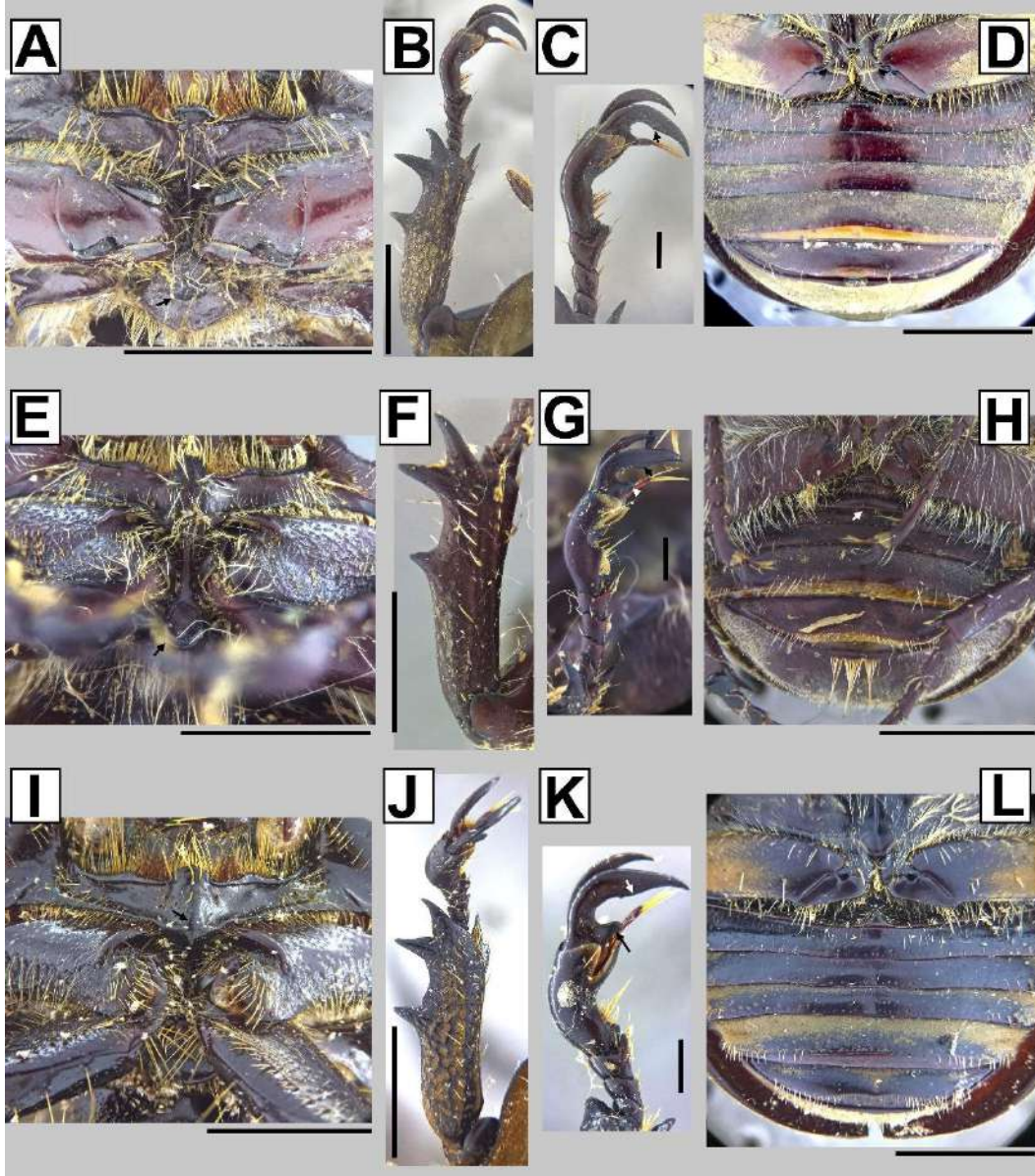


FIGURE 23. Male genitalia of *Lycomedes ohausi*, *Lycomedes enigmaticus* and *Lycomedes burmeisteri*. **A**, Parameres of *L. ohausi* in caudal view. Black arrows pointing to lateral protuberances of basal portion. **B**, Parameres of *L. ohausi* in lateral view. Double-headed black arrow showing thickness of apical portion. **C**, Parameres of *L. ohausi* in ventral view. Left black arrow pointing to ventral suture; right black arrow pointing to ventrolateral portion of parameres. **D**, Aedeagus *L. ohausi* in lateral view. Black arrow pointing to apical corner of posterior phallobase. **E**, Parameres of *L. enigmaticus* in caudal view. Superior black arrow pointing to apex of inner margin; inferior black arrows pointing to carinae on basal portion. **F**, Parameres of *L. enigmaticus* in lateral view. Superior black arrow pointing to apex of parameres; white arrow pointing to carina; inferior black arrow pointing to basal margin. **G**, Parameres of *L. enigmaticus* in ventral view. Black arrow pointing to lateral margin of base; black square showing wrinkles. **H**, Aedeagus of *L. enigmaticus* in lateral view. Left black arrow pointing to apical corner of posterior phallobase; right black arrow pointing to apical margin of posterior phallobase. **I**, Parameres of *L. burmeisteri* in caudal view. **J**, Parameres of *L. burmeisteri* in lateral view. Black arrow pointing to lateral carina; white arrow pointing to dorsal depression. **K**, Parameres of *L. burmeisteri* in ventral view. Superior black arrow pointing to apical portion of lateral margin; inferior black arrow pointing to medial concavity. **L**, Aedeagus of *L. burmeisteri* in lateral view. White arrow pointing to apical corner of posterior phallobase. Scale bars: 1 mm.

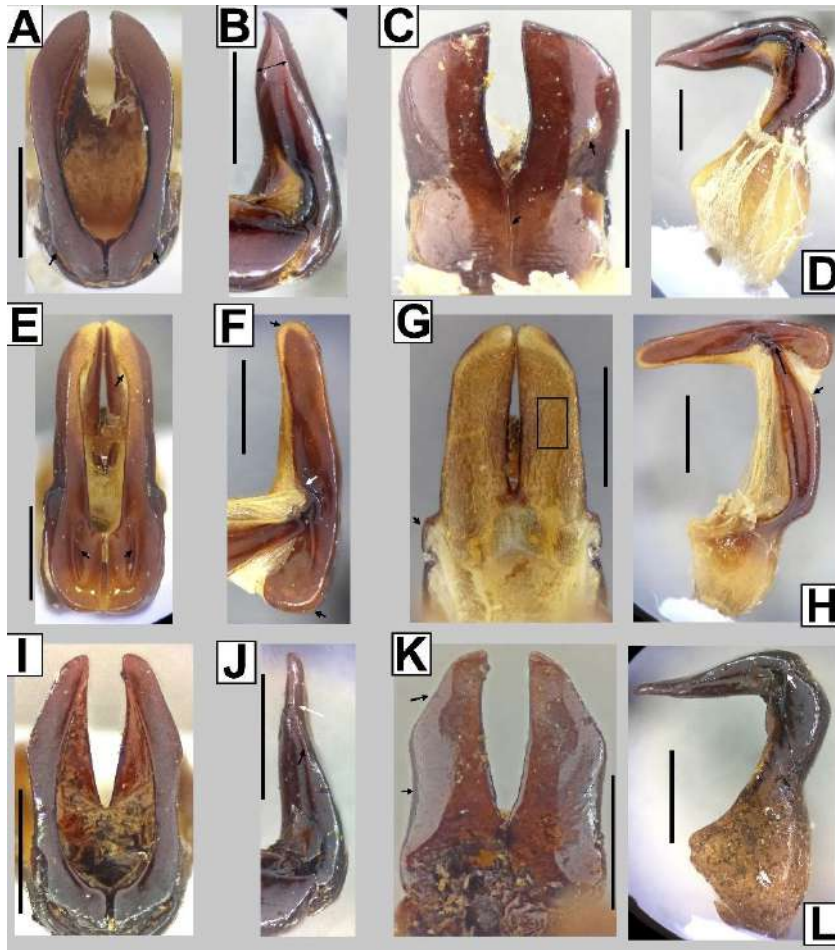


FIGURE 24. Female head of *Lycomedes ohausi* and *Lycomedes burmeisteri*. **A**, Head of *L. ohausi* in dorsal view. Black arrow pointing to anterior margin of ocular canthus. **B**, Head of *L. ohausi* in frontal view. Double-headed black arrows comparing clypeal apex with base; simple black arrow pointing to clypeal apex. **C**, Head of *L. ohausi* in lateral view. Black arrows pointing to clypeal base projections. **D**, Head of *L. burmeisteri* in dorsal view. Black arrow pointing to tomentum. **E**, Head of *L. burmeisteri* in frontal view. **F**, Head of *L. burmeisteri* in lateral view. Black arrows pointing to clypeal base projections. Scale bars: 1 mm.

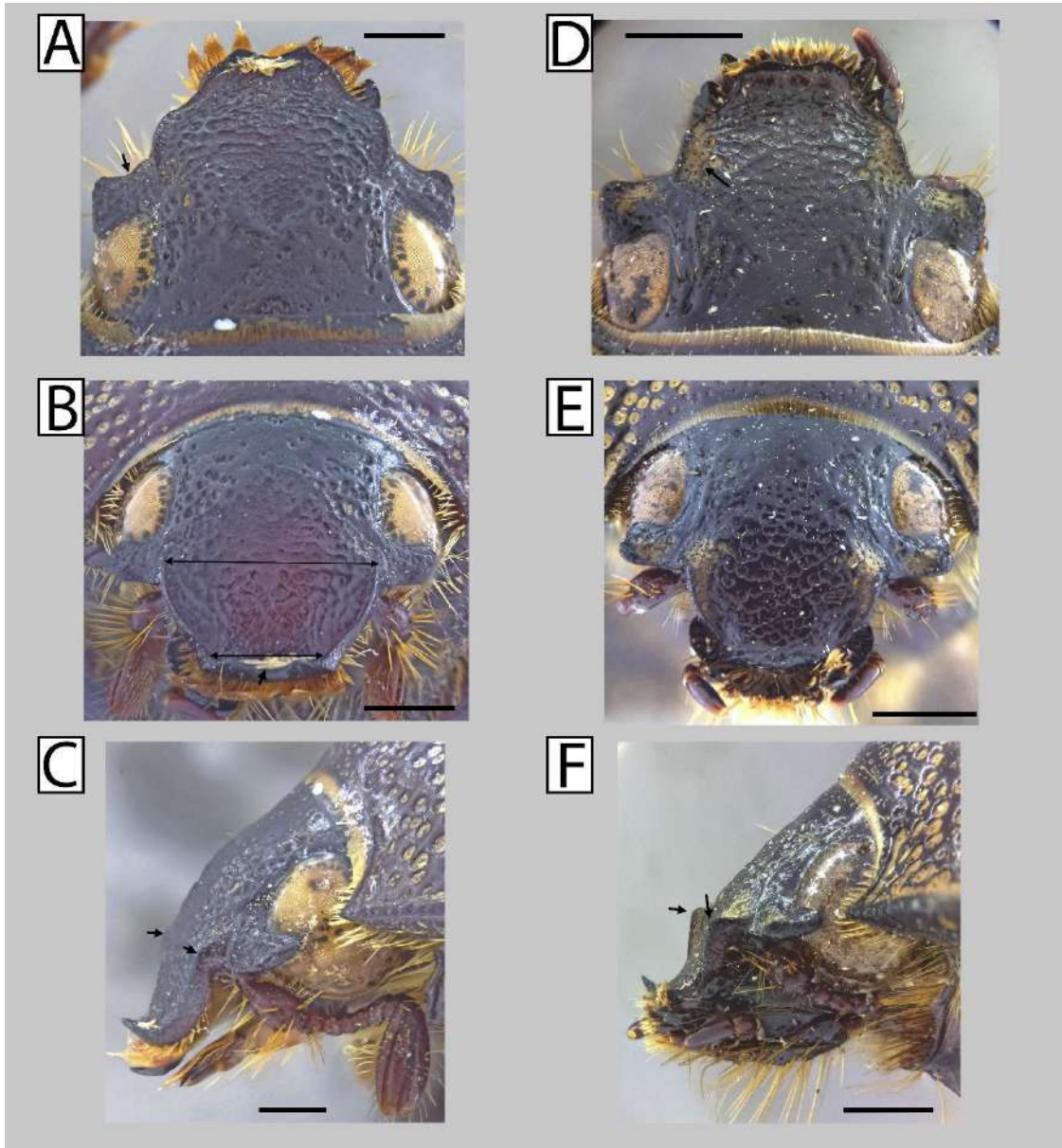


FIGURE 25. Female mouthparts of *Lycomedes ohausi*. **A**, Mandible in ventral view. Black arrow pointing to molar protuberance. **B**, Mandible in dorsal view. Black arrow pointing to outer basal projection. **C**, Maxilla in ventral view. Black arrow pointing to tooth. **D**, Labrum in dorsal view. Scale bars: 1 mm.



FIGURE 26. Female thorax, legs and abdomen of *Lycomedes ohausi* and *Lycomedes burmeisteri*. **A**, Pronotum of *L. ohausi* in dorsal view. Black arrow pointing to anterior border. **B**, Prosternum of *L. ohausi* in ventral view. Black arrow pointing to medial portion of prosternum. **C**, Part of abdomen, metafemur and metatibia of *L. ohausi* in ventral view. Black arrows pointing to tomentose areas; white arrows pointing to setae insertion. **D**, Pronotum of *L. burmeisteri* in dorsal view. **E**, Prosternum of *L. burmeisteri* in ventral view. White arrow pointing to prosternal process. **F**, Part of abdomen, metafemur and metatibia of *L. burmeisteri* in ventral view. Black arrows pointing to setae insertion. Scale bars: 5 mm.

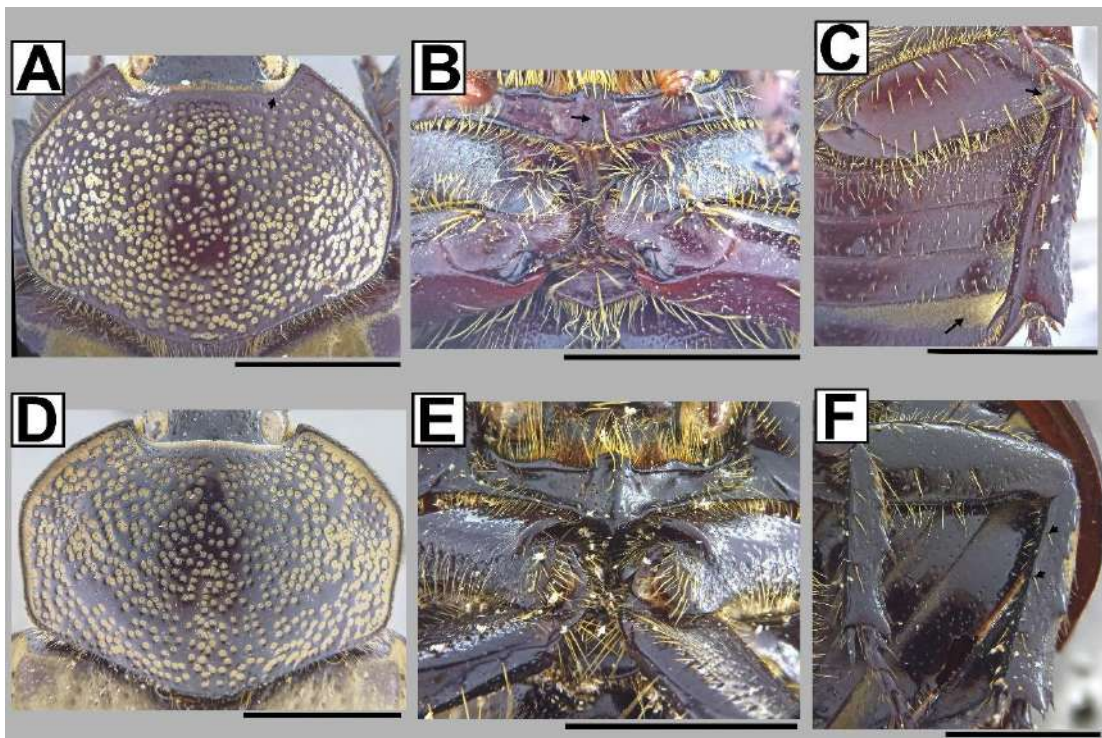


FIGURE 27. Male of *Lycomedes enigmaticus*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm.

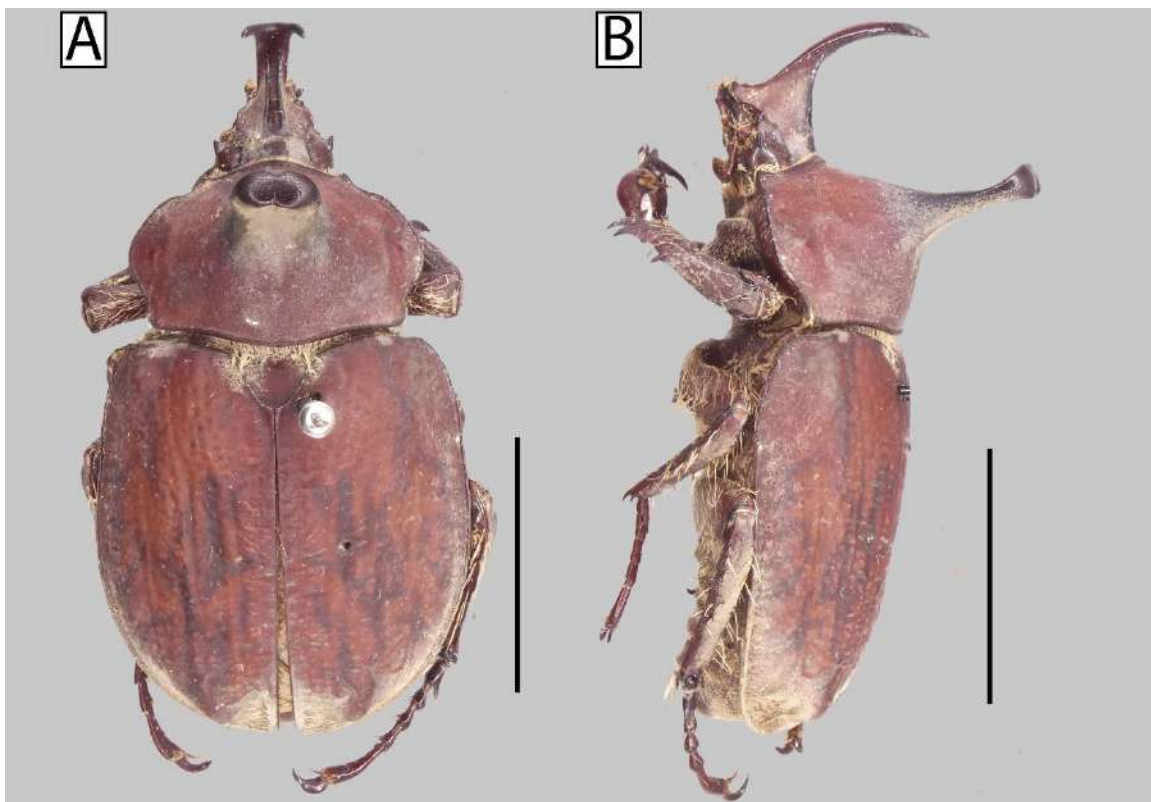


FIGURE 28. Male and female of *Lycomedes burmeisteri*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.

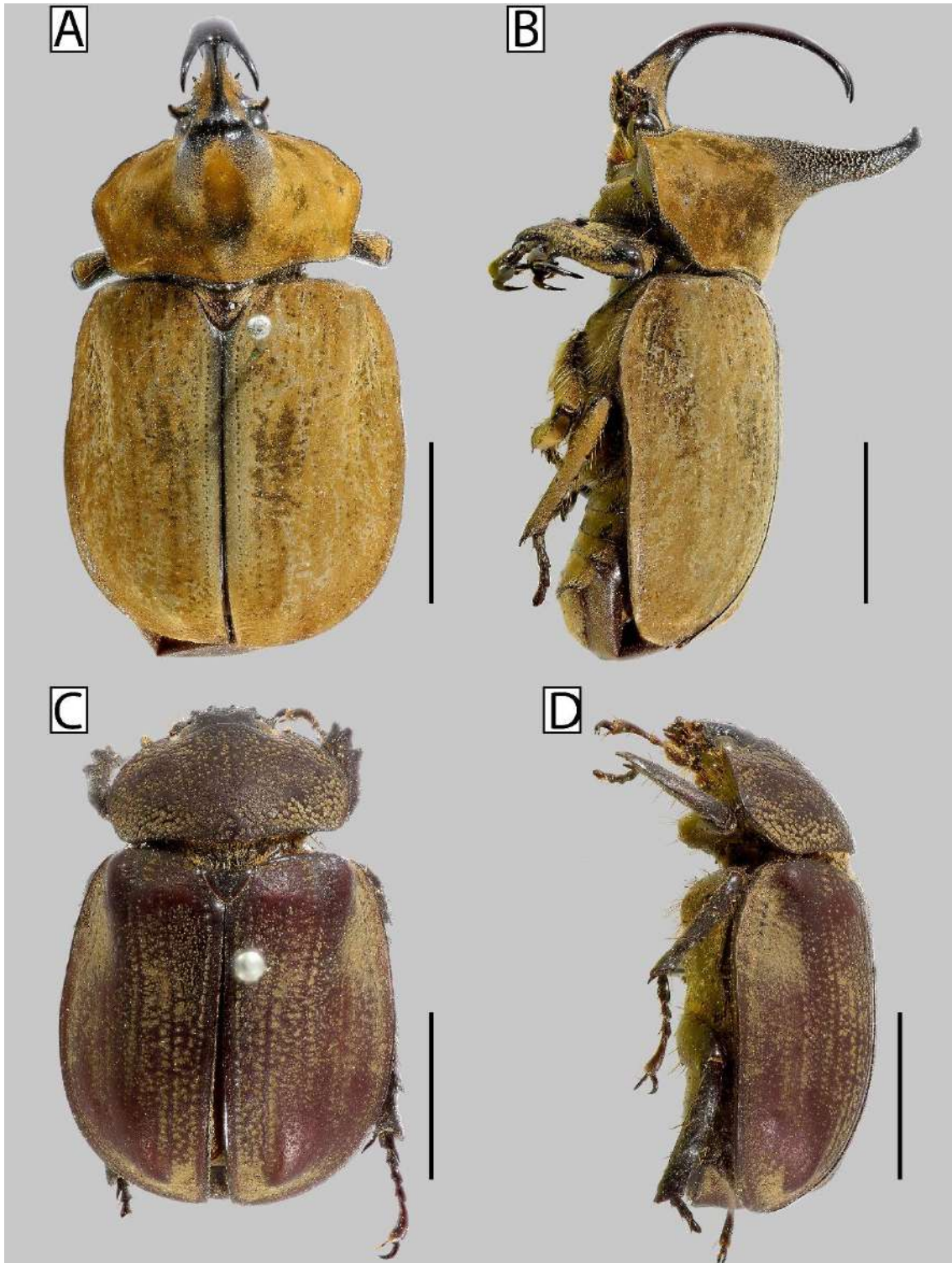


FIGURE 29. Male and female of *Horridocalia peruviana*. **A**, Habitus of male in dorsal view; **B**, habitus of male in lateral view; **C**, habitus of female in dorsal view; **D**, habitus of female in lateral view. Scale bars: 10 mm.

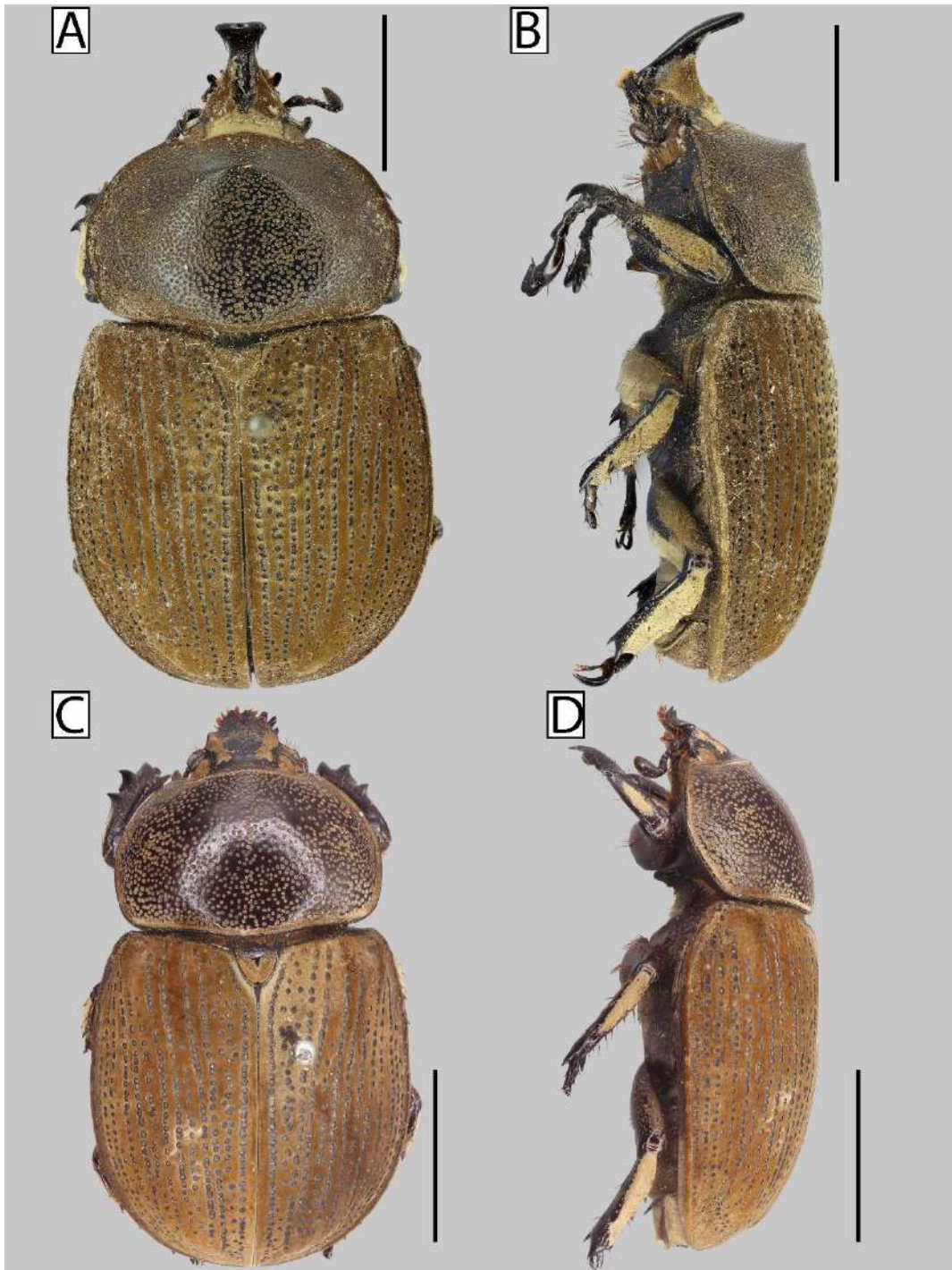


FIGURE 30. Male head and thorax of *Horridocalia delislei* and *Horridocalia peruviana*. **A**, Head of *H. delislei* in dorsal view. Black arrow pointing to keel. **B**, Pronotum of *H. delislei* in dorsal view. Black arrow pointing to apex of horn. **C**, Head and thorax of *H. delislei* in lateral view. Superior black arrow pointing to horn carina; inferior black arrow pointing to prosternal process; black square showing pronotal punctures. **D**, Head of *H. peruviana* in dorsal view. Black arrow pointing to small fovea; white arrows pointing to carinae. **E**, Pronotum of *H. peruviana* in dorsal view. Black arrow pointing to apex of horn. **F**, Head and thorax of *H. peruviana* in lateral view. Black arrow pointing to prosternal process; black square showing pronotal punctures. Scale bars: A-B, D-E, 5 mm; C,F, 10 mm. Figure A-B extracted from Neita-Moreno & Ratcliffe (2019); figure C by Antoine Mantilleri.

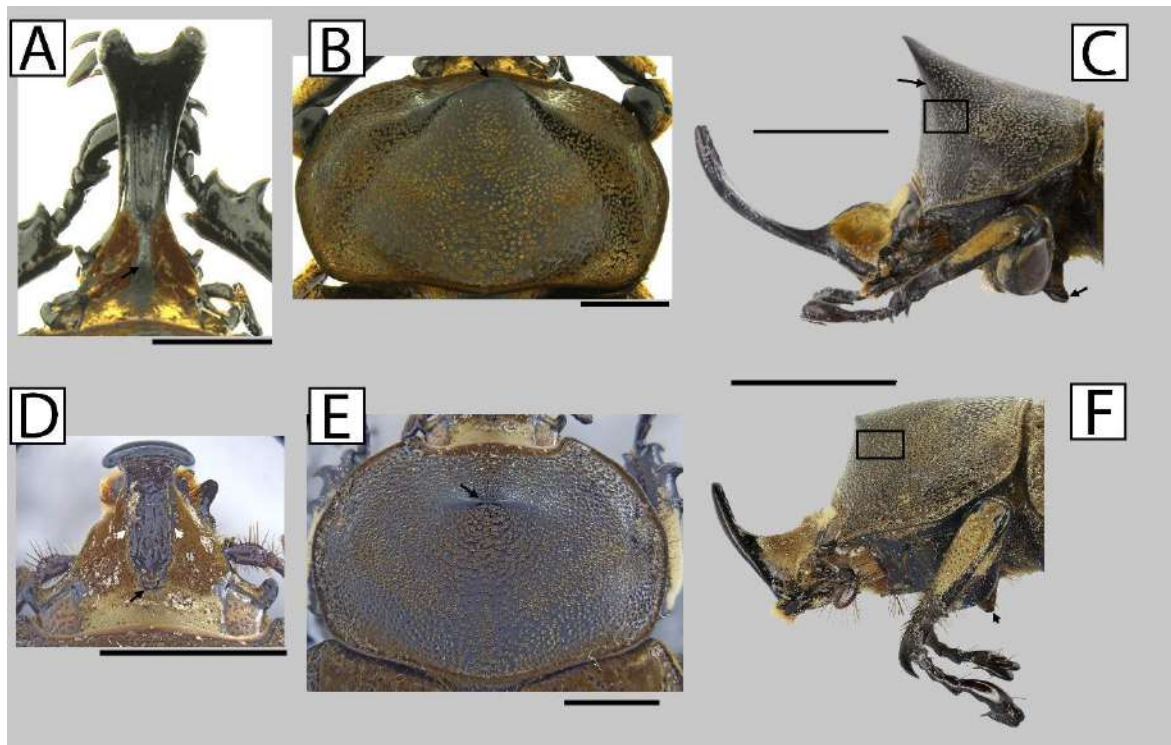


FIGURE 31. Male and female mouthparts of *Horridocalia peruviana*. **A**, Mandible of male *H. peruviana* in ventral view. Black arrow pointing to carina on inner tooth. **B**, Mandible of male *H. peruviana* in dorsal view. Black arrow pointing to apical outer margin. **C**, Maxilla of male *H. peruviana* in ventral view. Black arrow pointing to carina. **D**, Labrum of male *H. peruviana* in dorsal view. **E**, Mandible of female *H. peruviana* in ventral view. Left black arrow pointing to basal inner depression; right black arrow pointing to molar protuberance. **F**, Mandible of female *H. peruviana* in dorsal view. Black arrow pointing to carina between teeth. **G**, Maxilla of female *H. peruviana* in ventral view. **H**, Labrum of female *H. peruviana* in dorsal view. Scale bars: 1 mm.

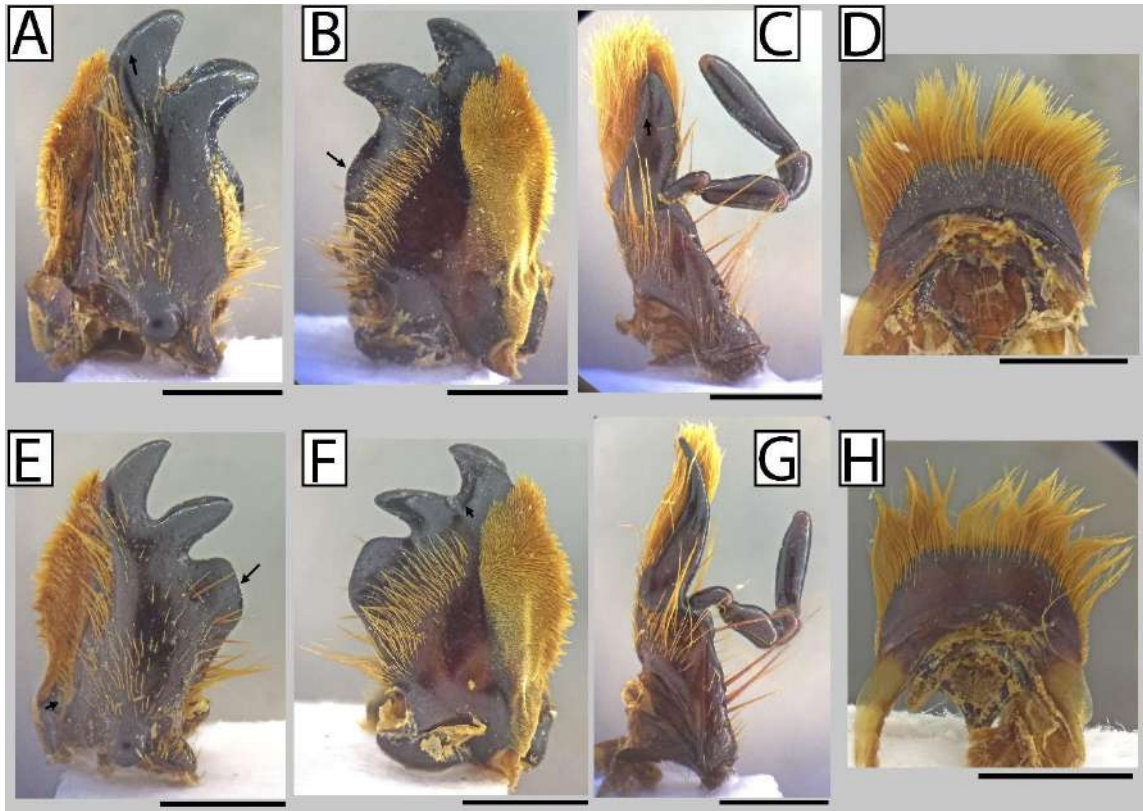


FIGURE 32. Male genitalia of *Horridocalia peruviana*. **A**, Parameres in caudal view. **B**, Parameres in lateral view. Left black arrow pointing to ventral slight protuberance; right black arrow pointing to apical protuberance; white arrow pointing to lateral carina. **C**, Parameres in ventral view. Superior black arrow pointing to apical emargination; inferior black arrow pointing to ventrolateral carina; white arrow pointing to basal ventral carina. **D**, Aedeagus *L. ohausi* in lateral view. Scale bars: 1 mm.

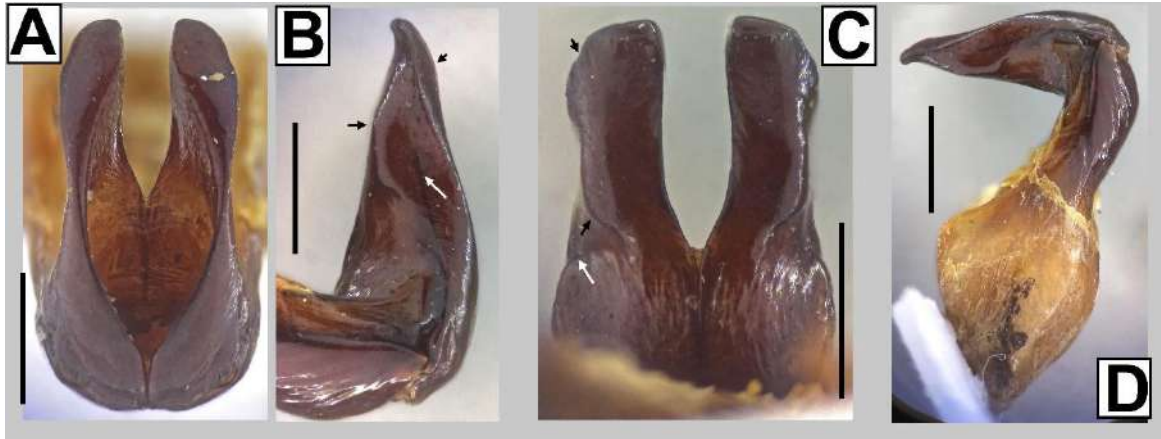


FIGURE 33. Female head of *Horridocalia peruviana*. **A**, Head in dorsal view. Simple black arrow pointing to anterior corner of clypeus; double-headed arrows comparing clypeal apex with base. **B**, Head in frontal view. Black arrows pointing to tomentum. **C**, Head in lateral view. **D**, Pronotum in dorsal view. **E**, Prosternum in ventral view. Black arrow pointing to prosternal process. **F**, Part of abdomen, metafemur and metatibia in ventral view. Scale bars: 5 mm.

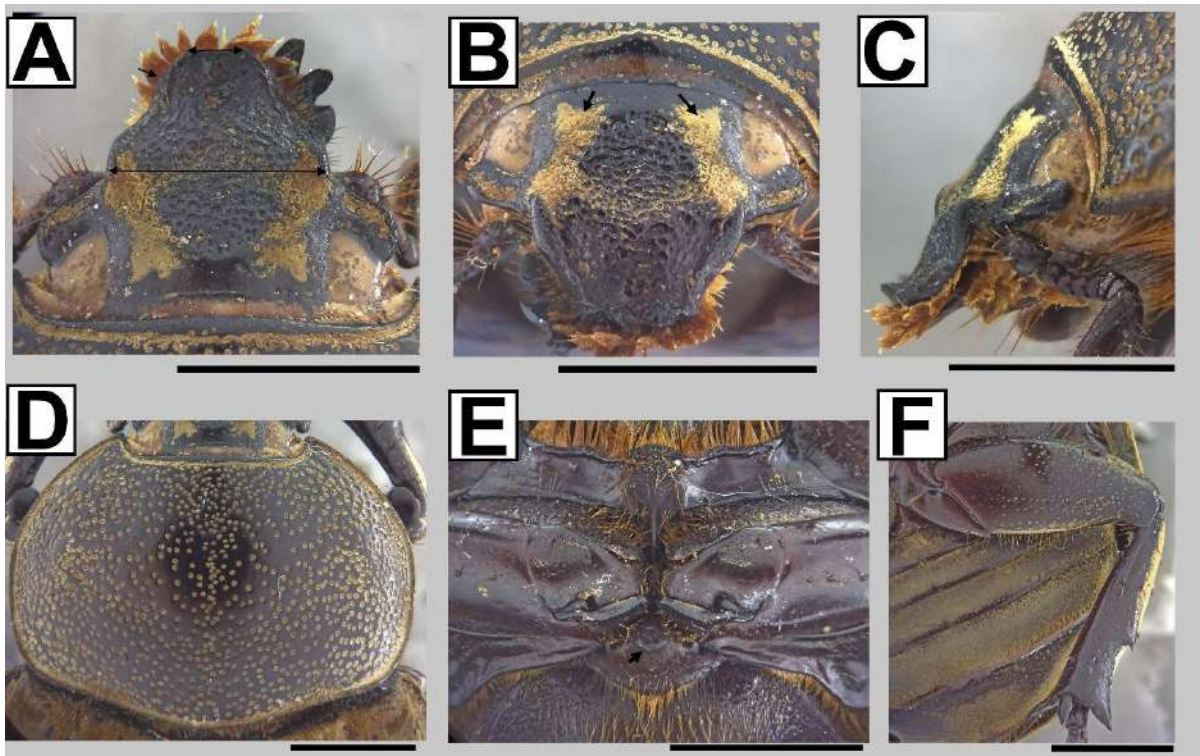


FIGURE 34. Male of *Horridocalia delislei*. **A**, Habitus in dorsal view; **B**, habitus in lateral view. Scale bars: 10 mm. Photos by Antoine Mantilleri (MNHN).

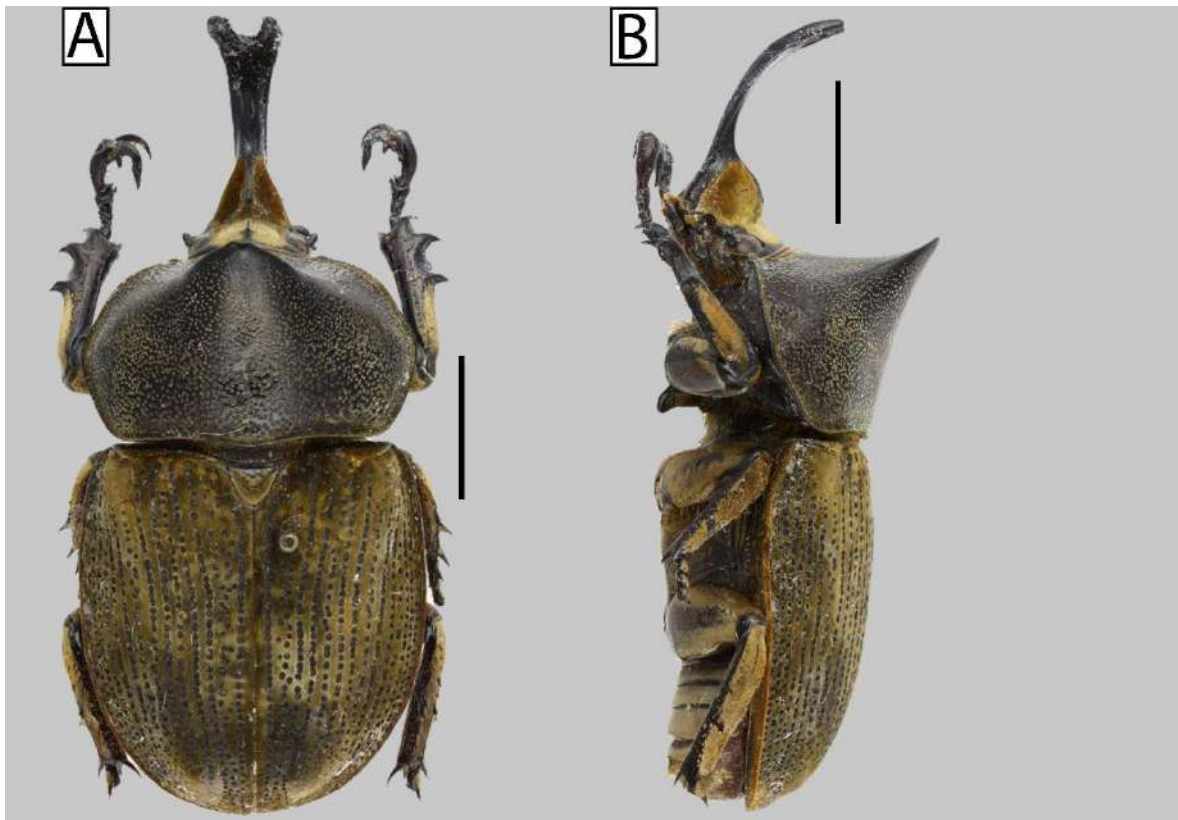


FIGURE 35. Distribution map of *Lycomedes*.

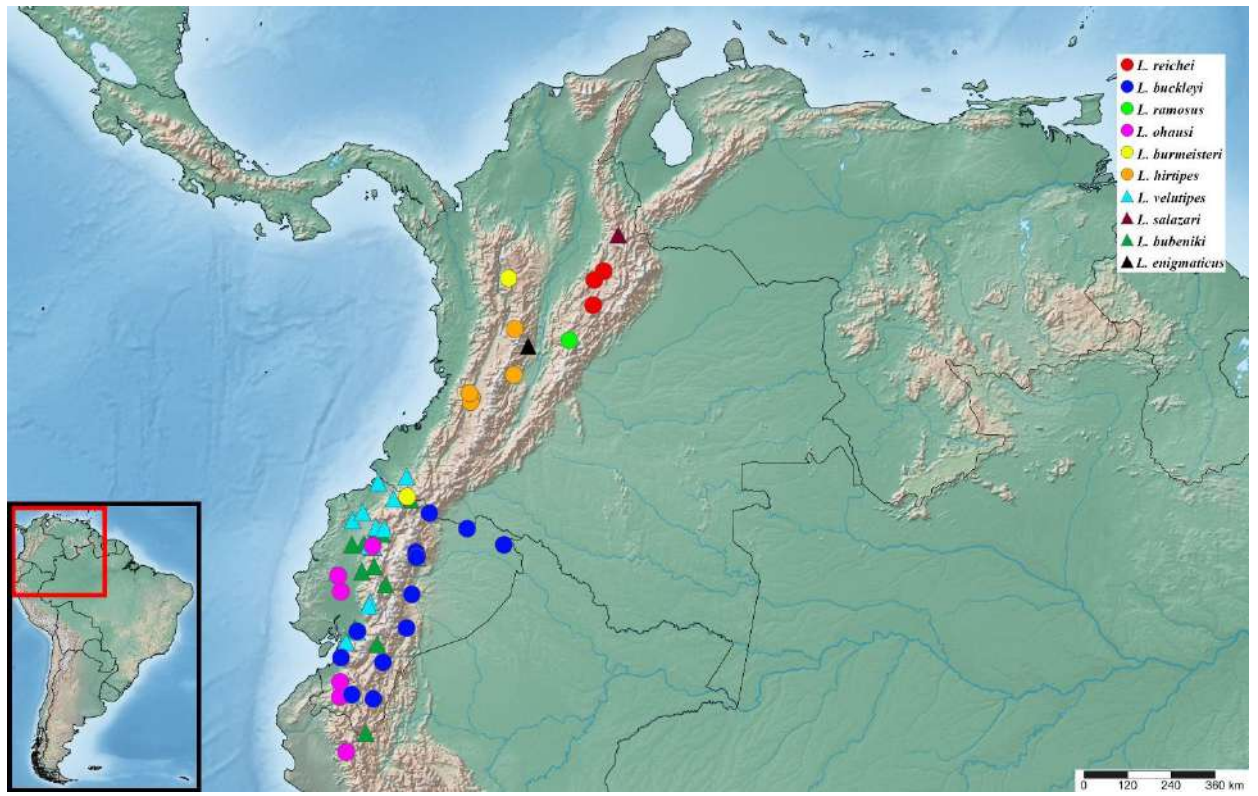
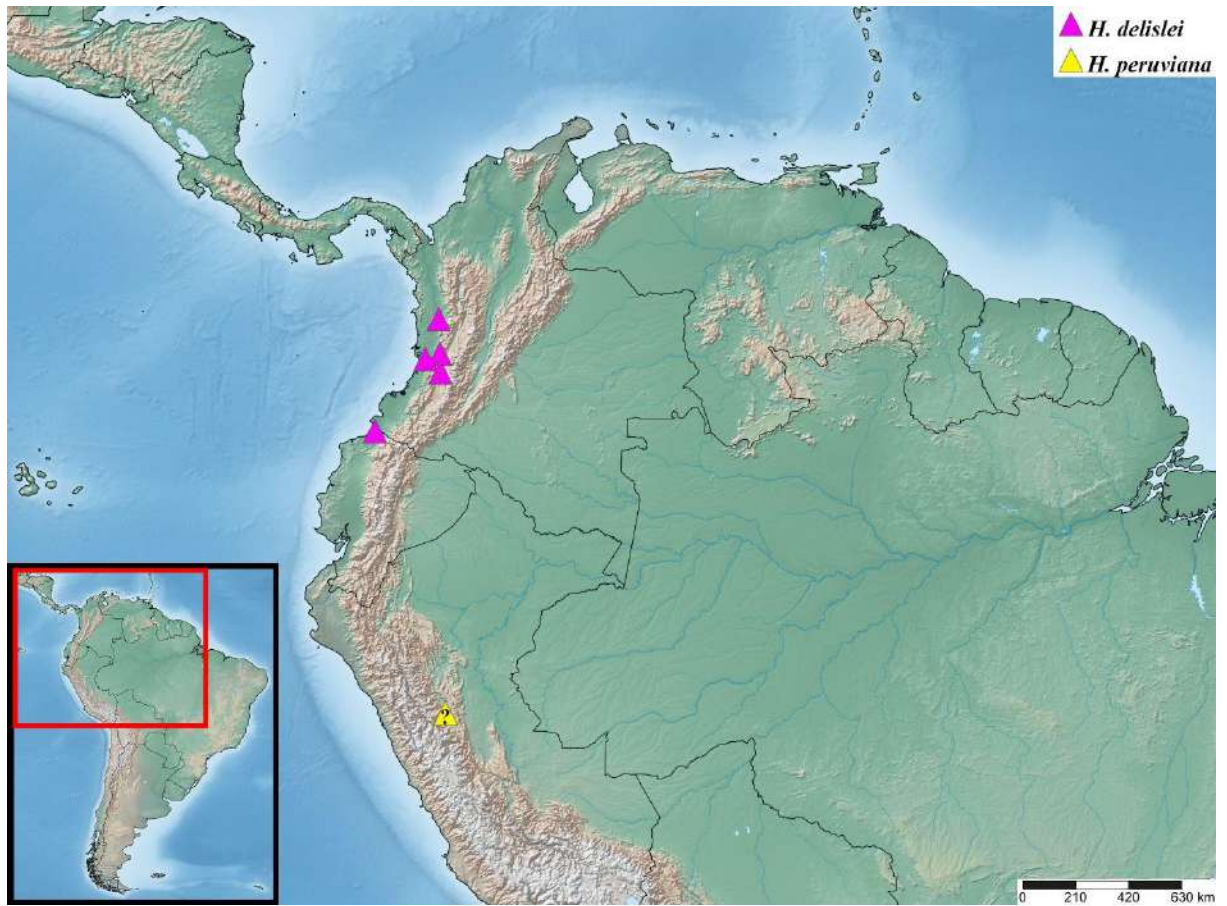


FIGURE 36. Distribution map of *Horridocalia*.



CAPÍTULO VI

Sobral, R., Morais, J.W. de & Grossi, P.C. (2019).
A new species of *Colacus* Ohaus, 1910 (Coleoptera:
Scarabaeoidea: Dynastinae) from the Mata Seca
biotope of Brazil, and notes on *Colacus morio*
Ohaus, 1910. Manuscrito publicado na revista
Zootaxa.

A new species of *Colacus* Ohaus, 1910 (Coleoptera: Scarabaeidae: Dynastinae) from the Mata Seca biotope of Brazil, and notes on *Colacus morio* Ohaus, 1910

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Abstract

In this contribution, *Colacus rubrofemoratus* Sobral, Morais, & Grossi **new species** (Coleoptera: Scarabaeidae: Dynastinae: Agaocephalini) is described and illustrated based on male specimens found in a transitional area of Caatinga, Atlantic Forest, and Cerrado in Brazil. In addition, the female of *Colacus morio* Ohaus, 1910 is redescribed, a distribution map for the genus is provided, and a new key to the species of *Colacus* is presented.

Key words: Agaocephalini, rhinoceros beetles, Scarabaeoidea, taxonomy

Introduction

Colacus Ohaus, 1910 (Coleoptera: Scarabaeidae: Dynastinae: Agaocephalini) is a Neotropical genus previously known from the High Monte and Central Andean Puna ecoregions of northwestern Argentina. Three species occur in Argentina: *Colacus bicolor* Ohaus, 1910, *Colacus morio* Ohaus, 1910, and *Colacus moroni* Neita-Moreno, 2015. In this contribution, we describe a new species of *Colacus* from Brazil collected in a biotope known as the Mata Seca. Additionally, we update the identification key of Neita-Moreno (2015) to include the new species, redescribe the female of *Colacus morio*, and present a distribution map for the four known species.

Material and methods

Terminology partially follows Endrödi (1985) and Neita-Moreno (2015) for general aspects of the body, and Nel & Scholtz (1990) for mouthparts. The distribution map of the species was made using SimpleMapp (Shorthouse 2010). The records in the map of the Argentinian species of *Colacus* were extracted from Martínez (1988) and Neita-Moreno (2015).

Specimens were deposited in the following collections: CERPE, Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil; EPGC, Everardo and Paschoal Grossi Collection, Nova Friburgo, Rio de Janeiro, Brazil; and IFML, Colección de Entomología del Instituto e Fundación Miguel Lillo, Tucumán, Argentina.

***Colacus rubrofemoratus* Sobral, Morais, & Grossi, new species**

(Figs. 1–5)

Diagnosis. *Colacus rubrofemoratus* is distinct from the other species of the genus as it has the cephalic tubercle transverse, emarginate on its apex (Fig. 2A–B), and red legs (Fig. 1B), visible even when specimens are walking

O artigo foi enviado na íntegra para a banca como um arquivo separado juntamente com a tese.

ANEXO I

Sobral, R., Grossi, P.C. & de Morais, J.W. (2018).
Two new species of *Aegopsis* Burmeister, 1847
(Coleoptera: Scarabaeidae: Dynastinae) from the
central Brazilian Cerrado. Manuscrito publicado na
revista Zootaxa.

Two new species of *Aegopsis* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae) from the central Brazilian Cerrado

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Abstract

Two new species of *Aegopsis* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae: Agaocephalini), *Aegopsis diceratops* Sobral & Grossi **new species** and *Aegopsis vazdemelloi* Sobral & Grossi **new species**, are described and illustrated based on specimens collected in Cerrado habitat in the Brazilian states of Minas Gerais and Mato Grosso. The new species are similar to *A. bolboceoides* (Thomson, 1860). A redescription of *A. bolboceoides* is provided along with remarks comparing characters among these three species. A distribution map and a male and female key to the species in the genus are provided.

Key words: Scarabaeoidea, rhinoceros beetles, South America, Neotropical region

Resumo

Duas novas espécies de *Aegopsis* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae: Agaocephalini), *Aegopsis diceratops* Sobral & Grossi **nova espécie** e *Aegopsis vazdemelloi* Sobral & Grossi **nova espécie**, são descritas e ilustradas baseadas em espécimes coletados no Cerrado, nos estados de Minas Gerais e Mato Grosso, Brasil. As novas espécies se assemelham com *A. bolboceoides* (Thomson, 1860). A redescricao de *A. bolboceoides* é feita, adicionalmente com comentários comparando os caracteres entre essas espécies. Um mapa de distribuição e uma chave para machos e fêmeas das espécies do gênero são fornecidos.

Introduction

Aegopsis Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae: Agaocephalini) is a Neotropical genus of rhinoceros beetles, with four known species distributed from southern Costa Rica to central Brazil: *A. bolboceoides* (Thomson, 1860), *A. chaminadei* Dechambre, 1999, *A. curvicornis* Burmeister, 1847, and *A. peruvianus* Arrow, 1941 (Endrödi 1985; Dechambre & Grossi 1990; Ratcliffe 2003). Adults of this genus can be recognized by their shiny black to brown color and three prominent horns (two cephalic and one prothoracic) in males. These horns are reduced in size according to male development and are absent in females, which instead possesses tubercles on the head.

Biological information about *Aegopsis* species is still incipient. Immatures are described only for *A. bolboceoides* and *A. curvicornis*, differing from other known larvae of Agaocephalini by the apex of the lacinia with three unci, the intermediate uncus smaller than the lateral unci, and external frontal setae present (Neita-Moreno *et al.* 2014). Records show that at least two species of this genus (*A. bolboceoides* and *A. curvicornis*) are univoltine. Their larvae develop underground in a chamber made with feces and fragments of soil, where they stay

O artigo foi enviado na íntegra para a banca como um arquivo separado juntamente com a tese.

SÍNTESE

Após o presente trabalho, Agocephalini foi dividida em duas subtribos novas para distinguir os gêneros predominantes no escudo das Guianas e planalto brasileiro (Agocephalina **subtrib. nov.**) dos gêneros predominantes nos Andes e na América Central (Lycomedina **subtrib. nov.**). Essa divisão serve para mostrar que dentro da tribo provavelmente ocorreram processos evolutivos que resultaram na formação de dois grupos próximos, que possuem um ancestral em comum mais próximo entre eles do que com outros Dynastinae (com base no conjunto de traços morfológicos), mas, com um conjunto robusto de caracteres morfológicos e um padrão de distribuição geográfica compartilhados somente entre os gêneros incluídos nas respectivas subtribos. Após os resultados deste estudo, houve uma reformulação nos gêneros da tribo, uma vez que nem todos os gêneros inseridos nela correspondiam à sua diagnose. Dessa forma, a tribo passou a ter um novo gênero (*Lycocephala* **stat. nov.**) e houve a transferência de três gêneros previamente incluídos em Agocephalini (*Colacus*, *Democrates* e *Gnathogolofa*) para a tribo Pentodontini. Foram feitas revisões para seis gêneros da tribo (*Agacephala*, *Brachysiderus*, *Horridocalia*, *Lycomedes*, *Minisiderus* e *Spodistes*), resultando na descrição de nove espécies novas, na descrição inédita de cinco fêmeas, na descrição pioneira do macho maior de *Lycomedes enigmaticus*, na revalidação de *Brachysiderus breyeri* **stat. rev.**, no primeiro registro de cópula em *Spodistes*, na sinonimização de *Agacephala urus* **syn. nov.** com *Agacephala mannerheimi*, e na redescrição de machos e fêmeas (quando possível) de 36 espécies. Além disso, foram publicados dois artigos relacionados à tribo Agocephalini. O primeiro deles foi a descrição de duas novas espécies de *Aegopsis* para o Cerrado (*A. diceratops* e *A. vazdemelloi*) junto da redescrição de *A. bolboceridus*; e o segundo foi a descrição de uma nova espécie de *Colacus* (*C. rubrofemoratus*) para o Brasil, também sendo o primeiro registro do gênero para o país. Até agora, a última revisão desses gêneros havia sido feita por Endrödi (1970) e as chaves para identificação das espécies ou eram com base em Endrödi (1985) ou chaves específicas para espécies que ocorrem no mesmo país. Tanto as descrições quanto as chaves desses trabalhos eram de difícil uso pela falta de caracteres para identificação de fêmeas. A maioria das referências para identificação tinham como base poucos desenhos das estruturas. No presente trabalho, elaboramos chaves de identificação para machos e fêmeas de todas as espécies estudadas na revisão de cada um dos gêneros, enfatizando as imagens dos caracteres diagnósticos de cada uma. A maioria das novas espécies estava

identificada nas coleções como sendo parte de alguma espécie conhecida, de tal forma que a distinção delas como espécies só foi possível examinando em conjunto material recente com material antigo de coleções nacionais e internacionais. O uso de caracteres subutilizados na taxonomia tradicional de Dynastinae, como é o caso das peças do aparelho bucal e a parte ventral da genitália masculina, foi de muita relevância para a distinção entre espécies, especialmente aquelas morfologicamente mais similares. Portanto, o conjunto da revisão taxonômica, que envolve as novas chaves dicotômicas para machos e fêmeas, as novas diagnoses e ilustrações, facilitará que novos trabalhos com o grupo sejam realizados, permitindo uma comparação mais nítida entre espécies.

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