

**UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO**  
**CENTRO DE CIÊNCIAS HUMANAS E NATURAIS**  
**PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS**

**Sistemática de *Apenesia* Westwood:  
abrindo a caixa de Pandora dos Pristocerinae  
(Hymenoptera, Bethylidae)**

**Isabel De Conte Carvalho de Alencar**

**Vitória, ES  
Janeiro, 2017**

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**Orientador(a):** Celso Oliveira Azevedo

**Coorientador(a):** Cecília Waichert Monteiro

**Tese submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para a obtenção do grau de Doutor em Biologia Animal.**

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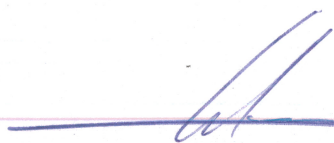
ISABEL DE CONTE CARVALHO DE ALENCAR

**“Sistemática de *Apenesia* Westwood: abrindo a caixa de Pandora dos *Pristocerinae*”**

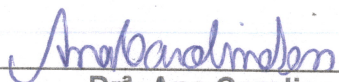
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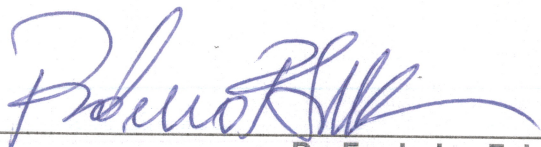
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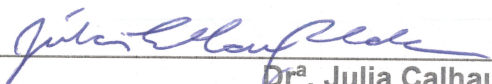
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Aos meus queridos pais, em alegria.

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*in memoriam*

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## Resumo

As vespas achatadas incluídas em *Apenesia* Westwood são cosmopolitas e apresentam alto dimorfismo sexual. As fêmeas são pouco coletadas, sem olhos ou ocelos, sem asas e pequenas, enquanto os machos são alados, robustos, com olhos desenvolvidos e ocelos, e costumam ser maiores do que a fêmea da mesma espécie. Existem 191 espécies descritas, a maioria conhecidas apenas pelo sexo masculino. Além do dimorfismo sexual e da sub-representação das fêmeas, os caracteres que delimitam a *Apenesia* são compartilhados por vários gêneros de *Pristocerinae*, tornando a classificação incerta e dificultando a compreensão da evolução do caráter e da variação entre táxons. Aqui objetivamos 1) testar se *Apenesia* é monofilético; 2) delimitar o gênero cladisticamente com base em dados morfológicos e moleculares (genes COI e 28S); 3) associar machos e fêmeas; e 4) revisar as espécies de *Apenesia*, fornecendo descrições e ilustrações quando necessário. Foram analisados 163 caracteres morfológicos no TNT e a Inferência Bayesiana foi realizada nos dados moleculares concatenados a partir de 1.553 pares de bases de nucleotídeos através de MrBayes. Em ambas as análises foi usada uma espécie de *Bethylinae* para o enraizamento. *Apenesia* foi recuperado como polifilético em todas as análises, composto por 10 linhagens distintas que puderam ser associados a padrões morfológicos. Mapeamos caracteres morfológicos estruturais de fêmeas nas árvores moleculares para esclarecer padrões morfológicos femininos nos grupos e recuperar a evolução morfológica. Concluímos que as fêmeas adicionam um conjunto de características que podem ajudar na delimitação de gêneros. Com base em nossos resultados, alguns atos nomenclaturais precisam ser propostos: 1) dois gêneros de *Pristocerinae* serão sinônimos a dois clados distintos de *Apenesia*; 2) dois táxons deverão ser revalidados em seus *status* genérico; 3) oito novas combinações serão propostas; e 4) seis novos gêneros serão propostos e nomeados. *Apenesia* é agora definido como aquelas vespas chatas tendo machos com o mesossomo giboso, a genitália com parâmero estreito e densamente pilosa e edeago com lobo apical ventral elíptico e coberto de verrugas. As fêmeas de *Apenesia* podem ser distinguidas de outras *Pristocerinae* pela cabeça mais larga que o mesossomo, as antenas muito curtas, mandíbula longa, e a base do clipeo ultrapassando os toruli na frente. Também incluímos uma revisão mundial da *Apenesia* com uma redescrição de todas as espécies conhecidas e a descrição de 21 novas espécies. Finalmente, nossos dados reforçam os problemas para definir *Apenesia* e outros gêneros em *Pristocerinae*.



## Abstract

The flat wasp *Apenesia* Westwood is a worldwide genus with high sexual dimorphism. Females are rare, without eyes or ocelli, wingless and small, whereas males are fully winged, robust, with developed eyes and ocelli, and are larger than the conspecific female. There are 191 species described, which are mostly known only by the male sex. Several nomenclatural and taxonomic problems are observed in *Apenesia*. Besides sexual dimorphism and females' underrepresentation, the characters delimiting *Apenesia* are shared by several *Pristocerinae* genera, making classification uncertain and hampering understanding of character evolution and variation between taxa. Here we aimed 1) to test if *Apenesia* is monophyletic; 2) to delimit the genus cladistically based on morphological and molecular data (COI and 28S genes); 3) to associate males and females; and 4) to review the species of *Apenesia*, providing descriptions and illustrations when necessary. We analyzed 163 morphological characters in TNT. Bayesian Inference was performed on the concatenated molecular data from 1,553 base pairs of nucleotides through MrBayes. In both analyzes we used a species of *Bethylinae* for rooting the tree. *Apenesia* was recovered as polyphyletic with 10 distinct lines associated to morphological patterns. We mapped structural morphological characters from females onto the molecular trees to enlighten female morphological patterns in the groups and to recover morphological evolution. We conclude that females add a set of features that can help genera delimitation. Although historically considered as an easy genus to classify, the structural analyses and phylogenetic inferences report multiple independent lineages within *Apenesia* species, indicating high convergence within *Pristocerinae*. Based on our results, some nomenclatural acts need to be proposed: 1) two *Pristocerinae* genera will be synonymies with *Apenesia* lines; 2) two taxa need to revalidate their generic status; 3) eight new combinations; and 4) six new genera will be nominated. *Apenesia* is now defined as flat wasps having males with the mesoscutum gibbous, the genitalia with paramere narrow and densely pilose and aedeagus with ventral apical lobe elliptical and covered in warts. Females of *Apenesia* can be distinguished from other *Pristocerinae* by having the head wider than the mesosoma, the antennae is short, the mandible is long, and the clypeus surpasses the toruli in the frons. We also provide a worldwide revision of *Apenesia* with a redescription of all known species and the description of 21 new species. Finally, our data reinforce the problems to define *Apenesia* and other genera in *Pristocerinae*.

## **Apresentação**

### *Sobre mim*

Nasci em 05 de junho de 1984, dia mundial do meio ambiente, em São Paulo – São Paulo. Sou a mais velha e única mulher do universo de três filhos dos meus pais, Celio e Regina. Desde criança já demonstrava interesse pelas palavras escritas tendo meus primeiros poemas e contos registrados aos oito anos de idade. Sempre fui um pouco diferente dos meus amigos: gostava de colecionar revistas de divulgação científica, dentre as que meus pais assinavam, como a Globo Ciência, Galileu e Superinteressante enquanto os meus colegas colecionavam histórias em quadrinho e revistas sobre adolescentes. Nas férias escolares, gostava de brincar replicando experiências descritas na coleção “Como a Ciência Funciona” da editora Globo além de brincar muito de “escolinha”. Em paralelo a isso, a paixão por animais dos meus pais, especialmente minha mãe, fez com que desde cedo me despertasse paixão pelo cuidado com os bichos e, mais para frente, com o ambiente onde eles vivem. Aos 12 anos, tive uma professora de Ciências (cujo nome só me recordo o primeiro, Helena) que me apresentou ao mundo biológico e, por conta das suas aulas, passei a esperar pelas aulas de ciências mesmo quando tinha prova. Nesta mesma época, as revistas de divulgação que eu tinha contato começaram a discutir temas como clonagem e a famosa ovelha Dolly além de alimentos transgênicos.

Desde essa época tinha em mente um desejo enorme de trabalhar como jornalista científica, aliando o meu gosto para a escrita e o intrigante mundo científico. Pois muito aconteceu na vida e, por motivos de força maior, a família teve que se mudar para Vitória, Espírito Santo. A época da notícia da mudança coincidiu com o findar do meu Ensino Médio e, ainda em São Paulo, fiz minha inscrição para o vestibular da UFES/2002 para o curso “ Ciências Biológicas”. Em 2001, as Universidades Federais enfrentaram uma longa greve que adiou até mesmo o calendário do vestibular daquele ano que aconteceu, salvo engano, em janeiro de 2002 a primeira fase e logo após o carnaval em fevereiro de 2002 a segunda. Quem me deu a notícia de que eu havia passado no vestibular foi minha grande amiga Juliana Pirola com quem tenho o prazer de dividir muitas histórias e amizade até os dias de hoje, apesar de toda a distância que surgiu. Estagiei desde o ingresso no curso no Laboratório de Sistemática de Bethylidae, onde desenvolvi projetos de iniciação científica com bolsa do CNPq durante a graduação. Durante a graduação tive a oportunidade de participar de eventos na área de Zoologia, publicar trabalhos em

eventos e periódicos. Formei em 2007 como bióloga bacharel e licenciada pelo Centro de Ciências Humanas e Naturais da Universidade Federal do Espírito Santo (CCHN UFES).

Ao final de 2007, fui aprovada no Mestrado em Biologia Animal pela UFES, com início em março de 2008 e término em fevereiro de 2010. Fui aprovada e nomeada no concurso para professores de Biologia do estado do Espírito Santo em 2008 não tendo assumido a função. Em 2009, fui aprovada e nomeada para o cargo de professor do Ensino Básico, Técnico e Tecnológico do Instituto Federal do Espírito Santo, *Campus* Santa Teresa onde leciono componentes curriculares de Zoologia dos Invertebrados, Zoologia Geral, Biologia Celular, Bioética e Legislação do Profissional Biólogo, Estágio III e Introdução à Biologia para os cursos de Agronomia e Licenciatura em Ciências Biológicas. Em 2012, fui aprovada no Doutorado em Biologia Animal na UFES, tendo iniciado as atividades em março de 2012.

Os dois anos e meio iniciais do doutorado foram conturbados visto que meus pais tiveram problemas de saúde e, durante este tempo, além das atividades do doutorado, ainda estava lecionando no Ifes com carga horária real acima das mencionadas em documentos. Apenas em agosto de 2014 minha licença foi concedida e então eu pude me dedicar às atividades de doutorado. Em maio de 2015, meu tio, Celso Carvalho de Alencar, faleceu e em julho do mesmo ano, perdi de maneira inesperada a estagiária, aluna e amiga Leonora Pereira dos Santos. Reflito que o aprendizado incorporado durante o desenvolvimento da tese foi para além da desenvoltura profissional, mas especialmente, do amadurecimento pessoal para priorizar a vida, os encontros e as relações firmadas.

Durante o doutorado pude visitar e trabalhar no NIAES (National Institute of Agro-Environmental Sciences, Japão) através do Pronex#52263010/2011, no MNHN (Museum National d'Histoire Naturelle, França), no MRAC (Musée Royale d'Afrique Centrale, Bélgica) e no MSNG (Museo Civico di Storia Naturale Giacomo Doria, Itália) através do financiamento CNPq#305746/2014-6. Sem dúvidas foram momentos de muito aprendizado e eu certamente os incluo como os melhores do desenvolvimento da tese. Conheci pessoas fantásticas, vivenciei culturas distintas e analisei tipos e exemplares importantíssimos para a conclusão desta tese.

Ao findar da licença do Ifes, casei com o também biólogo e entomólogo Felipe Berthodi Fraga. A seguir, regressei às atividades docentes em Santa Teresa. De lá e, entre idas e vindas a Vitória, encerramos o texto e o submetemos à análise. Seja qual for o parecer, alegre-me ter escolhido a carreira acadêmica a qual pretendo me dedicar até o final da vida, salvo novidades que possam surgir e eu não tenha como prever hoje.

### *Sobre meu encontro com a docência*

Não tenho em mim o discurso de que professor nasce pronto. Para mim, ser professor é escolher uma carreira em que me especializo e me reinvento todo o tempo. Sou, portanto, professora em formação e assim pretendo ser até o fim da vida. Porque conhecimento novo surge a todo instante. Tecnologias também. Se o professor se coloca como mediador de um processo em contínua transformação assim também deve estar.

Não tive muito tempo para pensar no que exatamente eu queria como um objetivo maior, profissionalmente falando. Já havia em mim desejos concretos sobre trabalhar com ciência (vide descrições sobre brincadeiras que gostava) e a curiosidade de que a ciência chegasse até às pessoas (como as preferências por colecionar revistas de divulgação científica, ainda que ingênuas). Desde que me inseri no contexto universitário, agarrei as oportunidades que surgiram com todo potencial que eu tinha. Sei que me dediquei, grande parte, para uma formação profissional acadêmica voltada para pesquisa. No entanto, a real oportunidade do mercado foi a docência, ainda que com brechas para as atividades de pesquisa e extensão.

E sim, foi no Ifes que, ao longo dos sete anos em que ali trabalho, aprendi a amar a profissão e vislumbrar desdobramentos consequentes da formação de pessoas. Em qualquer nível. Trabalho com Ensino Médio, Técnico e Superior. Neste último nível, trabalho com formação de licenciados em Biologia. Os próprios alunos são a engrenagem que preciso para vencer um grande desafio: levar a biologia (ou qualquer aspecto dela) para a vida de cada um, transformando ou potencializando as relações existentes entre homem e ambiente, no sentido mais integrador possível. Certamente não tenho 100% de sucesso, mas tenho sido feliz. Em sete anos de trabalho um de meus orientados já se encontra ingressando no doutorado e outros alunos já estão empregados e/ou cursando graduações, mestrados e doutorados em instituições de renome. Através do sucesso deles é que vislumbro o meu. E é assim que me encontro na docência: na felicidade de saber que há um ciclo no qual o sucesso só existe se o outro também o obtém.

### *Sobre meu encontro com Bethylidae<sup>1</sup>*

Meu ingresso na Biologia tinha mais a ver com a genética e seus desdobramentos do que pela minha relação com qualquer paixão pelos animais. Naquele momento, meus

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<sup>1</sup> família de vespas parasitoides representada por 3090 espécies válidas distribuídas em 100 gêneros alocados em sete subfamílias: Bethylinae, Epyrinae, Scleroderminae, Mesitiinae, Pristocerinae, Lancepyrinae, Holopsenellinae.

anseios profissionais me guiavam para um trabalho engenhoso e muito ambicioso: desejava investigar novas drogas para curas de doenças como o câncer através da engenharia genética.

No entanto, os Bethylidae foram a primeira oportunidade realmente aberta para que eu iniciasse as atividades científicas durante a graduação. Logo como caloura desesperada, acompanhei alguns trabalhos sobre genética humana, animal e vegetal. Percebendo a possibilidade potencial de trabalho, o único professor que realmente abriu as portas foi este que permanece me orientando desde novembro de 2002. Por ele trabalhar com Bethylidae, assim fui apresentada ao grupo com o qual permaneço trabalhando até os dias de hoje.

Bethylidae atualmente são denominadas vespas achatadas, tentativa de nome popular cunhado por Azevedo (2014) para essas vespas de tamanho reduzido, geralmente pretas, achatadas e difíceis de serem reconhecidas pelo público leigo de maneira espontânea. São espécies parasitoides de larvas de Coleoptera e Lepidoptera (Evans, 1978) tendo algumas espécies associadas ao controle de pragas agrícolas e grãos armazenados (Azevedo, 1999). De acordo com Azevedo (1999), *Cephalonomia stephanoderis* Betrem (Vespa-do-Togo) e *Prorops nasuta* Waterston (Vespa-da-Uganda) são espécies afrotropicais de betilídeos que tem sido utilizadas em programas de controle biológico da broca do café (*Hypothenemus hampei* (Ferrari), Scolytidae) na região neotropical. Ao compreender o potencial econômico e ecológico destas vespas foi impossível me desvencilhar da ideia fascinante de que um dia, através delas, o cafezinho servido em todas as casas poderia ter valor agroecológico agregado, diminuindo custos de produção (quem sabe?), melhorando a qualidade de vida não só das pessoas de forma direta, mas também dos rios, lençóis freáticos, florestas, enfim, do ambiente. Pela oportunidade de trabalhar com Bethylidae, vislumbrei oportunidades para trabalhar com controle biológico.

Mas, após o árduo trabalho de identificar a primeira espécie de Bethylidae da minha vida, *Nothepyrus brasiliensis* Evans, descobri o prazer em compreender a diversidade e, mais que isso, em reconhecê-la. E de saber o quanto isto está conectado com o ambiente. O significado real do meu encontro com Bethylidae, na verdade, foi meu encontro com a sistemática biológica. Área vasta e pouco compreendida por muitas pessoas, incluindo muitos professores que tive na graduação. Sou grata por tudo que tenho aprendido com a sistemática: de conhecer espécies a compreender processos. E desejo

que um dia todos possam ser gratos à sistemática também por tudo aquilo que ela nos traz: de conhecimento básico à aplicação prática.

### *Sobre o projeto desta tese*

Esta tese é produto de pelo menos sete anos do início de sua ideia. Durante o mestrado<sup>2</sup>, realizado entre março de 2008 a fevereiro de 2010, estudei as vespas pertencentes a subfamília Epyrinae. Durante este período, revisei muitos gêneros incluídos em Epyrinae que haviam sido negligenciados e não tinham a sua identidade claramente estabelecida sequer para que novos exemplares fossem endereçados a eles.

Dentre os gêneros de Epyrinae negligenciados, analisei as duas únicas espécies de *Neurepyris* Kieffer: *N. tagala* (Ashmead) e *N. rufiventer* Kieffer. Após estudo, conclui que ambas as espécies pertenciam a gêneros diferentes da subfamília Pristocerinae<sup>3</sup> (Alencar & Azevedo, 2011). A espécie-tipo, *N. rufiventer*, foi combinada a *Pristocera* e, devido a regras nomenclaturais de prioridade, *Neurepyris* foi considerado sinônimo de *Pristocera*. A outra espécie, *N. tagala*, foi transferida para *Apenesia*. A espécie agora então denominada *Apenesia tagala* (Ashmead) se assemelhava a algumas espécies de *Apenesia* descritas por Kieffer, Benoît e Terayama cujo hipopígio é bastante peculiar por apresentar área mediana menos esclerotizada e forte concavidade na superfície ventral<sup>4</sup>. Esta característica se destacou e trouxe diversos questionamentos taxonômicos. O principal deles é que, estas espécies, além do hipopígio característico, apresentavam outras condições morfológicas únicas incluindo a genitália com parâmetro muito largo na sua base e cúspide simples, o que as tornava muito distintas das demais espécies de *Apenesia*, inclusive pela ausência da cúspide dividida, considerada por Terayama (1996) como autapomorfia do gênero.

Após o findar do mestrado, meu orientador, intrigado com os questionamentos gerados a partir do estudo de *Apenesia tagala*, iniciou uma revisão de *Apenesia* para compreender melhor o táxon e se *Apenesia* poderia representar mais do que um gênero. Este projeto foi iniciado por ele sem minha participação. No final de 2011 surgiu a

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<sup>2</sup> A dissertação de mestrado versou sobre análise cladística de Epyrini (Alencar & Azevedo, 2013).

Alencar, I.D.C.C. & Azevedo, C.O. (2013) Reclassification of Epyrini (Hymenoptera: Bethyloidea): a tribal approach with commentary on their genera. *Systematic Entomology*, 38, 45–80.

<sup>3</sup> Subfamília caracterizada pelo forte dimorfismo sexual, no qual fêmeas são ápteras e sem ocelos, enquanto os machos são alados com ocelos e olhos desenvolvidos. Os machos apresentam ainda o metanoto com região mediana elevada, que os diferenciam de todos os demais representantes das vespas chatas. Veja figura 26.C do capítulo III, página 243. Alguns gêneros apresentam cópula forética.

<sup>4</sup> Como na ilustração da figura 40.H do capítulo III, página 324.

oportunidade de me preparar para o doutorado e, sob sua supervisão, a proposta de trabalhar com o delineamento de *Apenesia* surgiu quase como continuidade ao trabalho nascido a partir de dados gerados durante a dissertação de mestrado. Antes mesmo do projeto de doutorado ser escrito, muitos levantamentos e estudos já haviam sido realizados pelo orientador desta tese. Isto, sem dúvidas, facilitou o delineamento dos objetivos e metas a serem cumpridas durante o desenvolvimento da tese.

O projeto e a tese propriamente dita representam trabalhos distintos. A proposta inicial consistia em duas linhas de trabalho o que representaria dois capítulos ou dois artigos. A primeira correspondia à validação do gênero *Apenesia* através de ferramentas cladísticas (morfológicas e moleculares) bem como sua delimitação. A segunda correspondia a uma revisão taxonômica mundial das espécies que eram incluídas em *Apenesia* que apresentavam o hipopígio como descrito para *Apenesia tagala*. Nossa hipótese inicial correspondia ao ilustrado abaixo (Fig. 1).

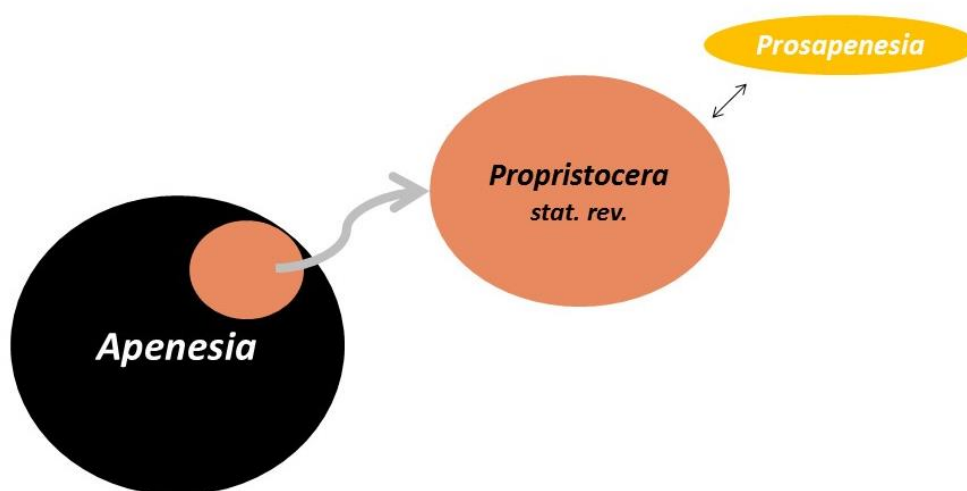


Fig. 1. Hipótese inicial do projeto de doutorado. *Apenesia*, um gênero cosmopolita, representado por um conjunto de 191 espécies em preto. Um subconjunto de espécies das regiões Paleártica, Oriental e Afrotropical que apresentam hipopígio semelhante ao descrito para *Apenesia tagala* corresponderia a um táxon distinto. Entre suas espécies, o subconjunto apresenta espécies-tipo de gêneros sinonimizados a *Apenesia* por Evans (1963). Através de análises prévias, nossa hipótese incluía a revalidação de *Propriostocera*. Devido a semelhanças do hipopígio compartilhadas com *Prosapenesia*, o trabalho previa a investigação desta relação.

Considerando a ideia inicial, durante o primeiro ano de doutorado, aprofundi o levantamento histórico de descrição de *Apenesia*. Construí um banco de dados com as informações disponíveis de descrição através da literatura ou análise direta de cada espécie de *Apenesia* bem como das ilustrações disponíveis em artigos e bancos de

ilustrações<sup>5</sup> e fotografias mantidos pelo laboratório. Sempre que possível, a análise do tipo foi solicitada e preferida para compreender a espécie. No início de 2013, após análise morfoestrutural aprofundada da maioria das espécies, somado às informações já levantadas pelo orientador, foi encontrado um novo panorama para *Apenesia*. A hipótese inicial foi modificada e o novo panorama para compreensão de *Apenesia* até então está ilustrado abaixo (Fig. 2).

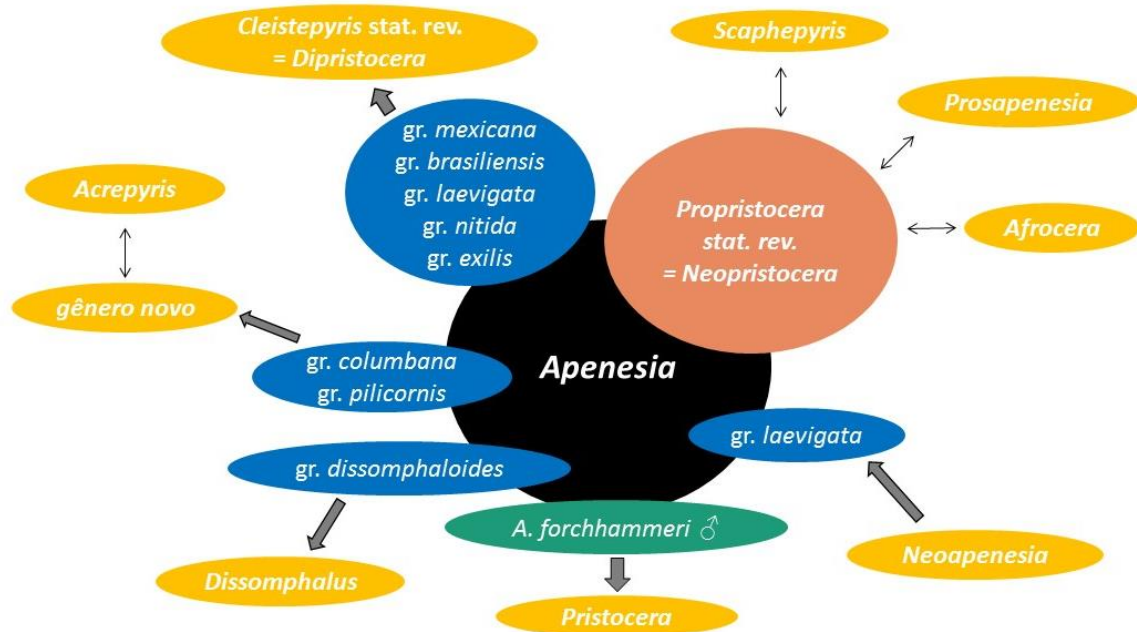


Fig. 2. Hipótese reformulada após primeiro ano de estudo. *Apenesia* permanece como grupo focal, destacado como conjunto em preto. Os grupos de espécies de *Apenesia* propostos por Evans (1963) para a fauna Neotropical estão representados por “gr.” e estão destacados como subconjuntos em azul. As possíveis transferências, combinações e proposições estão indicadas pelas setas cinzas. Os gêneros relacionados a serem profundamente investigados estão destacados em amarelo e conectados por setas de dois sentidos. A espécie *Apenesia forchhammeri* Krombein foi analisada através da ilustração no artigo original (Krombein, 1989) e constatou-se que o tipo da espécie é representante de *Pristocera*. A espécie está destacada em verde.

Após este levantamento, os direcionamentos da tese mudaram. Com a constatação de que era mais provável que *Apenesia* fosse um gênero polifilético e que muitos táxons precisariam ser reorganizados, o capítulo de revisão das espécies com hipopígio de superfície ventral fortemente côncava foi retirado. O objetivo agora era concentrar na

<sup>5</sup> O laboratório tem investido em visitar coleções biológicas do mundo, revisando todos os tipos de Bethyidae, atualizando suas diagnoses e fotografando ou desenhando seus principais caracteres.



delimitação de *Apenesia* e para onde seriam alocadas suas espécies, visto que constatamos proximidade com vários gêneros.

Para garantir que os esforços responderiam a estes anseios, tentamos ao logo de 2013 e 2014 estudar o máximo das espécies de *Apenesia* a partir das séries tipos (holótipos, sítipos e parátipos). Uma grande lacuna de informação contemplava as espécies de *Apenesia* descritas por Terayama que, em grande parte, não apresentavam ilustração ou descrição de estruturas que passamos a considerar importantes e decisivas tais como o hipopígio e a genitália. Como a quantidade de tipos estava concentrada em uma única coleção, realizei uma visita ao NIAES no final de 2013. Nesta visita pude estudar diversos tipos que não haviam sequer sido dissecados. Ao dissecá-los, encontrei novos padrões morfoestruturais para *Apenesia* que em muito diferiam dos padrões potenciais já estabelecidos e ilustrados na figura 2. Reforço que durante esta visita muita informação importante foi levantada e, sem ela, a tese não poderia apresentar os dados que aqui estão.

Durante os anos de 2014 e 2015 conheci as técnicas da biologia molecular e iniciei o processo de extração e sequenciamento de DNA de *Apenesia* e gêneros correlatos. Esta etapa teve apoio fundamental do colega de laboratório, Arturo Martinelli, e da bióloga do NGACB (Núcleo de Genética Aplicada à Conservação da Biodiversidade, UFES), Juliana Justino. Posteriormente, as etapas de análise dos dados moleculares só foram possíveis devido a parceria da orientação da Dra. Cecília Waichert.

De forma concomitante ao levantamento de dados moleculares, as análises morfológicas foram sendo amadurecidas e debatidas, especialmente durante o workshop de *Pristocerinae*, organizado em 2014/2. Todo conselho e conversa informal sobre caracteres e homologias trouxeram reflexões para este trabalho. No final de 2015 visitei as coleções MNHN, MRAC e MSNG onde encerrei as análises morfológicas dos tipos de *Apenesia*. Os resultados obtidos em análises parciais sempre indicaram a polifilia de *Apenesia*. Diversas linhagens foram reveladas tanto através dos dados moleculares quanto dos dados morfológicos. As análises sempre trouxeram reflexão sobre os dados e agrupamentos formados, em um processo de retroalimentação. Cada passo dado nos reconduziu a reinterpretar e reanálises mais aprofundadas de nossos próprios dados.

Somado a isto, as dificuldades de associar os sexos macho-fêmea de um mesmo gênero trouxeram desafios para a compreensão de *Apenesia*. Isto era essencial pois a espécie-tipo de *Apenesia* é representada por uma fêmea. Portanto, compreender *Apenesia* refletia compreender associação ente machos e fêmeas em nível genérico dentro de

Pristocerinae. Constatamos diversos padrões morfoestruturais entre as fêmeas de *Apenesia* registradas a partir de dados de acasalamento e dados de criação. Não era possível prever o que seria diagnóstico para cada linhagem de Pristocerinae uma vez que as fêmeas são crípticas e muito semelhantes entre si. Por este motivo, resolvemos adicionar a análise de mapeamentos dos caracteres das fêmeas para averiguar possíveis padrões de evolução da apteria em *Apenesia* e, conseqüentemente, para Pristocerinae.

Como resultado de todo estudo que foi possível ao longo dos quase cinco anos de doutoramento, apresentamos a hipótese a ser defendida para a tese (Fig. 3), propondo, no mínimo, melhor compreensão de *Apenesia* a partir do que foi proposto por Evans (1963) e que vem sendo seguido por autores como Terayama, Azevedo e Mita e seus respectivos colaboradores.

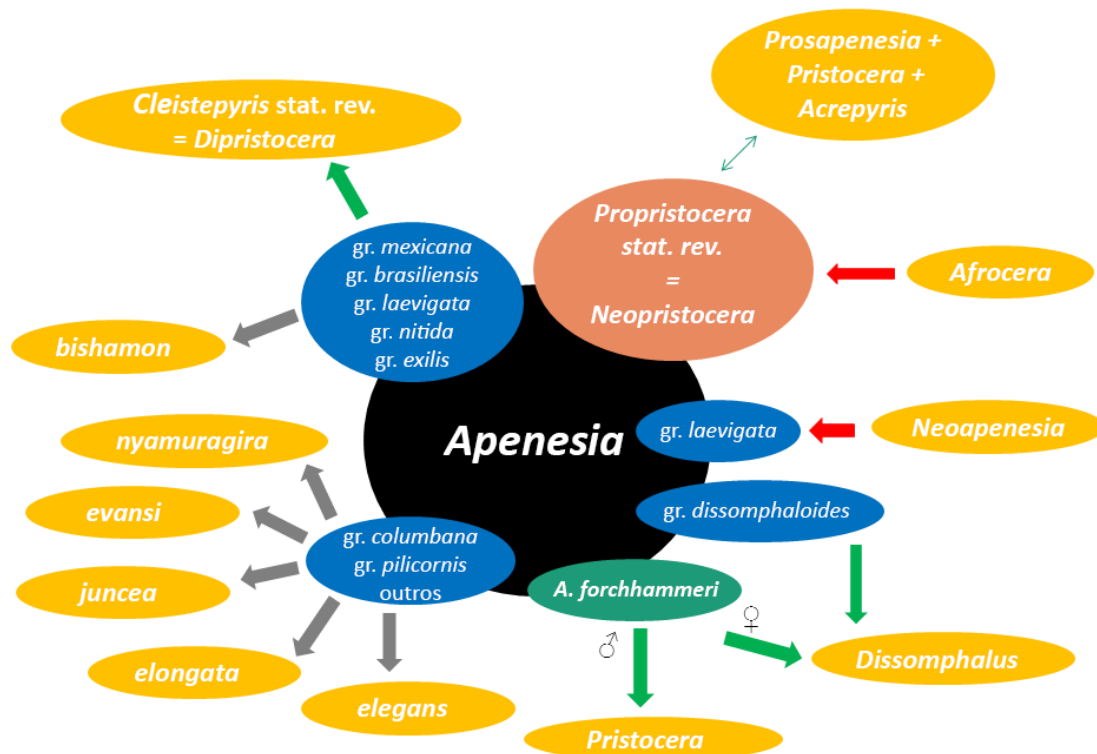


Figura 3. Hipótese a ser defendida por esta tese. O gênero *Apenesia* é redefinido baseado em machos e fêmeas. Dois gêneros, hoje, sinônimos de *Apenesia* terão seu status revalidado. Os grupos de espécies de *Apenesia* não foram recuperados como linhagens e, de maneira fragmentada, formaram subconjuntos aqui nomeados com epítetos específicos de espécies representantes das linhagens obtidas em nossas análises. Os subconjuntos representados por “*bishamon*”, “*nyamuragira*”, “*evansi*”, “*juncea*”, “*elongata*” e “*elegans*” representam táxons a serem descritos e propostos como gêneros novos. As setas cinzas representam combinações a serem realizadas para estes novos táxons. As setas verdes representam combinações a serem realizadas. As setas vermelhas representam sinonímias entre gêneros a serem propostas. A seta bidirecional representa a relação estabelecida com demais gêneros de Pristocerinae.

Tradicionalmente, trabalhos de sistemática apresentam títulos rígidos. Nos últimos anos, temos observado uma maior maleabilidade para caracterizar os problemas taxonômicos e vinculá-los a visões de mundo mais ampla ou mesmo fazer analogias com grandes marcos para sintetizar ideias e despertar o interesse de leitores potenciais.

No tópico anterior, mostramos que a construção da hipótese a ser defendida é complexa e nos surpreendeu muito. O gênero *Apenesia* sempre foi considerado “de taxonomia fácil” mas o estudo aprofundado realizado aqui nos mostrou que seu grau de complexidade estava oculto e sua delimitação se mostrou frágil. A proposta final a ser submetida como artigo, inclui a delimitação de *Apenesia*, a revalidação de dois gêneros até então considerados sinônimos juniores de *Apenesia*, além da descrição de seis gêneros novos. Nesta perspectiva, consideramos os resultados aqui propostos como muitos dados novos lançados ao mesmo tempo e que terão, certamente, grande impacto na compreensão da subfamília *Pristocerinae*. Postos estes motivos, resolvemos associar estas mudanças taxonômicas advindas de um único estudo ao resgatar a história mitológica de Pandora.

Na mitologia grega, Pandora ("a que possui todos os dons") foi a primeira mulher criada por Zeus com o intuito de punir os homens pela ousadia do titã Prometeu em roubar dos céus o segredo do fogo. Prometeu foi condenado a ficar 30.000 anos acorrentado no Monte Cáucaso, tendo seu fígado comido pelo abutre Éton todos os dias. Pandora foi enviada a Epimeteu, irmão de Prometeu, como um presente de Zeus. Pandora recebeu dos deuses, como presente de seu casamento com Epimeteu, uma caixa que nunca deveria ser aberta. Com a proibição de abertura da caixa, Pandora ficou instigada e, tomada pela curiosidade a abriu, liberando todos os males da humanidade: a doença, a guerra, a velhice, a mentira, os roubos, o ódio, etc. Na caixa sobrou apenas a esperança.

A “caixa de Pandora” é uma expressão utilizada para fazer referência a algo que gera curiosidade, mas que ao ser revelado ou estudado extrapola as expectativas, podendo fugir de controle. O estudo sobre *Apenesia* demonstrou que o gênero na verdade corresponde a diversas linhagens escondidas sob este nome, surpreendendo-nos com tamanha diversidade revelada. Acreditamos que as proposições taxonômicas aqui realizadas serão geradoras de diversos outros questionamentos para *Pristocerinae*. Desta forma, ao investigarmos o gênero “*Apenesia*” abrimos uma “caixa” de novas informações para *Pristocerinae* cujas consequências serão reveladas em diversos trabalhos a serem desenvolvidos no futuro.

### *Sobre os capítulos desta tese*

Esta tese apresenta três capítulos (Fig. 4). Os atos nomenclaturais aqui propostos são provisórios e inválidos para o ICZN. O primeiro capítulo apresenta hipótese filogenética de *Pristocerinae*, com ênfase em *Apenesia*, gerada através das análises morfoestruturais e moleculares. Pretendemos submetê-lo ao periódico “*Systematic Entomology*” ([http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1365-3113](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1365-3113)) e, por isto, o texto já se encontra na formatação necessária.

O segundo capítulo propõe a revisão taxonômica mundial das espécies que são incluídas na concepção de *Apenesia* proposta no capítulo 1. Devido ao perfil do trabalho, pretendemos submetê-lo ao periódico “*Zootaxa*” (<http://www.mapress.com/j/zt/>) após a publicação do primeiro capítulo. O texto já se encontra na formatação especificada do referido periódico.

O terceiro capítulo pretende resgatar, reunir e compilar toda a informação existente em *Pristocerinae*, considerando, inclusive, os resultados dos capítulos 1 e 2. Este último capítulo representa o estado da arte de *Pristocerinae* após análise do gênero *Apenesia* e, no contexto desta tese, atualiza e disponibiliza dados para futuros questionamentos taxonômicos, completando a abertura da “caixa de Pandora” de *Pristocerinae*. Este capítulo faz parte do projeto “Atlas dos gêneros de Bethyloidea (Hymenoptera, Chrysidoidea)” e tem intenção de ser publicado como parte de um livro que objetiva organizar e atualizar o conhecimento a respeito dos gêneros de Bethyloidea em escala global, através da construção de um manual ilustrado que pretende figurar entre as principais referências de Bethyloidea. O livro não tem data estabelecida para publicação, mas se dará posteriormente à publicação do capítulo 2 e, por isso, estará aberto a atualizações. A intenção é publicá-lo também na “*Zootaxa*” e, por isso, o texto já se encontra na formatação solicitada.

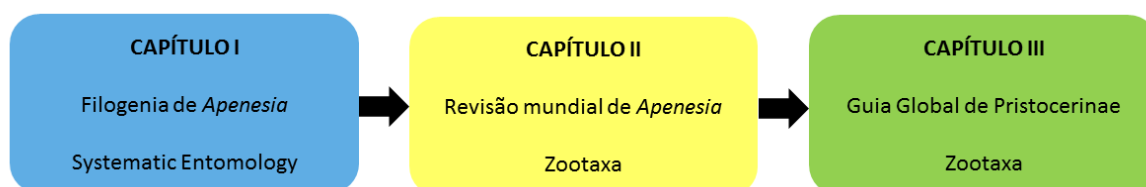


Fig. 4. Fluxograma e resumo dos capítulos que compõem esta tese.

Pelo fato do capítulo 3 fazer parte de um livro, não apresento aqui a parte de Material e Métodos e a literatura citada diz respeito a parte relacionada ao capítulo, pois estas sessões fazem parte de todo o livro e possuem juntas mais de 200 páginas. Além

disto, as figuras deste texto estão enumeradas já na formatação e ordem de entrada do livro e, por isso, a primeira prancha não inicia na “figura 1”.

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# CAPÍTULO I

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<http://www.umsabadoqualquer.com/>

# Opening the Pandora box of *Pristocerinae*:

molecular and morphological phylogenies of *Apenesia* (Hymenoptera, Bethyridae)  
reveal several hidden genera

## Abstract

The flat wasp *Apenesia* Westwood is one of the largest genera in *Pristocerinae* with 191 species worldwide. The lack of a single diagnostic morphological character has resulted in many distinct ground plans within *Apenesia*. Some authors have suggested *Apenesia* is polyphyletic. Here we aimed to investigate and delimit the genus based on morphological and molecular data. We analyzed 163 morphological characters on TNT using “Traditional Search”. Bayesian and Maximum Likelihood Inferences were performed on 1,553 concatenated nucleotide base pairs from COI and 28S sequences. All analyses were rooted with *Bethylinae* species. *Apenesia* was recovered as polyphyletic in all analyses. We observed 10 different lineages with species of *Apenesia* spread throughout the tree. *Neoapenesia* was recovered as paraphyletic and sister group to a partial *laevigata* species-group of *Apenesia*. We mapped female morphological characters onto the molecular tree to enlight patterns and to recover morphological evolution. We determined a set of features that can aid genera delimitation. Based on our analyses, we propose six new genera; revalidation of two genera, eight combinations and two species names; four new generic synonymies and one at the species level; 164 new combinations and one new name are proposed to avoid homonymy. *Apenesia* is now defined as flat wasps having males with the mesoscutum gibbous, the genitalia with paramere narrow and densely hairy and aedeagus with ventral apical lobe elliptical and covered in warts. Females of *Apenesia* can be distinguished from other *Pristocerinae* by having the head wider than the mesosoma, the antenna short, the mandible long, and the clypeus surpassing the toruli in the frons. This analysis reinforces the difficulties in defining *Apenesia* and other *Pristocerinae* genera.

**Key words.** Integrative taxonomy, *Afrocera*, *Tiphiidae*, male-female association, high sexual dimorphism, aptery evolution.

## Introduction

Pristocerinae are the most diverse subfamily of flat wasps (Bethyridae), containing 21 genera (see Terayama 1996; Várkonyi & Polaszek 2007; Zamprogno & Azevedo 2014, Gobbi & Azevedo 2016) and 1,017 species distributed from the tropics to the temperate regions of the world. Pristocerine species are remarkable because of a strong sexual dimorphism with males that are robust, winged and with ocelli and eyes developed, whereas females are delicate, wingless, with eyes reduced to few facets or absent and without ocelli (Ramos *et al.* 2010).

Sex associations at specific and generic levels are hampered by the acute morphological differentiation (Lanes & Azevedo 2007). Moreover, these apterous females are rarely collected in the commonly used flight interception and ground-level traps, resulting in poor collection sampling of females. Therefore, taxonomic studies and classification of Pristocerinae are mostly based on males (Evans 1978). Because females of Pristocerinae are known as parasitoids of coleopterous larvae (Terayama 2006) that live in cryptic habitats such as soil, litter, wood and seeds (Evans 1964), the wingless condition in females is probably an adaptation to live in this kind of habitat (Azevedo 1999d). Phoretic copulation has been reported for two genera of Pristocerinae, where the two sexes can be caught *in copula* in flight interception traps. Capture of these male-female pairs along with molecular tools are essential for trustful sex association (Azevedo *et al.* 2016).

*Apenesia* Westwood, 1874 is one of the largest genera in Pristocerinae. It was originally described based on two species known only from females. Despite the difficulty in proposing male-female associations, Evans (1963) combined four genera (with unknown females) with *Apenesia*: *Propristocera* Kieffer, 1905, *Cleistepyris* Kieffer, 1910, *Dipristocera* Kieffer, 1914 and *Neopristocera* Benoit, 1957. Evans (1963) justified the synonymy with the overlapped diagnostic characteristics between these taxa. Furthermore, he reared an undescribed bethylid couple from *Pantorhytes plutos* Oberthür (Curculionidae) larvae, and considered the female similar in characteristics to *Apenesia amazonica* Westwood, the type species of *Apenesia*. He finally proposed that *Apenesia* houses residual Pristocerinae females that do not fit the standards of other genera in the subfamily.

*Apenesia* has 191 species described worldwide. Only seven species are known from both sexes, whereas 29 species are known from females only. The few species described based on females generally consist on one or two exemplars. Even so, *Apenesia*



is one of the most studied genera within *Pristocerinae*. In the last decades, studies on the genus were mainly focused in the Neotropical fauna (e.g. Corrêa & Azevedo 2001; Leal & Azevedo 2001; Waichert & Azevedo 2003; Lanes & Azevedo 2004; Corrêa & Azevedo 2006; Ramos & Azevedo 2009; Ramos *et al.* 2010) and few studies were done on the Palaearctic (e.g. Terayama 2006) and Oriental regions (e.g. Azevedo & Waichert 2006). Phenotypic plasticity runs through the diagnostic features of several *Pristocerinae* genera (Evans 1964) and *Apenesia* plays a central role by having most of its diagnostic characters overlapping other genera's boundary features.

Terayama (1996) reconstructed the phylogenetic relationships of *Pristocerinae* based on morphological characters. He suggested that the genital cuspis split into ventral and dorsal arms is autapomorphic in *Apenesia*. However, several species of *Apenesia* have been described as having a simple cuspis (e.g. *Apenesia tagala* Ashmead and *Apenesia triloba* (Benoit)). The species with simple cuspis also present many other particular features such as triangular clypeus and hypopygium with ventral surface strongly concave, which disagree with diagnostic characters for the genus. The placement and relationships of *Apenesia* within *Pristocerinae* were poorly investigated by Terayama (1996), where *Apenesia* representatives we sampled only from the Palaearctic and Oriental regions . Later, Zamprogno & Azevedo (2014) pointed out to the polyphyly of *Apenesia* while cladistically investigating the generic boundaries of *Pristocera* Klug, 1808. Evans (1963) illustrated what he believed would be the intra- and intergeneric relationships of *Apenesia* through a dendrogram. In this diagram, he clearly demonstrated his idea that some species-groups of *Apenesia* would have originated other genera of *Pristocerinae*, such as *Pristocera* (which included *Acrepyris* Kieffer, 1905 as a subgenus in that time), *Dissomphalus* Ashmead, 1893 and *Pseudisobrachium* Kieffer, 1904. Nonetheless, an accurate phylogenetic approach to delimit *Apenesia* is still lacking despite the potential use of this genus for management of agricultural pests (Azevedo & Waichert 2006).

Recently, there has been an increased effort to study the worldwide flat wasp fauna and revision of previously described types. The outcomes of these studies suggest that *Apenesia* genus is poorly delimited. Beyond, there are many distinct ground plans within *Apenesia* that should be investigated. For instance, male genital characteristics have been widely used as main characteristics for species identification in Bethyridae. The lack of genitalia descriptions for delimiting Bethyridae species can lead to conflicts of interpretation and misidentification of species (see Lanes & Azevedo 2004; Alencar &

Azevedo 2008; Colombo & Azevedo 2016) and genus (see Alencar & Azevedo 2011; Azevedo & Alencar 2009). Finally, historically used taxonomic characters, including male genitalia and female morphological characters, have never been studied in light of molecular phylogenetic analyses. Uncovering how these characters evolved in *Pristocerinae* might solve gaps in our understanding of flat wasps, sex associations, species and generic boundaries, and natural history. Here we propose 1) to delimit the generic boundaries of *Apenesia sensu* Evans (1963) through phylogenetic analyses based on molecular and morphological characters, 2) to test the *Apenesia* sex associations proposed by Evans (1963), and 3) to reconstruct morphological character evolution to enlighten both taxonomy and aptery in *Pristocerinae* with particular emphasis in *Apenesia*.

## Material and methods

### *Material examined*

We studied almost all *Apenesia* species by directly observation during collections visits or loans (Table 1). The material was provided by the following institutions (curators at the time material was accessed):

ACC – Instituto de Ecología y Sistemática de Cuba (R. N. Aguilla)

AEIC – American Entomological Institute, USA (D. Wahl)

AMNH – American Museum of Natural History, New York, U.S.A. (J. M. Carpenter)

BMNH – Natural History Museum, United Kingdom (K. Goodger)

BPBM – Bernice Pauahi Bishop Museum, USA (A. Ramsdale)

CASC – California Academy of Sciences, San Francisco, U.S.A. (R. Zuparko)

CMNH – Carnegie Museum of Natural History (J. Ashe)

CNCI – Canadian National Collection of Insects, Canada (J. Huber)

CUIC – Cornell University, USA (E. R. Hoebecke)

CZMA – Coleção Zoológica do Maranhão, São Luis, Brazil (F. Limeira-de-Oliveira)

DZUP – Universidade Federal do Paraná, Brazil (K. Zanol)

FIML – Fundación y Instituto Miguel Lillo, Argentina (V. Colomo)

HNHM – Magyar Természettudományi Múzeum, Budapest, Hungary (S. Csösz)

IAVH – Instituto Alexander von Humboldt, Colombia (M. Ospina)

INHS – Illinois Natural History Survey, USA (C. Favret)

INPA – Instituto Nacional de Pesquisas da Amazônia, Brazil (J. A. Rafael)

ISAM – Iziko South African Museum, Cape Town, South Africa (S. van Noort)

LACM – Los Angeles County Museum of Natural History, USA (B. Brown)

MACN – Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Argentina (A. R. Alsina)

MCZH – Museum of Comparative Zoology, USA (S. Cover & P.D. Perkins)

MCSN/MSNG – Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy (M. Tavano)

MNHN – Museum National d’Histoire Naturelle, Paris, France (A. Touret-Alby)

MPEG – Museu Paraense Emílio Goeldi, Brazil (A. Harada)

MRAC – Musée Royale d’Afrique Centrale, Tervuren, Belgium (S. Hanot)

NIAES – National Institute of Agro-Environmental Sciences, Tsukuba, Japan (S. Yoshimatsu)

NHMW - Naturhistorisches Museum Wien, Vienna, Austria (D. Zimmermann)

NMKE – National Museum of Kenya, Nairobi, Kenya (R. Copeland)

OXUM – Oxford University Museum of Natural History (C. O’Toole and J. E. Hogan)

PMAE – Royal Alberta Museum, Alberta, Canada (M. Buck)

QMSB – Queensland Museum South Bank, South Brisbane, Australia (C. Burwell)

QSBG – Queen Sirikit Botanical Garden, Mae Rim, Chiang Mai, Thailand (W. Srisuka)

RMNH – Nationaal Natuurhistorische Museum, Holland (C. van Achterberg)

SEMC – Snow Entomological Collection, The University of Kansas, USA (Z. Falin)

UFES – Universidade Federal do Espírito Santo, Vitória, Brazil (C. O. Azevedo)

UQIC – The University of Queensland Insect Collection, Brisbane, Australia (S. Wright)

USNM – National Museum of Natural History, USA (T. Schultz, D. Furth)

YNU – Yeungnam University, Gyeongsan(-si), South Korea (J. W. Lee)

ZMHB – Museum für Naturkunde, Berlin, Germany (F. Koch)

### *Terminology and treatment*

Terminology for general body structures, measurements and indices follows Evans (1964), Azevedo (1999a), Lanes & Azevedo (2008), Alencar & Azevedo (2013), Zamprogno & Azevedo (2014) and Kawada *et al.* (2015). Wing morphology nomenclature follows Ramos & Azevedo (2012, 2016). Integument sculpture

terminology follows Harris (1979), except for the term coriaceous, which follows Eady (1968).

Taxonomic characters related to the male genitalia and hypopygium were examined after their dissection. Each dissected genitalia e hypopygium were placed in a glass vial containing 10% potassium hydroxide solution for 24 hours for diaphanization. Once clarified, the structures were submitted to a 25% acetic acid solution to neutralize potassium hydroxide action. After this step, the genitalia were transferred into a microvial filled with glycerin for preservation. Each microvial was pinned together with the specimens for morphological analyses and illustration. Genital and hypopygeal characters were examined under a Leica DM2500 light microscope.

### *Terminal taxa*

To test the hypothesis of *Apenesia* monophyly, we treated Pristocerinae as the ingroup in both morphological and molecular phylogenetic analyses. Although previous phylogenetic trees of Bethyridae establish the monophyly of Pristocerinae (Sorg 1988; Terayama 1996; Carpenter 1999; Carr *et al.* 2010), they disagree on the placement of *Apenesia* within the subfamily (Terayama 1996; Zamprogno & Azevedo 2014). Our taxon sampling heavily focused on *Apenesia* morphological and geographical diversity, including representatives from a broad range of zoogeographical regions, males, females and different species-group representatives (e.g., *brasiliensis*, *columbana*, *dissomphaloides*, *exilis*, *laevigata*, *mexicana*, *nitida* and *pilicornis*). As outgroup we selected species of Bethylinae, Epyrinae and Scleroderminae based on the topologies proposed by Sorg (1988), Evans (1964), Terayama (2003, 2006), Azevedo & Lanes (2009) and Carr *et al.* (2010) (Tables 2, 3).

**Morphological data sampling.** Our morphological analyses were performed from the selection of 61 terminal taxa which represent the most morphological diversity possible (Table 2). We included representatives of type species and holotype specimens whenever possible for potential nomenclatural actions. We included 36 species of *Apenesia* and 23 species representing other 13 genera of Pristocerinae: *Acrepyris* Kieffer, 1905; *Afrocera* Benoît, 1983; *Caloapenesia* Terayama, 1995; *Calobrachium* Gobbi & Azevedo 2016; *Dissomphalus* Ashmead, 1893; *Foenobethylus* Kieffer, 1913; *Neoapenesia* Terayama, 1995; *Parascleroderma* Kieffer, 1904; *Pristocera* Klug, 1808; *Prosapenesia* Kieffer, 1910; *Protisobrachium* Benoît, 1957; *Pseudisobrachium* Kieffer, 1904 and *Trichiscus* Benoît, 1956. Only male specimens were included in this analysis

because high levels of sexual dimorphism characterize Pristocerinae and association between sexes is uncertain at both species and genus levels (Table 2).

**Molecular data sampling.** Our molecular analyses were performed from the selection of 58 terminal taxa. We sampled specimens of *Apenesia* and Pristocerinae preserved in ethanol 100% and stored at -4° C. We included 25 species of *Apenesia* and 27 species representing ten genera of Pristocerinae: *Acrepyris*, *Caloapenesia*, *Dissomphalus*, *Foenobethylus*, *Neoapenesia*, *Parascleroderma*, *Pristocera*, *Protisobrachium*, *Pseudisobrachium* and *Trichiscus*.

All terminal taxa information for molecular data are listed in Table 3.

#### *Morphological data*

Two morphological matrices were coded for this study. The male morphological data (characters and states) were mainly taken from previous studies (Evans 1961, 1963, 1964; Terayama 1996; Lanes & Azevedo 2004; Corrêa & Azevedo 2006; Lanes & Azevedo 2008; Ramos & Azevedo 2009; Ramos *et al.* 2010; Alencar & Azevedo 2013; Zamprogno & Azevedo 2014; Gobbi & Azevedo 2016). One hundred sixty-three adult characters were coded using Leica M80 microscopes and LED light sources (Appendix 1). We coded the character states through direct analyses of the specimens.

The second morphological matrix was coded based on female Pristocerinae representatives (listed below). The characters were chosen aiming to seek female's diagnostic characters and to enlighten evolution of aptery in Pristocerinae with particular emphasis in *Apenesia*. The data were obtained from examination of several pinned and wet-preserved specimens, photographs and from the literature. Any genera belonging to Pristocerinae with biological data, phoretic copulation report or molecular-based male-female association were included in this matrix.

All character states were treated as unordered and not polarized in the morphological matrices. Inapplicable and unknown characters were represented as '-'. Data were included in two matrices (Tables 4 and 5) using the program DELTA Editor (DEscription Language TAXonomy) by Dallwitz (1980) and Dallwitz *et al.* (1999). We used DELTA to generate a nexus file from the matrix. Trees were manipulated using WINCLADA by Nixon (2000).

### *DNA extraction and molecular protocols*

DNA was extracted from muscle tissues of the last metasomal segments using a NucleoSpin® Tissue (Macherey-Nagel) DNA extraction kit, diluting the sample on average 30µl instead of the 200µl recommended by the protocol..

We used one mitochondrial and one nuclear gene, respectively, cytochrome c oxidase subunit I (COI) and ribosomal subunit 28S. The amplification of these markers was performed using a 50µl polymerase chain reaction (PCR) in a ABI Veriti® thermocycler. Each PCR reaction included 2µl of extracted DNA, 5µl of buffer solution, 2.5µl MgCl<sub>2</sub>, 0.4µl dNTP, 0.4µl of each primer and 0.125µM Platinum® Taq DNA Polimerase (Invitrogen, Inc.). The total volume of DNA stock was 25µl. The adopted profile followed three steps: (1) an initial step of denaturation of double-stranded DNA at 95°C for 3 minutes; (2) 43 cycles of 95°C for 45 seconds (denaturation), 47°C in COI and 55°C in 28S for 45 seconds (annealing), 72°C for 45 seconds (elongation); (3) a final period at 72°C for 5 minutes. For COI amplification (~630bp) we used the reverse and forward universal primers primers HCO2198 (5'-GGT CAA CAA ATC ATA AAG ATA TTT GG-3') and LCO2198 (5'-TAA ACTT CAG GGT GAC CAA AAA ATCA-3') described by Folmer *et al.* (1994). For 28S amplification (~680bp) we used the forward primer F2 (5'-CGT GTT GCT TGA TAG TGC AGC-3') described by Belshaw & Quicke (1997) and the reverse primer D3 (5'-TAG TTC ACC ATC TTT CGG GTC-3') described by Mardulyn & Whitfield (1999).

Successfully amplified DNA fragments were purified with the ExoSAP-IT® (USB Corporation) enzyme purification protocol kit. Sequences were generated in MACROGEN Inc. (Seoul, Korea) (<http://dna.macrogen.com>). Only the sequence of the sense strand DNA was generated using the forward primers. The identity of each sequence was confirmed by using BLAST, comparing against the GenBank nucleotide databaste (Altschul *et al.* 1997).

The COI resulting sequences were aligned by the ClustalW aligner in Geneious 7.0.1 (<http://www.geneious.com>, Kearse *et al.* 2012) and subsequently refined manually for quality. The 28S resulting sequences were aligned by the MAFFT (Kato, 2013). A molecular concatenated matrix was produced resulting in 1,553 nucleotide base pairs.

### *Phylogenetic analyses*

**Morphological matrix.** The searches for the most parsimonious trees were carried out with the software TNT ver. 1.1 (Goloboff *et al.* 2008) for the male morphological matrix. Characters were treated under two weighting schemes: equal weights and implied weights (Goloboff 1993, Goloboff *et al.* 2008). We used Traditional Search algorithms with parameter sets as follows: space for 10,000 trees in memory; Wagner trees; random seed 5; 1,000 replications; TBR algorithm; 100 trees save per replication; other parameter as in default mode; the tree was rooted in *Eupsenella insulana* Gordh & Harris, 1996. This procedure was repeated with trees from RAM. For implied weighting we used a TNT script (setk.run) written by Salvador Arias to calculate the appropriate value for the constant k (according to Goloboff *et al.* 2008). The script returned a value of  $k = 12.392578$  for our data set, which was used for subsequent analyses. Branch support was investigated using symmetric resampling (Goloboff *et al.* 2003). The Symmetric Resampling (SR) analyses were run in TNT with the traditional search (default parameters) and 1,000 replications.

The morphological cladograms recovered with TNT were manipulated and edited with Winclada ver. 1.00.08 (Nixon 1999–2002). Only unambiguous changes were optimized as fast (ACCTRAN) on the trees except character 11, which was optimized as slow (DELTRAN) based on the assumption of maxillary palpi number reduction in Bethylidae (Evans 1964).

**Molecular matrix.** We implemented both Maximum Likelihood (ML) and Bayesian inference (BI) approaches to reconstruct the molecular topology. Gene trees were reconstructed through BI to check for topological incongruence. The optimal partition strategy and models of molecular evolution for the data were determined in PartitionFinder 1.01 (Lanfear *et al.* 2012). We set SYM + I + G as the model for the nuclear marker, whereas the mitochondrial marker was partitioned by codon and set as follows: codon 1 as SYM + I + G model; codon 2 as K81uf + I + G model; and codon 3 as HKY + I + G model.

We carried out BI on the concatenated matrix. The BI was performed in MrBayes (Ronquist & Huelsenbeck 2003) with four Bayesian Markov chain Monte Carlo chains running simultaneously for a total of 10 million generations, with sampling every 1,000 generations. Trace plots and effective sample size (ESS) were examined in TRACER v. 1.5 to determine MCMC mixing and convergence. Trees from the first 25% of the samples were removed as burn-in. A majority-rule consensus tree was computed with



posterior probabilities for each node. ML analyses were conducted with RAxML through the Cipres Science Gateway service (Miller *et al.* 2010, <https://www.phylo.org/>) under the model GTRGAMMA. We performed 1,000 bootstrap replications to assess node supports. Phylogenetic tree viewing and editing were performed in FigTree v1.0.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

#### *Female character reconstruction analyses*

We conducted a morphological study to identify potential characters for circumscribing *Pristocerinae* genera using female characters. A final set of twelve discrete characters was selected for ancestral character state reconstruction analyses. Our sample represents eight *Pristocerinae* genera of the 21 known, and belonging to 24 species (Table 6). We mapped the morphological characters onto the molecular phylogeny using a maximum likelihood approach. The ML approach was implemented using the rayDISC command in the package corHMM developed by Beaulieu *et al.* (2013) and available through CRAN (<http://cran.us.r-project.org>) executed in RStudio Version 0.98.1103 (R Core Team 2015).

Three models of character evolution were evaluated under the ML method: equal rates (ER), symmetrical (SYM) and all rates different (ARD). A likelihood-ratio test was performed to compare the fit of each model and select among these varying models of character evolution. The alternative hypothesis of better fit to the more complex model was rejected with P-value under 0.05.

The following discrete characters and states included are: (1) head width (0 wider than mesosoma/ 1 narrower than mesosoma); (2) antenna size (0 short, never surpassing head length/ 1 long, always surpassing head length); (3) posterior margin of clypeus (0 surpassing toruli on frons/ 1 never surpassing toruli on frons); (4) Mesopleuron border in dorsal view (0 keeled/ 1 convex); (5) mesopleuron, dorsal view (0 very large/ 1 narrow and badly visible); (6) mesopleuron, shape (0 callus-like/ 1 elongate); (7) petiolar body expansion (0 present/ 1 absent); (8) antero-lateral fovea on metapectal-propodeal complex (0 present/ 1 absent); (9) mesonotum size (0 short/ 1 long); (10) anterior region of metapectal-propodeal complex width (0 wide/ 1 narrow); (11) petiole size (0 long/ 1 short); and (12) anterior margin of mesonotum (0 concave/ 1 straight).



### *Illustrations*

Specimens were photographed under a Leica Z16 APO stereomicroscope fit with a camera adaptor coupled to a Leica DFC 295 video camera (Leica Microsystems, Switzerland). The software Leica Application Suite V3. 6.0 and Microsystems by Leica (Switzerland) Limited (LAS) were used to capture individual focal planes. We used a scalable and modular LED illumination dome for microscopic scientific photography as described by Kawada & Buffington (2016). Helicon Focus (HeliconSoft version 4.2.9) software was responsible for stacking the layers into a single combined-focus image using the following parameters: method C and full resolution.

The hypopygium and genitalia drawings were performed using a camera lucida attached to an Olympus CH30 or Leica DM 2500 compound microscope. The hypopygium was compressed with a cover slip for illustration.

For micrographs, the selected specimens were dehydrated in ascending ethanol series (30%-100%). Each specimen was critical point dried (Autosandri-815, Tousimis) using liquid CO<sub>2</sub>. After that, dissected parts were prepared and mounted on stubs using a double-sided carbon tape, then sputtered with gold (Desk V, Denton Vacuum) and finally observed with a scanning electron microscope (JEOL, JEM6610 LV) at Laboratório de Ultraestrutura Celular Carlos Alberto Redins in the Health and Science Center (LUCCAR/CCS-UFES).

All illustrations and plates were edited and vectorized using the adjustments (e.g., levels, shadows/highlights), tools (e.g., healing brush, clone stamp) and filters (e.g., unsharp mask), respectively using image edition software.

## **Results**

### *Phylogenetic analyses*

Molecular and morphological topologies recovered a monophyletic Pristocerinae (Figs. 1-3) and confirmed the polyphyly of *Apenesia*. Both approaches presented similar species composition in the lineages formed by species of *Apenesia*; the phylogenetic relationships among them, however, varied mostly based on the level of resolution achieved, except for those species not included in molecular analyses (lineages C and D, Figs. 1-2). Moreover, the ML and BI trees were congruent. In all phylogenies, the *Apenesia* terminal taxa clustered within 10 different lineage (A-G) spread through the ingroup with good statistical supports (symmetric resampling, SR>60; bootstrap, B> 60

and posterior probability,  $pp \geq 0.80$ ). Finally, the topologies held the monophyly of *Protisobrachium*, *Trichiscus*, *Acrepyris*, and *Pristocera*, the last two supporting Terayama (1996) and Zamprogno & Azevedo (2014), respectively.

The phylogenetic reconstruction of the 163 morphological male characters returned 496 equally parsimonious cladograms with 664 steps under equal weights. The consistency index (CI) was 0.30 and the retention index (RI) was 0.77. The strict consensus tree had 22 nodes collapsed (Fig. 1). The implied weighting returned only one tree that agrees mostly in topology with the cladogram recovered under equal weights (Fig. 2, Appendix 3 with a hypothesis to the character distribution). Although the subfamilial node is supported (SR = 100), the generic relationships remain unclear for most of our outcome. All features we report here are first highlighted through phylogenetic analysis to *Apenesia* and *Pristocerinae*.

The morphological male synapomorphies that support *Pristocerinae* are: clypeal medial lobe semicircular (15:2); occipital carina present (26:1); anterior fovea of mesopleura present (43:0); mesopleural fovea present (44:0); esternalus present (51:0); median region of metanotum elevated (56:0); metapostnotal texture rugulose (67:0); propodeal disc area polished (68:1); forefemur not enlarged (71:1); anterior trochanter conical and long (72:0); forewing with r-rs & RS1 joint somewhat continuous (83:1); forewing with 3Cu vein spectral (89:1); forewing with 2A vein absent (92:1); medial flexion line divided (99:0); one paramere present (125:0); paramere narrow (127:1); aedeagus dorsal cover present (155:0); and basal ring of genitalia incomplete (162:1).

We named *Apenesia* lineages with letters (A to G) on the topology recovered and will be using this nomenclature from this point on. Lineage A (SR = 100; bootstrap = 100,  $pp = 1.00$ ) clusters some species of *Apenesia* from the Neotropical and Oriental regions and formed a polytomy with species of *Neoapenesia*. This lineage is supported by the synapomorphies: four maxillary palpi (11:2); basiparamere with apical and membranous projection (138:1) (Fig. 8.D-E) and cuspis apex developed dorsad (141:1) (Fig. 8.C) besides other several homoplastic features.

Lineage B is represented by *dissomphaloides* species-group belonging to *Apenesia*. They nested into the lineage composed by species of *Dissomphalus* (RS = 57, B = 78,  $pp = 1.00$ ). The *dissomphaloides* species-group and representatives of *Dissomphalus* included in the analysis share the homoplasies: body robust (1:0); mandible with three teeth (10:2); pronotal disc short (29:0); mesopleural anterior sulcus

trabeculate (42:1); radial flexion line long (97:1); and sinuous (98:1) and metasoma oval (106:1).

*Apenesia nyamuragira* Benoît and *Ap. bishamon* Terayama did not nest within any lineage. They seem to represent two distinct lineages in Pristocerinae due to the morphological pattern. They were named as lineage C and D, respectively, for discussion purposes, and were not included in the molecular phylogenetic hypothesis because DNA amplification failed in these specimens. *Apenesia bishamon* and *Ap. nyamuragira* differ from all other Pristocerinae by various autapomorphies. *Apenesia bishamon* has the mesopleuron with posterior fovea (Fig. 12.C), which is usually present in Epyrinae only and *Ap. nyamuragira* presents the apical margin of hypopygium deeply concave and the lateral and median stalks short (Fig. 11.D).

Lineage E (RS = 69, B = 97, pp = 1.00) is mostly composed by Neotropical species, which are specimen-abundant in South American collections. The phylogenetic relationships within the lineage are obscured by the polytomy recovered in equal analysis (Fig. 1). This lineage is supported by the synapomorphy “shape of paramere narrow basally and extended apically” (127:3) (Fig. 9.K-L) and other several homoplasies. Lineage E differs in ML and BI approaches by the resolution of phylogenetic relationships. In ML and BI, lineage E is sister to (*Parascleroderma* + *Foenobethylus*) (B = 27, pp = 0.77).

Lineage F (RS = 99, B = 80, pp = 0.83) represents the largest body-sized Neotropical species of Pristocerinae. In implicit analysis, lineage F is sister to lineage G (Fig. 2), in equal weighting it breaks into a polytomy (Fig. 1). Finally, BI and ML recover lineage F as sister to a lineage that includes lineages A, E, H, *Parascleroderma* and *Foenobethylus* (Fig. 3). Only homoplastic characters are reported for F lineage such as: mandible with upper tooth curved posterad (8:1); antennal flagellomere narrow (21:1); ocellar triangle close to the vertex (25:0); mesopleural anterior sulcus absent (41:1); mesopleural fovea absent (44:1); metanotal trough narrow (61:1); radial flexion line present (96:1); cubital-medial flexion line absent (103:1); hypopygium with apex side distant to lateral stalk (120:0); paramere thick (127:0); and with apex beveled (128:0); basivolsella rounded (153:1); aedeagus without dorsal cover (155:1) and basal ring incomplete and ventral (163:0) (Fig. 8. I).

Some species of *Apenesia* from the Oriental region formed lineage G (RS = 95, B = 100, PP = 1.00, Figs. 1-3). This lineage is characterized by the synapomorphic characteristic of hypopygium plate thick with inner membrane with sclerotized borders

(109:0), which is unique among the Pristocerinae lineages. Lineage G is placed in polytomy with many lineages of Pristocerinae (parsimony, Fig. 1), sister to lineage F (Fig. 2) or it is one of the lineages to first branch off (BI, pp = 94, Fig. 3).

Lineage H is similar in all analyses, even with low support (RS = 56, B = 24, pp = 0.68). It is formed by the lineages I (RS = 100, B = 100, pp = 1.00) and J (RS = 100, B = 90, pp = 1.00). In BI and ML topologies lineage H is sister to ((*Neoapenesia* + *Apenesia*) + ((*Parascleroderma* + *Foenobethylus*) + lineage E)), whereas in parsimony lineage H is included in a polytomy with lineages C, D, E, F, G and ((*Pristocera* + *Acrepyris*) + (*Prosapenesia* + lineage K)). Lineage H is supported morphologically by the synapomorphies: projection on inner margin of paramere (134:0) (Fig. 9.F); basivolsella with dorsal callus on median margin (137:0) (Fig. 9.G); and digital projection on base of volsella (148:0).

Lineage I represents Neotropical species as large as the ones in lineage F, whereas lineage J includes small sized species from the Australian region. Lineage I is delimited by the synapomorphies: mesopleural oblique sulcus polished (40:4), metapostnotum carinate (67:7) (Fig. 10.B), digital projections on inner margin of volsella base wide (Fig. 10.D), and other homoplasies such as paramere apex beveled (128:0) and paramere dorsally fused to basiparamere (132:1) (Fig. 10.D). Distinctly, morphological phylogenetic analysis pointed to several homoplastic features supporting the lineage such as: frons with projection (3:1), prepectus wide (48:1), propodeal disc area coriaceous (68:4) (Fig. 9.B), hypopygium with translucent pair of spots on its surface (112:1) and median stalk base enlarged (114:1) (Fig. 9.C), and volsella reduced (139:1).

Some particular species of *Apenesia* from the Oriental region formed lineage G. This lineage is characterized by the synapomorphic character “hypopygium plate thick and inner membrane with sclerotized borders” (109:0) (Fig. 10.K), which is unique among the Pristocerinae lineages. Lineage G is placed at a polytomy among many lineages of Pristocerinae (Fig. 1) or as a deficiently supported cluster (Figs. 2), or it is one of the basalmost lineages (Fig. 3).

Finally, lineage K (RS = 63, B = 92, pp = 0.83) clusters species of *Apenesia* from the Afrotropical and Oriental regions. The position of lineage K is similar in all analyses. They differ especially because of the low sampling of *Prosapenesia* and *Afroceras* in BI and ML topologies. In the morphological cladogram, *Afroceras* is part of lineage K (RS = 63) and together they are sister to *Prosapenesia* (RS = 78), which is supported by the synapomorphy hypopygium with less sclerotization of the median region (111:0) (Fig.

11.C). In parsimony, ((lineage K + *Afrocera*) + *Prosapenesia*) are sister to (*Acrepyris* + *Pristocera*) (RS = 66), whereas in the molecular topology *Acrepyris*, *Pristocera* and lineage K form a polytomic relationship (B = 82, pp = 0.90). In the cladistic approach, lineage K is supported only by homoplastic characters such as mandible with two teeth (10:1); antennal flagellomere wide (21:0); pronotal disc without anterior carina (31:0); pronotal disc without transverse depression (33:0); scutellar groove arched (37:1), forewing 4Cu vein tubular (91:0); and medial flexion line trifurcated (100:1).

The phylogenetic relationships within the remaining genera of Pristocerinae slightly disagree between molecular and morphological phylogenetic approaches. In the BI and ML trees *Dissomphalus*, *Trichiscus*, *Protisobrachium* and lineage B clustered with *Pristocera*, *Acrepyris* and lineage K (B = 60, pp = 0.71), whereas in the parsimony analysis, there is no support to conclude which lineage is sister to *Pristocera*, *Acrepyris* and lineage K. The morphological data analyses returned *Dissomphalus* as polyphyletic (including lineage B and *Trichiscus*), but monophyletic for the molecular data analysis. *Pseudisobrachium*, *Caloapenesia* and lineage G positions are also different between morphological/molecular data. In ML and BI topologies, species of *Pseudisobrachium* are the first lineage to branch off of Pristocerinae (B = 90, pp = 1.00), whereas for parsimony the earliest branching is lineage A. *Caloapenesia* appears as a long branch in the molecular phylogenies, sister to ((*Acrepyris* + *Pristocera* + lineage K) + (*Trichiscus* + (*Protisobrachium* + (*Dissomphalus* + lineage B)))). On the other hand, TNT outcomes supported the clade ((*Caloapenesia* + *Calobrachium*) + *Pseudisobrachium*) by sharing the basal ring complete and curved ventrad (160:1). Other differences include *Caloapenesia* not closely related to *Pseudisobrachium* in the molecular analyses. Besides, most major lineages have low support (RS < 60) and many *Apenesia* lineages form a polytomy through morphological data analysis.

#### *Female character reconstruction analyses*

The likelihood-ratio test selected the ER model as the best-fit model for all characters, except for characters 3 and 4, for which the SYM model fit better.

The head wider than mesosoma (1:0), short antenna (2:0), basal margin of clypeus surpassing toruli (3:0) (Fig. 13.A) and keeled dorsal margin of mesopleuron (Fig. 13.B), had a single origin in Pristocerinae. These traits appeared in lineage A and also in *Neoapenesia* (Fig. 4.A). Inconspicuousness of the mesopleuron margin in dorsal view (5:0) (Fig. 13.B) and callus-shaped mesopleuron (6:0) (Fig. 13.L) was likely the condition

seen in the ancestor of *Dissomphalus* and lineage B (Fig. 4.B). The origin of these characters was dubious in the lineages (*Dissomphalus*+ *Protisobrachium*) + *Trichiscus* and *Dissomphalus* + *Protisobrachium*. The petiolar body expansion (7:1) and the antero-lateral fovea on the metapectal-propodeal complex (8:0) arose once in *Pristocera* (Fig. 5.A). The mesonotum long (9:1) and the anterior region of metapectal-propodeal complex narrow (10:1) had two independent origins, one in lineage K and another in *Pseudisobrachium* (Fig. 5.B). The length of the petiole also changed in two distinct lineages in Pristocerinae, the long petiole (11:0) was likely the condition seen in the ancestor of (*PI*+ (*Parascleroderma*+ *Foenobethylus*)) and in (*Dissomphalus* + lineage B) (Fig. 6.A). Finally, the anterior margin of the mesonotum straight (12:1) evolved multiple times in Pristocerinae, arising in *Pristocera*, in the ancestor of (lineage A + *Neoapenesia*) and also in the ancestor of (*Dissomphalus* + lineage B) (Fig. 6.B). The lineages (*Dissomphalus* + *Protisobrachium*) + *Trichiscus* and *Dissomphalus* + *Protisobrachium* had dubious origin of the anterior margin of mesonotum (Fig. 6.B).

## Discussion

### *Polyphyly in Apenesia*

Our results recovered 10 distinct lineages in *Apenesia*, which reflects the wide geographic range and high morphological diversities currently found in this genus. The polyphyly of *Apenesia*, as proposed by Zamprogno & Azevedo (2014) and suggested by Evans (1963), is confirmed. Evans (1963) revised and delimited *Apenesia*, but assumed that the generic boundaries proposed by him were probably polyphyletic. He proposed that *Apenesia* has been “used in this broad sense, to apply to a rather large, heterogeneous, and protean complex of species, most of which are known from the male sex only” (Evans 1963, page 251). The newly proposed phylogenetic hypothesis of *Apenesia* contradicts those suggested by Sorg (1988), Evans (1963) and Terayama (1996), which considered *Apenesia* monophyletic.

Our molecular and morphological analyses justify our nomenclatural actions to elevate various lineages found under the name *Apenesia* to the generic level (see Taxonomic Accounts section). Although the internal relationships remain uncertain, they are unquestionably lineages evolving independently several times in Pristocerinae, and they are distinguishable morphologically. Based on the phylogenetic result and on the taxonomic revision of holotypes and specimens, we propose six new genera in the



Pristocerinae and revalidate the generic status of two: *P4 gen. nov. to be proposed*; *P6 gen. nov. to be proposed*; *P1 stat. rev. to be proposed*; *P5 gen. nov. to be proposed*; *P7 gen. nov. to be proposed*; *P9 gen. nov. to be proposed*; *P10 gen. nov. to be proposed*; *P3 stat. rev. to be proposed* To summarize all phylogenetic data we present a consensus diagram (Fig. 7). Furthermore, our study shows that geographic component might be helpful delimiting taxa in Pristocerinae. Although the subfamily had an old origin (~ 90 Mya with the main lineages arising around 70-55 Mya, unpublished data), the apterous condition and cryptic habitat of females limits dispersal in this group.

Several characters historically used to diagnose taxa within Pristocerinae have been shown to be homoplastic (Zamprogno & Azevedo 2014). Thus, most of the generic boundaries in the subfamily have been based on homoplasies only, which points out taxonomic and nomenclatural issues in Pristocerinae. Homoplasies were also pointed out in other subfamilies of Bethylidae. Epyrinae, for example, have several genera delimited based on homoplasies, which lead to misidentifications (Waichert & Azevedo 2009; Alencar & Azevedo 2013). For instance, Sorg (1988) defined *Apenesia* as monophyletic, supported by the synapomorphic character “reduction of palpal formula number to 4:2”. We found that only lineage A shares this synapomorphy, where the palpal formula is diagnostic for both male and female. Lineage A remains as *Apenesia* because it contains the type species, but *Neoapenesia* is added to it. *Apenesia amazonica*, the type species of *Apenesia*, has the same morphological pattern as in all females included in lineage A + *Neoapenesia*. Terayama (1996) considered male genitalia with cuspis split into two arms as synapomorphy of *Apenesia*. Our results show that the cuspis's shape evolved several times in Pristocerinae. The cuspis divided is also found in some genera of Epyrinae and Scleroderminae, and in all genera of Mesitiinae. Perhaps the division in the cuspis may be related to male-female genitalia attachment and similar shape would have evolved through parallel evolution. Shape and function of cuspis, and other genitalic characters, need further investigation in Bethylidae in order to better establish primary homologies in the family.

The most used diagnostic features for *Apenesia* species-groups overlap those used for other genera and generate difficulties in defining the variations between species and species-groups. Nevertheless, we were able to define and propose for the first time diagnostic characters for *Apenesia*, and the new taxa, based on phylogenetic studies (Fig. 1-4). For instance, genitalia characters such as paramere shape, basivolsella length and projections were helpful to delimit several taxa.

### *Phylogenetic redefinition of Apenesia*

Although the relationships among Pristocerinae lineages are not established herein, the lineages are well delimited.

The relationship between lineage A and *Neoapenesia* was corroborated on morphological and molecular phylogenetic analyses. This lineage occurs in the Neotropical, Nearctic, Afrotropical, Oriental and Australian regions. This lineage is less frequent in collections, and perhaps for this reason, it has not yet been registered in the Palearctic. Terayama (1996) proposed *Neoapenesia* to be monophyletic and sister to (*Pseudisobrachium* + *Protisobrachium*) because of the lack of notauli and the stalked subgenital ring. This relationship has not been retrieved in analyses that followed Terayama (1996), such as Zamprogno & Azevedo (2014). The notauli absent or indistinct is commonly seen as interspecific variation in Bethyliidae (e.g. Azevedo 2008 for *Pseudisobrachium*; Gobbi & Azevedo 2016 for *Calobrachium*). The main morphological characters for *Neoapenesia*, such as clypeus projecting medially, pronotal disc short and paramere long, proposed by Terayama (1996), short antenna (Sawada *et al.*, 2014) and the mesosoma gibbous in profile (studied here), overlap those present in some species of the *laevigata* species-group of *Apenesia*. Similarity in morphological pattern precludes distinguishing *Neoapenesia* from *laevigata* species-group *in partim*. Besides, those male diagnostic features may be addressed for specimens of *Dissomphalus* as well, especially the clypeus with median tooth and the mesosoma gibbous. However, these taxa differ by the genital characteristics: *Dissomphalus* has the paramere wide, the basiparamere simple and the aedeagus with two distinct laminae, whereas *Apenesia* has the paramere narrow, the basiparamere with apical projection and the aedeagus with one single laminae. Recently, Sawada *et al.* (2014) described a species for *Neoapenesia* with male-female association based on biological observation (raised from same dead wood) and confirmed by molecular data. Sawada *et al.* (2014) pointed *Neoapenesia* female “appear to be *Apenesia*”. In fact, they were right. Female of *Neoapenesia makiharai* Sawada, Terayama & Mita is undistinguished from *Apenesia amazonica*, type species of *Apenesia*, except for clypeus shape. Sorg, (1988) analyzed females of *Apenesia* and conclude the palpal formula 4:3 is unique among the Pristocerinae genera. Here we observed the palpal formula 4:3 in males of *Apenesia* lineage A (which includes *laevigata* species-group of *Apenesia in partim*), *Apenesia amazonica*, beyond males and females of *Neoapenesia*. Due to all the arguments set out above, lineage A represents the real core sense of *Apenesia*, including *Neoapenesia* as a junior synonym (**n. syn. to be proposed**). Then,



we propose and justify the synonymy of *Neoapenesia* under *Apenesia* based on the characters previously discussed.

Lineage B represents the species of *dissomphaloides* species-group proposed by Evans (1963), recovered with species of *Dissomphalus* in both analyses. Ashmead (1893) delimited *Dissomphalus* by having a tergal process. Later the genus was defined by having the aedeagus divided into ventral and dorsal laminae (Azevedo, 2001; Azevedo, 2000; Azevedo 1999a, b, c, Azevedo 2003). Since then, several species of *Dissomphalus* have been described including variations in the presence/absence of tergal processes (see for example, Alencar & Azevedo 2008; Mugrabi & Azevedo 2013 and Colombo & Azevedo 2016). Characteristics such as body robust, metasoma wide and short, clypeus tridentate and aedeagus divided into two distinct laminae are present in *Dissomphalus* and *dissomphaloides*. Our results reinforce Azevedo's (2003) definition of *Dissomphalus* and justify transferring *dissomphaloides* species-group to *Dissomphalus*.

The dorsal and ventral laminae in the aedeagus of *Dissomphalus* are morphologically complex (see Azevedo 2001), hampering the whole understanding of its structure. The proposals for primary homologies in each lamina of the aedeagus are restricted to a few conditions because the aedeagus has a large range of morphological diversity making comparison among species hard or dubious. The aedeagus divided into dorsal and ventral laminae is not synapomorphic to *Dissomphalus* as Azevedo (2003) established. *Pristocera*, *Acrepyris*, *Trichiscus*, *Protisobrachium* and *P3* (lineage K) also present this condition. In the molecular analyses, these taxa were recovered as a single lineage, suggesting only one event of origin for the division of aedeagus in laminae. Differently, in our morphological analyses this condition appeared at least three times independently. The study of male genitalia is essential to define species and genera in Bethyloidea, mostly in Pristocerinae, where phoretic copulation has been reported (Evans 1978). To improve the resolution of lineages and to test the genital characteristics as diagnostic for Pristocerinae genera (and for Bethyloidea in general), new studies are required to determine homologies in most of the aedeagus.

*Apenesia nyamuragira* Benoît and *Ap. bishamon* Terayama are divergent from all other lineages in *Apenesia* and in Pristocerinae. Their close relative remains unknown. *Apenesia nyamuragira* has an elongated body and a triangular median lobe in the clypeus, similar to species of *Afroceras*. *Apenesia nyamuragira* has the male genitalia with paramere very narrow (Fig. 11.K), aedeagus with long setae in the apical lobe (Fig. 11.J-L) and hypopygium with posterior margin strongly concave but its plate is complete and

flat (Fig. 11.I), whereas *Afroceras* has the male genitalia with the paramere very wide, the aedeagus without setae in the apical lobe and hypopygium with posterior margin usually trilobate and the median surface of its plate strongly concave. We analyzed specimens from the Afrotropical region identified as *Apenesia* in many collections that also had the characteristics we aforementioned to *Ap. nyamuragira* what lead us to propose ***P10* gen. nov. to be proposed** to accommodate this species.

*Apenesia bishamon* is a Palaearctic species characterized by the presence posterior margin of lower fovea on mesopleuron. This characteristic is unique in Pristocerinae, but it is seen in Epyrinae (see Alencar & Azevedo 2013). Other genitalic features such as the short paramere strongly curved mesad and at least partially fused to a very long basiparamere, a small volsella and the long aedeagus define *A. bishamon* as an independent lineage of *Apenesia*. We propose ***P9* gen. nov. to be proposed** to include this single species since any other Pristocerinae genera present these distinct characteristics.

Lineage E is a supported lineage in Pristocerinae. Although we were unable to include representatives of the type species in the phylogenetic studied, we have directly analyzed the types species that represent the currently invalid names *Cleistepyris* and *Dipristocera*, both names were synonymized by Evans (1963) with *Apenesia*. Thus, our results support the resurrection of *Cleistepyris* to the generic level. Synapomorphies that support ***P1* stat. rev. to be proposed** are: median lobe of clypeus rounded or triangular but usually very short (Fig. 9.H), with absent or barely visible lateral lobes, male genitalia with paramere ax-like with base narrow and apex expanded (Fig. 9.K-L) and cuspis divided into ventral and dorsal arm, ventral one elongate (Fig. 9.K). ***P1* stat. rev. to be proposed** includes the majority of the species currently included in *Apenesia* and represent the common sense of the genus boundaries, mostly because of Evans' (1963) influence. The genus is more abundant in the Neotropics but is also found in the Nearctic region. Records from Palaearctic, Afrotropical and Oriental regions need to be checked. ***P1* stat. rev. to be proposed** includes most of the species belonging to *brasiliensis* and *nitida* species-group of *Apenesia* in Evans' conception, as well as some species from other groups as *columbana*, *exilis*, *mexicana*, *pilicornis* beyond residual *laevigata*.

We propose ***P4* gen. nov. to be proposed** composed by species of *columbana* and *pilicornis* species-group (lineage F). Species of ***P4* gen. nov. to be proposed** are similar to *Acrepyris* because of the large body size, the very long antenna, the median lobe of clypeus rectangular and projected forward, and the uppermost tooth of mandible usually

curved inward. Similarities among these lineages are homoplastic (Terayama 1996) and have evolved independently. **P4 gen. nov. to be proposed**, however, is unique within Pristocerinae by having the male genitalia with paramere usually fused to the basiparamere (Fig. 8.I-J), the apex is beveled, the volsella is long, the basivolsella is short and wide (Fig. 8.J) and the basal ring reduced to the latero-ventral region (Fig. 8.J).

**P7 gen. nov. to be proposed** (lineage G) represents part of the current Oriental species of *Apenesia*. It also resembles *Acrepyris* by having a rectangular clypeus. They are distinguishable by body size, which is small and large, respectively. **P7 gen. nov. to be proposed** is unique in the family by presenting the hypopygium with a large and thin membrane, delimited laterally by an extension of lateral stalks and covering its median long stalk (Fig. 10.J-K). Moreover, the hypopygium plate is large and thick near the posterior margin, noticeable even without dissecting the specimens (see Fig. 02 in Lim *et al.* 2011). Finally, the male genitalia have the paramere unusually narrow, curved mesad and with the margins densely setose (Fig. 10.L-M); the volsella is small, with cuspis divided, the basivolsella is elongate, and basal ring is reduced to lateral part. We are aware of at least five undescribed species belonging to **P7 gen. nov. to be proposed**, which will be described elsewhere.

Lineage H has Australian and Neotropical species. These species share genitalia features such as: a spine projection in the inner surface of paramere, basivolsella with two projections upward and the presence of a projection in dorsal margin between the delimitation of paramere and basiparamere. This dorsal projection differs from that present in *Apenesia* by being continuous to the basiparamere; it has a soft membrane joining the projection to the genital ring, while in lineage H the projection is sclerotized and never exceeds the limit of the paramere and basiparamere. Although lineage H presents many synapomorphic states, the support values that maintain lineages I + J together is not as high as the one supporting each of the lineages separately (Fig. 1-3). Species of lineage I occur only in the eastern Neotropical region and are included in **P5 gen. nov. to be proposed**; whereas the lineage J, **P6 gen. nov. to be proposed**, includes the Australian and Andean species. Other differences justify treating each one as distinct taxa. **P5** presents species with large body specimens (Fig. 10.A-B), male genitalia with apex of paramere beveled, basivolsella with upward projections short with wide base and aedeagus elongate (Fig. 10.D), basal ring absent, whereas the **P6 gen. nov. to be proposed** presents species with small body size (Fig. 9.A-B), male genitalia with paramere apex rounded (Fig. 9.F), basivolsella upward projections long and narrow (Fig.

9.D), aedeagus wide and short (Fig. 9.F) and basal ring incomplete (Fig. 9.D). ***P5* gen. nov. to be proposed** is composed of representatives of *columbana* and *pilicornis* species-groups that are not morphologically related to the species belonging to ***P4* gen. nov. to be proposed**. Else, ***P6* gen. nov. to be proposed** has Australian species, for instance *Apenesia evansi* Gordh, 1990. However, we have seen at least 10 new species among material from Australia and Chile in UQIC and AMNH collections.

Lineage K is a lineage with about 20 known and hundreds of undescribed species from the Oriental, Afrotropical and Palaearctic regions. It is characterized by having the clypeus triangular (Fig. 11.A), long and wide basally, and the hypopygium strongly concave on its outer surface (Fig. 11.C). Our morphological topology shows *Afrocera* clustering within lineage K, whose other members share the lineage aforementioned *Afrocera* characteristics. Thus, all these species belong to the same genus. Because the characteristics described here for lineage K are present in *Propristocera* and *Neopristocera* (synonyms of *Apenesia*) type species (which we analyzed directly, see Table 1), our results support the revalidation of *Propristocera*, which is older than *Neopristocera* and *Afrocera*.

The peculiar hypopygium plate of ***P3* stat. rev. to be proposed** is also reported in *Prosapenesia*, which is endemic from the Afrotropical region near Namibia. In all morphological analyses, *Prosapenesia* is the sister group of ***P3* stat. rev. to be proposed** (Fig. 1-2). This group was also recovered in Zamprogno & Azevedo (2014). The lineage *Prosapenesia* + ***P3* stat. rev. to be proposed** is supported by the following synapomorphies: the hypopygium with concavity in its outer median surface (111:1), the stalks of hypopygium stub-like (116:1), paramere wide (127:1), volsella wide and aedeagus wide (154:1). However, the area occupied by the concavity in the hypopygium plate of ***P3* stat. rev. to be proposed** is quite large compared to the short one in *Prosapenesia*, which is restricted near to the posterior margin. In ***P3* stat. rev. to be proposed**, the concavity can reach the vicinity of the apical margin.

#### *Phoretic copulation, male-female association and Pristocerinae female evolution evidences*

Several genitalic characters were found to have phylogenetic signal; the cuspis shape and size, the presence of division in the cuspis, projections on paramere, basiparamere and basivolsella, paramere shape and number of laminae in the aedeagus

helped us to reconstruct the phylogenetic history of *Pristocerinae*. Almost all genera may be delimited by a set of male genital characteristics.

Currently, the most relevant taxonomic studies in *Bethylidae* emphasize the understanding of hypopygium and genital characteristics for delimitation at species, genera and subfamilies levels (see Azevedo 1999d; Alencar & Azevedo 2013; Zamprogno & Azevedo 2014; Gobbi & Azevedo 2016). The male needs to hold the female by the genitalia during coupling, especially in *Pristocerinae*, in which phoretic copulation occurs during flight (Gordh 1990). For this reason, the male-female genital system needs an accurate fitting for a successful mating. Therefore, morphological similarities and differences in the genitalia are useful to delimit different taxonomic levels. Genital features are useful to delimit *Pristocerinae* genera in a cladistics context.

Previously to our study, only one female had been associated with its conspecific male based on nucleotide sequences (Sawada *et al.* 2014). We associate females of *Pseudisobrachium*, *Parascleroderma*, *Pristocera* and *Dissomphalus* to their congeneric males based on molecular phylogenetic analyses. The number of *Pristocerinae* genera with known female, is herein significantly increased, tending toward better labeling of phoretic copulation and biological records in the subfamily.

#### *Female morphological character evolution*

Mapping analyses of morphological females characteristics were enlightening, showing recognizable patterns within *Pristocerinae* genera (Fig. 13-14). Females of the subfamily are hardly distinguishable specific and generically and this is the first time we have reliable data to make male-female generic association.

The female character mapping analysis supports the distinct lineages found within *Apenesia*. Our results indicate that the shape of the head, the size of the antenna, the posterior margin of the clypeal median lobe, the length and shape of the mesonotum, the shape of the mesopleuron, the metapectal-propodeal complex sides and the constriction at the anterior portion of the metapectal-propodeal complex are helpful characters to delimit generic boundaries in females of *Pristocerinae*.

The head wider than mesosoma evolved once in *Pristocerinae* (Fig. 13.A). Females belonging to the *Apenesia* (lineage A + *Neoapenesia*) have, besides the large head, the posterior margin of clypeus surpassing toruli on frons, and the metapectal-propodeal complex strongly constricted (Figs. 13.B). The size of the head reflects the overall specimen size. Moreover, females with large head seem to be unusually larger

than the male associated. These species lack records of phoretic copulation. Sawada *et al.* (2014) associated the absence of phoretic copulation to the females be larger than male's specimens. Biological data indicate that these species attack cerambycid larvae inside infested stem (Seetharama *et al.* 2007; Sawada *et al.* 2014).

The shape of the anterior margin of mesonotum is another helpful feature to identify Pristocerinae. According to our mapping analyses, the probable female ancestor of Pristocerinae presented a straight anterior margin in the mesonotum, which evolved to concave in *Apenesia* (lineage A), (*Dissomphalus* + lineage B) and *Pristocera* were independently (Fig. 6B).

The female of *Ap. simulata* Evans, 1969 (lineage B) was first found *in copula*. *Apenesia simulata*, and other species from *dissomphaloides* species-group, is characterized by having the mesonotum conspicuous below the margin of the mesosoma, and the mesopleuron callus in dorsal view and the metapectal-propodeal complex with parallel sides. These features have a single origin in the subfamily, being recorded to lineage B and *Dissomphalus*. These are the most sampled females in Pristocerinae, usually collected in yellow pan trap, pit fall, sweeping on forest trail, and Malaise traps. It suggests that females of *Dissomphalus* are free living in the soil and litter of forested areas. Based on our morphological, molecular and mapping analyses, we are confident that *Ap. simulata* is indeed a representative of *Dissomphalus*. The characteristics listed above are here reported as diagnostic for females of *Dissomphalus*.

Females of *Dissomphalus*, *Parascleroderma* and ***P1 stat. rev. to be proposed*** (lineage E) have the petiole long. The petiole appeared in Apocrita conferring a high plasticity level for the movement of metasoma. In our date the long petiole arises twice independently in two non-related lineages: (*Dissomphalus* + lineage B) and (*Parascleroderma* + ***P1 stat. rev. to be proposed***). According to Turrisi & Vilhelmsen (2010), long petiole possibly allows a wider range of vertical movement of the metasoma with respect to the mesosoma and may improve oviposition. Perhaps females of *Dissomphalus* and *Parascleroderma* oviposit inserting the ovipositor in their hosts.

*Apenesia elongata* Evans, 1963 is the only one to be included in ***P4 gen. nov. to be proposed*** (lineage F) with male-female association. ***P6 gen. nov. to be proposed*** (lineage J) has one species with male-female associate by phoretic copulation, *P6 evansi* (Gordh) **comb. nov. to be proposed**. The elongate and oval head of this species is also similar to *Dissomphalus* and ***P4 gen. nov. to be proposed***. But as ***P1 stat. rev. to be proposed*** this female pattern presents an obsolete ommatidium, whereas ***P4 gen. nov. to***



**be proposed** presents some distinct ommatidia. The female of this pattern needs to be better investigated. The assemblage of features is unique to the *P6* **gen. nov. to be proposed** but its own synapomorphies are lacking.

Even the lineage K, *P3* **stat. rev. to be proposed**, being clarified for males in this study no female was reported up to date. We have sorted hundreds of specimens from Thailand (QSBG) and Madagascar (CASC), and we were able to find a couple caught in copula. The couple is probably a new species and will be described elsewhere. Finally, the female specimens identified as *Prosapenesia* by Mugrabi & Azevedo (2010) from Madagascar are actually *P3* **stat. rev. to be proposed**. Males of *Prosapenesia* were not recorded to Madagascar even after many years of collecting efforts made by CASC collection. Krombein (1989) described the female of *Pro. lacteipennis* Kieffer, 1910 because of it had been collected in the same locality of the male. Assuming that *Prosapenesia* and lineage K are different genera, the sex association made by Krombein is possibly mistaken and the females currently described as *Prosapenesia* belong, in fact, to *P3* **stat. rev. to be proposed**. Recently, Santhosh & Ranjith (2016) added two female-based species to *Prosapenesia* following Krombein's concept. Here we propose to transfer these two species to *P3*.

Concluding, females of Pristocerinae might be cryptic interspecific but not intergenerically. The morphological characteristics studied here are reliable to differentiate the genera. Lastly, it was possible to confirm association of male-female in *Parascleroderma*, *Pristocera* and *Pseudisobrachium* based on nucleotide sequences, what led us to propose diagnostic features for these three genera (see Taxonomic accounts). Pristocerinae females have been neglected especially because they are hard to find. Many efforts have been done to collect males in the past two decades. These efforts allowed several improvements to pristocerine taxonomy. However, it is still necessary to deeply investigate male genitalia homologies to better understand genera patterns. Our results show it is necessary to also understand female's taxonomy and biology to improve resolutions in phylogenies and genera delimitations. New sampling methods need to be tested to collect females efficiently. After all that, Pristocerinae phylogenies must be revisited.

Here we showed *Apenesia* delimitation was fragile and hidden high complexity. Our proposal includes a new set of species for precisely define *Apenesia*, revalidation of two genera hitherto considered junior synonyms of *Apenesia*, in addition to the description of six new genera. In this perspective, we consider the results proposed here

as many new data released at the same time and that will certainly have great impact in the Pristocerinae understanding. Given these reasons, we associate these taxonomic changes from a single study by rescuing the mythological history of Pandora. Pandora's box is an artifact in Greek mythology, which contained all the evils of the world. Pandora opened the jar and all the evils flew out, leaving only "Hope" inside once she had closed it again. Today the phrase "to open Pandora's box" means to perform an action that may seem small or innocent, but that turns out to have far-reaching consequences. Then, this study is just the opening of the "Pandora box" of Pristocerinae.

#### *Taxonomic accounts*

According to the phylogenies recovered from our analyses, a rearrangement of the generic boundaries in Pristocerinae is necessary. Here we propose a new delimitation for *Apenesia*, two genera are revalidated, six new genera are proposed and some species are transferred to other genera. We provide a checklist for each taxa, most of the species we analyzed directly from the holotype, others by pictures, draws and literature.

#### ***Apenesia* Westwood, 1874** (Figs. 8.A-E; 13.A-B)

*Apenesia* Westwood, 1874, 170. Type-species: *Apenesia amazonica* Westwood, 1874. Subsequent designation by Westwood 1881, 130.

*Aeluroides* Tullgren, 1904, 1: 429-428. Type-species: *Aeluroides sjostedti* Tullgren, 1904. Original monotypy. Synonymy by Kieffer 1914, 41: 391.

*Neoapenesia* Terayama, 1995, 63: 886. Type-species: *Neoapenesia leytensis* Terayama, 1995. Original monotypy. **Syn. to be proposed**

**Diagnosis. Male:** head usually wider than long; mandible narrow; palpal formula 4:3; clypeus with median lobe projected and usually with median small tooth; antenna with flagellomere short; mesosoma gibbous; pronotal disc very short; forewing with R1a long; R1b absent; Cub spectral and long, usually subdivided; hypopygium plate short, with three anterior stalks, median one very long; genitalia with paramere narrow and long, cuspis developed dorsad, apical projection on basiparamere with membranous area with chitinous projections. **Female:** head quadrate and distinctly larger than pronotal width; clypeus short, with posterior margin surpassing torulus; mandible long and narrow, palpal formula 4:3; antenna short, not reaching posterior margin of head; mesopleuron with



lateral surface concave; mesocoxa very developed; metapectal-propodeal complex with strong anterior constriction; anterior region of metapectal-propodeal complex with lateral margin bulging.

**Remarks.** It represents lineage A + *Neoapenesia* in our analyses (Figs. 1-3).

**Distribution.** Cosmopolitan.

**Check list.**

*amazonica* Westwood, 1874

*amoena* Evans, 1963

*bicolor* Vargas & Terayama, 2002

*chontalica* Westwood, 1881

*conradti* Kieffer, 1910

*delicata* Evans, 1963

*dominica* Evans, 1963

*flavipes* Cameron, 1888

*formosa* Vargas & Terayama, 2002

*laevigata* (Evans, 1958)

*leytensis* (Terayama, 1995) **comb. nov. to be proposed** from *Neoapenesia*

*levis* Kieffer, 1904

*makiharai* (Sawada *et al.*, 2014) **comb. nov. to be proposed** from *Neoapenesia*

*malaitensis* Brues, 1918

*modesta* (Smith, 1864)

*nigra* Kieffer, 1904

*parasitica* (Smith, 1864)

*perlonga* Corrêa & Azevedo, 2006

*proxima* Kieffer, 1904

*punctalata* Krombein, 1989

*sahyadrica* Azevedo & Waichert, 2006

*singularis* Lanes & Azevedo, 2004

*sjostedti* (Tulgren, 1904)

*substriata* Kieffer, 1904

*unicolor* Kieffer, 1904

*vaurieorum* Evans, 1969

**PI Kieffer, 1910** *stat. rev. to be proposed* (Figs. 9.H-M; 13.G-H)

PI Kieffer 1910, 79: 48. Type-species: *Cleistepyris punctatus* Kieffer, 1910 = *Apenesia peruana* new name Evans, 1963 and syn. jr. of *Cleistepyris brasiliensis* **nec** *Apenesia punctata* (Cameron, 1888). Subsequent designation by Kieffer 1914, 41: 490.

*Dipristocera* Kieffer 1914, 41: 471. Type-species: *Pristocera microchela* Kieffer, 1911b. Original monotypy. **Syn. to be proposed**

**Diagnosis. Male:** median clypeal lobe with variable shape but usually triangular and short, eye glabrous; antenna long, first antennomeres larger than distal ones; palpal formula 6:3; forewing with pterostigma short and triangular, R1b short, Rsc very long with distal end spectral and almost touching the wing margin, r-rs&Rsc junction almost smooth; genitalia with paramere with base narrow and apex very expanded; cuspis divided into ventral and dorsal arms, ventral one usually large. **Female:** head globoid, antenna reaching pronotum, mandibles with from two to four teeth; clypeus usually short; eye absent or very small, indistinct; mesonotum caliciform with anterior margin strongly concave and rounded behind; mesopleuron conspicuous dorsally, lateral surface convex; metapectal-propodeal complex weakly to moderately constricted near spiracles; petiole long.

**Remarks.** It represents lineage E in our analyses (Figs. 1-3). Phoretic copulation is recorded to few species (Table 1).

**Distribution.** Pan-american, but abundant in the Neotropical region.

#### **Check list.**

*acius* (Lanes & Azevedo, 2004) **comb. nov. to be proposed** from *Apenesia*

*alutaceus* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*

*angustatus* (Evans, 1958) **comb. nov. to be proposed** from *Apenesia*

*apicilatus* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*

*atlanticus* (Corrêa & Azevedo, 2006) **comb. nov. to be proposed** from *Apenesia*

*auriculus* (Lanes & Azevedo, 2004) **comb. nov. to be proposed** from *Apenesia*

*auritus* (Waichert & Azevedo, 2003) **comb. nov. to be proposed** from *Apenesia*

*brasiliensis* (Kieffer, 1909) **comb. nov. to be proposed** from *Apenesia*

*bugabensis* (Cameron, 1888) **comb. nov. to be proposed** from *Apenesia*

*chiricahua* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*

*clypeatus* (Leal & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*cochise* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*columbanus* (Westwood, 1874) **comb. nov. to be proposed** from *Apenesia*  
*conconvatus* (Corrêa & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*crenulatus* (Kieffer, 1909) **comb. nov. to be proposed** from *Apenesia*  
*cubensis* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*curvatus* (Lanes & Azevedo, 2004) **comb. nov. to be proposed** from *Apenesia*  
*distinctus* (Corrêa & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*exiguus* (Corrêa & Azevedo, 2006) **comb. nov. to be proposed** from *Apenesia*  
*fulvicollis* (Westwood, 1874) **comb. nov. to be proposed** from *Apenesia*  
*hepaticus* (Corrêa & Azevedo, 2006) **comb. nov. to be proposed** from *Apenesia*  
*inca* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*jamaica* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*laceratus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*laevicornis* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*lapsus* (Lanes & Azevedo, 2004) **comb. nov. to be proposed** from *Apenesia*  
*leucophthalmus* (Evans, 1964) **comb. nov. to be proposed** from *Apenesia*  
*lobatus* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*longus* (Ramos & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*magnus* (Ramos & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*malinche* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*maya* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*megaventrifera* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*membranaceus* (Lanes & Azevedo, 2004) **comb. nov. to be proposed** from *Apenesia*  
*mexicana* (Cameron, 1904) **comb. nov. to be proposed** from *Apenesia*  
*microchelus* (Kieffer, 1911) **comb. nov. to be proposed** from *Apenesia*  
*mohave* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*neotropica* Kieffer, 1910 **comb. rev.** from *Apenesia*  
*nitidus* Kieffer, 1910 **comb. rev.** from *Apenesia*  
*ocullatus* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*olmeca* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*percurrens* (Kieffer, 1910) **comb. nov. to be proposed nov. rev.** to be reinstall from  
*Apenesia pando* Evans, 1963 = replaced name for *Plutobethylus percurrens* Kieffer, 1910  
*paradoxus* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*

*paraensis* (Kieffer, 1910) **comb. nov. to be proposed** from *Apenesia*  
*patens* (Corrêa & Azevedo, 2006) **comb. nov. to be proposed** from *Apenesia*  
*peccatus* (Ramos & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*pectinatus* (Corrêa & Azevedo, 2006) **comb. nov. to be proposed** from *Apenesia*  
*peculiaris* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*perconcavus* (Ramos & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*permaximus* (Ramos & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*quadratus* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*quadrimerus* (Leal & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*quelatus* (Ramos, Araújo & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*rectus* (Ramos & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*rostrum* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*rotundum* (Leal & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*santaecatarinae* (Evans, 1964) **comb. nov. to be proposed** from *Apenesia*  
*serrulatus* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*simplex* (Corrêa & Azevedo, 2006) **comb. nov. to be proposed** from *Apenesia*  
*spatulatus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*spinipes* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*striatulus* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*strictus* (Corrêa & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*strigulatus* (Lanes & Azevedo, 2004) **comb. nov. to be proposed** from *Apenesia*  
*sulcatus* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*tarascana* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*testaceipes* (Cameron, 1888) **comb. nov. to be proposed** from *Apenesia*  
*tlahuicana* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*transversus* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*triangulum* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*triapicalis* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*trivisum* (Ramos, Araújo & Azevedo, 2010) **comb. nov. to be proposed** from *Apenesia*  
*unipilosus* (Corrêa & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*ventosus* (Azevedo & Batista, 2002) **comb. nov. to be proposed** from *Apenesia*  
*williamsi* (Evans, 1966) **comb. nov. to be proposed** from *Apenesia*  
*zamorum* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*

***P3* Kieffer, 1905** *stat. rev. to be proposed* (Figs. 11.A-F; 13.I-J)

*P3* Kieffer 1905, 9: 247 in Kieffer & Marshall (1904-1906). Type-species:

*Propristocera interrupta* Kieffer, 1905. Subsequent designation by Kieffer 1914, 41: 484.

*Afrocera* Benoît 1983, 97: 674-675. Type-species: *Afrocera bamboutoana* Benoît, 1983.

Original designation. **Syn. to be proposed**

*Neopristocera* Benoît 1957, 88: 44. Type-species: *Neopristocera triloba* Benoît, 1957.

Original designation. **Syn. to be proposed**

**Diagnosis. Male:** median clypeal lobe projected and triangular; hypopygium short with three short stalks stub-like, median ventral surface less sclerotized and strongly concave; apical margin trilobate when compressed in cover slip; genitalia with paramere large and very developed dorsally, with strong concavity to fit volsella; basivolsella short, distinct to basiparamere; volsella large; aedeagus usually with two distinct lamina; basal ring narrow and present latero-dorsally. **Female:** head elongate; antennae long; eye usually absent; pronotum elongate; mesonotum elongate and triangular; mesopleuron does not cover lateral of metapectal-propodeal complex in dorsal view, strongly constricted at its extreme anterior end.

**Remarks.** It represents lineage K + *Afrocera* in our analyses (Figs. 1-3). *P3* is one of the most abundant genera in Afrotropical samples. There are many new species to be described only from Madagascar samples that we have sorted. Phoretic copulations is record.

**Distribution.** Afrotropical, Oriental and Palaeartic.

#### **Check list.**

*acuta* (Benoît, 1957) **comb. nov. to be proposed** from *Apenesia*

*aegyptia* Kieffer, 1921 **comb. rev.** from *Apenesia*

*bamboutoana* (Benoît, 1983) **comb. nov. to be proposed** from *Afrocera*

*carinicollis* (Terayama, 2004) **comb. nov. to be proposed** from *Apenesia*

*emarginata* (Santhosh & Ranjith, 2016) **comb. nov. to be proposed** from *Prosapenesia*

*formosimonticola* (Terayama, 1996) **comb. nov. to be proposed** from *Apenesia*

*flavipes* (Fouts, 1930) **comb. nov. to be proposed and nom. rev.** to be reinstall from

*Apenesia foutsii* Gordh & Móczár, 1990 = replaced name for *Misepyrus flavipes* Fouts

*interrupta* Kieffer, 1905 **comb. rev.** from *Apenesia*  
*kusigematii* (Terayama, 1999) **comb. nov. to be proposed** from *Apenesia*  
*luzonica* (Fouts, 1930) **comb. nov. to be proposed** from *Apenesia*  
*mindanaensis* (Fouts, 1930) **comb. nov. to be proposed** from *Apenesia*  
*neavei* (Turner & Waterson, 1917) **comb. nov. to be proposed** from *Pristocera*  
*nyama* Benoît, 1957 **comb. rev.** from *Apenesia*  
*okinawensis* (Terayama, 1999) **comb. nov. to be proposed** from *Apenesia*  
*orientalia* (Ranjith & Santhosh, 2016) **comb. nov. to be proposed** from *Prosapenesia*  
*percurrens* Kieffer, 1905 **comb. rev.** from *Apenesia*  
*pingtungensis* (Terayama, 1996) **comb. nov. to be proposed** from *Apenesia*  
*polita* (Fouts, 1930) **comb. nov. to be proposed** from *Apenesia*  
*pseudosuzannae* Benoît, 1957 **comb. rev.** from *Apenesia*  
*pulchella* (Terayama, 2004) **comb. nov. to be proposed** from *Apenesia*  
*sinensis* (Xu, Terayama & He, 2002) **comb. nov. to be proposed** from *Apenesia*  
*suzannae* Benoît, 1957 **comb. rev.** from *Apenesia*  
*tagala* (Ashmead, 1905) **comb. nov. to be proposed** from *Apenesia* = *Apenesia minor*  
(Kieffer, 1913) **Syn. to be proposed**  
*tengu* (Terayama, 2006) **comb. nov. to be proposed** from *Apenesia*  
*triloba* (Benoît, 1957) **comb. nov. to be proposed** from *Apenesia*

**P4 Alencar & Azevedo new genus to be proposed** (Figs. 8.F-J; 13.C-D)

P4 Alencar & Azevedo. Type-species: *Apenesia elongata* Evans, 1963.

**Diagnosis. Male:** clypeus rectangular or trapezoidal, always very projected forward; anteromesoscutum long; notaulus badly impressed; metaposnotal median carina present, incomplete; metaposnotal area with divergent carinae; forewing with pterostigma lanceolate, R1b long, Rsc very long with distal end spectral, r-rs&Rsc junction distinct and angled; hypopygium with median stalk long; genitalia with paramere with apex beveled, basiparamere short and wide, cuspis and digitus long, basal ring narrow and ventrad. **Female:** head elongate, antenna long; scape with same width along its length; eye small and distinct; pronotum long; mesoscutum triangular, with anterior margin concave and posterior one convex; metapectal-propodeal complex with an inconspicuous constriction; spiracle small and oval, placed latero-dorsally; petiole short.

**Remarks.** It represents lineage F in our analyses (Figs. 1-3). This genus is less abundant than *P1 stat. rev. to be proposed* but it is common in the Neotropical samples. *P4 elongata* (Evans, 1963) is the only species with known female.

**Distribution.** Pan-american, but most abundant in the Neotropical region.

**Etymology.** The name derives from *Acrepyris*, another genus in Pristocerinae which *P4* resembles morphologically.

#### **Check list.**

*angusticeps* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*coarctata* (Kieffer, 1909) **comb. nov. to be proposed** from *Apenesia*  
*elongata* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*exilis* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*fusilis* (Corrêa & Azevedo, 2001) **comb. nov. to be proposed** from *Apenesia*  
*guatemalensis* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*luteola* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*martini* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*ornata* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*pilicornis* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*punctata* (Cameron, 1888) **comb. nov. to be proposed** from *Apenesia*  
*reducta* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*tenebrosa* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*venezuelana* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*

#### ***P6* Alencar & Azevedo new genus to be proposed (Figs. 9.A-G; 13.E-F)**

*P6* Alencar & Azevedo. Type-species: *Apenesia evansi* Gordh, 1990.

**Diagnosis. Male:** body size small; clypeus short, with apical slightly convex or straight; prepectus divided and large; forewing with pterostigma short and oval, R1*b* short, Rsc very long, r-rs&Rsc junction smooth, hypopygium with three stalks, median stalk long with base very large, median surface with light spots; genitalia with paramere very narrow and curved mesad, usually with a median spine projection at inner surface; dorsal base of paramere with a hard projection variable in size and position; basivolsella long with an apical spine; basiparamere apical margin without distinction to paramere; basal ring large



and placed laterally on genital ring. **Female:** head elongate; clypeus produced and not continuous to frons; antenna long; eye absent mesoscutellum triangular, with anterior margin slightly concave and posterior one convex; metapectal-propodeal complex constriction weak; petiole short.

**Remarks.** It represents lineage J in our analyses (Figs. 1-3). It presents phoretic copulation.

**Distribution.** Australian region and Chile.

**Etymology.** The name derives from Australia, zoogeographical region in which the genus occurs.

#### **Check list.**

*australiense* (Kieffer, 1906) **comb. nov. to be proposed** from *Apenesia*

*chilena* (Evans, 1967) **comb. nov. to be proposed** from *Apenesia*

*evansi* (Gordh, 1990) **comb. nov. to be proposed** from *Apenesia*

*tofti* (Ward, 2013) **comb. nov. to be proposed** from *Apenesia*

#### ***P5* Alencar & Azevedo new genus to be proposed (Figs. 10.A-G)**

*P5* Alencar & Azevedo. Type-species: *Apenesia juncea* Evans, 1966.

**Diagnosis. Male:** body size large; clypeus usually rectangular; forewing with: pterostigma short and oval, R1b long, Rsc long with distal end spectral, r-rs&Rsc junction smooth; hypopygium with three stalks, median stalk long with base narrow; genitalia with paramere narrow and curved mesad; dorsal base of paramere with a hard projection hook-like; basivolsella short with an apical spine; basiparamere apical margin without distinction to paramere; basal ring absent. **Female:** unknown.

**Remarks.** It represents lineage I in our analyses. The body shape of *P5 gen. nov. to be proposed* is quite similar to *P4 gen. nov. to be proposed*. However, *P5 gen. nov. to be proposed* has the basivolsella long and narrow with mesial apical projection, whereas *P4 gen. nov. to be proposed* has the basivolsella short and wide without mesial apical projection. *P5 gen. nov. to be proposed* presents many morphologically similar species that should be investigated under molecular analyses.

**Distribution.** Pan-american.

**Etymology.** Random combination of letters + termination “nesia” from *Apenesia*.



### Check list.

*cusco* (Evans, 1966) **comb. nov. to be proposed** from *Apenesia*  
*flammicornis* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*funebri* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*juncea* (Evans, 1966) **comb. nov. to be proposed** from *Apenesia*  
*pallidicornis* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*pallidula* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*  
*polita* (Evans, 1958) **nom. rev. and comb. nov. to be proposed** from *Apenesia parapolita*  
Evans, 1963 = replaced name for *Propristocera polita* Evans, 1958, replacement name  
*photophila* (Ogloblin, 1930) **comb. nov. to be proposed** from *Apenesia*  
*pima* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*

### P7 Alencar & Azevedo new genus to be proposed (Figs. 10.H-N)

P7 Alencar & Azevedo. Type-species: *Apenesia elegans* Terayama, 1999.

**Diagnosis. Male:** antenna long; clypeus usually short with apical margin convex; forewing with pterostigma lanceolate, R1b long, r-rs&Rsc junction distinct and angled; hypopygium with inner surface with distinct setae, median stalk long; inner membrane very developed overlapping median stalk, with delimited borders, apical margin thick, shape variable; genitalia with paramere very narrow, curved mesad and with ventral margin setose; basivolsella long and narrow; basal ring large and placed laterally on genital ring. **Female:** unknown.

**Remarks.** It represents lineage G in our analyses (Figs. 1-3).

**Distribution.** Palaearctic, Oriental region.

**Etymology.** Elegan from elegans epithet + termination “nesia” from *Apenesia*.

### Check list.

*chitouensis* (Terayama, 1996) **comb. nov. to be proposed** from *Apenesia*  
*clara* (Xu, Terayama & He, 2002) **comb. nov. to be proposed** from *Apenesia*  
*consobrina* (Kieffer, 1922) **comb. nov. to be proposed** from *Apenesia*  
*daikoku* (Terayama, 1999) **comb. nov. to be proposed** from *Apenesia*  
*electriphila* (Cockerell, 1917) **comb. nov. to be proposed** from *Apenesia*  
*elegans* (Terayama, 1999) **comb. nov. to be proposed** from *Apenesia*

*intricata* (Kieffer, 1922) **comb. nov. to be proposed** from *Apenesia*  
*kaguyahime* (Terayama, 2006) **comb. nov. to be proposed** from *Apenesia*  
*kakaniensis* (Terayama, 2004) **comb. nov. to be proposed** from *Apenesia*  
*ktmdana* (Terayama, 2004) **comb. nov. to be proposed** from *Apenesia*  
*lathrobioides* (Westwood, 1874) **comb. nov. to be proposed** from *Apenesia*  
*levicollis* (Kieffer, 1905) **comb. nov. to be proposed** from *Apenesia*  
*liukueiensis* (Terayama, 1996) **comb. nov. to be proposed** from *Apenesia*  
*meifuiae* (Terayama, 1996) **comb. nov. to be proposed** from *Apenesia*  
*minima* (Kieffer, 1913) **comb. nov. to be proposed** from *Apenesia*  
*nepalensis* (Terayama, 2004) **comb. nov. to be proposed** from *Apenesia*  
*otohime* (Terayama, 1999) **comb. nov. to be proposed** from *Apenesia*  
*philippinensis* (Kieffer, 1913) **comb. nov. to be proposed** from *Apenesia*  
*takasago* (Terayama, 1996) **comb. nov. to be proposed** from *Apenesia*  
*tianmuensis* (Xu, Terayama & He, 2002) **comb. nov. to be proposed** from *Apenesia*  
*xanthoptera* (Kieffer, 1922) **comb. nov. to be proposed** from *Apenesia*

**P9 Alencar & Azevedo new genus to be proposed** (Figs. 12.A-F)

P9 Alencar & Azevedo. Type-species: *Apenesia bishamon* Terayama, 1999.

**Diagnosis. Male:** clypeus very projected and triangular; notaulus irregularly foveolate; mesopleuron with opened anterior and inferior foveae; metanotum with three median foveae; metaposnotal median carina present; hypopygium with three stalks, median stalk long, genitalia with paramere and basiparamere fused, without distinction; apex of paramere with at least one thin and long projection; basivolsella very long; basal ring narrow and placed dorsal-laterally above genital ring. **Female:** unknown.

**Remarks.** It represents lineage D in our analyses (Fig. 1-3).

**Distribution.** Palaearctic region, but we have seen undescribed species from Afrotropical region.

**Etymology.** The name derives from Epyrinae, another subfamily in Bethyilidae, which presents lower fovea in many species.

**Check list.**

*bishamon* (Terayama, 1999) **comb. nov. to be proposed** from *Apenesia*

***P10* Alencar & Azevedo new genus to be proposed** (Figs. 11.A-F)

*P10* Alencar & Azevedo. Type-species: *Apenesia nyamuragira* Benoît, 1957.

**Diagnosis. Male:** antenna long and setose; clypeus long and triangular; metapectal-propodeal complex elongate; metaposnotal median carina present; hypopygium with three short stalks, basal margin strongly concave between stalks, apical margin strongly concave, u-shaped, median surface very short; genitalia with paramere long and very narrow; apex of paramere with at least one thin and long projection; basivolsella very short; aedeagus with apical long setae; basal ring narrow and placed dorsal-laterally above genital ring. **Female:** unknown.

**Remarks.** It represents lineage C in our analyses (Figs. 1-3). Although this genus is currently monotypic, we have seen some undescribed species from Kenya and Madagascar.

**Distribution.** Afrotropical region.

**Etymology.** The name derives from *Pristocera*, another genus in Pristocerinae which *P10* resembles morphologically.

**Check list.**

*nyamuragira* (Benoît, 1957) **comb. nov. to be proposed** from *Apenesia*

*Species transferred to other taxa from Apenesia*

***Dissomphalus* Ashmead, 1893** (Figs. 13.K-L)

*browni* (Evans, 1964) **comb. nov.** from *Apenesia*

*caribbeanus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*

*denticulatus* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia denticulata*, Evans, 1963 (= *Propristocera tridentata*, Evans 1958, replacement name)

*dissomphaloides* (Evans, 1963) **comb. nov. to be proposed** from *Apenesia*

*flaviscapus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*

*forchhammeri* (Krombein, 1989) **comb. nov.** from *Apenesia*

*insulanus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*

*kiefferi* (Benoît, 1957) **comb. nov. to be proposed** from *Pseudisobrachium*

*lilloanus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*matticum* (Benoît, 1957) **comb. nov. to be proposed** from *Pseudisobrachium*  
*neobrowni* Alencar & Azevedo **nom. nov.** for *Dissomphalus browni* Terayama, 2001  
*pygmaeus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*sarawakensis* (Terayama & Yamane, 1997) **comb. nov. to be proposed** from *Apenesia*  
*simulatus* (Evans, 1969) **comb. nov. to be proposed** from *Apenesia*  
*tridentata* (Kieffer, 1912) **comb. nov.** from *Apenesia*  
*yu* (Snelling, 1996) **com. nov.** from *Apenesia*

#### ***Protisobrachium* Benoît, 1957**

*pallidimanus* (Kieffer, 1912) **comb. nov. to be proposed** from *Apenesia*

#### ***Pseudisobrachium* Kieffer, 1904** (Figs. 13.O-P)

*beggsae* (Ward, 2013) **comb. nov. to be proposed** from *Apenesia*

#### ***Holepyris* Kieffer, 1904**

*coronatus* (Ashmead, 1893) **comb. nov. to be proposed** from *Apenesia*

#### **Tiphiidae, *Eirone* Westwood, 1844**

*harrisi* (Ward, 2013) **comb. nov. to be proposed** from *Apenesia*

#### *Conclusion*

Although *Apenesia* has been considered a genus of easy taxonomy history, morphological and phylogenetic analyses uncovered its evolutionary complexity. The difficulties inherent to taxon understanding are mostly related to the problem of male-female association in Pristocerinae. Absence of well-founded hypotheses to relate males and females, at both species and genus levels, can result in erroneous classification. Here we demonstrate that molecular tools and biological data such as couple taken during copulation, breeding observation and so on, can provide safe male-female association. The concept of *Apenesia* that we defend here corresponds to Westwood's (1874) concept of *Apenesia* females added to Terayama's (1995) concept of *Neoapenesia* males. That reinforces that the proposal of new generic taxa based only on females should be carefully done. In addition, better understanding of morphological structures in light of phylogenetic hypotheses may improve the delimitation of taxa at the genus level.

Genitalia structures have been used to clarify species delimitation notably in the last two decades. Now we got data to define many *Pristocerinae* genera by genital features as well. Phylogenetic studies such as Alencar & Azevedo (2013) and Zamprogno & Azevedo (2014) clearly demonstrate that understanding homologies in the flat wasps genitalia is essential to set relationships at taxonomic levels above species.

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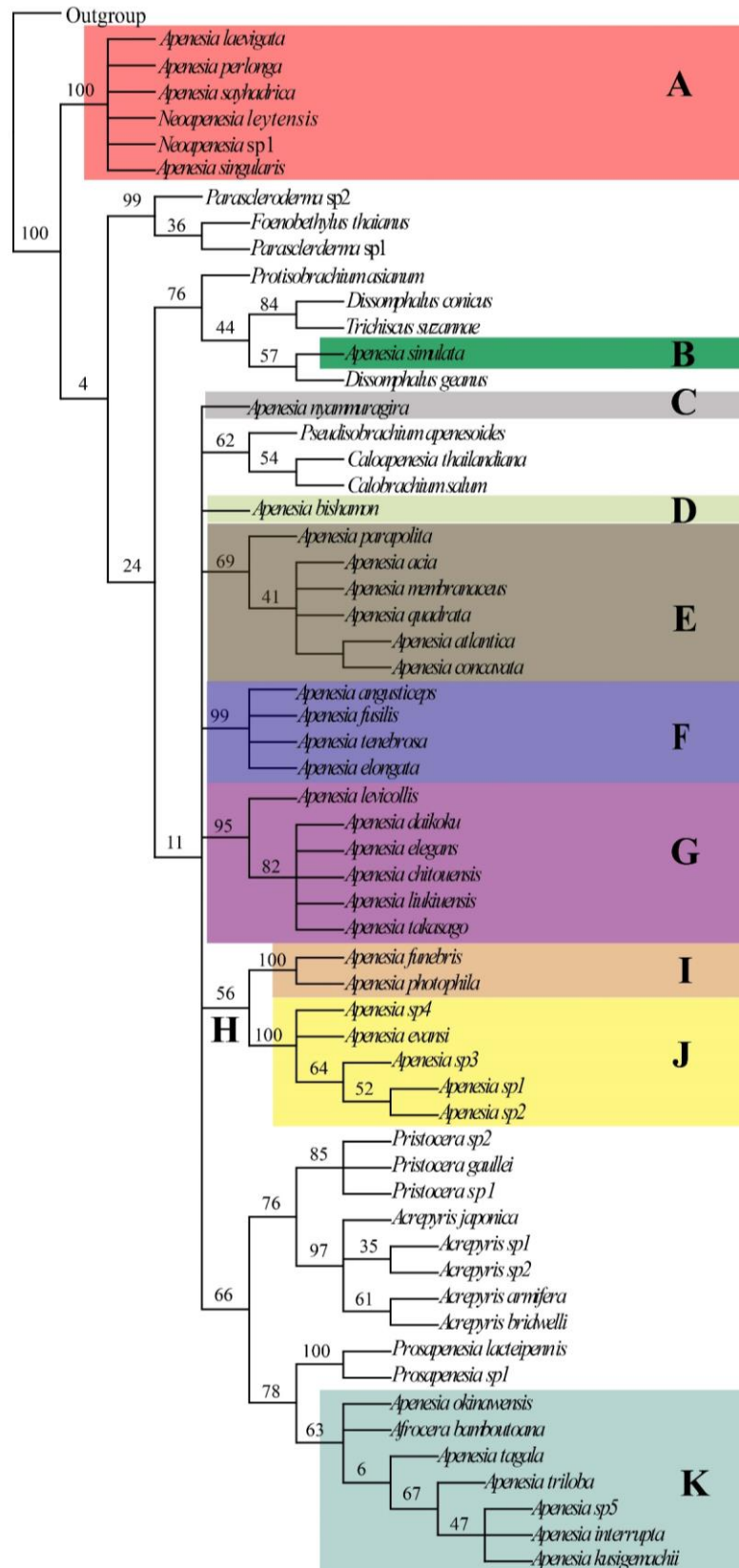
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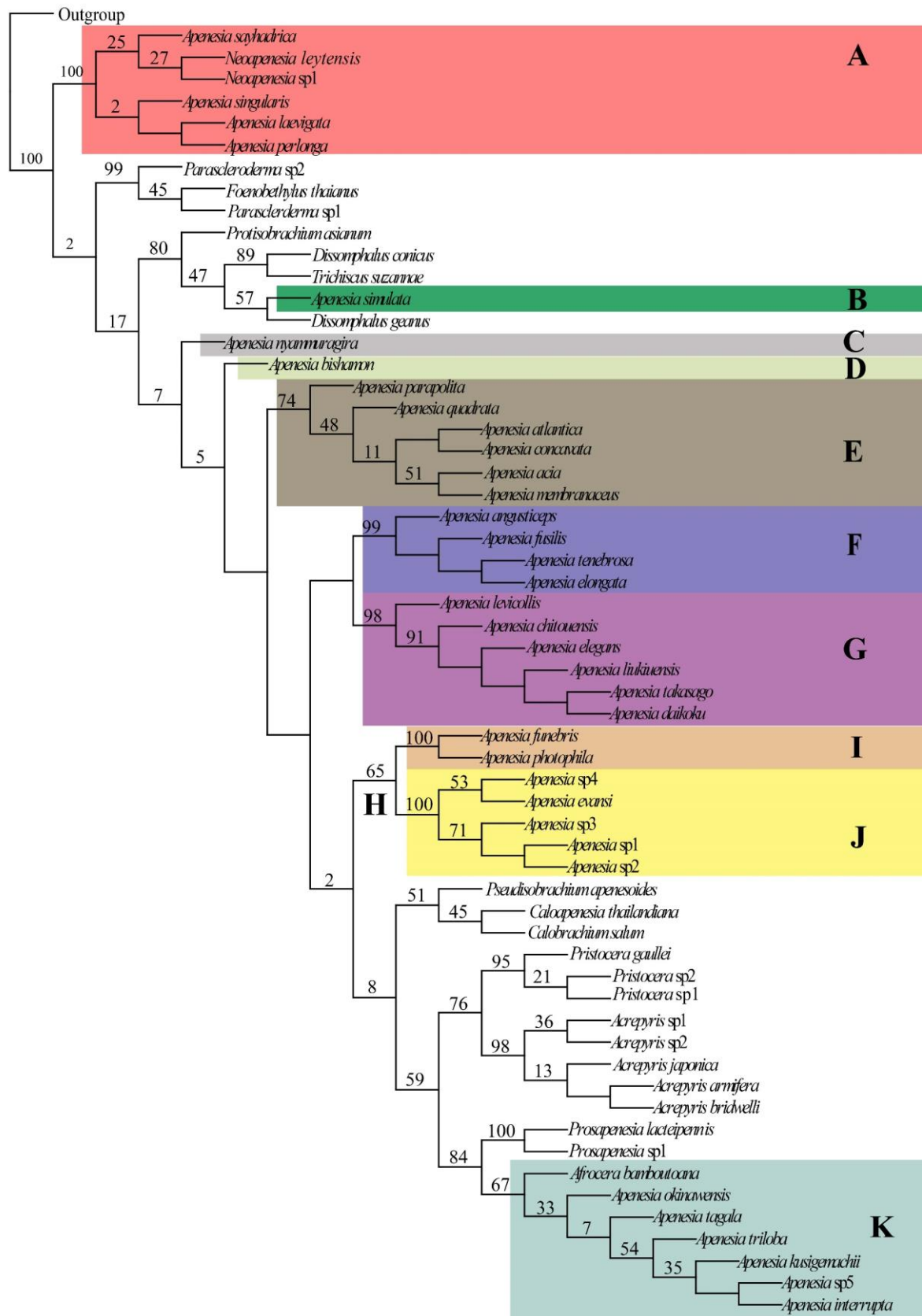
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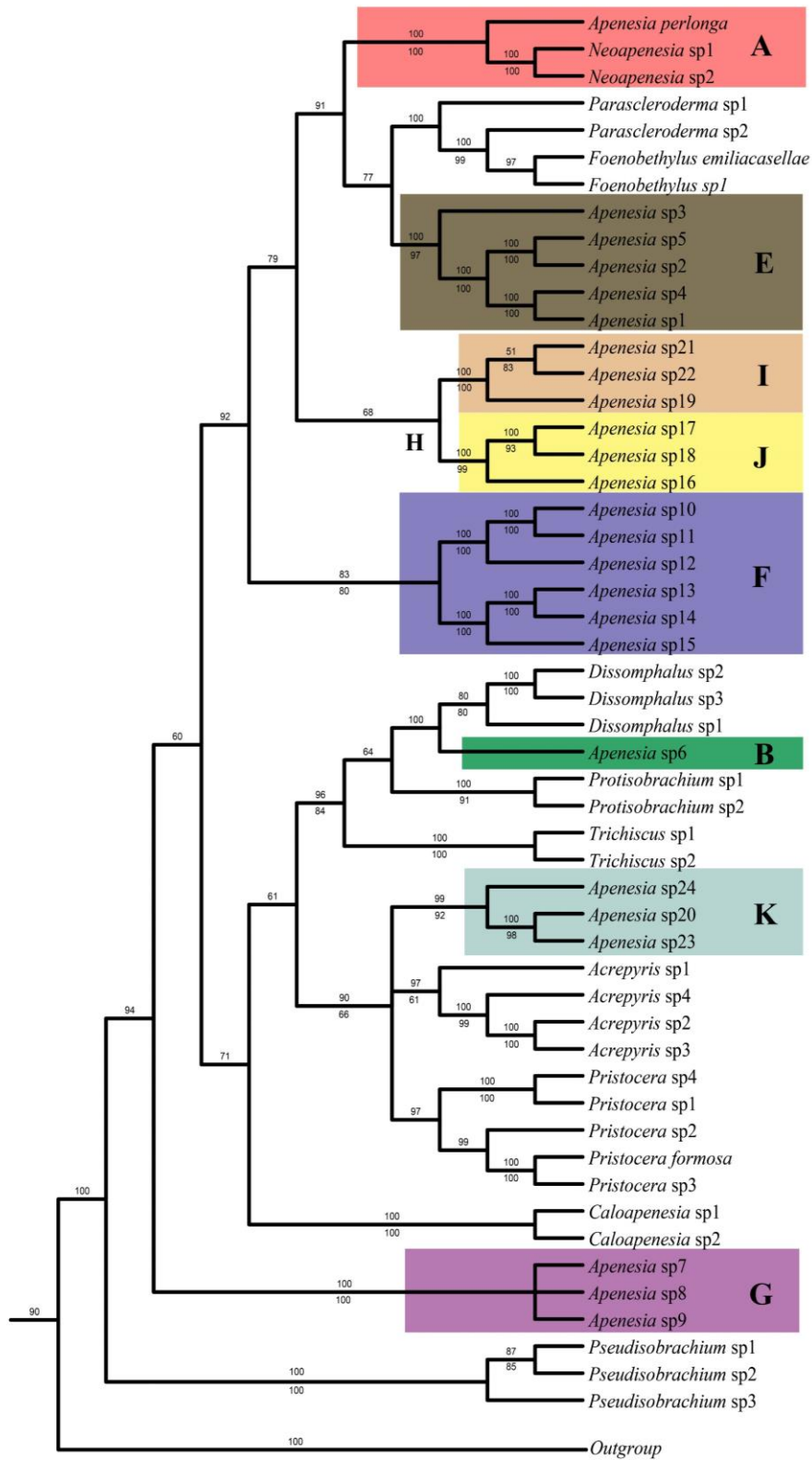


**Fig. 1.** Strict consensus of 496 equally parsimonious trees (664 steps, CI = 30, RI = 77) with equal weights based on morphological data. *Apenesia* lineages A-K are color detached. Values for GC frequencies (symmetric resampling) are shown above branches.



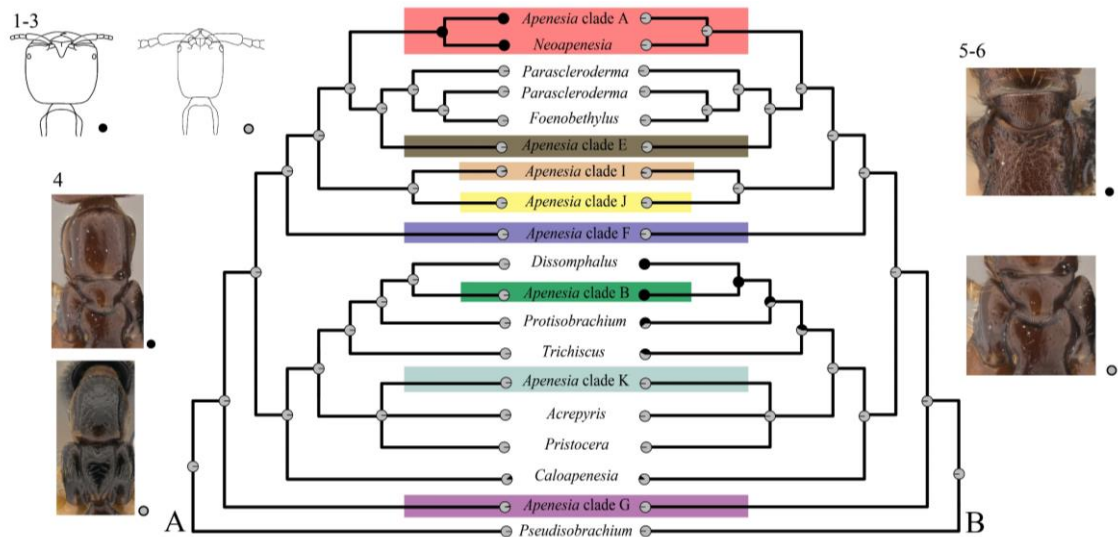
**Fig. 2.** Cladogram obtained under implied weighting scheme of the characters ( $k = 12.392578$ ). Values for GC frequencies (symmetric resampling) are shown above branches.



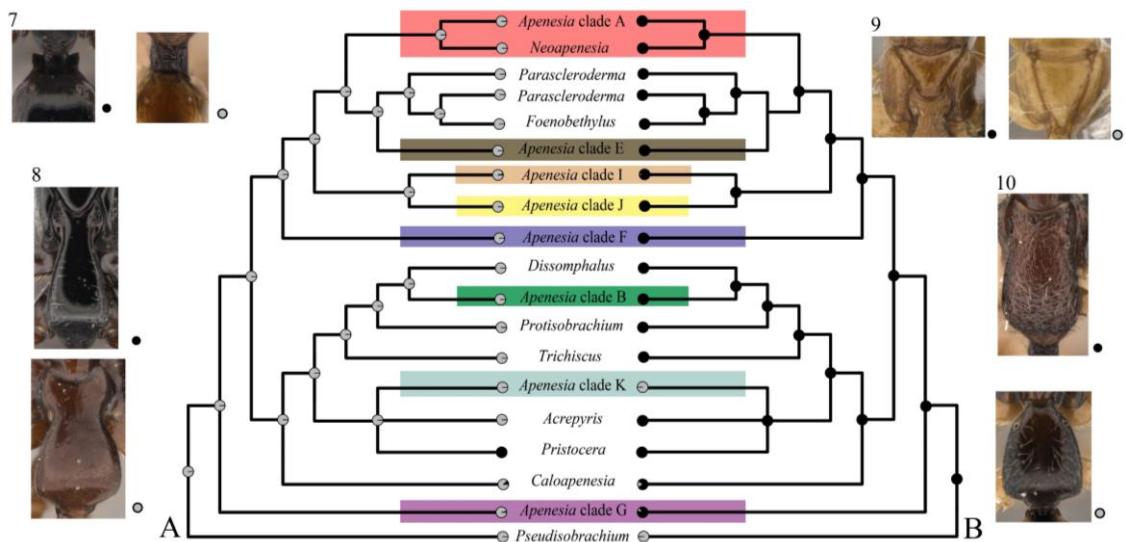


**Fig. 3.** Phylogenetic Bayesian and Maximum Likelihood reconstruction of Pristocerinae based on concatenated sequence data (COI and 28S rDNA). Values of posterior probability ( $\geq 60$ ) are shown above the branches. Maximum likelihood bootstrap values ( $\geq 80\%$ ) are represented below the branches.

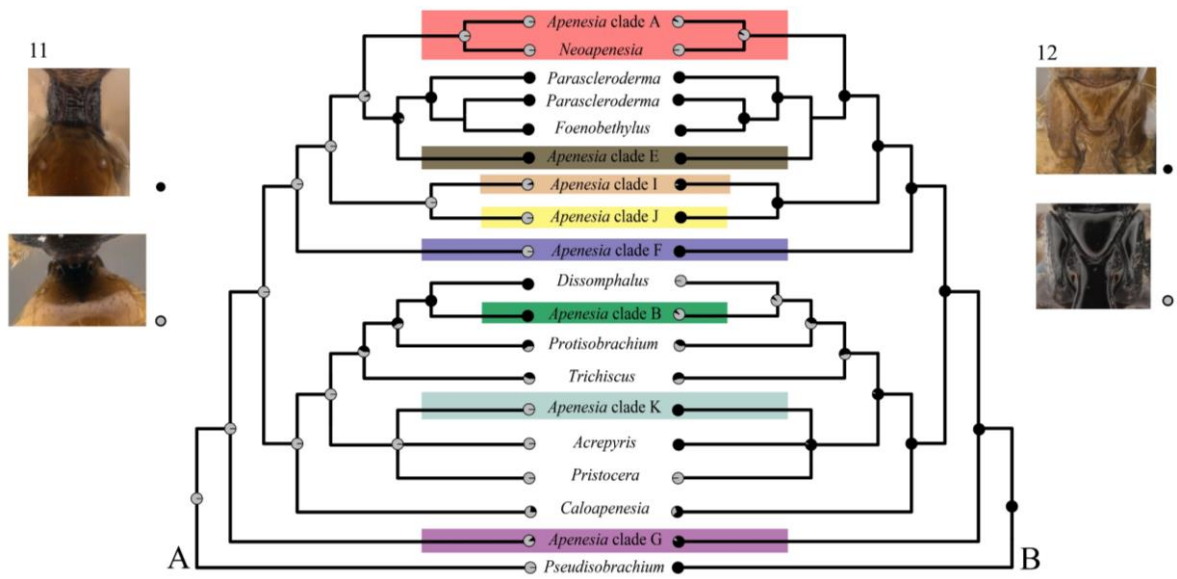




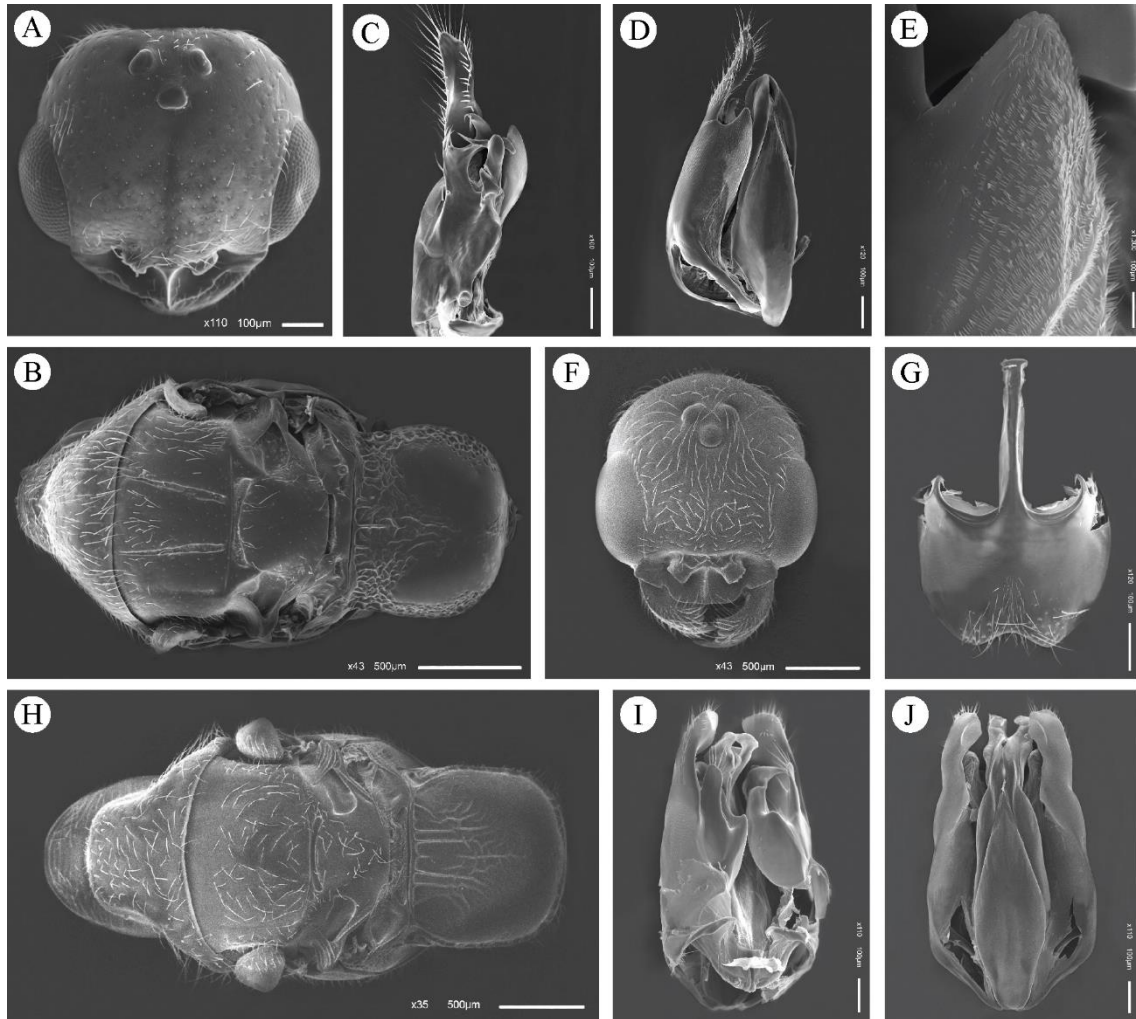
**Fig. 4.** Bayesian ancestral character state reconstruction (BI-ASR) of Pristocerinae female morphological characters. A. (1) head width (0 wider than mesosoma/ 1 narrower than mesosoma); (2) antenna size (0 short/ 1 long); (3) posterior margin of clypeus (0 surpassing toruli on frons/ 1 never surpassing toruli on frons); (4) Mesopleuron border in dorsal view (0 keeled/1 convex). B. (5) mesopleuron, dorsal view (0 visible/ 1 badly visible); (6) mesopleuron, shape (0 callus-like/ 1 elongate). Black circle (0); grey circle (1).



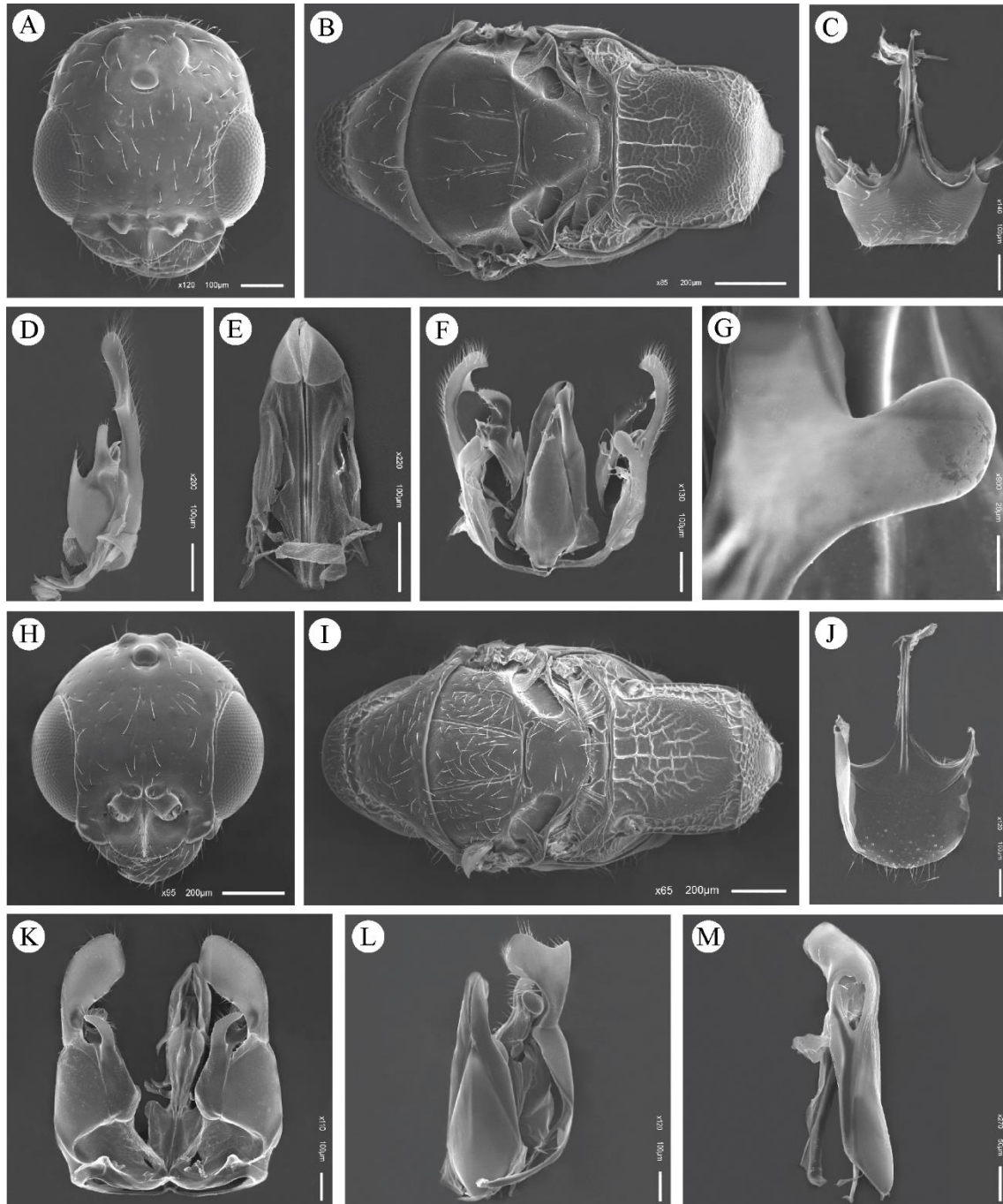
**Fig. 5.** Bayesian ancestral character state reconstruction (BI-ASR) of Pristocerinae female morphological characters. A. (7) petiolar body expansion (0 present/ 1 absent); (8) anterolateral fovea on metapectal-propodeal complex (0 present/ 1 absent). B. (9) mesonotum size (0 short/ 1 long); (10) anterior region of metapectal-propodeal complex width (0 wide/ 1 narrow). Black circle (0); grey circle (1).



**Fig. 6.** Bayesian ancestral character state reconstruction (BI-ASR) of Pristocerinae female main features. A. (11) petiole size (0 long/ 1 short). B. (12) anterior margin of mesonotum (0 concave/ 1 straight). Black circle (0); grey circle (1).

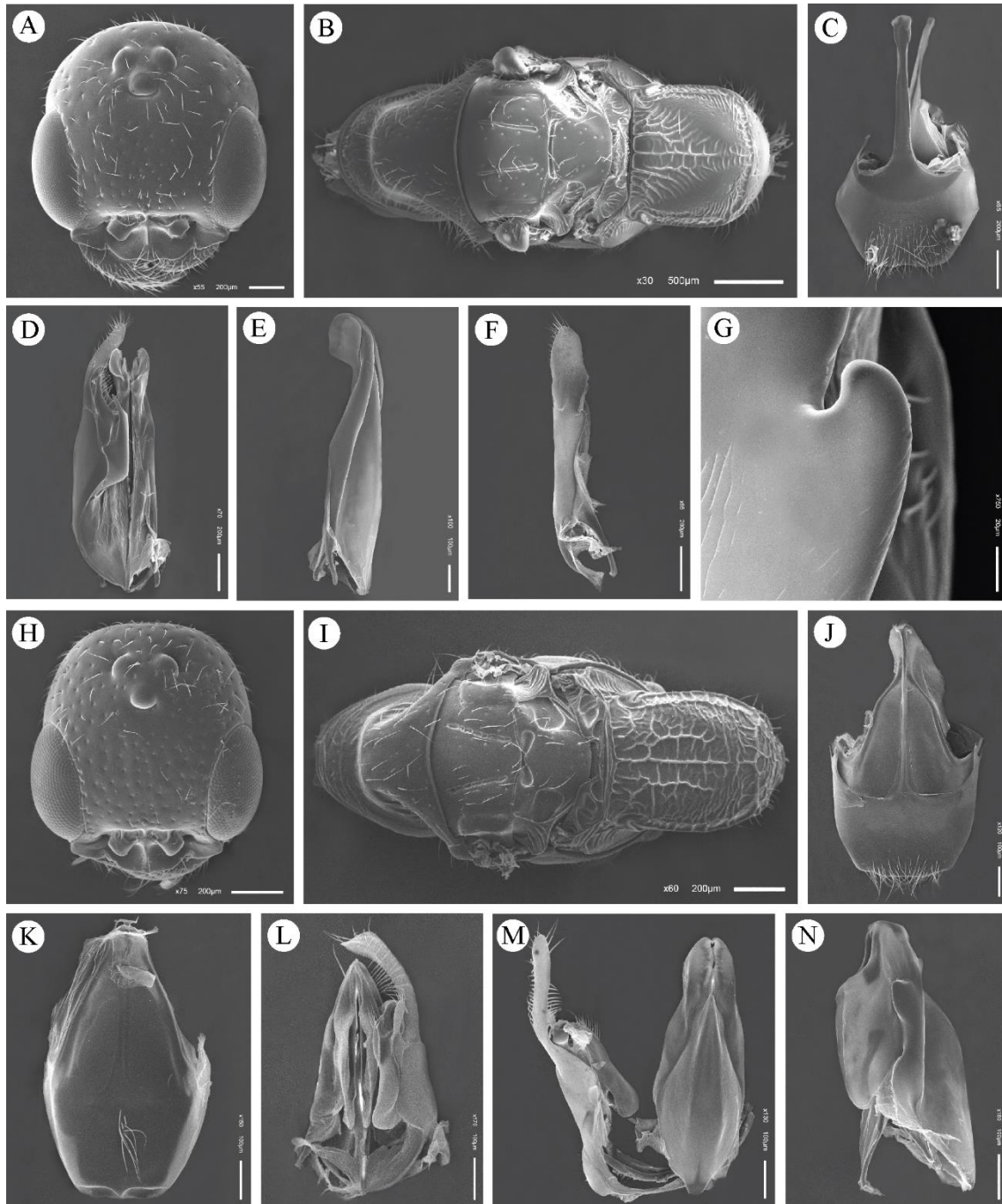


**Fig. 7.** Males. A-E *Apenesia*. A. Head, dorsal view; B. Mesosoma, dorsal view; C. Basivolsella, inner view; D. Genitalia, dorsal view; E. Apical projection of basiparamere, dorsal view. F-G *P4 gen. nov.* F. Head, dorsal view; G. Hypopygium, ventral view; H. Mesosoma, dorsal view, I. Genitalia, latero-ventral view; J. Genitalia, dorsal view.

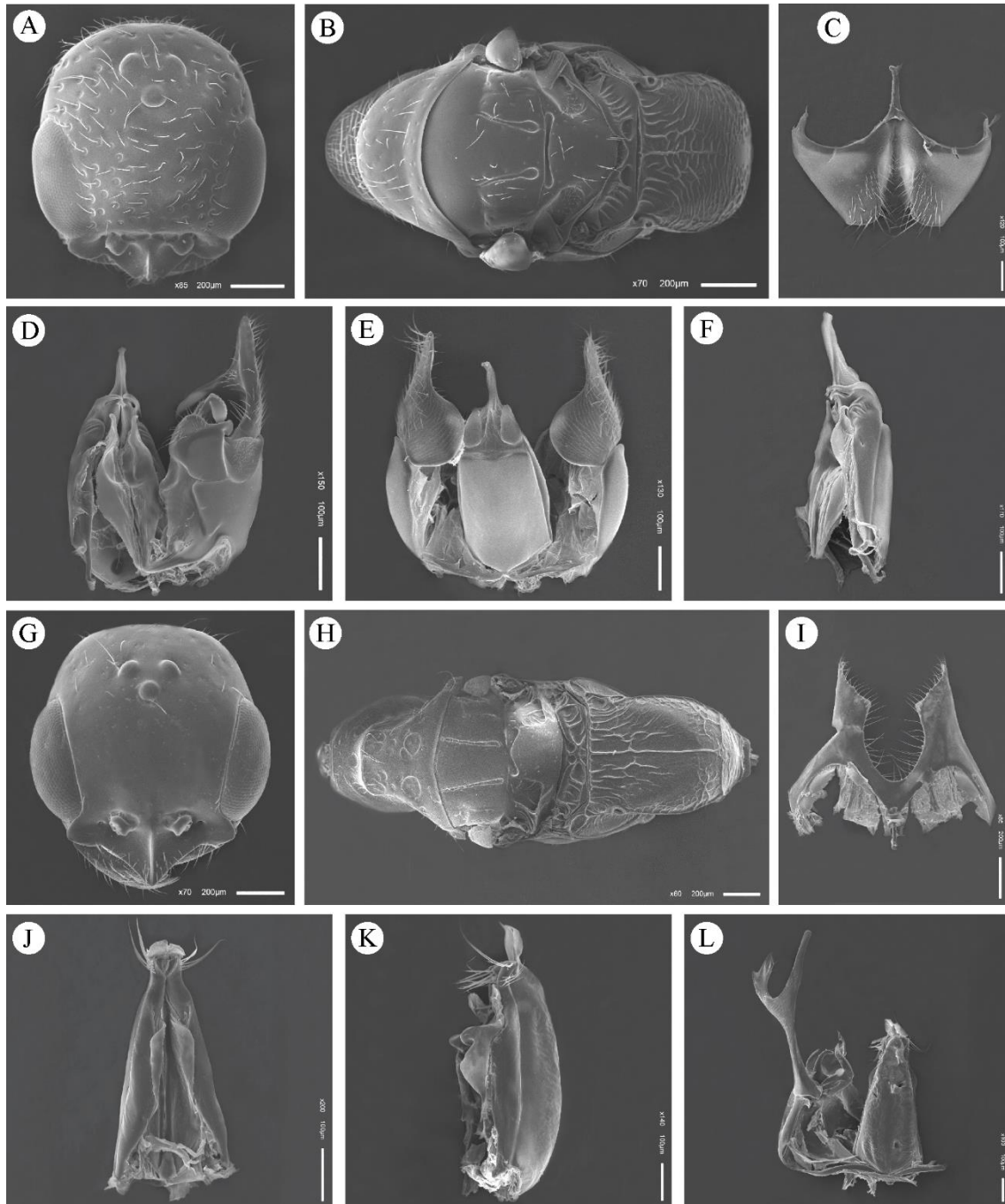


**Fig. 8.** Males. A-G *P6 gen. nov.* A. Head, dorsal view; B. Mesosoma, dorsal view; C. Hypopygium, ventral view; D. Basivolsella, ventral view; E. Aedeagus, ventral view; F. Genitalia, dorsal view; G. Projection between paramere and basiparamere, dorsal view. H-M *P1 stat. rev.* H. Head, dorsal view; I. Mesosoma, dorsal view, J. Hypopygium, dorsal view; K. Genitalia, ventral view; L. Genitalia, dorsal view; M. Aedeagus, lateral view.

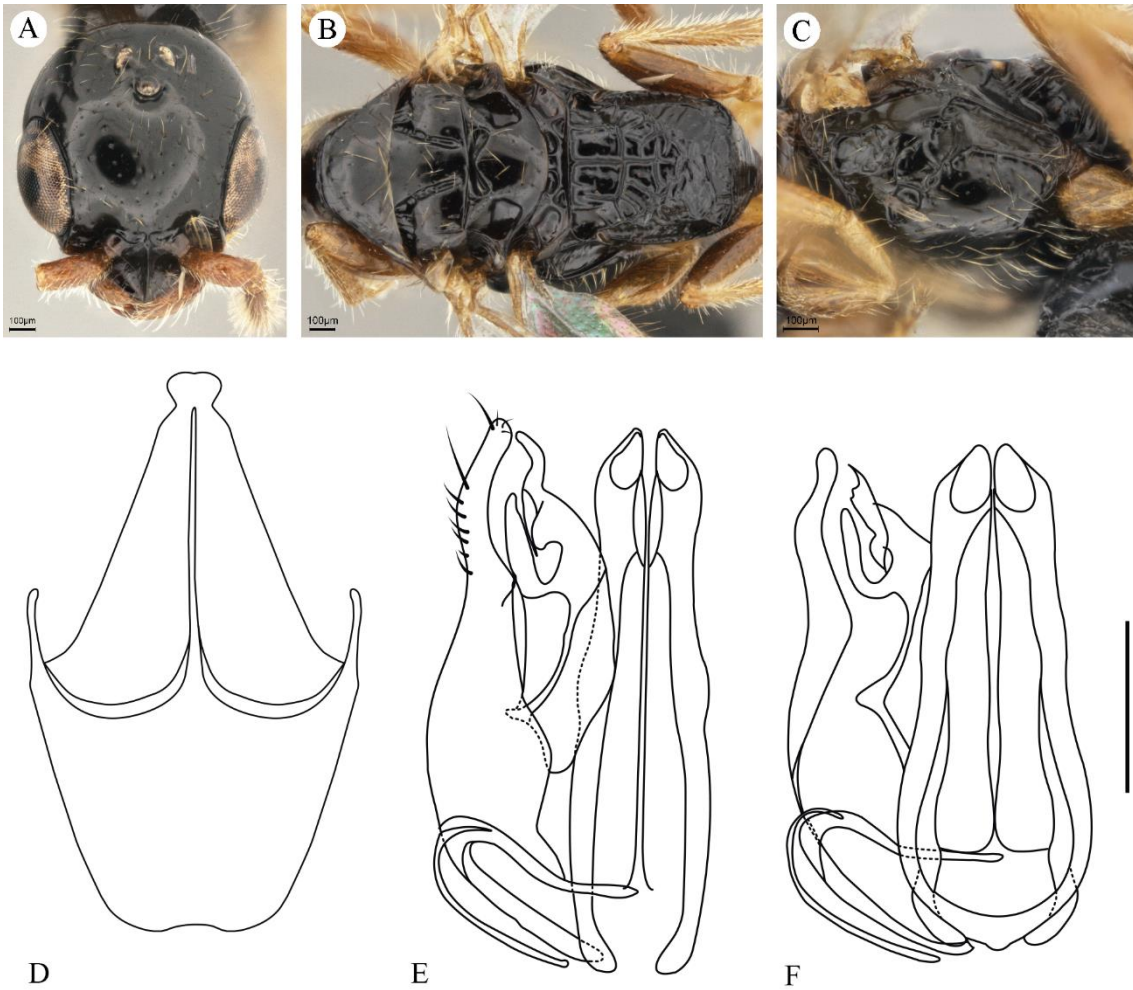




**Fig. 9.** Males. A-G *P5 gen. nov.* A. Head, dorsal view; B. Mesosoma, dorsal view; C. Hypopygium, ventral view; D. genitalia ventral view; E. Aedeagus, lateral view; F. Paramere and basiparamere, dorsal view; G. Projection between paramere and basiparamere, dorsal view. H-N *P7 gen. nov.* H. Head, dorsal view; I. Mesosoma, dorsal view; J. Hypopygium, dorsal view; K. Hypopygium, ventral view; L. Genitalia, ventral view; M. Genitalia, dorsal view; N. Aedeagus, lateral view.

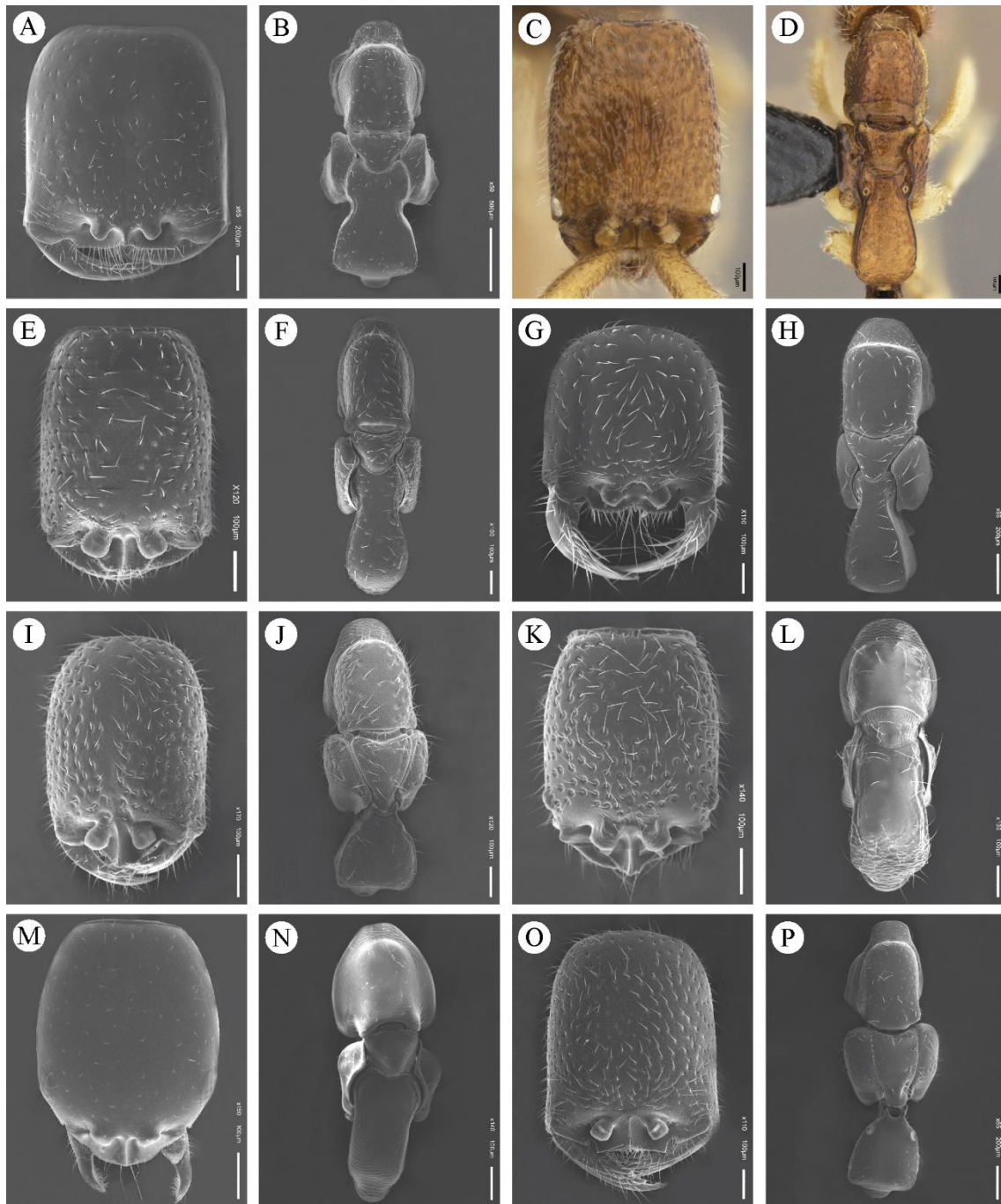


**Fig. 10.** Males. A-G *P3 stat. rev.* A. Head, dorsal view; B. Mesosoma, dorsal view; C. Hypopygium, ventral view; D. Genitalia, ventral view; E. Genitalia, dorsal view; F. Aedeagus, lateral view. G-L *P10 gen. nov.* G. Head, dorsal view; H. Mesosoma, dorsal view; I. Hypopygium, ventral view; J. Aedeagus, ventral view; K. Aedeagus, lateral view; L. Genitalia, dorsal view.



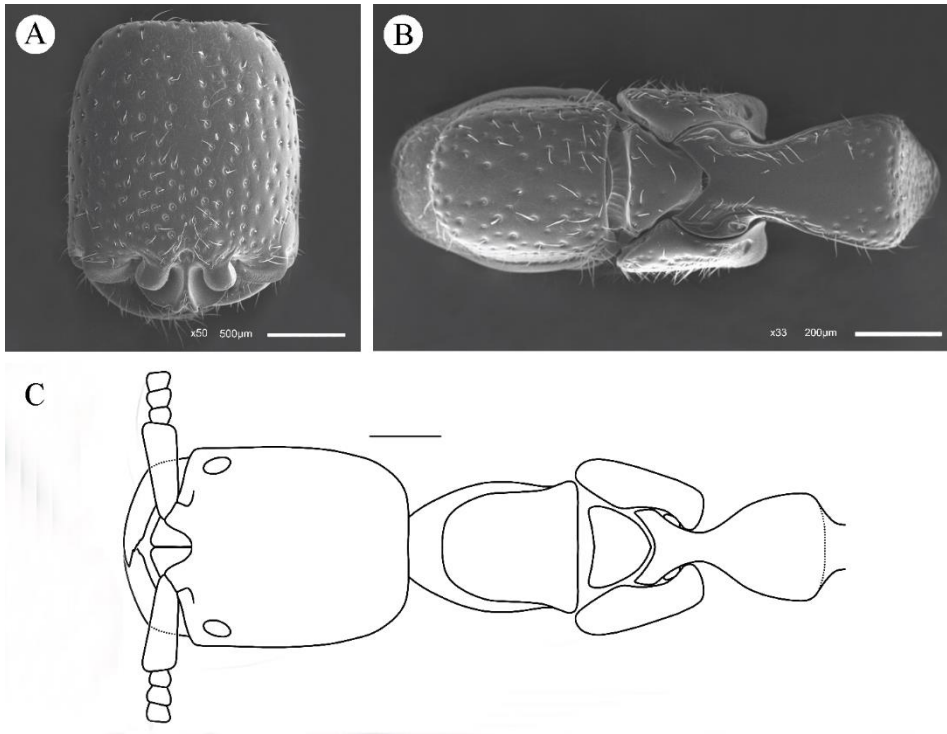
**Fig. 11.** Male. A-F *P9* gen. nov. A. Head, dorsal view; B. Mesosoma, dorsal view, C. Mesopleuron, lateral view; D. Hypopygium, ventral view; E. Genitalia, ventral view; F. Genitalia, dorsal view. (D-E scale bar 250 $\mu$ m)





**Fig. 12.** Females. A-B *Apenesia*. A. Head, dorsal view; B. Mesosoma, dorsal view. C-D *P4 gen. nov.* C. Head, dorsal view; D. Mesosoma, dorsal view. E-F *P6 gen. nov.* E. Head, dorsal view; F. Mesosoma, dorsal view. G-H *P1 stat. rev.* G. Head, dorsal view; H. Mesosoma, dorsal view. I-J *P3 stat. rev.* I. Head, dorsal view; J. Mesosoma, dorsal view. K-L *Dissomphalus* K. Head, dorsal view; L. Mesosoma, dorsal view. M-N *Parascleroderma* M. Head, dorsal view; N. Mesosoma, dorsal view. O-P *Pseudisobrachium* O. Head, dorsal view; P. Mesosoma, dorsal view





**Fig. 13.** Females. A-B *Pristocera* A. Head, dorsal view; B. Mesosoma, dorsal view. C *Acrepyris*, body, dorsal view.

Tab. 1. List of *Apenesia* species examined with emphasis in which types were directly analyzed. When never it was not possible to check the type, we studied the description provided in the literature. Only 18 species were analyzed indirectly by literature data (around 9,4%). Male-female association is reported as \* found in phoretic copulation and \*\* biology data.

#	Original name to <i>Apenesia</i>	Sex	Collection	Occurrence	Study
1	<i>acia</i> , <i>Apenesia</i> Lanes & Azevedo, 2004	♂	MPEG	Neotropical	holotype seen
2	<i>acuta</i> , <i>Neopristocera</i> Benoit, 1957	♂	MRAC	Afrotropical	holotype seen
3	<i>aegyptia</i> , <i>Propristocera</i> Kieffer, 1921	♂	NHMW	Afrotropical	holotype seen
4	<i>alutacea</i> , <i>Apenesia</i> Evans, 1963	♂	AEIC	Neotropical	holotype seen
5	<b><i>amazonica</i>, <i>Apenesia</i> Westwood, 1874</b> (Type species of <i>Apenesia</i> )	♀	OXUM	Neotropical	holotype seen
6	<i>amoenia</i> , <i>Apenesia</i> Evans, 1963	♀	USNM	Neotropical	holotype seen
7	<i>angustata</i> , <i>Propristocera</i> Evans, 1958	♂	USNM	Neotropical	holotype seen
8	<i>angusticeps</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
9	<i>apicilata</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
10	<i>atlantica</i> , <i>Apenesia</i> Correa & Azevedo, 2006	♂	MZSP	Neotropical	holotype seen
11	<i>auricula</i> , <i>Apenesia</i> Lanes & Azevedo, 2004	♂	INPA	Neotropical	holotype seen
12	<i>aurita</i> , <i>Apenesia</i> Waichert & Azevedo, 2003	♂	UFES	Neotropical	holotype seen
13	<i>australiensis</i> , <i>Pseudisobrachium</i> Kieffer, 1906	♂	?	Australian	type lost, literature
14	<i>beggasae</i> , <i>Apenesia</i> Ward, 2013	♂♀	NZAC/ LUNZ	Australian	literature
15	<i>bicolor</i> , <i>Apenesia</i> Vargas & Terayama, 2002	♀	IAVH	Neotropical	holotype seen
16	<i>bishamon</i> , <i>Apenesia</i> Terayama, 1999	♂	NIAES	Palaeartic	holotype seen
17	<i>brasiliensis</i> , <i>Rhabdepyris</i> Kieffer, 1909	♂	CASC	Neotropical	holotype seen
	<b>= <i>peruana</i>, <i>Apenesia</i> Evans, 1963</b> (= <i>Cleistepyris punctatus</i> Kieffer, 1910, replacement name) (type species of <i>Cleistepyris</i> ) sin. junior = <i>brasiliensis</i> )	♂	ZMBH	Neotropical	holotype seen
18	<i>browni</i> , <i>Apenesia</i> Evans, 1964	♀	MCZH	Neotropical	holotype seen
19	<i>bugabensis</i> , <i>Epyris</i> Cameron, 1888	♂	BMNH	Neotropical	holotype seen
20	<i>caribbeana</i> , <i>Apenesia</i> Evans, 1969	♂	USNM	Neotropical	holotype seen
21	<i>carinicollis</i> , <i>Apenesia</i> Terayama, 2004	♂	PMAE	Oriental	holotype seen
22	<i>chilena</i> , <i>Apenesia</i> Evans, 1967	♂	CNCI	Neotropical	holotype seen
23	<i>chiricahua</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
				Nearctic	
24	<i>chitouensis</i> , <i>Apenesia</i> Terayama, 1996	♂	NIAES	Palaeartic	holotype seen
25	<i>chontalica</i> , <i>Apenesia</i> Westwood, 1881	♀	OXUM	Neotropical	holotype seen
26	<i>clara</i> , <i>Apenesia</i> Xu, Terayama & He, 2002	♂	ZU	Oriental	literature
27	<i>clypeata</i> , <i>Apenesia</i> Leal & Azevedo, 2001	♂	DZUP	Neotropical	holotype seen
28	<i>coarctata</i> , <i>Holepyris</i> Kieffer, 1909	♂	CASC	Neotropical	holotype seen
29	<i>cochise</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
30	<i>columbana</i> , <i>Pristocera</i> Westwood, 1874	♂	OXUM	Neotropical	holotype seen
31	<i>concovata</i> , <i>Apenesia</i> Corrêa & Azevedo, 2001	♂	UFES	Neotropical	holotype seen
32	<i>conradi</i> , <i>Apenesia</i> Kieffer, 1912	♀	ZMHB	Afrotropical	syntypes seen
33	<i>consobrina</i> , <i>Cleistepyris</i> Kieffer, 1922	♂	?	Oriental	type lost, literature
34	<i>coronata</i> , <i>Apenesia</i> Ashmead, 1893	♂	USNM	Nearctic	literature
35	<i>crenulata</i> , <i>Propristocera</i> (Kieffer, 1909)	♂	CASC	Neotropical	holotype seen
36	<i>cubensis</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
37	<i>curvata</i> , <i>Apenesia</i> Lanes & Azevedo, 2004	♂	INPA	Neotropical	holotype seen
38	<i>cusco</i> , <i>Apenesia</i> Evans, 1966	♂	MCZH	Neotropical	holotype seen
39	<i>daikoku</i> , <i>Apenesia</i> Terayama, 1999	♂	NIAES	Palaeartic	holotype seen
40	<i>delicata</i> , <i>Apenesia</i> Evans, 1963	♀	USNM	Neotropical	holotype seen
41	<i>denticulata</i> , <i>Apenesia</i> Evans, 1963 (= <i>Propristocera tridentata</i> , replacement name)	♂	USNM	Neotropical	holotype seen

Tab. 1. List of *Apenesia* species examined with emphasis in which types were directly analyzed. When never it was not possible to check the type, we studied the description provided in the literature. Only 18 species were analyzed indirectly by literature data (around 9,4%). Male-female association is reported as \* found in phoretic copulation and \*\* biology data.

#	Original name to <i>Apenesia</i>	Sex	Collection	Occurrence	Study
42	<i>dissomphaloides</i> , <i>Apenesia</i> Evans, 1963	♂	INHS	Neotropical	holotype seen
				Nearctic	
43	<i>distincta</i> , <i>Apenesia</i> Corrêa & Azevedo, 2001	♂	UFES	Neotropical	holotype seen
44	<i>dominica</i> , <i>Apenesia</i> Evans, 1963	♀	MCZH	Neotropical	holotype seen
45	<i>electriphila</i> , <i>Apenesia</i> Cockerell, 1917 (fossil)	♂	BMNH	Oriental	holotype seen
46	<i>elegans</i> , <i>Apenesia</i> Terayama, 1999	♂	NIAES	Palaeartic	holotype seen
				Oriental	
47	<i>elongata</i> , <i>Apenesia</i> Evans, 1963	♂♀*	USNM	Neotropical	holotype seen
48	<i>evansi</i> , <i>Apenesia</i> Gordh, 1990	♂♀*	QMSB	Australian	holotype seen
49	<i>exigua</i> , <i>Apenesia</i> Correa & Azevedo, 2006	♂	MZSP	Neotropical	holotype seen
50	<i>exilis</i> , <i>Apenesia</i> Evans, 1963	♂	INHS	Nearctic	holotype seen
51	<i>flammicornis</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
52	<i>flavipes</i> , <i>Apenesia</i> Cameron, 1888	♀	BMNH	Neotropical	holotype seen
53	<i>flaviscapus</i> , <i>Apenesia</i> Evans, 1969	♂	USNM	Neotropical	holotype seen
54	<i>forchhammeri</i> , <i>Apenesia</i> Krombein, 1989	♀	USNM	Afrotropical	holotype seen
	<i>forchhammeri</i> , <i>Apenesia</i> Krombein, 1989	♂	USNM	Afrotropical	non type seen
55	<i>formosa</i> , <i>Apenesia</i> Vargás & Terayama, 2002	♀	IAVH	Neotropical	holotype seen
56	<i>formosimonticola</i> , <i>Apenesia</i> Terayama, 1996	♂	NSMT	Palaeartic	literature
57	<i>foutsii</i> , <i>Apenesia</i> Gordh & Móczár, 1990 (= <i>Misepyris flavipes</i> Fouts, 1930, replacement name)	♂	USNM	Oriental	holotype seen
58	<i>fulvicollis</i> , <i>Pristocera</i> Westwood, 1874	♂	OXUM	Neotropical	holotype seen
	= <i>subangulata</i> , <i>Apenesia</i> Azevedo & Batista, 2002 sin. junior = <i>fulvicollis</i>	♂	UFES	Neotropical	holotype seen
59	<i>funebri</i> , <i>Apenesia</i> Evans, 1963	♂	USNM	Neotropical	holotype seen
60	<i>fusilis</i> , <i>Apenesia</i> Corrêa & Azevedo, 2001	♂	UFES	Neotropical	holotype seen
61	<i>guatemalensis</i> , <i>Apenesia</i> Evans, 1963	♂	USNM	Neotropical	holotype seen
62	<i>harrisi</i> , <i>Apenesia</i> Ward, 2013	♀	NZAC	Australian	literature
63	<i>hepatica</i> , <i>Apenesia</i> Correa & Azevedo, 2006	♂	MZSP	Neotropical	holotype seen
64	<i>inca</i> , <i>Apenesia</i> Evans, 1963	♂	CUIC	Neotropical	holotype seen
65	<i>insulana</i> , <i>Apenesia</i> Evans, 1969	♂	CNCI	Neotropical	holotype seen
66	<i>interrupta</i> , <i>Propristocera</i> Kieffer, 1905 (type species of <i>Propristocera</i> )	♂	HNHM	Oriental	holotype seen
67	<i>intricata</i> , <i>Clestepyris</i> Kieffer, 1922	♂	?	Oriental	type lost, literature
68	<i>jamaica</i> , <i>Apenesia</i> Evans, 1969	♂	CNCI	Neotropical	holotype seen
69	<i>juncea</i> , <i>Apenesia</i> Evans, 1966	♂	MCZH	Neotropical	holotype seen
70	<i>kaguyahime</i> , <i>Apenesia</i> Terayama, 2006	♀	NIAES	Palaeartic	holotype seen
71	<i>kakaniensis</i> , <i>Apenesia</i> Terayama, 2004	♂	PMAE	Oriental	holotype seen
72	<i>ktmdana</i> , <i>Apenesia</i> Terayama, 2004	♂	PMAE	Oriental	holotype seen
73	<i>kusigematii</i> , <i>Apenesia</i> Terayama, 1999	♂	NIAES	Palaeartic	holotype seen
74	<i>lacerata</i> , <i>Apenesia</i> Evans, 1969	♂	FIML	Neotropical	holotype seen
75	<i>laevicornis</i> , <i>Apenesia</i> Evans, 1969	♂	FIML	Neotropical	holotype seen
76	<i>laevigata</i> , <i>Propristocera</i> Evans, 1958	♂	USNM	Neotropical	holotype seen
77	<i>lapsa</i> , <i>Apenesia</i> Lanes & Azevedo, 2004	♂	MPEG	Neotropical	holotype seen
78	<i>lathrobioides</i> , <i>Epyris</i> Westwood, 1874	♂	OXUM	Oriental	holotype seen
79	<i>leucophthalma</i> , <i>Apenesia</i> Evans, 1964	♀	MCZH	Neotropical	holotype seen
80	<i>levicollis</i> , <i>Propristocera</i> Kieffer, 1905	♂	HNHM	Oriental	holotype seen
81	<i>levis</i> , <i>Apenesia</i> Kieffer, 1904	♀	MCSN	Afrotropical	holotype seen

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#	Original name to <i>Apenesia</i>	Sex	Collection	Occurrence	Study
82	<i>lilloana</i> , <i>Apenesia</i> Evans, 1969	♂	FIML	Neotropical	holotype seen
83	<i>liukueiensis</i> , <i>Apenesia</i> Terayama, 1996	♂	NIAES	Palaeartic	holotype seen
84	<i>lobata</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
85	<i>longa</i> , <i>Apenesia</i> Ramos & Azevedo, 2009	♂	CNCI	Neotropical	holotype seen
86	<i>luteola</i> , <i>Apenesia</i> Evans, 1969	♂	ACC	Neotropical	holotype seen
87	<i>luzonica</i> , <i>Misepyris</i> Fouts, 1930	♂	USNM	Oriental	holotype seen
88	<i>magna</i> , <i>Apenesia</i> Ramos & Azevedo, 2009	♂	CNCI	Neotropical	holotype seen
89	<i>malaitensis</i> , <i>Apenesia</i> Brues, 1918	♀	MCZH	Solomon	holotype seen
90	<i>malinche</i> , <i>Apenesia</i> Evans, 1963	♂	SEMC	Neotropical Nearctic	holotype seen
91	<i>martini</i> , <i>Apenesia</i> Evans, 1963	♂	CNCI	Nearctic	holotype seen
92	<i>maya</i> , <i>Apenesia</i> Evans, 1963	♂	USNM	Neotropical	holotype seen
93	<i>megaventris</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
94	<i>meifuiuae</i> , <i>Apenesia</i> Terayama, 1996	♂	NIAES	Palaeartic	holotype seen
95	<i>membranaceus</i> , <i>Apenesia</i> Lanes & Azevedo, 2004	♂	INPA	Neotropical	holotype seen
96	<i>mexicana</i> , <i>Epyris</i> Cameron, 1904	♂	BMNH	Neotropical	holotype seen
97	<i>microchela</i> , <i>Pristocera</i> Kieffer, 1911 (type species of <i>Dipristocera</i> )	♂	BMNH	Neotropical	holotype seen
98	<i>mindanaensis</i> , <i>Misepyris</i> Fouts, 1930	♂	USNM	Oriental	holotype seen
99	<i>minima</i> , <i>Cleistepyris</i> Kieffer, 1913	♂	?	Oriental	type lost, literature
100	<i>minor</i> , <i>Cleistepyris</i> Kieffer, 1913	♂	MNH	Oriental	holotype seen
101	<i>modesta</i> , <i>Scleroderma</i> Smith, 1864	♀	OXUM	Oriental	holotype seen
102	<i>mohave</i> , <i>Apenesia</i> Evans, 1963	♂	SEMC	Neotropical	holotype seen
103	<i>neotropica</i> , <i>Cleistepyris</i> Kieffer, 1910	♂	CASC	Neotropical	holotype seen
104	<i>nepalensis</i> , <i>Apenesia</i> Terayama, 2004	♂	PMAE	Oriental	holotype seen
105	<i>nigra</i> , <i>Apenesia</i> Kieffer, 1904	♀	MCSN	Afrotropical	holotype seen
106	<i>nitida</i> , <i>Cleistepyris</i> Kieffer, 1910	♂	ZMBH	Neotropical	holotype seen
	<i>nitida</i> , <i>Cleistepyris</i> Kieffer, 1910	♀*	AMNH	Neotropical	alotype seen
107	<i>nyama</i> , <i>Propristocera</i> Benoit, 1957	♂	MRAC	Afrotropical	holotype seen
108	<i>nyamuragira</i> , <i>Propristocera</i> Benoit, 1957	♂	MRAC	Afrotropical	holotype seen
109	<i>ocullata</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
110	<i>okinawensis</i> , <i>Apenesia</i> Terayama, 1999	♂	NIAES	Palaeartic Oriental	holotype seen
111	<i>olmecca</i> , <i>Apenesia</i> Evans, 1963	♂	CASC	Neotropical	holotype seen
112	<i>ornata</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
113	<i>otohime</i> , <i>Apenesia</i> Terayama, 1999	♀	NIAES	Palaeartic	holotype seen
114	<i>pallidicornis</i> , <i>Apenesia</i> Evans, 1963	♂	CMNH	Neotropical	holotype seen
115	<i>pallidimanus</i> , <i>Pristocera</i> Kieffer, 1912	♂	BMNH	Afrotropical	holotype seen
116	<i>pallidula</i> , <i>Apenesia</i> Evans, 1963	♂	SEMC	Nearctic	holotype seen
117	<i>pando</i> , <i>Apenesia</i> Evans, 1963 (= <i>Plutobethylus percurrens</i> Kieffer, 1910, replacement name)	♂	ZMBH	Neotropical	holotype seen
118	<i>paradoxa</i> , <i>Apenesia</i> Evans, 1963	♀	USNM	Neotropical	holotype seen
	<i>paraensis</i> , <i>Propristocera</i> Kieffer, 1910	♂	Baker?	Neotropical	non type seen at USNM
119	= <i>boliviensis</i> , <i>Propristocera</i> Ogloblin, 1938 sin. junior = <i>paraensis</i>	♂	MACN	Neotropical	holotype seen
	= <i>truncaticeps</i> , <i>Cleistepyris</i> Kieffer, 1910 sin. junior = <i>paraensis</i>	♂	ZMBH	Neotropical	holotype seen
120	<i>parapolita</i> , <i>Apenesia</i> Evans, 1963 (= <i>Propristocera polita</i> Evans, 1958, replacement name)	♂	AEIC	Nearctic	holotype seen

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#	Original name to <i>Apenesia</i>	Sex	Collection	Occurrence	Study
121	<i>parasitica</i> , <i>Scleroderma</i> Smith, 1864	♀	OXUM	Oriental	holotype seen
122	<i>patens</i> , <i>Apenesia</i> Correa & Azevedo, 2006	♂	MZSP	Neotropical	holotype seen
123	<i>peccata</i> , <i>Apenesia</i> Ramos & Azevedo, 2009	♂	CNCI	Neotropical	holotype seen
124	<i>pectinata</i> , <i>Apenesia</i> Correa & Azevedo, 2006	♂	MZSP	Neotropical	holotype seen
125	<i>peculiaris</i> , <i>Apenesia</i> Evans, 1963	♂	SEMC	Neotropical	holotype seen
126	<i>perconcava</i> , <i>Apenesia</i> Ramos & Azevedo, 2009	♂	CNCI	Neotropical	holotype seen
127	<i>percurrans</i> , <i>Propriocera</i> Kieffer, 1905	♂	HNHM	Oriental	holotype seen
128	<i>perlonga</i> , <i>Apenesia</i> Correa & Azevedo, 2006	♂	MZSP	Neotropical	holotype seen
129	<i>permaxima</i> , <i>Apenesia</i> Ramos & Azevedo, 2009	♂	CNCI	Neotropical	holotype seen
130	<i>philippinensis</i> , <i>Cleistopyris</i> Kieffer, 1913	♂♀*	Baker	Oriental	type lost, literature
131	<i>photophila</i> , <i>Pristocera</i> Oglöblin, 1930	♂	MCZH	Neotropical	holotype seen
132	<i>pilicornis</i> , <i>Apenesia</i> Evans, 1963	♂	USNM	Neotropical	holotype seen
133	<i>pima</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Nearctic	holotype seen
134	<i>pingtungensis</i> , <i>Apenesia</i> Terayama, 1996	♂	NSMT	Palaeartic	literature
135	<i>polita</i> , <i>Misepyris</i> Fouts, 1930	♂	USNM	Oriental	holotype seen
136	<i>proxima</i> , <i>Apenesia</i> Kieffer, 1904	♂	MCSN	Australian	holotype seen
137	<i>pseudosuzannae</i> , <i>Propriocera</i> Benoit, 1957	♂	MRAC	Oriental	holotype seen
138	<i>pulchella</i> , <i>Apenesia</i> Terayama, 2004	♂	PMAE	Oriental	holotype seen
139	<i>punctalata</i> , <i>Apenesia</i> Krombein, 1989 (= <i>Apenesia punctata</i> Kieffer, 1904, replacement name)	♀	MCSN	Afrotropical	holotype seen
140	<i>punctata</i> , <i>Epyris</i> Cameron, 1888	♂	BMNH	Neotropical	holotype seen
141	<i>pygmaea</i> , <i>Apenesia</i> Evans, 1969	♂	FIML	Neotropical	holotype seen
142	<i>quadrata</i> , <i>Apenesia</i> Evans, 1963	♂	CUIC	Neotropical	holotype seen
	<i>quadrata</i> , <i>Apenesia</i> Evans, 1963	♀*	IBGE	Neotropical	alotype seen
	= <i>laticeps</i> , <i>Apenesia</i> Evans, 1963 sin. junior = <i>quadrata</i>	♂	CUIC	Neotropical	holotype seen
143	<i>quadrimera</i> , <i>Apenesia</i> Leal & Azevedo, 2001	♂	DZUP	Neotropical	holotype seen
144	<i>quelata</i> , <i>Apenesia</i> Ramos, Araujo & Azevedo, 2010	♂	MPEG	BRASIL	holotype seen
145	<i>raonis</i> , <i>Apenesia</i> Kurian, 1955	♀	IFRI	Oriental	literature
146	<i>recta</i> , <i>Apenesia</i> Ramos & Azevedo, 2009	♂	CNCI	Neotropical	holotype seen
147	<i>reducta</i> , <i>Apenesia</i> Evans, 1963	♂	CMNH	Neotropical	holotype seen
148	<i>remota</i> , <i>Pristocera</i> Kieffer, 1912	♂	BMNH	Afrotropical	holotype seen
149	<i>rostrum</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
150	<i>rotunda</i> , <i>Apenesia</i> Leal & Azevedo, 2001	♂	DZUP	Neotropical	holotype seen
151	<i>sahyadrica</i> , <i>Apenesia</i> Azevedo & Waichert, 2006	♂♀**	UFES	Oriental	holotype seen
152	<i>santacatarinae</i> , <i>Apenesia</i> Evans, 1964	♂	BMNH	Neotropical	holotype seen
153	<i>sarawakensis</i> , <i>Apenesia</i> Terayama & Yamane, 1997	♀	SMSM	Oriental	literature
154	<i>serrulata</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
155	<i>simplex</i> , <i>Apenesia</i> Correa & Azevedo, 2006	♂	MZSP	Neotropical	holotype seen
156	<i>simulata</i> , <i>Apenesia</i> Evans, 1969	♂	FIML	Neotropical	holotype seen
157	<i>sinensis</i> , <i>Apenesia</i> Xu, Terayama & He, 2002	♂	ZU	Oriental	literature
158	<i>singularis</i> , <i>Apenesia</i> Lanes & Azevedo, 2004	♂	MPEG	Neotropical	holotype seen
159	<i>sjostedti</i> , <i>Aleurodes</i> Tulgren, 1904 (type species of <i>Aleurodes</i> )	♀	NHRS	Afrotropical	literature
160	<i>spatulata</i> , <i>Apenesia</i> Evans, 1969	♂	FIML	Neotropical	holotype seen
161	<i>spinipes</i> , <i>Apenesia</i> Evans, 1969	♂	FIML	Neotropical	holotype seen
162	<i>striatula</i> , <i>Apenesia</i> Evans, 1963	♂	USNM	Neotropical	holotype seen

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163	<i>stricta</i> , <i>Apenesia</i> Corrêa & Azevedo, 2001	♂	UFES	Neotropical	holotype seen
164	<i>strigulata</i> , <i>Apenesia</i> Lanes & Azevedo, 2004	♂	MPEG	Neotropical	holotype seen
165	<i>substriata</i> , <i>Apenesia</i> Kieffer, 1904	♀	MCSN	Neotropical	holotype seen
166	<i>sulcata</i> , <i>Apenesia</i> Evans, 1963	♂	SEMC	Neotropical	holotype seen
167	<i>suzannae</i> , <i>Propriostocera</i> Benoit, 1957	♂	MRAC	Afrotropical	holotype seen
168	<i>tagala</i> , <i>Neurepyris</i> Ashmead, 1905	♂	USNM	Philippines	holotype seen
169	<i>takasago</i> , <i>Apenesia</i> Terayama, 1996	♂	NIAES	Palearctic	holotype seen
170	<i>tarascana</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
171	<i>tenebrosa</i> , <i>Apenesia</i> Evans, 1963	♂	USNM	Neotropical	holotype seen
172	<i>tengu</i> , <i>Apenesia</i> Terayama, 2006	♂	NIAES	Palearctic	holotype seen
173	<i>testaceipes</i> , <i>Epyris</i> Cameron, 1888	♂	BMNH	Neotropical	holotype seen
174	<i>tianmuensis</i> , <i>Apenesia</i> Xu, Terayama & He, 2002	♂	ZU	Oriental	literature
175	<i>tlahuicana</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
176	<i>tofti</i> , <i>Apenesia</i> Ward, 2013	♂♀	NZAC	Australian	literature
177	<i>transversa</i> , <i>Apenesia</i> Evans, 1963	♂	USNM	Neotropical	holotype seen
178	<i>triangula</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
179	<i>triapicalis</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
180	<i>tridentata</i> , <i>Apenesia</i> Kieffer, 1912	♀	ZMHB	Afrotropical	holotype seen
181	<b><i>triloba</i>, <i>Neopristocera</i> Benoit, 1957</b> (type species of <i>Neopristocera</i> )	♂	MRAC	Afrotropical	holotype seen
182	<i>trivisa</i> , <i>Apenesia</i> Ramos, Araujo & Azevedo, 2010	♂	CNCI	TRINIDAD	holotype seen
183	<i>unicolor</i> , <i>Apenesia</i> Kieffer, 1904	♀	MCSN	Oriental	holotype seen
184	<i>unipilosa</i> , <i>Apenesia</i> Corrêa & Azevedo, 2001	♂	UFES	Neotropical	holotype seen
185	<i>vauricorum</i> , <i>Apenesia</i> Evans, 1969	♀	AMNH	Neotropical	holotype seen
186	<i>venezuelana</i> , <i>Apenesia</i> Evans, 1963	♂	MCZH	Neotropical	holotype seen
187	<i>ventosa</i> , <i>Apenesia</i> Azevedo & Batista, 2002	♂	UFES	Neotropical	holotype seen
188	<i>williamsi</i> , <i>Apenesia</i> Evans, 1966	♂	BPBM	Neotropical	holotype seen
189	<i>xanthoptera</i> , <i>Cleistopyris</i> Kieffer, 1922	♂	?	Oriental	type lost, literature
190	<i>yu</i> , <i>Apenesia</i> Snelling, 1996	♂	LACM	Neotropical	holotype seen
191	<i>zamora</i> , <i>Apenesia</i> Evans, 1963	♂	AMNH	Neotropical	holotype seen

**Tab. 2.** Terminal taxa of morphological analysis. In bold type species, \*holotype, \*\*paratype.

Species	Locality	Deposit.	code
<b>Ingroup</b>			
<i>Apenesia acia</i> Lanes & Azevedo, 2004	Trinidad & Tobago	UFES	#56473
<i>Apenesia angusticeps</i> ** Evans, 1963	Brazil	UFES	#10353
<i>Apenesia atlantica</i> Correa & Azevedo, 2006	Brazil	UFES	#10347
<i>Apenesia bishamon</i> * Terayama, 1999	Japan	NIAES	HYM-100
<i>Apenesia chitouensis</i> * Terayama, 1996	Taiwan	NIAES	HYM-88
<i>Apenesia concavata</i> * Corrêa & Azevedo, 2001	Brazil	UFES	#37717, #10496
<i>Apenesia daikoku</i> * Terayama, 1999	Japan	NIAES	HYM-101
<i>Apenesia elegans</i> * Terayama, 1999	Japan, South Korea	NIAES, YNU	HYM-102
<i>Apenesia elongata</i> Evans, 1963	Brazil	UFES	#10738
<i>Apenesia evansi</i> * Gordh, 1990	Australia	UQIC	
<i>Apenesia funebris</i> Evans, 1963	Brazil	UFES	#10748
<i>Apenesia fusilis</i> ** Corrêa & Azevedo, 2001	Brazil	UFES	#10755
<b><i>Apenesia interrupta</i></b> * (Kieffer, 1905)	Sri Lanka	HNMN	
<i>Apenesia kusigematii</i> *, ** Terayama, 1999	Japan	NIAES, HNMN	HYM-103
<i>Apenesia laevigata</i> * (Evans, 1958)	Argentina	USNM	#64114
<i>Apenesia levicollis</i> * (Kieffer, 1905)	India	HNMN	
<i>Apenesia liukueiensis</i> Terayama, 1996	Taiwan	NIAES	HYM-090
<i>Apenesia membranaceus</i> ** Lanes & Azevedo, 2004	Brazil	UFES	#10829
<i>Apenesia nyamuragira</i> * (Benoit, 1957)	Congo	MRAC	
<i>Apenesia okinawensis</i> Terayama, 1999	Japan	NIAES	HYM-104
<i>Apenesia parapollita</i> Evans, 1963	USA	UFES	#10882
<i>Apenesia perlonga</i> Correa & Azevedo, 2006	Brazil	UFES	#10915
<i>Apenesia photophila</i> (Ogloblin, 1930)	Brazil	UFES	#10917
<i>Apenesia quadrata</i> Evans, 1963	Brazil	UFES	#55922
<i>Apenesia sahyadrica</i> * Azevedo & Waichert, 2006	India	UFES	#11128
<i>Apenesia simulata</i> ** Evans, 1969	Argentina	UFES	#11131
<i>Apenesia singularis</i> Lanes & Azevedo, 2004	Brazil	UFES	#11137
<i>Apenesia tagala</i> * (Ashmead, 1905)	Philippines, South Korea	USNM, YNU	#8439
<i>Apenesia takasago</i> Terayama, 1996	Taiwan	NIAES	HYM-092
<i>Apenesia tenebrosa</i> Evans, 1963	Brazil	UFES	#11162
<b><i>Apenesia triloba</i></b> * (Benoit, 1957)	Congo, Uganda	MRAC, ISAM	ISA 21
<i>Apenesia</i> sp1	Australia	UQIC	sp1 aust
<i>Apenesia</i> sp2	Australia	UQIC	sp2 aust
<i>Apenesia</i> sp3	Australia	UQIC	sp3 aust
<i>Apenesia</i> sp4	Australia	UQIC	sp4 aust
<i>Apenesia</i> sp5	United Arab Emirates	UFES	Isa 14
<i>Acrepyris armiferus</i> (Say, 1828)	USA	UFES	UFES09176
<i>Acrepyris bridwelli</i> (Evans, 1963)	USA	UFES	UFES092204
<i>Acrepyris japonicus</i> (Yatsumatsu, 1955)	Japan	UFES	UFES09256
<i>Acrepyris</i> sp1	Vietnam	RMNH	
<i>Acrepyris</i> sp2	Vietnam	RMNH	
<b><i>Afrocerca bamboutoana</i></b> * Benoît, 1983	Cameroon	MNH	
<b><i>Caloapenesia thailandiana</i></b> Terayama, 1995	Thailand	RMNH	
<b><i>Calobranchium salum</i></b> * Gobbi & Azevedo, 2016	Thailand	QSBG	
<i>Dissomphalus conicus</i> Azevedo, 2003	Brazil	UFES	UFES12353
<i>Dissomphalus geanus</i> Mugarib & Azevedo, 2013	Vietnam	RMNH	
<i>Foenobethylus thaianus</i> (Terayama, 1998)	Thailand	PMAE	
<b><i>Neoapenesia leytensis</i></b> * Terayama, 1995	Japan	PMAE, NIAES	
<i>Neoapenesia</i> sp1	Uganda	ISAM	Ibes n°14385
<i>Parascleroderma</i> sp1	Thailand	RMNH	
<i>Parascleroderma</i> sp2	South Africa	PMAE	
<i>Pristocera gaullei</i> Kieffer, 1908	South Africa	UFES	UFES17899
<i>Pristocera</i> sp1	Madagascar	CASC	CASENT2085691
<i>Pristocera</i> sp2	Uganda	ISAM	Isa22
<i>Prosapenesia lacteipennis</i> Kieffer, 1910	Namibia	PMAE	Isa219
<i>Prosapenesia</i> sp1	Namibia	PMAE	Isa220
<i>Protisobranchium asianum</i> Terayama, 1995	Thailand	QSBG	
<i>Pseudisobranchium apenesoides</i> Waichert & Azevedo, 2004	Brazil	UFES	UFES57661
<i>Trichiscus suzannae</i> Benoît, 1986	Uganda	PMAE	
<b>Outgroup</b>			
<i>Eupsenella insulana</i> Gordh & Harris, 1996	New Zeland	UFES	
<i>Goniozus</i> sp	Brazil	UFES	

**Tab. 3.** Terminal taxa of molecular analysis. Different species belonging to the same cluster are represented by ~ and a species which has similar structures.

Species		Sex	Locality	Deposit.	Code
<b>Ingroup</b>					
<i>Apenesia perlonga</i>	~laevigata	♂	Brazil	UFES	Isa288
<i>Apenesia</i> sp1	~brasiliensis	♂	Brazil	UFES	Isa17
<i>Apenesia</i> sp2	~brasiliensis	♂	Brazil	UFES	Isa20
<i>Apenesia</i> sp3	~brasiliensis	♂	Brazil	UFES	Isa212
<i>Apenesia</i> sp4	~brasiliensis	♂	Brazil	UFES	Isa214
<i>Apenesia</i> sp5	~brasiliensis	♂	Brazil	UFES	Isa296
<i>Apenesia</i> sp6	~dissomphaloides	♂	Kenya	NMKE	ABM280
<i>Apenesia</i> sp7	~elegans	♂	Thailand	QSBG	Isa92
<i>Apenesia</i> sp8	~elegans	♂	Thailand	QSBG	Isa93
<i>Apenesia</i> sp9	~elegans	♂	Thailand	QSBG	Isa94
<i>Apenesia</i> sp10	~elongata	♂	Brazil	UFES	Isa12
<i>Apenesia</i> sp11	~elongata	♂	Brazil	UFES	Isa213
<i>Apenesia</i> sp12	~elongata	♂	Brazil	UFES	Isa291
<i>Apenesia</i> sp13	~elongata	♂	Brazil	CZMA	Isa298
<i>Apenesia</i> sp14	~elongata	♂	Brazil	CZMA	Isa299
<i>Apenesia</i> sp15	~elongata	♂	Brazil	CZMA	Isa300
<i>Apenesia</i> sp16	~evansi	♂	Australia	UFES	Isa130
<i>Apenesia</i> sp17	~evansi	♂	Australia	UFES	Isa136
<i>Apenesia</i> sp18	~evansi	♂	Australia	UFES	Isa316
<i>Apenesia</i> sp19	~funebriis	♂	Brazil	UFES	Isa11
<i>Apenesia</i> sp20	~interrupta	♂	Thailand	QSBG	Isa336
<i>Apenesia</i> sp21	~photophila	♂	Brazil	UFES	Isa209
<i>Apenesia</i> sp22	~photophila	♂	Brazil	UFES	Isa210
<i>Apenesia</i> sp23	~triloba	♂	Thailand	QSBG	Isa249
<i>Apenesia</i> sp24	~triloba	♂	Kenia	NMKE	Isa279
<i>Acrepyris</i> sp1		♂	Thailand	QSBG	Isa251
<i>Acrepyris</i> sp2		♂	Thailand	QSBG	Isa260
<i>Acrepyris</i> sp3		♂	Thailand	QSBG	Isa266
<i>Acrepyris</i> sp4		♂	USA	UFES	Isa352
<i>Caloapenesia</i> sp1		♂	Papua New Guinea	MNHN	Isa240
<i>Caloapenesia</i> sp2		♂	Papua New Guinea	MNHN	Isa241
<i>Dissomphalus</i> sp1		♀	French Guiana	UFES	Isa205
<i>Dissomphalus</i> sp2		♂	Nigeria	AMNH	Isa387
<i>Dissomphalus</i> sp3		♂	Nigeria	AMNH	Isa388
<i>Foenobethylus emiliacasellae</i>		♂	Thailand	QSBG	GU213952
<i>Foenobethylus</i> sp1		♂	Thailand	QSBG	Doc242
<i>Neoapenesia</i> sp1	~leytensis	♂	Papua New Guinea	MNHN	Isa236
<i>Neoapenesia</i> sp2	~leytensis	♂	Papua New Guinea	MNHN	Isa239
<i>Parascleroderma</i> sp1		♂	Australia	UQIC	Isa273
<i>Parascleroderma</i> sp2		♂	Australia	UFES	Isa312
<i>Pristocera formosa</i>		♀	South Korea	UFES	Isa343
<i>Pristocera</i> sp1	~rosmarum	♂	Kenya	NMKE	Isa278
<i>Pristocera</i> sp2		♂	United Arab Emirates	UFES	ABM51
<i>Pristocera</i> sp3		♂	Thailand	QSBG	Isa252
<i>Pristocera</i> sp4		♂	Kenya	NMKE	Isa284
<i>Protisobrachium</i> sp1		♂	Kenya	NMKE	ABM283
<i>Protisobrachium</i> sp2		♂	Madagascar	CASC	A76
<i>Pseudisobrachium</i> sp1		♂	Brazil	CZMA	CZMA14
<i>Pseudisobrachium</i> sp2		♀	Brazil	UFES	Isa191
<i>Pseudisobrachium</i> sp3		♂	USA	UFES	Isa359
<i>Trichiscus</i> sp1		♂	Kenya	NMKE	ABM95
<i>Trichiscus</i> sp2		♂	Kenya	NMKE	ABM96
<b>Outgroup</b>					
<i>Sierola gracile</i>		♀	USA	BPBM	Doc262
<i>Sierola</i> sp	~anthacina	♀	USA	BPBM	Doc260
<i>Goniozus</i> sp					
<i>Prorops nasuta</i>					Doc75
<i>Formosiepyris</i> sp					Doc218
<i>Holepyris</i> sp					Doc 70





Data matrix of characters 56-110 used in the phylogenetic analyses.

Taxa (cont)	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
<i>Acrepyris armifera</i>	0	0	1	1	0	0	0	1	0	1	0	0	5	0	0	1	0	1	0	1	0	0	-	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	0	-	-	0	0	0	1	0	0	1	0	0	2	1	0
<i>Acrepyris bridwelli</i>	0	0	1	1	1	0	0	1	0	1	0	0	5	0	0	1	0	1	0	1	0	0	-	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	0	-	-	0	0	0	1	0	0	1	0	0	2	1	0	
<i>Acrepyris japonica</i>	0	0	1	1	1	0	0	1	0	1	0	0	5	0	0	1	0	1	0	1	0	0	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	0	-	-	0	0	0	1	0	0	1	0	0	2	1	0	
<i>Acrepyris sp1</i>	0	0	1	1	1	0	0	1	0	1	0	0	5	0	0	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	0	-	-	0	0	0	1	0	0	1	0	0	2	1	0	
<i>Acrepyris sp2</i>	0	0	1	1	1	0	0	1	0	1	0	0	5	0	0	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	0	-	-	0	0	0	1	0	0	1	0	0	2	1	0	
<i>Afrocerca bamboutoana</i>	0	0	1	1	1	0	0	0	1	1	2	5	1	0	1	0	1	1	1	1	1	1	0	1	0	1	0	1	1	0	1	0	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	2	1	0		
<i>Apenesia acia</i>	0	1	0	1	1	0	0	1	0	1	1	0	2	1	1	1	0	1	1	1	0	0	1	1	0	0	1	1	1	1	1	0	1	1	-	1	1	-	1	1	0	0	0	0	0	0	0	0	0	1	2	1	0		
<i>Apenesia angusticeps</i>	0	1	1	1	2	1	0	1	0	0	1	0	1	1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	1	1	1	1	0	2	0	2	1	0	1	1	0	-	-	0	1	0	1	1	0	1	0	0	2	1	0
<i>Apenesia atlantica</i>	0	1	0	1	1	0	0	1	0	1	1	0	3	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	1	1	0	1	1	-	1	1	-	1	1	0	0	0	0	0	0	0	0	0	1	2	1	0			
<i>Apenesia bishamon</i>	0	1	1	1	1	0	1	0	1	0	1	0	4	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	0	1	0	2	1	-	1	1	-	0	0	-	-	0	0	0	1	0	0	0	0	0	2	1	0		
<i>Apenesia chitouensis</i>	0	1	0	1	0	0	0	0	1	1	0	4	1	0	1	0	1	0	1	0	1	1	0	1	1	1	1	0	1	1	1	0	2	0	2	0	1	-	0	1	0	0	0	1	0	0	0	1	0	0	2	0	0		
<i>Apenesia concavata</i>	0	1	0	1	1	0	1	1	0	1	1	0	3	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	1	1	0	1	1	-	1	1	-	0	1	1	0	0	0	0	0	0	0	1	2	1	0				
<i>Apenesia daikoku</i>	0	1	0	1	0	0	0	0	1	1	0	4	1	0	1	0	1	0	1	0	1	1	1	1	1	0	1	1	0	1	1	0	2	0	2	0	1	-	0	1	0	0	0	1	0	0	0	1	0	0	2	0	0		
<i>Apenesia elegans</i>	0	1	0	1	0	0	0	0	1	1	0	4	1	0	1	0	1	0	1	0	1	1	0	1	1	1	1	1	0	1	1	0	2	0	2	0	1	-	0	1	0	0	1	0	0	0	1	0	0	2	0	0			
<i>Apenesia elongata</i>	0	1	1	2	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	1	1	1	0	2	0	2	1	0	1	1	0	-	0	1	0	1	1	0	1	0	0	2	1	0			
<i>Apenesia evansi</i>	0	1	1	1	1	2	0	0	1	1	0	3	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	1	1	0	1	0	2	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0			
<i>Apenesia funebris</i>	0	1	1	1	0	0	0	0	1	1	6	1	1	1	1	0	1	0	1	1	0	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	1	0	-	-	0	1	0	0	0	1	0	0	2	1	0				
<i>Apenesia fusilis</i>	0	1	1	2	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	1	1	1	0	2	0	2	1	0	1	1	0	-	-	0	1	0	1	1	0	1	0	0	2	1	0		
<i>Apenesia interrupta</i>	0	0	1	1	2	0	0	1	0	1	1	0	2	1	0	1	0	1	1	1	1	0	-	1	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	2	1	0			
<i>Apenesia kusigemachii</i>	0	0	1	1	2	0	0	1	0	1	1	0	2	1	0	1	0	1	1	1	1	0	-	1	0	1	0	1	1	0	1	0	0	0	0	0	1	0	0	-	-	0	1	0	0	0	0	0	0	2	1	0			
<i>Apenesia laevigata</i>	0	1	0	1	1	0	1	0	0	0	1	0	1	1	1	0	1	0	1	0	1	0	0	-	1	1	1	1	1	0	2	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0		
<i>Apenesia levicollis</i>	0	0	1	1	2	0	0	1	0	1	1	0	2	1	0	1	0	1	1	1	1	0	-	1	0	1	0	1	1	0	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	2	0	0			
<i>Apenesia liukuensis</i>	0	1	0	1	0	0	0	0	1	1	0	4	1	0	1	0	1	0	1	0	1	1	1	1	1	0	1	1	0	1	1	0	2	0	2	0	1	-	0	1	0	0	0	1	0	0	0	1	0	0	2	0	0		
<i>Apenesia membranaceus</i>	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	1	-	1	1	-	1	1	1	0	0	0	0	0	0	0	0	1	2	1	0			
<i>Apenesia nyammuragira</i>	0	1	1	1	2	0	1	0	0	1	1	0	1	1	1	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	1	0	
<i>Apenesia okinawensis</i>	0	0	1	1	2	0	0	1	0	1	1	0	5	1	0	1	0	1	1	1	1	0	1	0	1	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	-	-	0	1	0	0	0	0	0	2	1	0	
<i>Apenesia parapoliia</i>	0	1	0	1	1	1	1	0	1	1	0	3	1	1	1	0	1	0	1	0	1	0	0	-	1	1	1	1	1	0	2	0	1	1	-	1	1	-	1	1	0	0	0	0	0	0	0	0	0	1	2	1	0		
<i>Apenesia perlonga</i>	0	1	0	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	0	-	1	1	1	1	0	1	0	2	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	
<i>Apenesia photophila</i>	0	1	1	1	0	0	0	0	1	1	6	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	
<i>Apenesia quadrata</i>	0	1	0	1	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	0	1	0	0	1	1	0	0	1	1	1	1	0	1	1	-	1	1	-	1	1	0	0	0	0	0	0	0	0	0	1	2	1	0		
<i>Apenesia sayhadrica</i>	0	1	0	1	1	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	-	1	1	1	1	0	1	0	2	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	2	1	0	2	1	0
<i>Apenesia simulata</i>	0	1	1	1	1	2	0	0	1	1	0	2	1	1	1	0	1	0	0	1	0	1	0	1	1	0	0	1	1	0	0	1	1	-	1	1	-	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0		
<i>Apenesia singularis</i>	0	1	0	1	1	0	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	-	1	1	1	0	1	0	2	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	2	1	0	1	1	0		
<i>Apenesia sp1</i>	0	1	1	1	1	1	2	0	0	1	1	0	2	1	1	1	0	1	0	1	1	0	0	1	1	1	1	1	1	0	1	0	2	1	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0	2	1	0			
<i>Apenesia sp2</i>	0	1	1	1	1	2	0	0	1	1	0	2	1	1	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0	1	0	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	2	1	0		
<i>Apenesia sp3</i>	0	1	1	1	1	2	0	0	1	1	3	3	1	1	1	0	1	0	1	0	1	0	0																																

Data matrix of characters 111-163 used in the phylogenetic analyses.

Taxa (cont.)	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163		
<i>Acropyris armifera</i>	1	1	1	1	0	1	1	1	0	1	1	1	-	1	0	0	0	1	1	0	1	2	0	1	-	1	1	0	1	0	0	1	1	0	-	-	0	1	-	1	0	1	0	1	0	0	0	1	0	0	1	1			
<i>Acropyris bridwelli</i>	1	1	1	1	0	1	1	1	0	1	1	1	-	1	0	0	0	1	1	0	1	2	0	1	-	1	1	0	1	0	0	1	1	0	-	-	0	1	-	1	0	1	0	1	0	0	0	1	0	0	1	1			
<i>Acropyris japonica</i>	1	1	1	1	0	1	1	1	1	1	1	1	-	0	0	0	1	1	0	1	2	0	1	-	1	1	0	1	0	0	1	1	0	-	-	0	1	-	1	0	1	0	1	0	0	0	1	0	0	1	1				
<i>Acropyris</i> sp1	1	1	1	1	0	1	1	1	1	0	1	1	-	1	0	0	0	1	1	0	1	2	1	1	-	1	1	0	1	0	0	1	1	0	-	-	0	1	-	1	0	1	0	1	0	0	0	1	0	0	1	1			
<i>Acropyris</i> sp2	1	1	1	1	0	1	1	1	1	1	1	1	-	1	0	0	0	1	1	0	1	2	1	1	-	1	1	0	1	0	0	1	1	0	-	-	0	1	-	1	0	1	0	1	0	0	0	1	0	0	1	1			
<i>Afrocerca bamboutoana</i>	0	1	0	1	0	0	1	1	0	1	1	1	-	1	0	0	0	1	1	1	0	2	0	1	-	1	1	0	1	1	0	1	0	0	-	-	1	1	-	1	0	1	0	1	0	0	1	-	0	0	1	1			
<i>Apenesia acia</i>	1	1	1	1	1	-	-	1	-	-	1	0	1	1	0	1	2	1	1	-	1	1	0	1	1	0	1	1	0	1	1	0	1	1	1	3	1	1	1	-	1	1	1	0	1	0	1	1	-	-	0	0	1	2	
<i>Apenesia angusticeps</i>	1	1	1	1	0	1	1	1	1	0	1	1	-	1	0	0	0	0	1	0	0	2	1	1	-	1	1	0	1	1	0	1	1	1	0	-	-	1	1	-	1	1	1	1	1	1	-	1	-	-	0	0	1	0	
<i>Apenesia atlantica</i>	1	1	1	1	1	-	-	1	-	-	1	0	1	1	0	1	2	1	0	0	0	2	1	1	-	1	1	0	1	1	0	1	1	1	1	0	1	1	-	1	1	-	1	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia bishamon</i>	1	1	1	1	0	1	0	1	0	1	1	0	1	1	0	1	3	1	1	0	0	0	1	1	-	1	1	0	1	1	0	1	1	0	-	-	1	1	-	1	1	1	0	1	0	1	1	-	-	0	0	1	1		
<i>Apenesia chitouensis</i>	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	1	0	0	1	1	1	-	0	1	0	0	1	0	0	1	1	0	0	0	1	-	1	1	1	0	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia concavata</i>	1	1	1	1	1	-	-	1	-	-	1	0	1	1	0	0	2	1	0	0	0	2	1	1	-	1	1	0	1	1	0	1	1	1	0	1	1	-	1	1	0	1	1	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia daikoku</i>	1	0	1	1	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	0	1	1	-	0	1	0	0	1	0	0	1	1	0	0	1	-	1	1	0	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia elegans</i>	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	1	0	0	1	1	1	-	0	1	0	0	1	0	0	1	1	0	0	0	1	-	1	1	1	0	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia elongata</i>	1	1	1	1	0	1	1	0	1	0	1	1	1	1	0	0	0	1	0	0	0	2	1	1	-	1	1	0	1	1	0	1	1	1	0	-	-	1	1	-	1	1	1	1	1	-	1	-	-	0	0	1	0		
<i>Apenesia evansi</i>	1	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	0	0	1	0	1	0	0	1	0	1	0	1	0	1	1	-	-	0	0	1	2
<i>Apenesia funebris</i>	1	1	1	1	0	1	0	0	1	1	1	0	1	1	0	0	1	0	1	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	-	-	1	0	1	1	0	0	1	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia fusilis</i>	1	1	1	1	0	1	1	0	1	0	1	1	-	1	0	0	0	1	0	0	2	1	1	-	1	1	0	1	1	0	1	1	1	0	-	-	1	1	-	1	1	1	1	1	1	-	1	-	-	0	0	1	0		
<i>Apenesia interrupta</i>	0	1	0	1	0	0	1	1	0	1	1	1	-	1	0	0	0	1	1	1	0	2	0	1	-	1	1	0	1	1	0	1	0	0	-	-	1	1	-	1	0	1	0	1	0	0	0	1	-	-	0	0	1	1	
<i>Apenesia kusigemachii</i>	0	1	0	1	0	0	1	1	0	1	0	1	-	1	0	0	0	1	1	1	0	2	0	1	-	1	1	0	1	1	0	1	0	0	-	-	1	1	-	1	0	1	0	0	1	0	0	1	-	-	0	0	1	1	
<i>Apenesia laevigata</i>	1	1	1	1	0	1	0	0	1	1	1	1	0	1	0	1	1	1	0	1	1	2	1	1	-	1	1	1	1	1	1	0	1	0	-	-	1	1	-	1	0	0	1	0	1	1	-	-	0	0	1	2			
<i>Apenesia levicollis</i>	1	0	1	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	0	0	1	1	1	-	0	1	0	0	1	0	0	1	1	0	0	0	1	-	1	1	1	0	1	0	1	1	-	-	0	0	1	2			
<i>Apenesia liukuensis</i>	1	0	1	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	0	1	1	-	0	1	0	0	1	1	0	0	1	-	-	1	1	0	1	-	1	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia membranaceus</i>	1	1	1	1	1	-	-	1	-	-	1	0	1	1	0	0	2	1	0	0	0	0	1	1	-	1	1	0	1	1	0	0	1	1	3	1	1	1	-	1	1	1	0	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia nyammuragira</i>	1	1	0	0	1	-	-	0	0	-	1	1	-	1	0	0	1	1	1	0	0	2	1	1	-	1	1	0	1	0	0	1	0	1	2	0	1	1	-	1	0	1	0	1	1	-	-	0	1	-	-	0	1	-	
<i>Apenesia okinawensis</i>	0	1	0	1	0	0	1	1	0	1	1	1	-	1	0	0	0	1	1	1	0	2	0	1	-	1	1	0	1	1	0	1	0	0	-	-	1	1	-	1	0	1	0	0	0	1	-	-	0	0	1	1			
<i>Apenesia parapoliia</i>	1	1	1	1	0	1	0	1	1	1	1	0	1	1	0	1	2	1	1	0	0	2	1	1	-	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	-	-	0	0	1	2					
<i>Apenesia perlonga</i>	1	1	1	1	0	1	0	0	1	1	1	1	0	1	0	1	1	1	1	0	1	2	1	1	-	1	1	1	1	1	0	1	0	-	-	1	1	-	1	0	0	0	1	0	1	1	-	-	0	0	1	2			
<i>Apenesia photophila</i>	1	1	1	1	0	1	0	0	1	1	1	0	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	-	-	1	0	1	1	0	1	1	0	1	1	-	-	0	0	1	2				
<i>Apenesia quadrata</i>	1	1	1	1	1	-	-	1	-	-	1	0	1	1	0	0	2	1	0	0	0	2	1	1	-	1	1	0	1	1	0	0	1	2	1	1	1	-	1	1	1	1	0	1	1	-	-	0	0	1	2				
<i>Apenesia sayhadrica</i>	1	1	1	1	0	1	0	0	0	1	1	0	0	1	0	1	1	1	1	0	1	2	1	1	-	1	1	1	1	1	0	1	0	-	-	1	1	-	1	0	0	0	1	0	1	1	-	-	0	0	1	2			
<i>Apenesia simulata</i>	1	1	1	0	0	1	1	1	1	1	1	-	1	0	0	0	1	1	0	0	2	0	1	-	1	1	0	1	0	0	1	1	0	-	-	1	1	-	0	0	1	0	0	1	-	0	1	-	-	0	1	-			
<i>Apenesia singularis</i>	1	1	1	1	0	1	0	0	1	1	1	0	1	1	0	1	1	1	0	1	2	1	1	-	1	1	1	1	1	0	1	0	-	-	1	1	-	1	0	0	1	0	1	1	-	-	0	0	1	2					
<i>Apenesia</i> sp1	1	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	0	1	1	0	0	0	1	0	1	1	1	3	1	1	0	0	1	0	1	0	1	0	1	1	-	-	0	0	1	2		
<i>Apenesia</i> sp2	1	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	3	1	1	0	0	1	0	1	0	1	0	1	1	-	-	0	0	1	2				
<i>Apenesia</i> sp3	1	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	1	0	0	0	1	0	1	1	1	3	1	1	0	0	1	0	1	0	1	0	1	1	-	-	0	0	1	2			
<i>Apenesia</i> sp4	1	0	1																																																				

**Tab. 5.** Data matrix of characters 1-12 used in the female mapping character analyses.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12
<i>Apenesia elongata</i>	1	1	1	1	0	0	1	1	0	0	1	0
<i>Apenesia evansi</i>	1	1	1	1	0	0	1	1	0	0	1	0
<i>Apenesia nitida</i>	1	1	1	1	0	0	1	1	0	0	1	0
<i>Apenesia quadrata</i>	1	1	1	1	0	0	1	1	0	0	1	0
<i>Apenesia simulata</i>	1	1	1	1	1	1	1	1	0	0	0	1
<i>Apenesia sahyadrica</i>	0	0	0	0	0	0	1	1	0	0	1	1
<i>Apenesia</i> sp	1	1	1	1	0	0	1	1	1	1	1	0
<i>Dissomphalus connubialis</i>	1	1	1	1	1	1	1	1	0	0	0	1
<i>Dissomphalus bifuratus</i>	1	1	1	1	1	1	1	1	0	0	0	1
<i>Dissomphalus bisserratus</i>	1	1	1	1	1	1	1	1	0	0	0	1
<i>Dissomphalus megadentatus</i>	1	1	1	1	1	1	1	1	0	0	0	1
<i>Dissomphalus xanthopus</i>	1	1	1	1	1	1	1	1	0	0	0	1
<i>Dissomphalus uncus</i>	1	1	1	1	1	1	1	1	0	0	0	1
<i>Dissomphalus</i> sp	1	1	1	1	1	1	1	1	0	0	0	1
<i>Neoapenesia makihari</i>	0	0	0	0	0	0	1	1	0	0	1	1
<i>Parascleroderma</i> sp	1	1	1	1	0	0	1	1	0	0	0	0
<i>Pristocera</i> sp1	1	1	1	1	0	0	0	0	0	0	1	1
<i>Pristocera</i> sp2	1	1	1	1	0	0	0	0	0	0	1	1
<i>Pristocera</i> sp3	1	1	1	1	0	0	0	0	0	0	1	1
<i>Pristocera</i> sp4	1	1	1	1	0	0	0	0	0	0	1	1
<i>Pseudisobrachium</i> sp	1	1	1	1	0	0	1	1	1	1	1	0

**Tab. 6.** Pristocerinae females with male-female association.

Lineages	Phoretic copulation	Molecular association	Biological data
	clade A		<i>Apenesia sahyadrica</i> Azevedo & Waichert (Azevedo & Waichert 2006)
	clade B	<i>Apenesia simulata</i> Evans (this study; Azevedo <i>et al.</i> in press)	
<i>Apenesia</i>	clade E	<i>Apenesia nitida</i> (Kieffer); <i>Ap. quadrata</i> Evans (Evans 1969; Ramos <i>et al.</i> 2010)	
	clade F	<i>Apenesia elongata</i> Evans (Corrêa & Azevedo 2006)	
	clade J	<i>Apenesia evansi</i> Gordh (Gordh 1990)	
	clade K	<i>Apenesia</i> sp (this study)	
<i>Dissomphalus</i>	<i>Dissomphalus connubials</i> Evans; <i>D. bifuratus</i> Azevedo; <i>D. bisserratus</i> Azevedo; <i>D. megadentatus</i> Azevedo; <i>D. xanthopus</i> Ashmead; <i>D. uncus</i> Alencar & Azevedo (Evans 1966; Azevedo 1999a; Azevedo 2001; Azevedo 2003; Vargas 2007; Alencar & Azevedo 2008)	<i>Dissomphalus</i> sp., lineage association (this study; Martinelli, personal communication)	
<i>Neoapenesia</i>		<i>Neoapenesia makiharai</i> Sawada <i>et al.</i> (Sawada <i>et al.</i> 2014)	<i>Neoapenesia makihara</i> (Sawada <i>et al.</i> 2014)
<i>Parascleroderma</i>		<i>Parascleroderma</i> sp. (this study)	
<i>Pristocera</i>		<i>Pristocera</i> sp., lineage association (this study)	<i>Pristocera</i> spp. (Azevedo <i>et al.</i> in press a)
<i>Pseudisobrachium</i>		<i>Pseudisobrachium</i> sp., lineage association (this study)	

*Appendix 1. Character list for males*

1. Body: (0) robust; (1) slender.
2. Head: (0) as long as large; (1) larger than long; (2) longer than large.
3. Frons projection: (0) present; (1) absent.
4. Relative length of the mandible: (0) long, when mandible length is less than 0.7x the head width; (1) very long, when mandible length is equal to or more than 0.7x the head width; (2) short.
5. Relative width of the mandible apex: (0) as wide as the base; (1) wider than the base.
6. Mandible surface: (0) plane; (1) convex.
7. Mandible with keel on upper margin: (0) present; (1) absent.
8. Mandible with upper tooth curved posterad: (0) absent; (1) present.
9. Mandible with upper tooth distinctly large: (0) present; (1) absent.
10. Mandible teeth number: (0) 1; (1) 2; (2) 3; (3) 4; (4) 5.
11. Number of maxillary palpi: (0) 6; (1) 5; (2) 4; (3) 3; (4) 2; (5) 1.
12. Number of labial palpi: (0) 3; (1) 2; (2) 1.
13. Clypeus: (0) projected forward; (1) shortly truncate.
14. Clypeal lobes: (0) distinct; (1) indistinct.
15. Clypeal median lobe shape: (0) triangular; (1) rectangular; (2) trapezoidal; (3) semicircular.
16. Clypeal median lobe margin: (0) truncate; (1) convex; (2) sharpened, sides divergent posterad.
17. Clypeal small median tooth: (0) present; (1) absent.
18. Clypeal continuity with frons: (0) present, posterior margin surpassing torulli; (1) absent, posterior margin not surpassing torulli.
19. Antenna with long setae on flagellomeres: (0) absent; (1) present.
20. Antennae length: (0) short; (1) long.
21. Flagellomere width: (0) wide; (1) narrow.
22. Flagellomere margin: (0) parallel; (1) diverging posterad.
23. Placoid sensillae: (0) present; (1) absent.
24. Eye: (0) glabrous; (1) densely hairy.
25. Ocellar triangle: (0) close to vertex; (1) far from vertex crest.
26. Occipital carina: (0) absent; (1) present.

27. Mesosoma gibbous in lateral view: (0) absent, head at same level of mesosoma; (1) present, head at lower level than mesosoma.
28. Projection of the pronotal collar, lateral view: (0) projected laterally over the propleuron; (1) not projected.
29. Pronotal disc, size: (0) short; (1) long.
30. Pronotal disc, width: (0) wide; (1) narrow.
31. Pronotal disc with anterior carina: (0) absent; (1) present.
32. Lateral of pronotum strigate: (0) present; (1) absent.
33. Pronotal disc with transverse depression: (0) absent; (1) present.
34. Propleuron elongate anterad: (0) absent; (1) present.
35. Prosternum area: (0) small; (1) large.
36. Scutellar disc, size: (0) short; (1) long.
37. Scutellar groove: (0) straight; (1) arched; (2) angled.
38. Mesopleural callus: (0) present; (1) absent.
39. Mesopleural posterior oblique sulcus: (0) present; (1) absent.
40. Texture of mesopleural oblique sulcus: (0) punctuated; (1) trabeculate; (2) with one puncture; (3) shallow punctuated; (4) polished.
41. Mesopleural anterior sulcus: (0) present; (1) absent.
42. Texture of mesopleural anterior sulcus: (0) punctuated; (1) trabeculate.
43. Anterior fovea: (0) present; (1) absent.
44. Mesopleural fovea: (0) present; (1) absent.
45. Connection of subtegular sulcus and mesepimeral sulcus: (0) present; (1) absent.
46. Posterior fovea of mesopleural callus, when continuity is present: (0) present; (1) absent.
47. Prepectus: (0) divided into two plates; (1) fused.
48. Prepectus width: (0) wide; (1) narrow.
49. Prepectus texture: (0) coriaceous; (1) foveolate.
50. Prepectus anterior margin: (0) narrow; (1) wide.
51. Sternaulus: (0) present; (1) absent.
52. Sternaulus shape: (0) long; (1) rounded.
53. Epicnemium: (0) large; (1) reduced.
54. Epicnemial sulcus: (0) present; (1) absent.
55. Mesodiscrimen: (0) carinate; (1) sulcate.
56. Median region of metanotum: (0) elevated; (1) depressed.

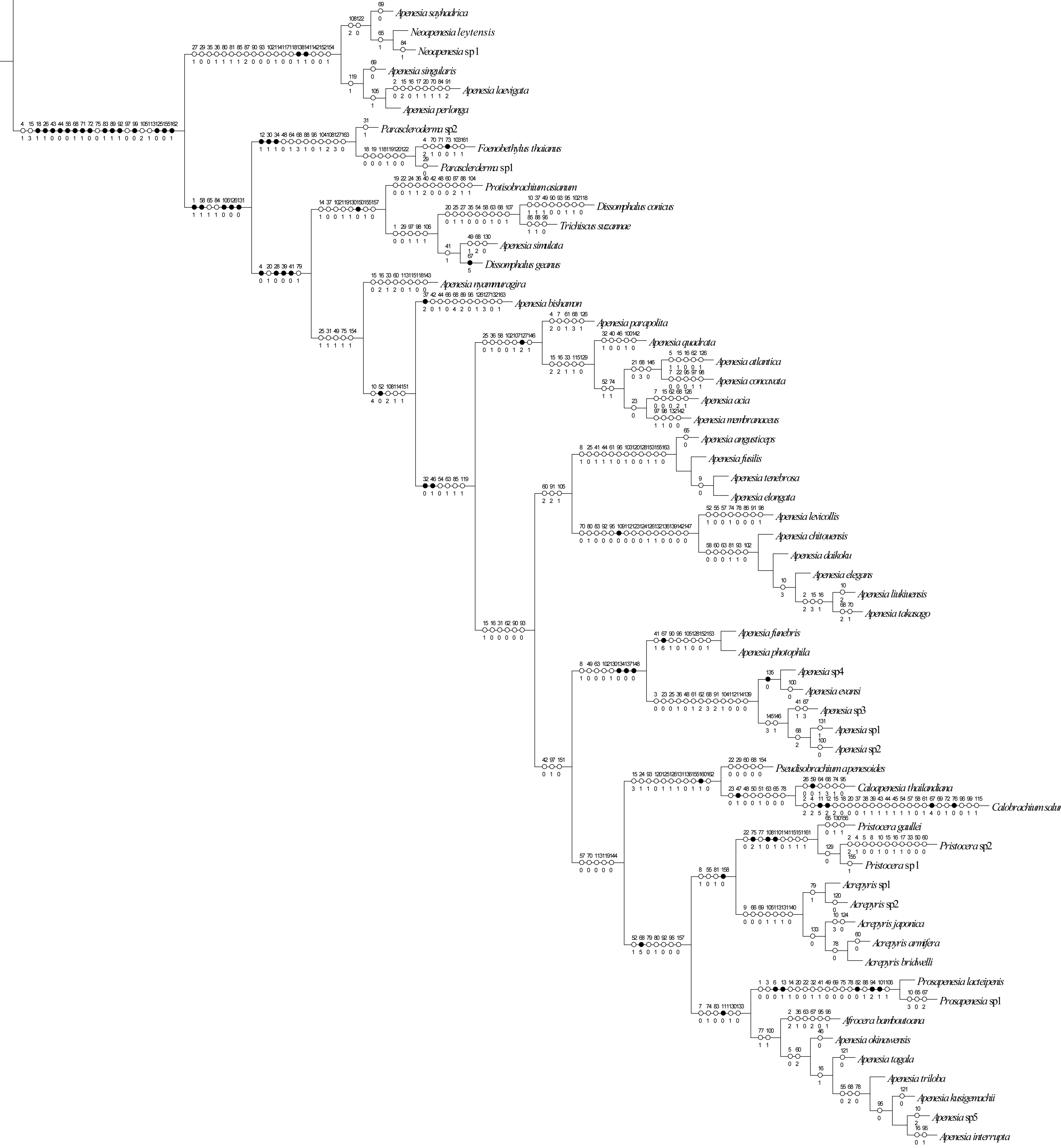
57. Median region of metanotum width: (0) wide; (1) narrow.
58. Median region of metanotum length: (0) long; (1) short.
59. Median metanotal fovea: (0) absent; (1) present.
60. Median metanotal fovea shape: (0) rounded; (1) oval; (2) subtriangular.
61. Metanotal trough: (0) large; (1) narrow.
62. Metanotal trough texture: (0) distinctly foveolate; (1) fovea badly impressed; (2) imbricate.
63. Metapectal-propodeal complex length: (0) long, 1.3x as long as wide; (1) short, as long as wide.
64. Transverse anterior carina of propodeum: (0) present; (1) absent.
65. Metaposnotal median carina: (0) absent or short; (1) long.
66. Metaposnotal-propodeal suture: (0) present; (1) absent.
67. Metaposnotal texture: (0) rugulose; (1) foveolate; (2) strigate; (3) coriaceous; (4) areolate; (5) polished; (6) carinate.
68. Propodeal disc area: (0) foveolate; (1) polished; (2) imbricate; (3) coriaceous; (4) finely rugulose; (5) strigate.
69. Metapleural carina: (0) absent; (1) present.
70. Transverse posterior carina of the propodeum: (0) absent; (1) present.
71. Profemur enlarged: (0) present; (1) absent.
72. Protrochanter: (0) conical and long; (1) arched and short.
73. Metafemur enlarged: (0) present; (1) absent.
74. Mesotibia with strong spines: (0) absent; (1) present.
75. Number of teeth on tarsal claw: (0) one; (1) two; (2) three.
76. Forewing anterior margin angulate: (0) present, margin discontinuous, forewing abruptly wider after costal vein; (1) absent, margin continuous, forewing progressively wider distally.
77. Costal cell: (0) wide, even partially near to stigma; (1) narrow.
78. Forewing with 3C: (0) absent; (1) present.
79. 3C vein length: (0) short; (1) long.
80. Forewing with stigma remarkably large: (0) absent; (1) present.
81. Forewing with radial vein emerging from the middle of 2R1 stigma: (0) absent; (1) present.
82. Forewing with radial vein tubular and distinct: (0) absent; (1) present.
83. Forewing with r-rs and RS1 join: (0) abruptly angled; (1) somewhat continuous.



84. Forewing with 4M vein near radial vein: (0) present; (1) absent.
85. Forewing with 1R1 distant from stigma: (0) present; (1) absent.
86. Forewing with Rsa: (0) inclined; (1) concave; (2) straight.
87. Forewing 2Cu vein: (0) long, 2Cu longer than cu-a; (1) short, 2Cu shorter than Cu-a; (2) 2Cu as long as Cu-a.
88. Forewing 3Cu vein: (0) present; (1) absent.
89. Forewing 3Cu vein: (0) tubular; (1) spectral; (2) nebulose.
90. Forewing 4Cu vein: (0) present; (1) absent.
91. Forewing 4Cu vein: (0) tubular; (1) spectral; (2) nebulose.
92. Forewing m-cu vein: (0) present; (1) absent.
93. Forewing 2A vein: (0) present; (1) absent.
94. Forewing 2A vein: (0) tubular; (1) spectral; (2) nebulose.
95. Radial flexion line: (0) present; (1) absent.
96. Radial flexion line: (0) absent; (1) present.
97. Radial flexion line length, when present: (0) very short; (1) long.
98. Radial flexion line direction, when present: (0) parallel to radial vein; (1) sinuous.
99. Medial flexion line division, when present: (0) present; (1) absent.
100. Medial flexion line divided, when present: (0) bifurcated; (1) trifurcated.
101. Medial-radial flexion line: (0) present; (1) absent.
102. Cubital flexion line: (0) present; (1) absent.
103. Cubital-medial flexion line: (0) present; (1) absent.
104. Hind wing jugal lobe: (0) long; (1) reduced; (2) absent.
105. Jugal lobe recess: (0) long; (1) short; (2) very short.
106. Metasoma oval: (0) absent; (1) present.
107. Tergal process on metasoma: (0) absent; (1) present.
108. Hypopygium plate: (0) longer than large; (1) larger than long; (2) as long as large.
109. Hypopygium plate thickness in transversal section: (0) thick, inner membrane with sclerotized borders; (1) thin.
110. Hypopygium division: (0) absent; (1) present.
111. Hypopygium with sclerotization of the median region, when single plate: (0) less strong than lateral areas; (1) as strong as other areas.
112. Translucent pair of spots on hypopygeal surface: (0) present; (1) absent.

113. Relative length of the median stalk of hypopygium: (0) short, when the length of that stalk is smaller than half of the total length of hypopygium; (1) long, when the length of that stalk is longer or equal to half of the total length of the hypopygium.
114. Base of median stalk: (0) enlarged; (1) narrow.
115. Hypopygium with lateral stalk: (0) present; (1) absent.
116. Shape of lateral stalk of hypopygium, when present: (0) short, stub-like; (1) elongate.
117. Lateral stalk length: (0) long; (1) short.
118. Hypopygium side projected as stalk-like: (0) present; (1) absent.
119. Basal margin of the hypopygium side: (0) truncate; (1) concave.
120. Distance between apex side to lateral stalk; (0) distant, nearly same measure between median stalk to lateral stalk; (1) close, less than the measure between median stalk to lateral stalk.
121. Presence of an inner projection in the triangular shape on inner surface of the hypopygium: (0) present; (1) absent.
122. Inner membrane of hypopygium: (0) broad, extending median stalk; (1) restricted to inner surface of hypopygium.
123. Inner membrane of hypopygium detached apically: (0) present; (1) absent.
124. Bristle line on median inner surface of hypopygium: (0) present; (1) absent.
125. Number of parameres: (0) one; (1) two.
126. Paramere thickness: (0) thick; (1) thin.
127. Shape of the paramere: (0) completely wide; (1) completely narrow; (2) narrow basally and extended apically; (3) narrow and slightly extended apically.
128. Paramere apex beveled: (0) present; (1) absent.
129. Apical margin of paramere with recess: (0) present; (1) absent.
130. Paramere excavated basally to accommodated cuspis: (0) absent; (1) present.
131. Paramere apex direction: (0) inward; (1) upward.
132. Paramere and basiparamere distinction: (0) totally fused; (1) dorsally fused; (2) completely distinct.
133. Dorsal margin of paramere with subapical small concavity: (0) present; (1) absent.
134. Projection on inner margin of paramere: (0) present; (1) absent.
135. Projection shape on inner margin of paramere, when present: (0) filiform; (1) expanded.
136. Bristle line inside paramere: (0) present; (1) absent.

137. Basiparamere with dorsal callus on median margin: (0) present; (1) absent.
138. Basiparamere with apical and membranous projection: (0) absent; (1) present.
139. Volsella reduced: (0) present; (1) absent.
140. Volsellar base: (0) long; (1) short.
141. Cuspis apex: (0) simple; (1) developed dorsad.
142. Setae on apex of cuspis: (0) present; (1) absent.
143. Cuspis length upward: (0) short; (1) long.
144. Cuspis with ventral arm: (0) absent; (1) present.
145. Ventral arm of cuspis width: (0) uniformly narrow; (1) apex dilated; (2) base dilated; (3) uniformly wide.
146. Direction of ventral arm of cuspis apex: (0) upward; (1) outward.
147. Distinct setae on basal margin of digitus: (0) present; (1) absent.
148. Digital projection on base of volsella: (0) present; (1) absent.
149. Width of digital projections on inner margin of base of volsella: (0) very narrow; (1) wide.
150. Basivolsella outlined from basiparamere: (0) absent; (1) present.
151. Basivolsella length: (0) long, almost touching genital ring; (1) short, not touching genital ring.
152. Basivolsella with basal inner margin folded: (0) present; (1) absent.
153. Basivolsellar shape: (0) elongate; (1) rounded.
154. Aedeagus shape: (0) oval, wide; (1) rectangular, narrow.
155. Aedeagus dorsal cover: (0) present; (1) absent.
156. Aedeagus dorsal cover apical margin: (0) straight; (1) pointed.
157. Aedeagus divided into two valvae: (0) present; (1) absent.
158. Dorsal valva of aedeagus with two plates: (0) present; (1) absent.
159. Ventral plate of aedeagus dorsal valva, when two plates: (0) attached to the dorsal one; (1) not completely attached to the dorsal one.
160. Genital ring curved ventrad: (0) absent; (1) present.
161. Basal ring: (0) present; (1) absent.
162. Basal ring, when present: (0) complete; (1) incomplete.
163. Basal ring incomplete position, when present: (0) ventral; (1) dorsal; (2) lateral.



App. 2. Cladogram obtained under implied weighting of the characters (k = 12.392578), illustrating one of the hypothesis for the distribution of characters.

## CAPÍTULO II



[http://www.ib.usp.br/~mvdomingues/funny\\_cartoons.htm](http://www.ib.usp.br/~mvdomingues/funny_cartoons.htm)

# Revision of the world *Apenesia* Westwood (Hymenoptera, Bethyridae)

## Abstract

The world species of *Apenesia* are revised. Twenty-seven previously described species of *Pristocerinae* are addressed to *Apenesia*. Additionally, 21 new species are described and illustrated: *Apenesia* #001 **sp. nov.**; *A.* #002 **sp. nov.**; *A.* #003 **sp. nov.**; *A.* #004 **sp. nov.**; *A.* #005 **sp. nov.**; *A.* #006 **sp. nov.**; *A.* #007 **sp. nov.**; *A.* #008 **sp. nov.**; *A.* #009 **sp. nov.**; *A.* #010 **sp. nov.**; *A.* #011 **sp. nov.**; *A.* #012 **sp. nov.**; *A.* #013 **sp. nov.**; *A.* #014 **sp. nov.**; *A.* #015 **sp. nov.**; *A.* #016 **sp. nov.**; *A.* #017 **sp. nov.**; *A.* #018 **sp. nov.**; *A.* #019 **sp. nov.**; *A.* #020 **sp. nov.** and *A.* #021 **sp. nov.** The sexual association of two species was possible due to biological data in *A.* #007 and *A.* #003. A key to species based on males is presented. The genus *Apenesia* is parasitoid of beetles who live in gallery in dead wood or seeds.

**Key words:** Chrysoidea, *Pristocerinae*, sex association, *Cerambycidae*, *Curculionidae*.

## Introduction

The flat wasp genus *Apenesia* was described by Westwood (1874) based on two species: *A. amazonica* Westwood, 1874 and *A. modesta* (Smith, 1864), both based only on females. Kieffer (1914d) synonymized *Aeluroides* Tullgren, 1904 under *Apenesia* which had only one species also based only on female. He classified *Apenesia* in Epyrini, although the females of this genus are apterous, the ocelli are absent and the eyes reduced to few facets as all females of *Pristocerinae* concept (see Evans, 1963 and Gordh & Móczár, 1990).

Evans (1963) synonymized many *Pristocerinae* genera known only by species based on males under *Apenesia*. He did not provide any reason why he made the sex association among those taxa. Alencar (chapter 1, this volume) analyzed cladistically *Apenesia* sensu Evans (1963) and concluded *Apenesia* as polyphyletic genus. Alencar (chapter 1, this volume) splitted *Apenesia* into nine different genera based on morphology, molecular and sex association.

*Apenesia* sensu Alencar (chapter 1, this volume) included *Neoapenesia* Terayama, 1995 as a synonymous junior and few species of *Apenesia* sensu Evans (1963). It fits in *Pristocerinae* because all males have the metanotum developed medially and the strong dimorphism between male and

female. In *Apenesia*, males are alate, usually dark coloured, with eyes and ocelli developed, whereas females are apterous, usually yellow or reddish coloured, eyes badly developed with few facets and without ocelli.

In the new concept of *Apenesia*, males are easily recognized among *Pristocerinae* by the body robust; antennae short; clypeus with median lobe trapezoidal usually with a median tooth; pronotum short; prosternum aligned to pronotum; mesoscutum gibbous; hypopygium short, with three stalks; median stalk very long; genitalia with paramere long, narrow and pilose; cuspis developed dorsad, its base articulate in basivolella; basiparamere subdivided ventrally; apical projection on basiparamere apex in dorsal view; aedeagus with ventral apical lobe with warts and dorsal cover long. Usually, *Pristocerinae* females are ant similar and hardly separable, because they are highly modified. However, *Apenesia* females have the head wider than mesosoma; antennae very short, never surpassing head size; clypeus not prominent and extending back frons; mesopleuron developed with frontal surface concave and metapectal-propodeal complex with strong anterior constriction. The few male-female associations indicate males are much smaller than females (see Sawada *et al.* 2014; Azevedo & Waichert 2006).

Today the genus is cosmopolitan and represented by 26 species according to Alencar (chapter 1, this volume): four known only by males, 20 only by females and two have both sexes known. Atypically to *Pristocerinae* genera, the majority of species in *Apenesia* is known from the females. However, as often in *Pristocerinae*, most species based on females are recorded from usually only one or few specimens. That happens because females are rarely collected (Azevedo & Waichert 2006) by the usual successful methods to get *Bethylidae*. Despite this should seem a rule for *Pristocerinae*, Sawada *et al.* (2014) observed females of *Apenesia* inside wood gallery and male-female contact actually happens on wood-borers with no phoretic copulation records. Phoretic copulation is common in some *Pristocerinae*, as in *Dissomphalus* Ashmead, 1893 and *Cleistepyris* Kieffer, 1910. This reinforces the few female specimens collected in Malaise trap and sweeping because *Apenesia* females do not fly or are carried during copula and they live inside wood gallery.

This work intended to be the first revision of *Apenesia* in Alencar (chapter 1, this volume) sensu. The revision is based on 372 new specimens sorted and loan from many different collections and museums of the world. We present a new diagnose for the genus, redescriptions of known species; a worldwide key to all male species, including the new ones described here. All species had their mainly features illustrated except for *Apenesia malaitensis* Brues, *A. modesta* (Smith); *A. punctata* Kieffer and *A. sjostedti* Tullgren because the material was not available for this study.

## Material and methods

### Collections

The following collections (the name of the curator in charge follows the name of the institutions) provided the material examined:

AEIC – American Entomological Institute, U.S.A. (David Wahl)

AMNH – American Museum of Natural History, U.S.A. (James M. Carpenter)

BMNH – The Natural History Museum, United Kingdom (David Notton)

BPBM – Bernice Pauahi Bishop Museum, U.S.A. (James Boone)

CASC – California Academy of Sciences, U.S.A. (R. Zuparko)

CEPLAC – Comissão Executiva do Plano da Lavoura Cacaueira Bahia, Brazil (José Luis Pires)

CNCI – Canadian National Collection of Insects, Canada (J. Huber)

IAVH – Instituto Alexander von Humboldt, Colombia (Monica Ospina)

INPA – Instituto Nacional de Pesquisas da Amazônia, Brazil (J.A. Rafael, Márcio L. Oliveira)

ISAM – Iziko South African Museum, South Africa (Simon van Noort)

LACM – Los Angeles County Museum of Natural History, U.S.A. (Brian Brown)

MSNG – Museo Civico di Storia Naturale Giacomo Doria, Italy (Maria Tavano, Fabio Penati, Roberto Pogany)

MCZH – Museum of Comparative Zoology, U.S.A. (Stephan Cover, Philip Perkins)

MIUP – Museo de Invertebrados Graham Fairchild, Universidad de Panama, Panama (D. Quinteros A.)

MNHN – Museum National d'Histoire Naturelle, France (Agnière Touret-Alby, Claire Villement)

MPEG – Museu Paraense Emílio Goeldi, Brazil (Orlando Tobias)

MUSM – Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Peru

NIAES – National Institute of Agro-Environmental Sciences, Japan (Shin-ichi Yoshimatsu)

OXUM – Oxford University Museum of Natural History (C. O'Toole and J. E. Hogan)

PMAE – Royal Alberta Museum, Canada (A. T. Finnermore and Mathias Buck)

QSBG – Queen Sirikit Botanical Garden, Thailand (Wichai Srisuka)

RMNH – Nationaal Natuurhistorische Museum, Holand (C. van Achterberg)

UFES – Universidade Federal do Espírito Santo, Brazil (Celso O. Azevedo)

UQIC – The University of Queensland Insect Collection, Australia (Susan Wright)

USNM – National Museum of Natural History, U.S.A. (David Furth)

ZMHB – Museum für Naturkunde, Germany (F. Koch)

Other collection cited in the text:



TULE – Tokyo University of Agriculture and Technology, Japan (Akihiko Shinohara)

NSMT – National Science Museum, Japan (Akihiko Shinohara).

### **Taxonomic treatment**

The terms of general body structures, measurements and indices used in this study follow Evans (1964), Azevedo (1999), Lanes & Azevedo (2008), Alencar & Azevedo (2013), Zamprogno & Azevedo (2014) and Kawada *et al.* (2015). The nomenclature of wings follows Ramos & Azevedo (2012) and Ramos & Azevedo (2016). The terms for integument sculpture follow Harris (1979), except for the term coriaceous that follows Eady (1968).

For taxonomic characters related to the genitalia and hypopygium, such structures were first dissected and then treated to be better to study under light microscope Leica DM2500. Each dissected part was placed in a glass vial containing a potassium hydroxide solution 10% during 24 hours for its diafanization. Once clarified, the structures were submitted to an acetic acid solution 25% to neutralize potassium hydroxide action. After this protocol, the material was transferred into a genitalia microvial with glycerin for preservation. Each microvial was pinned together with the specimens for the morphological analyses and illustration.

The descriptions were elaborated with DELTA (Descriptive Language for Taxonomy) as proposed by Dallwitz *et al.* (1993). The key was first generated by DELTA keyand then improved and edited manually.

The material examined information was transcribed without modification from the labels, except by the names of countries translated into English. The specific epithet of all new species was formed by a random combination of letters, added by the suffix “a” to address the female gender. The localities were shown at the Material examined item from North to South direction.

### **Illustrations**

The specimens were photographed under a Leica Z16 APO stereomicroscope fit with a camera adaptor coupled to a Leica DFC 295 video camera (Leica Microsystems, Switzerland). The softwares Leica Application Suite V3. 6.0 and Microsystems by Leica (Switzerland) Limited (LAS) were used to capture individual focal planes. We used a scalable and modular LED illumination dome for microscopic scientific photography as described in Kawada & Buffington (2016). Helicon Focus (HeliconSoft version 4.2.9) software was responsible for stacking the layers into a single combined-focus image using the following parameters: method C and full resolution.

The hypopygium and genitalia drawings were performed using a camera lucida attached to an Olympus CH30 or Leica DM 2500 compound microscope, most correspond to each species holotype. In the section “remarks” we informed whenever genitalia or hypopygium draw was done using a non type specimen. The hypopygium were compressed with cover slip to illustration.

For micrographs, the selected specimens were dehydrated in ascending ethanol series (30%-100%). Each specimen was critical point dried (Autosandri-815, Tousimis) using liquid CO<sub>2</sub>. After that, dissected parts were prepared and mounted on stubs using a double-sided carbon tape. Then sputtered with gold (Desk V, Denton Vacuum) and finally observed by a scanning electron microscope (JEOL, JEM6610 LV) at Laboratório de Ultraestrutura Celular Carlos Alberto Redins in Health and Science Center (LUCCAR/CCS-UFES).

All illustrations and plates were edited in a software for images edition and vectorization using the adjustments (e.g., levels, shadows/highlights), tools (e.g., healing brush, clone stamp) and filters (e.g., unsharp mask), respectively.

### ***Apenesia* Westwood, 1874**

*Apenesia* Westwood 1874: 170. Type-species: *Apenesia amazonica* Westwood, by subsequent designation in Westwood 1881: 130.

*Aeluroides* Tullgren 1904: 429–428. Type-species: *Aeluroides sjostedti* Tullgren, by monotypy. Synonymy by Kieffer 1914, 41: 391.

*Neoapenesia* Terayama 1995a: 886. Type-species: *Neoapenesia leytensis* Terayama, by monotypy.

**Synonymy by Alencar (chapter 1, this volume).**

*Archaeopristocera* Terayama 2004, 27: 44. Type-species: *Archaeopristocera miki* Terayama, by monotypy. **Synonymy to be proposed.**

**Diagnosis.** MALE. Head usually wider than long. Maxillar palpus short; palpal formula 4:3 (Fig. 1.A). Clypeus broad, projected medially and with median acute tooth. Antenna short, never surpassing mesoscutum; flagellomere equally sized and short. Thorax very high in profile. Pronotal disc short (Fig. 1.B). Pronotal collar short laterally; prosternum easily seen in dorsal view. Prosternum aligned to pronotum in ventral view. Mesoscutum gibbous and wide. Forewing with R1b absent; Cua spectral; m-cu and Cub nebulous; medial flexion line deeply divided (Fig. 1.C). Hypopygium short, with three stalks; median stalk very long; anterior corner stalk-shaped. Genitalia with paramere narrow and long, surface wholly pilose (Fig. 1.E-F); cuspis developed dorsad (Fig.

1.E), its base articulate in basivolella; basiparamere subdivided ventrally; apical projection on basiparamere apex in dorsal view; aedeagus with ventral apical lobe with warts and dorsal cover long and narrow. FEMALE. Head distinctly larger than pronotal width, usually square (Fig. 13.B). Mandible long and narrow (Fig. 13.A-D). Palpal formula 4:3. Clypeus with basal margin surpassing posterior margin of torulus. Antenna short, not reaching posterior margin of head. Pronotum with a short and shallow depression at anterior median margin. Mesopleuron with concave surface in frontal view (Fig. 13.J). Metapectal-propodeal complex with strong anterior constriction (Fig. 14.A-E). Anterior region of metapectal-propodeal complex with lateral margin bulging (Fig. 14.A-E).

**Species included.** *A. amazonica* Westwood, 1874; *A.* #001 **sp. nov.**; *A. amoena* Evans, 1963; *A.* #002 **sp. nov.**; *A.* #003 **sp. nov.**; *A.* #004 **sp. nov.**; *A.* #005 **sp. nov.**; *A. bicolor* Vargas & Terayama, 2002; *A.* #006 **sp. nov.**; *A.* #007 **sp. nov.**; *A.* #008 **sp. nov.**; *A. chontalica* Westwood, 1881; *A.* #009 **sp. nov.**; *A.* #010 **sp. nov.**; *A. conradti* Kieffer, 1910; *A. delicata* Evans, 1963; *A. dominica* Evans, 1963; *A.* #011 **sp. nov.**; *A.* #012 **sp. nov.**; *A.* #013 **sp. nov.**; *A.* #014 **sp. nov.**; *A. flavipes* Cameron, 1888; *A. formosa* Vargas & Terayama, 2002; *A.* #015 **sp. nov.**; *A.* #016 **sp. nov.**; *A.* #24 **sp. nov.**; *A.* #018 **sp. nov.**; *A.* #019 **sp. nov.**; *A.* #020 **sp. nov.**; *A.* #021 **sp. nov.**; *A. laevigata* (Evans, 1958); *A. levis* Kieffer, 1904; *A. leytensis* (Terayama, 1995); *A. makiharai* (Sawada, Terayama & Mita, 2014); *A. malaitensis* Brues, 1918; *A. miki* (Terayama, 2004) **comb. nov.**, *A. modesta* (Smith, 1864); *A. nigra* Kieffer, 1904; *A. parasitica* (Smith, 1865); *A. perlonga* Corrêa & Azevedo, 2006; *A. proxima* Kieffer, 1904; *A. punctata* Kieffer, 1904; *A. sahyadrica* Azevedo & Waichert, 2006; *A. singularis* Lanes & Azevedo, 2004; *A. sjostedti* (Tullgren, 1904); *A. substriata* Kieffer, 1904; *A. unicolor* Kieffer, 1904 and *A. vaurieorum* Evans, 1969a.

**Remarks.** In *Apenesia*, the typical male clypeus broad, projected medially and with median acute tooth resembles species of *Dissomphalus* and some of *P10*. Although, *A. laevigata* and *A.* #010 present trapezoidal clypeus without median acute tooth which is similar to the typical male *Pseudisobrachium*. Despite the difficult to count the number of labial and maxillar palps, the palpal formula in *Apenesia* is an exclusive diagnostic feature for both male and female.

Here we were able to understand the identity of fossil genus *Archaeopristocera* represented by a single female. We considered it junior synonymous of *Apenesia*. According to Terayama (2004), *Archaeopristocera* belongs to Pristocerinae by having the eyes small with several facets, the ocelli and forewing absent. He considered as autapomorphies of such genus the mandible long, with strongly angulate axe, the anterior margin of clypeus concave, with a pair of teeth laterally, and the tarsi longer than tibiae. All these characters are also found in many *Apenesia* female species. Moreover, the fossil presents the antennae short and the clypeus continuous to frons, both are remarkable characteristics of *Apenesia* females.

**Distribution.** Cosmopolitan.

## Key to *Apenesia* species (males)

1. Metaposnotal area mainly polished after spiracle (Fig. 1.C, G, H); metaposnotal median carina absent ... 2
  - Metaposnotal area mainly rugulose or foveolate (Fig. 7.A, B, D-F); metaposnotal median carina usually present (Fig. 7.A, F) ... 11
  
2. Notaulus present (Fig. 1.A, B, I) ... 3
  - Notaulus absent (Fig. 1.B) ... 7
  
3. Metapectal-propodeal complex long, posterior margin convex (Fig. 1.D); mesoscutellum elongate; mesoscutum-scutelar sulcus arched (Fig. 9.D) ... *Apenesia laevigata* (Evans, 1958)
  - Metapectal-propodeal complex short, posterior margin almost straight (Fig. 8.H); mesoscutellum elongate; mesoscutum-scutelar sulcus weakly arched or straight (Fig. 8.H) ... 4
  
4. Notaulus incomplete posteriorly (Fig. 8.H) ... *Apenesia* #017 **sp. nov.**
  - Notaulus complete (Fig. 9.I) ... 5
  
5. Mandible with four teeth (Fig. 6.Q); notaulus very convergent posteriorly; mesoscutum-scutelar sulcus short and shallow (Fig. 9.I); hypopygeal posterior margin straight (Fig. 14.L) ... *Apenesia singularis* Lanes & Azevedo, 2004
  - Mandible with one tooth (Fig. 5.K); notaulus convergent posteriorly; mesoscutum-scutelar sulcus long and deep (Fig. 7.H); hypopygeal posterior margin strongly concave (Fig. 14.F) ... 6
  
6. Eye not bulging (Fig. 2.H); pronotal disc long (Fig. 7.H); mesoscutum-scutelar sulcus weakly arched (Fig. 7.H) ... *Apenesia* #008 **sp. nov.**
  - Eye bulging (Fig. 4.E); pronotal disc very short (Fig. 9.C); mesoscutum-scutelar sulcus straight (Fig. 9.C) ... *Apenesia* #021 **sp. nov.**
  
7. Pronotal disc very short; mesoscutum-scutelar sulcus short and straight; axilla oval; metapectal-propodeal complex long (Fig. 8.A) ... *Apenesia* #010 **sp. nov.**
  - Pronotal disc long; mesoscutum-scutelar sulcus long and weakly arched; axilla trapezoidal; metapectal-propodeal complex short (Fig. 7.G) ... 8

8. Head larger than long (Fig. 2.G); metaposnotal area almost completely polished except by narrow strigate anterior area (Fig. 7.G); hypopygeal posterior margin almost straight (Fig. 13G) ... *Apenesia* #007 **sp. nov.**

- Head as large as long (Fig. 2.C); metaposnotal area foveolate or imbricate anteriorly (Fig. 7.C, 9.A, 9.F); hypopygeal posterior margin concave (Fig. 13.C) ... 9

9. Mandible with three teeth (Fig. 6.N); cuspis with three callus (Fig. 21.C); basivolsella apical inner margin with small projection (Fig. 21.A) ... 10

- Mandible with four teeth (Fig. 5.F); cuspis with two callus (Fig. 15.I); basivolsella apical inner margin with large projection (Fig. 15.G) ... *Apenesia* #003 **sp. nov.**

10. Metanotal fovea oval; median region of metanotum narrow and large; metaposnotum with row of anterior foveae, polished and weakly imbricate Fig. (9.A); hypopygeal membrane reaching more than half of hypopygium Length; hypopygeal lateral margin sinuous (Fig. 14.D) ... *Apenesia* #019 **sp. nov.**

- Metanotal fovea linear; median region of metanotum wide and narrow; metaposnotum imbricate and polished (Fig. 9.F); hypopygeal membrane not reaching half of hypopygium Length; hypopygeal lateral margin converging posterad (Fig. 14.I) ... *Apenesia makihari* (Sawada, Terayama & Mita, 2014)

11. Metaposnotal median carina distinctly present (Fig. 8.C, 9.E) ... 12

- Metaposnotal median carina absent (Fig. 7.E, 7.I, 8.B) ... 20

12. Notaulus incomplete posteriorly or absent (Fig. 8.C) ... 13

- Notaulus complete (Fig. 7.F) ... 15

13. Pronotal disc short; metaposnotal median carina short (Fig. 8.C); cuspis with one serrate callus (Fig. 18.I)... *Apenesia* #012 **sp. nov.**

- Pronotal disc very short; metaposnotal median carina long (Fig. 9.E); cuspis with more than one callus (Fig. 22.F) ... 14

14. Head nearly rounded with strong convex vertex (Fig. 4.G); notaulus absent or nearly so (Fig. 9.E); hypopygeal posterior margin convex (Fig. 14.H) ... *Apenesia leytensis* (Terayama, 1995)

- Head trapezoidal with vertex almost straight (Fig. 2.B); notaulus present, incomplete posteriorly (Fig. 7B); hypopygeal posterior margin concave (Fig. 13.B) ... *Apenesia* #002 **sp. nov.**

15. Head longer than large (Fig. 2.F); mandible with one tooth (Fig. 5.I) ... 16  
- Head nearly as long as large (Fig. 4.B), mandible with four or five teeth (Fig. 6.H) ... 18
16. Head with vertex convex; eye not bulging (Fig. 2.F); metaposnotum mostly imbricate; metanonal fovea oval (Fig. 7.F) ... *Apenesia* #006 **sp. nov.**  
- Head with vertex straight or nearly so; eye bulging (Fig. 4.D); metaposnotum mostly rugulose; metanonal fovea dropped-shaped (Fig. 9.B, 9.E) ... 17
17. Ocellar triangle with proximal edges (Fig. 4.D); pronotal disc very short; mesoscutum-scutelar sulcus weakly arched (Fig. 9.B); cuspis with two callus (Fig. 21.F) ... #020 **sp. nov.**  
- Ocellar triangle with distal edges (Fig. 5.A); pronotal disc short; mesoscutum-scutelar sulcus straight (Fig. 9.G); cuspis with one serrate callus (Fig. 23.C) ... *Apenesia perlonga* Corrêa & Azevedo, 2006
18. Mesoscutum-scutelar sulcus straight and shallow (Fig. 8I); aedeagus with dorsal lobe long and narrow (Fig. 20.H) ... *Apenesia* #018 **sp. nov.**  
- Mesoscutum-scutelar sulcus at least arched, deep or shallow (Fig. 7.A, 7.D); aedeagus with dorsal lobe short or, when long, not narrow (Fig. 15.B) ... 19
19. Mesoscutum-scutelar sulcus weakly arched and shallow (Fig. 7.A); hypopygium with posterior margin straight, without flap (Fig. 13.A); aedeagus with dorsal lobe long and wide (Fig. 15.B) ... *Apenesia* #001 **sp. nov.**  
- Mesoscutum-scutelar sulcus arched and deep (Fig. 7.D); hypopygium with posterior margin concave, with flap (Fig. 13.D); aedeagus with dorsal lobe short and wide (Fig. 16.B) ... *Apenesia* #004 **sp. nov.**
20. Pronotal disc short or very short (Fig. 7.I) ... 21  
- Pronotal disc long (Fig. 8.E) ... 24
21. Notaulus complete (Fig. 8.B); hypopygeal posterior margin concave (Fig. 13.K) ... 22  
- Notaulus incomplete posteriorly (Fig. 7.I); hypopygeal posterior margin straight (Fig. 13.I) ... *Apenesia* #009 **sp. nov.**

22. Mandible with one tooth (Fig. 5.H); mesoscutum-scutelar sulcus weakly arched (Fig. 7.E); hypopygium with flap (Fig. 14.A) ... 23

- Mandible with three teeth (Fig. 6.A); mesoscutum-scutelar sulcus wide and arched (Fig. 8.B); hypopygium without flap (Fig. 14.C) ... *Apenesia* #011 **sp. nov.**

23. Mesoscutum-scutelar sulcus narrow; metanotal fovea badly impressed; metapectal-propodeal complex with posterior margin almost straight; metaposnotum rugulose, polished and weakly imbricate (Fig. 8.G); paraspicular sulcus weakly foveolate; metapleural carina absent (Fig. 11.F); propodeal declivity polished-foveolate ... *Apenesia* #016 **sp. nov.**

- Mesoscutum-scutelar sulcus wide; metanotal fovea well impressed; metapectal-propodeal complex with posterior margin convex; metaposnotum strigate anteriorly, coriaceous medially, and weakly coriaceous (Fig. 7.E); paraspicular sulcus irregularly foveolate; metapleural carina present (Fig. 10.E); propodeal declivity imbricate ... *Apenesia* #005 **sp. nov.**

24. Metaposnotum texture in trapezoidal area (Fig. 8.E) ... *Apenesia* #014 **sp. nov.**

- Metaposnotum texture in triangular area (Fig. 8.D, 9.H) ... 25

25. Notaulus almost parallel (Fig. 8.D); cuspis with three callus (Fig. 19.C) ... *Apenesia* #013 **sp. nov.**

- Notaulus converging posterad (Fig. 8.F, 9.H); cuspis with one or two callus (Fig. 19.I) ... 26

26. Mandible with one tooth (Fig. 6.E); mesoscutum-scutelar sulcus wide and deep; metanotal fovea dropped-shaped; metaposnotum rugulose (Fig. 8.F); hypopygeal plate short (Fig. 13.O) ... #015 **sp. nov.**

- Mandible with four teeth (Fig. 6.P); mesoscutum-scutelar sulcus narrow and shallow; metanotal fovea oval; metaposnotum irregularly foveolate (Fig. 9.H); hypopygeal plate long (Fig. 14.K) ... *Apenesia sahyadrica* Azevedo & Waichert, 2006

***Apenesia amazonica* Westwood, 1874**

(Figs. 25.F)

*Apenesia amazonica* Westwood 1874: 171, pl 31, fig. 12. #f; Westwood 1881, 124: 131; Dalla Torre 1898, 5: 557 (catalog); Kieffer 1908, 76: 25 (catalog), pl 1, fig. 6; Kieffer 1911, 35: 200–233; Kieffer 1914, 41: 392, 395–396; Evans 1963, 130: 269, 356–357, fig. 131; Evans 1964, 132: 33; Gordh & Móczár 1990, 46: 199 (catalog).

**Diagnosis.** Female.- Length 7.6 mm. **Color.** Body castaneous, metasoma dark castaneous. Mandible with two apical teeth. Clypeus extending back frons, median lobe with apical margin strongly concave, so that clypeus is nearly absent medially, apical margin with bristles, median carina absent. Eye dark, elliptical, with about 11 facets. Malar space shorter than eye length. Frons aciculate, punctures sparse. Head quadrate with sides parallel, vertex concave,  $1.1 \times$  as long as wide. Pronotal disc with sides nearly parallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.77 \times$  its minimum width. Mesopleuron with longitudinal carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma shorter than head and mesosoma together, petiole short.

**Material examined.** Holotype #f: BRAZIL: Amazonia, D. Bates col. (OXUM).

**Comments.** This species may probably be the corresponding female of *A. singularis*, a species described only based on male specimens. *Apenesia singularis* is abundant in the Amazon region and due to the sympatric occurrence this hypothesis should be tested with molecular data.

**Distribution.** Neotropical (Brazil).

***Apenesia* #001 Alencar & Azevedo, sp. nov.**

(Figs. 2.A, 5.D, 7.A, 10.A, 13.A, 15.A-C)

**Description.** Holotype. Male. Length 4.2 mm. LFW 2.6 mm.

**Colors.** Head and mesosoma dark castaneous; antenna, clypeus and metasoma castaneous; legs castaneous and yellowish; wings hyaline, veins castaneous.

**Head.** Head as long as large, trapezoidal. Frons weakly coriaceous, sparsely puncticulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin crenulate, median carina short in profile. Mandible with five apical teeth, teeth with different size, upper tooth mesad, three upper teeth equally sized. Eye weakly bulging. Ocelli large, triangle with distal edges.



**Mesosoma.** Pronotal disc very short. Notaulus present, complete, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutelar sulcus weakly arched, without fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea drop-shaped; median region wide, narrow, with posterior margin straight. Metapectal-propodeal complex long, posterior margin convex; metaposnotal median carina present, metaposnotum rugulose. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum weakly coriaceous, inferior region coriaceous. Propodeal declivity coriaceous-foveolate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin almost straight, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, large, and acute. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, almost equally sized, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe long; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, MALAYSIA, Se. Sabah, nr Danum Valley Field C. W0N1, 2–23.viii.1987, Mal. trap. 5, C. V. Achterberg & D. Kennedy, c 150m (RMNH'87) (Ibes n° 14155) Paratypes: MALAYSIA, Pasoh Forest Res. Negri S., P. & M. Becker (AEIC): 1m#, XII.5.78, for. gap (Ibes n° 14103); 1m#, III.19.79, prim. for. (Ibes n° 14099); 1m#, V.26.79, for. gap (Ibes n° 14101); 1m#, XI.3.79, forest (Ibes n° 14102); 1m#, III.12.80, for. gap (Ibes n° 14100); 1m#, IV.17.80, prim. for. (Ibes n° 14104); PENINSULA MALAYSIA, Pasoh Forest Reserve, Negeri Sembilan (NIAES): 2m#, 25.iii–2.iv.1993, Fine Malaise Trap, K. Konishi & K. Maeto, (Ibes n° 14151, 14153); 1m#, 26.iii–3.iv.1993, Fine Malaise Trap, K. Konishi & K. Maeto, (Ibes n° 14154); 1m#, 26.ix-3.xii.1993, Fine Malaise Trap, K. Maeto (Ibes n° 14158); 1m#, 3–10.xii.1993, Fine Malaise Trap, K. Maeto, (Ibes n° 14159); 1m#, 26.ix-3.xii.1993, Coarse Malaise Trap, K. Maeto (Ibes n° 14152). INDONESIA, N Ceram, 20km E Wahai, nr Pasahari rainforest, 3–20. iii.1997, C. V. Achterberg & R. de Vries, c 25m, (RMNH'97): 1m#, Mal. trap. 17 (Ibes n° 14156), 1m#, Mal. trap. 19 (Ibes n° 14157).

**Comments.** This species is unique by having the head slightly larger than long with convex vertex; the mandible with five teeth and three upper very small; the pronotum very short; notaulus complete; the metaposnotum v-shaped and rugulose; the genitalia with basivolsella apical inner margin projected mesad, forming a deep concavity on base of digitus. This projection can be less prominent in some specimens.

**Distribution.** Oriental (Malaysia, Indonesia).

***Apenesia amoena* Evans, 1963**

(Figs. 25.G)

*Apenesia amoena* Evans 1963: 130: 269, 353–354, fig. 133. #f; Evans 1964, 132: 32; Gordh & Móczár 1990, 46: 199 (catalog).

**Diagnosis.** Female.- Length 4.61 mm. **Color.** Body castaneous, metasoma darker. Mandible with two apical teeth. Clypeus very short, emarginated and high medially so that it is triangular in frontal view, margin with bristles. Eye dark, elliptical, with about eight facets. Malar space shorter than eye length. Frons with very fine striations, punctures small and sparse, with two short sutures above clypeus, which join posteriorly. Head quadrate with sides parallel and vertex nearly straight (barely concave),  $1.16 \times$  as long as wide. Pronotal disc with sides diverging posteriorly. Maximum width of propodeal disc  $1.6 \times$  its minimum width. Mesotibia strongly spinose. Metasoma as long as head and mesosoma together, with very short petiole.

**Material examined.** Holotype #f: COSTA RICA, *S[an]ta Clara*, Hamburg Farm, 28.V.[19]25, F. Nevermann col. (USNM, #66015).

**Distribution.** Neotropical (Costa Rica).

***Apenesia* #002 Alencar & Azevedo, sp. nov.**

(Figs. 2.B, 5.E, 7.B, 10.B, 13.B, 15.D-F)

**Description.** Holotype. Male. Length 4 mm. LFW 3 mm.

**Colors.** Body reddish castaneous; mandible yellowish; legs castaneous; wings amber, veins dark castaneous.

**Head.** Head as long as large, trapezoidal. Frons weakly coriaceous, sparsely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with three apical teeth, teeth with similar size, upper tooth mesad. Eye weakly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc very short. Notaulus present, incomplete posteriorly, parallel. Parapsidal signal weakly impressed. Scutellum longer than large, posterior margin almost straight; mesoscutum-scutular sulcus weakly arched, with fovea on side edge, narrow, shallow. Axilla drop-shaped, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea drop-shaped; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metapostnotal median carina present, metapostnotum

irregularly foveolate, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina present; lateral surface of propodeum imbricate, inferior region strigulate. Propodeal declivity polished-foveolate.

**Metasoma.** Petiole short. Hypopygium with plate very short, posterior margin concave, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, large, and convex. Basiparamere with apical dorsal projection small, apex convex. Cuspis with apical margin with two apical callus, almost equally sized, dorsal end long. Aedeagus with two apical lobes, ventral lobe short; dorsal lobe short; subapical membrane long; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype #m, MALAYSIA, Pasoh Forest Res. Negri S., III.18.80, P. & M. Becker, forest (AEIC) (Ibes n° 14043).

**Comments.** This species is unique in having the head larger than long; the mandible with three teeth; the pronotum very short; the notaulus incomplete posteriorly; the metapostnotum t-shaped and irregularly foveolate; Hypopygium with plate short with posterior margin concave; genitalia with basivolsella apical inner margin projected mesad and convex. The mesosoma of #002 is similar to #009 because of the mesoscutum has incomplete notaulus. #002 and #009 differ from each other especially by the head trapezoidal and rectangular and the hypopygium posterior margin concave and straight, respectively.

**Distribution.** Oriental (Malaysia).

***Apenesia* #003 Alencar & Azevedo, sp. nov.**

(Figs. 2.C, 5.F, 7.C, 10.C, 13.C, 15.G-I, 24.A, E, 25.A)

**Description.** Holotype. Male. Length 4.2 mm. LFW 3.4 mm.

**Colors.** Body dark castaneus; mandible castaneus; legs castaneous and yellowish; wings light amber, veins castaneous.

**Head.** Head as long as large, quadrate. Frons coriaceous, densely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with four apical teeth, teeth with different size, upper tooth mesad, two upper teeth equally sized. Eye weakly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc short. Notaulus absent. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutular sulcus weakly arched, without fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, large. Metanotal trough

foveolate, metanotal fovea linear; median region wide, large, with posterior margin straight. Metapectal-propodeal complex long, posterior margin convex; metaposnotal median carina absent, metaposnotum row of anterior foveae, and polished. Propodeal disc polished. Paraspicular sulcus weakly punctulate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region strigulate. Propodeal declivity imbricate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin concave, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, large, and convex. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, almost equally sized, dorsal end long. Aedeagus with two apical lobes, ventral lobe short; dorsal lobe short; subapical membrane absent; aedeagal dorsal cover narrow.

**Female.** Known.

**Description.** Allotype. Female.- Length 4.9 mm. Body castaneous, metasoma dark castaneous. Mandible with two apical teeth. Clypeus extending back frons, median lobe with apical margin concave, apical margin with bristles, median carina absent. Eye gray, elliptical, with about 12 facets. Malar space shorter than eye length. Frons aciculate, punctures sparse. Head elongate with sides parallel, vertex concave,  $1.31 \times$  as long as wide. Pronotal disc with sides nearly parallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.75 \times$  its minimum width. Mesopleuron with longitudinal carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma longer than head and mesosoma together, petiole short.

**Material examined.** Holotype m#, [JAPAN], Kurima Is., Miyako Isls. Ryukyus, 25.x.2003, Collected dead plants, H. Makihara *Leucaena leucocephala*, 22–27.iv.2004, Hirroshi Makihara Collection (NIAES) (Ibes n° 14160). Allotype f#, [JAPAN], Kurima Is., Miyako Isls. Ryukyus, 25.x.2005, Collected dead plants, H. Makihara, *Leucaena leucocephala*, 22–27.iv.2004, Hirroshi Makihara Collection (NIAES) (Ibes n° 14162). Paratypes: [JAPAN]: Kurima Is., Miyako Isls. Ryukyus, Hirroshi Makihara Collection (NIAES): 1m#, 25.x.2006, Collected dead plants, H. Makihara, *Leucaena leucocephala*, 27.ii–11.iii.2004 (Ibes n° 14163); 1f#, 25.x.2004, Collected dead plants, H. Makihara, *Leucaena leucocephala*, 22–27.iv.2004 (Ibes n° 14161); Tarama Is., Miyako Isls. Ryukyus, 22–23.X.2003, Collected dead plants, H. Makihara (NIAES): 1 f#, *Diospyros ferres*, 27.ii–11.iii.2004, Hirroshi Makihara Collection (Ibes n° 14164); 1f#, *Diospyros ferres*, 27.ii–11.iii.2004, Hirroshi Makihara Collection (Ibes° 14195); 1f#, *Morus australis* Poiret, 6–22.iv.2004, Hirroshi Makihara Collection (Ibes n° 14196); 1f#, *Leucaena leucocephala*, 6–22.iv.2004, Hirroshi Makihara Collection (Ibes n° 14165); Mt. Nagodake, Okinawa Is. Ryukyus, 15.x.2003, Collected dead plants, H. Makihara (NIAES): 1m#, *Viburnum odoratissimm* var. *awabuki*, 11–18.iii.2004, Hirroshi Makihara Collection (Ibes n° 14166); 1f#, *Viburnum odoratissimm* var. *awabuki*, 27.ii–11.iii.2004, Hirroshi Makihara Collection (Ibes n° 14198); 3f#,

*Diospyros Morrisiana* Hance, 11–18.iii.2004, Hirroshi Makihara Collection (Ibes n° 14167, 14168, 14197); Mt. Ooyama, Okinoerabu Is. Kagoshima Pref., H. Makihara (NIAES):5f#, 12.x.2003, Collected dead plants, *Symplocos nakaharae*, 11–18.iii.2004, Hirroshi Makihara Collection (Ibes n° 14169, 14170, 14171, 14172, 14173); 1f#, *Pinus luchuensis* Mayr., 11–18.iii.2004, Hirroshi Makihara Collection (Ibes n° 14175); 1f#, *Elaeocarpus sylvestris* var. *ellipticus*, 6–22.iv..2004, Hirroshi Makihara Collection (Ibes n° 14174); 19f#, Mt. Omotodake, Ishigakil Is. Ryukyus, 21.x.2003, Collected dead plants, H. Makihara, *Machilus japonica* Sleb. et Zucc., 27.ii–11.iii.2004, Hirroshi Makihara Collection (Ibes n° 14176, 14177, 14178, 14179, 14180, 14181, 14182, 14183, 14184, 14185, 14186, 14187, 14188, 14189, 14190, 14191, 14192, 14193, 14194).

**Comments.** *Apenesia* #003 was collected manually by H. Makihara who observed contact behavior and copulation among specimens collected (personal communication). This species is similar to *Apenesia* #007 by having notaulus absent; pronotum short; metapostnotum almost completely polished and apical inner margin of basivolvella projected and convex. Although, males of #003 has head as long as large; mandible with four teeth; metanotal groove foveolate with linear median fovea; metapectal-propodeal complex with posterior margin convex; metapostnotum with row of anterior fovea and hypopygeal posterior margin concave, whereas males of *Apenesia* #007 has head longer than large; mandible with three teeth; metanotal groove mostly imbricate; metapectal-propodeal complex with posterior margin almost straight; metapostnotum with row of striae and hypopygeal posterior margin almost straight.

Based only on females, *Apenesia* #003 could represent *A. malaitensis* Brues because female size is similar, the mandible is bidentate and the head is elongate. Although, since Pristocerinae females, including *Apenesia*, seem to be cryptical, we decided to split the species until molecular data is available to test this hypothesis. For now, we were not able to analyze *A. malaitensis* unless by literature what makes us not comfortable to not keep both split.

**Distribution.** Palaearctic (Japan).

#### ***Apenesia* #004 Alencar & Azevedo, sp. nov.**

(Figs. 2.D, 5.G, 7.D, 10.D, 13.D, 16.A-C)

**Description.** Holotype. Male. Length 4.7 mm. LFW 4 mm.

**Colors.** Head and body dark castaneous; metasoma redish; antenna and mandible light castaneous; legs castaneous and yellowish; wings hyaline, veins castaneous.

**Head.** Head as long as large, trapezoidal. Frons coriaceous, sparsely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin smooth, median carina short in profile. Mandible with five apical

teeth, teeth with different size, upper tooth mesad, four upper teeth equally sized. Eye weakly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc very short. Notaulus present, complete, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum longer than large, posterior margin convex; mesoscutum-scutular sulcus strongly arched, with fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough imbricate, metanotal fovea oval; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina present, metaposnotum rugulose, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina present; lateral surface of propodeum imbricate, inferior region strigulate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate long, posterior margin concave, flap present. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, large, and acute. Basiparamere with apical dorsal projection large, apex acute. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end very short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane absent; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, MALAYSIA, Pasoh Forest Res. Negri S., IV.3.80, P. & M. Becker, prim. for. (AEIC) (Ibes n° 14097). Paratypes: 1m#, THAILAND, Nakhon Si Thammarat, Namtok Yong NP, 8°10.434'N, 99°44.508'E, 5–12.xi.2008, Malaise trap, U-pral;K. leg., T4254 (QSBG) (Ibes n° 14204). MALAYSIA: 1m#, Se. Sabah, nr Danum Valley Field C. W0N1, 13.ix-4.x.1987, Mal.trap 5, C. V. Acherberg & D. Kennedy, c 150m (RMNH'87) (Ibes n° 14199); 1m#, Se. Sabah, Danum Valley Field C. W0, 24.ii.-18.iii.1987, Mal. Trap 11, C. V. Acherberg, c 150m (RMNH'87) (Ibes n° 14200); 1m#, SW. Sabah, nr Long Pa Sai (West), 1–13.iv.1987, Mal. Trap 6, C. V. Acherberg, c. 1025m (RMNH'87) (Ibes n° 14201); 1m#, SW. Sabah, nr Long Pa Sai (East), 25.xi–8.xii.1987, Mal.trap 4, C. V. Acherberg, c. 1000m, (RMNH'87) (Ibes n° 14202); 1m#, SW. Sabah, nr Long Pa Sia, Payakalaba, 25.xi.-1.xii.1987, Mal.trap15, C. V. Acherberg, c. 1010m, stub #40 (SEM) (RMNH'87) (Ibes n° 14203); Pasoh Forest Res. Negri S., P. & M. Becker, for. gap (AEIC): 1m#, XII.31.79 (Ibes n° 14093); 1m#, XII.20.79 (Ibes n° 14095); 1m#, III.1.80 (Ibes n° 14090); 1m#, III.28.80 (Ibes n° 14091); 1m#, IV.10.80 (Ibes n° 14092); 1m#, IV.15.80 (Ibes n° 14096); 1m#, IV.22.80 (Ibes n° 14094); 1m#, IV.30.80 (Ibes n° 14098); 1m#, PENINSULA MALAYSIA, Pasoh Forest Reserve, Negeri Sembilan, 2–8.iv.1993, Fine Malaise Trap, K. Konishi & K. Maeto (NIAES) (Ibes n° 14150). 1m#, INDONESIA, Sula Isl. Mangole, near Buya, 12.x.-2.xi.1993, Mal.trap11, C. V. Acherberg, C 46 (RMNH'93) (Ibes n° 14205). 1m#, VANUATU {=New Hebrides}, Erromango I, Dillon Bay, ii.1981, N.L.H. Krauss, coll., 0–100m, Acc. #1981.131 (BPBM) (Ibes n° 14244).

**Comments.** *Apenesia* #004 is similar to *Apenesia* #018 by having the notaulus complete and the metaposnotum rugulose. However, #004 has the mandible with five teeth; the mesoscutum-mesoscutellar suture strongly arched and deep; the hypopygium with flap and posterior margin concave, whereas *Apenesia* #018 has the mandible with four teeth; the mesoscutum-mesoscutellar suture straight and shallow; the hypopygium without flap and posterior margin almost straight.

**Distribution.** Oriental (Thailand, Indonesia, Malaysia) and Australian (Vanuatu).

***Apenesia* #005 Alencar & Azevedo, sp. nov.**

(Figs. 2.E, 5.H, 7.E, 10.E, 13.E, 16.D-F)

**Description.** Holotype. Male. Length 3.7 mm. LFW 2.5 mm.

**Colors.** Body orange castaneus except antenna, mandible and legs yellowish.

**Head.** Head as long as large, trapezoidal. Frons weakly coriaceous, sparsely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye strongly bulging. Triangle with proximal edges.

**Mesosoma.** Pronotal disc very short. Notaulus present, complete, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough imbricate, metanotal fovea oval; median region narrow, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin convex; metaposnotal median carina absent, metaposnotum strigate anteriorly, coriaceous medially, and weakly coriaceous. Paraspicular sulcus irregularly foveolate; metapleural carina present; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity imbricate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex acute. Cuspis with apical margin serrate, dorsal end very short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe long; subapical membrane absent; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, ECUADOR, Pichincha, Tinalandia 16 km s., Santo Domingo, 15-vi-1975, S.+ J. Peck (PMAE) (Ibes n° 14207).

**Comments.** *Apenesia* #005 is promptly recognized by having the reddish-brown body since other species are usually dark brown or black. *Apenesia* #005 and *Apenesia* #001 have aedeagus dorsal lobe long which is unusual within *Apenesia* species. However, despite the body color,

*Apenesia* #005 has the mandible with one tooth; the metapostnotal median carina absent and the hypopygium flap and posterior margin concave, whereas *Apenesia* #001 has the mandible with five teeth; the metapostnotal median carina present and the hypopygium without flap and posterior margin almost straight.

**Distribution.** Neotropical (Ecuador).

***Apenesia bicolor* Vargas & Terayama, 2002**

(Figs. 25.H)

*Apenesia bicolor* Vargas & Terayama 2002: 27–29, figs. 5–8.

**Diagnosis.** Female.- Length 5.3 mm. **Color.** Body castaneous, metasoma dark castaneous. Mandible with two apical teeth. Clypeus extending back frons, median lobe with apical strongly concave, so that clypeus is nearly absent medially, apical margin with bristles, median carina absent. Eye dark, elliptical, with about 10 facets. Malar space shorter than eye length. Frons aciculate, punctures sparse. Head quadrate with sides parallel, vertex straight,  $1.17 \times$  as long as wide. Pronotal disc with sides nearly parallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.73 \times$  its minimum width. Mesopleuron with longitudinal carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma longer than head and mesosoma together, petiole very short.

**Material examined.** Holotype #: COLOMBIA, *Choco*, La Balsa, Corregimiento La Honda, Rio Sucio, L. Mendoza col., VJIC 0126. (IAVH-E 86696).

**Distribution.** Neotropical (Colombia).

***Apenesia* #006 Alencar & Azevedo, sp. nov.**

(Figs. 2.F, 5.I, 7.F, 10.F, 13.F, 16.G-I)

**Description.** Holotype. Male. Length 5.9 mm. LFW 4.3 mm.

**Colors.** Head and body castaneous; metasoma light castaneous; antenna, clypeus, mandible and legs yellowish; wings hyaline, veins castaneous.

**Head.** Head larger than long, rectangular. Frons coriaceous, densely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye weakly bulging. Ocelli large, triangle with proximal edges.



**Mesosoma.** Pronotal disc short. Notaulus present, complete, strongly converging posterad. Parapsidal signal well delimited. Scutellum as long as large, posterior margin convex; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, narrow, shallow. Axilla drop-shaped, deep, large. Metanotal trough foveolate, metanotal fovea oval; median region narrow, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina present, metaposnotum strigate anteriorly, and imbricate. Propodeal disc imbricate; Paraspicular sulcus imbricate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity imbricate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin projected mesad, small, and acute. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, GUATEMALA: Izabal, Las Escobas, 200 m, [15°41'N], [88°39'W], V-1987, [M.] Sharkey [col.] (PMAE) (Ibes n° 14208). Paratypes: 1m#, same data as holotype (Ibes n° 8347); 1m#, BRAZIL, Amazonas, 71°38'W, 4°33'S, IX.'80, Alvarenga (AEIC) (Ibes n° 14118).

**Comments.** This species is unique by having the dorsal part of metapectal-propodeal complex entire imbricate. *Apenesia* #006 is similar to *Apenesia* #008 and *A. perlonga* by having the head larger than long, rectangular; the mandible with one tooth; the pronotum short; notaulus complete and convergent posteriorly and the hypopygium with flap and posterior margin concave. However, *Apenesia* #006 has the head rectangular with vertex slightly convex as *Apenesia* #008, whereas *A. perlonga* has the head rectangular with vertex straight. *Apenesia* #006 differs from *Apenesia* #008 by the presence of a metaposnotal median carina.

**Distribution.** Neotropical (Guatemala, Brazil).

***Apenesia* #007 Alencar & Azevedo, sp. nov.**

(Figs. 2.G, 5.J, 7.G, 10.G, 13.G, 17.A-C, 24.B, F, 25.B)

**Description.** Holotype. Male. Length 5.3 mm. LFW 4.2 mm.

**Colors.** Body black or dark cast. Antenna, clipeo, mandible castaneus; Legs castaneous and yellowish; wings hyaline, veins castaneus.

**Head.** Head larger than long, trapezoidal. Frons coriaceous, densely punctulate; line on frons absent. Vertex straight. Clypeus broad with median lobe subtrapezoidal, median tooth present, and

large, apical margin crenulate, median carina high in profile. Mandible with three apical teeth, teeth with similar size, upper tooth mesad. Eye weakly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc short. Notaulus absent. Parapsidal signal well delimited. Scutellum as long as large, posterior margin convex; mesoscutum-scutelar sulcus weakly arched, without fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea oval; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum row of striae, and polished. Propodeal disc polished. Paraspicular sulcus weakly punctulate; metapleural carina absent; lateral surface of propodeum coriaceous, inferior region coriaceous. Propodeal declivity polished-punctulate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin almost straight, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, large, and convex. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end long. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Known.

**Description.** Allotype. Female.- Length 5,5 mm. Body light castaneous, metasoma castaneous. Mandible with three apical teeth. Clypeus extending back frons, median lobe with apical margin strongly concave, so that clypeus is nearly absent medially, apical margin with bristles, median carina absent. Eye grey, elliptical, with about 6 facets. Malar space wider than eye length. Frons aciculate, punctures sparse. Head quadrate with sides parallel, vertex slightly concave,  $1.1 \times$  as long as wide. Pronotal disc with sides nearly parallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.8 \times$  its minimum width. Mesopleuron with longitudinal carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma longer than head and mesosoma together, petiole very short.

**Material examined.** Holotype m#, [PAPUA NEW GUINEA], New Britain, Kerawat, x.1946, ex larva of *Pantorhytes plutus*, B. A. O'Connor, Imp. Inst. Ent. Coll. No. 10600 (BMNH) (Ibes n° 14253). Allotype f#, same data as holotype (Ibes n° 14257). Paratypes: 1m#, INDONESIA, N Ceram, 9 km E Wawai, nr PHPA-Q coastal rainforest, 28.ii–21.iii.1997, Mal.trap 6, C. V. Acherberg & R. de Vries (RMNH'97) (Ibes n° 14211). MALAYSIA, Pasoh Forest Res. Negri S., P. & M. Becker (AEIC): 3m#, III-23-78, for. gap (Ibes n° 14049, 14063, 14065); 1m#, III.30.78, for. gap (Ibes n° 14050); 1m#, IV.3.78, for. gap (Ibes n° 14060); 1m#, IV.15.78, for. gap (Ibes n° 14058); 1m#, IV.25.78, for. gap (Ibes n° 14061); 1m#, IV.30.78, for. gap (Ibes n° 14069); 1m#, V.9.78, for. gap (Ibes n° 14052); 1m#, V.16.78, for. gap (Ibes n° 14048); 1m#, V.24.78, for. gap (Ibes n° 14064);

1m#, VI.19.78, for. gap (Ibes n° 14072); 1m#, VIII.5.78, for. gap (Ibes n° 14057); 1m#, X.21.78, for. gap (Ibes n° 14071); 1m#, X.24.78, for. gap (Ibes n° 14056); 1m#, X.26.78, for. gap (Ibes n° 14070); 1m#, XII.29.78, for. gap (Ibes n° 14073); 1m#, I.15.79, for. gap (Ibes n° 14047); 1m#, I.16.79, forest (Ibes n° 14066); 1m#, II.5.79, for. gap (Ibes n° 14059); 1m#, II.9.79, for. gap (Ibes n° 14068); 1m#, II.27.79, for. gap (Ibes n° 14053); 1m#, III.7.79, for. gap (Ibes n° 14054); 1m#, III.8.79, for. gap (Ibes n° 14055); 1m#, III.11.79, forest (Ibes n° 14044); 1m#, VII.5.79, forest (Ibes n° 14046); 1m#, VIII.17.79, forest (Ibes n° 14045); 1m#, IX.26.79, for. gap (Ibes n° 14062); 1m#, XI.8.79, forest (Ibes n° 14067); 1m#, I.24.80, for. gap (Ibes n° 14051). PENINSULA MALAYSIA, Pasoh Forest Reserve, Negeri Sembilan (NIAES): 1m#, 2–8.iv.1993, Fine Malaise Trap, K. Konishi & K. Maeto (Ibes n° 14133); 1m#, 9–16.IV.1993, Coarse Malaise Trap, K. Konishi & K. Maeto (Ibes n° 14129); 1m#, 26.xi–3.xii.1993, Coarse Malaise Trap, K. Maeto (Ibes n° 14130). 1m#, N[EW]. GUINEA, Saruwaged Mts., I.22–II.16.1979, J. Sedlacek, 500m (AEIC) (Ibes n° 14041); NEW GUINEA (BPBM): 1m#, (NW), SE Biak I., 1.vii.1962, J. L. Gressitt & J. Sedlacek collectors (Ibes n° 14239); 1m#, NE Zenag- Lae Road, 1.v.1965, Malaise Trap, J. Sedlacek, 100m (Ibes n° 14242). PAPUA NEW GUINEA: 3m#, New Britain, Kerevat, 29-x-1973, P. T. Bailey (PMAE) (Ibes n° 14209, 14210, 14384); 1m#, 5f#, same data as holotype (Ibes n° 14252, 14254, 14255, 14256, 14258, 14259); 1m#, Wanang, 03/12/2012–04/12/2012, PNG MAL-WAN01-D16, P4915, 11066 (MNHN) (Ibes n° 14273); 1m#, Wanang, 26/11/2012–27/11/2012, PNG MAL-WAN-D-11/16-d11, P0542, 867 (MNHN) (Ibes n° 14275).

**Comments.** According to label data, some males and females of this species were reared from Curculionidae beetle larvae *Pantorhytes plutus* Faust, 1892. This species is similar to *Apenesia* #003 by having the notaulus absent; pronotum short; the metapostnotum almost all polished and basivolvella apical inner margin projected and convex. Although, males of *Apenesia* #003 have the head as long as large; the mandible with four teeth; the metanotal groove foveolate with linear median fovea; the metapectal-propodeal complex with posterior margin convex; the metapostnotum with row of anterior fovea; the hypopygeal posterior margin concave and females have two teeth, whereas males of *Apenesia* #007 has the head longer than large; the mandible with three teeth; the metanotal groove mostly imbricate; the metapectal-propodeal complex with posterior margin almost straight; the metapostnotum with row of striae; the hypopygeal posterior margin almost straight and females have three teeth.

**Distribution.** Oriental (Indonesia, Malaysia); Australian (Papua New Guinea).

***Apenesia* #008 Alencar & Azevedo, sp. nov.**

(Figs. 2.H, 5.K, 7.H, 10.H, 13.H, 17.D-F)

**Description.** Holotype. Male. Length 4.5 mm. LFW 3.8 mm.

**Colors.** Body castaneus; antenna, clipeo, mandible and legs yellowish; wings hyaline, veins castaneus.

**Head.** Head larger than long, rectangular. Frons weakly coriaceous, densely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin smooth, median carina high in profile. Mandible with one apical tooth. Eye weakly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, complete, strongly converging posterad. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin convex; mesoscutum-scutelar sulcus weakly arched, without fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough foveolate, metanotal fovea drop-shaped; median region narrow, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum strigate anteriorly, coriaceous medially, and polished. Propodeal disc polished. Paraspicular sulcus weakly punctulate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin projected mesad, small, and acute. Basiparamere with apical dorsal projection large, apex acute. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, COSTA RICA, Puntarenas, R.F. Golfo Dulce, 24km w. Pietdras Blancas, xii-1989–iii-1990, P. Hanson, 200m (PMAE) (Ibes n° 14213). Paratype: 1m#, COSTA RICA, Alajuela, Penas Blancas, 23-v-1987, MT, E. Cruz, 700m (PMAE) (Ibes n° 14212).

**Comments.** *Apenesia* #008 is similar to *A.* #006 and *A. perlonga* by having the head larger than long, rectangular; the mandible with one tooth; the pronotum short; the notaulus complete and convergent posteriorly and the hypopygium with flap and posterior margin concave. However, *A.* #008 has the head rectangular with vertex slightly convex as *A.* #006, whereas *A. perlonga* has the head rectangular with vertex straight. *Apenesia* #006 differs from *A.* #008 by the presence of metaposnotal median carina present in *A.* #006 and absent in *A.* #008.

**Distribution.** Neotropical (Costa Rica).

***Apenesia chontalica* Westwood, 1881**

(Figs. 25.I)

*Apenesia chontalica* Westwood 1881, 131, pl 7, fig. 3. #f; Cameron 1888, 1: 448; Dalla Torre 1898, 5: 558 (catalog); Kieffer, 1908, 76, 25 (catalog); Kieffer 1914, 41: 392, 395; Evans 1963, 130: 269, 358-359, figs 132, 134; Evans 1964, 132: 32, figs. 13, 15; Gordh & Móczár 1990, 46: 201 (catalog).

**Diagnosis.** Female.- Length 7.0 mm. **Color.** Body castaneous. Mandible with two apical teeth. Clypeus extending back frons, broad short trapezoidal median lobe, margin with few bristles. Eye dark, elliptical, with about 12 facets. Malar space slightly shorter than eye length. Frons nearly polished, punctures small and very sparse. Head subquadrate,  $0.95 \times$  as long as wide, sides convex, vertex straight, occipital carina visible in dorsal view. Pronotal disc with lateral margin parallel, sides diverging downward. Maximum width of propodeal disc  $1.6 \times$  its minimum width, slope between propodeal disc and declivity rounded. Mesotibia strongly spinose. Metasoma much longer than head and mesosoma together, petiole very short.

**Material examined.** Non type #f: MEX[ICO], in decayed, log. {?=10g}, XII'.20', Laredo, 24745, lot #41-459 [det. by Evans, 1962] (USNM).

**Comments.** Type material was not available to this study. The type material is supposed be deposited at OXUM, but we were not able to find it there.

**Distribution.** Neotropical (Mexico, Guatemala, Nicaragua, Costa Rica).

***Apenesia* #009 Alencar & Azevedo, sp. nov.**

(Figs. 3.A, 5.L, 7.I, 10.I, 13.I, 17.G-I)

**Description.** Holotype. Male. Length 5 mm. LFW 4 mm.

**Colors.** Body black; antenna, clypeus and metasoma dark castaneous; legs and mandible castaneous; wings ambar, veins dark castaneous.

**Head.** Head larger than long, rectangular. Frons coriaceous, sparsely puncticulate; line on frons absent. Vertex straight. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin smooth, median carina high in profile. Mandible with one apical tooth. Eye strongly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc very short. Notaulus present, incomplete posteriorly, parallel. Parapsidal signal weakly impressed. Scutellum longer than large, posterior margin convex; mesoscutum-scutelar sulcus almost straight, without fovea on side edge, narrow, shallow. Axilla

subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea oval; median region wide, narrow, with posterior margin convex. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina present, metaposnotum row of anterior foveae, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity polished-foveolate.

**Metasoma.** Petiole short. Hypopygium with plate long, posterior margin almost straight, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, small, and acute. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, dorsal larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe short; dorsal lobe short; subapical membrane long; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, MADAGASCAR: Antsiranana, Prov., Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW, Manantenina, 11–14.Dec.2005, 14° 26' 06" S 049° 45' 36" E, California Academy of Sciences, coll. B.L.Fisher et al., elev 775m, malaise trap, rainforest, collection code: BLF13383 (Ibes n° 1462). Paratypes: 2m#, same data as holotype (Ibes n° 14263, 14279). MADAGASCAR: 2 #m, Toamasina, Prov., Reserve Betampona Camp Vohitsivalana, 37.1 km 338° Toamasina, elev 520 m, 1–3.Dec.2005, 17° 53' 12" S 049° 12' 09" E, California Acad. of Sciences, coll. Brian L. Fisher et al., malaise trap, rainforest, collection code: BLF13244 (Ibes n° 14266, 14267); 1 #m, Toamasina, Montagne d'Akirindro, 7.6 km 341° NNW Ambinanitelo, elev 600m 17–21.Mar.2003, 15° 17' 18" S 049° 32' 54" E, California Acad. of Sciences, coll. Fisher, Griswold et al., malaise trap, in rainforest, collection code: BLF8253 (CASENT 2087999); 1 #m, Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, el 450m, 12–25 November 2003, 14° 26' 12" S 049° 46' 30" E California Acad. of Sciences coll. B.L.Fisher et al, malaise, trap in rainforest, BLF8723 (CASENT 2089579); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Vohiparara, at broken bridge, el 1110 m, 21–28 January 2002, 21° 13.57' S, 47° 22.19' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise trap in high altitude, rainforest, MA-02-09A-13 (CASENT 2064412); 4 #m, Province Fianarantsoa, Parc National Ranomafana, radio tower at forest edge, elev 1130 m, 14 - 21 January 2002, 21° 15.05' S, 47° 24.43' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, mixed tropical forest, MA-02-09B-12 (CASENT 2063509, 2063615; Ibes n° 14268, 14269); 1 #m, Province Fianarantsoa, Parc National Ranomafana, radio tower at forest edge, elev 1130 m, 18 - 27 February 2003, 21° 15.05' S, 47° 24.43' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, mixed tropical forest, MA-02-09B-53 (CASENT 2116482); 1 #m, MADAGASCAR: Province

Fianarantsoa, Parc National Ranomafana, radio tower at forest edge, elev 1130 m, 9 - 20 March 2003, 21° 15.05' S, 47° 24.43' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, mixed tropical Forest, MA-02-09B-55 (CASENT 2063924); 2 #m, Province Fianarantsoa, Parc National Ranomafana, radio tower at forest edge, elev 1130 m, 6–17 July 2003, 21° 15.05' S, 47° 24.43' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, mixed tropical forest, MA-02-09B-66 (CASENT 2064187, 2064236); 2 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 15–22 November 2001, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, secondary tropical forest, MA-02-09C-03 (CASENT 2088481, 2088517); 2 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 6–15 December 2001, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, secondary tropical forest, MA-02-09C-06 (CASENT 2088787, 2088809); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 2–10 January 2002, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, secondary tropical forest, MA-02-09C-10 (CASENT 2089026); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 10–14 January 2002, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, secondary tropical forest, MA-02-09C-11 (CASENT 2078428); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 12–19 February 2002, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, secondary tropical forest, MA-02-09C-16 (CASENT 2078642); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 23–28 April 2002, 21° 15.99' S, 47° 25.21' E coll: M. Irwin, R. Harin'Hala, California Acad of Sciences malaise, secondary tropical forest, MA-02-09C-26 (CASENT 2088991); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 26 Feb-10 March 2003, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences malaise, secondary tropical forest, MA-02-09C-55 (Ibes n° 14270); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 10–21 March 2003, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, secondary tropical forest, MA-02-09C-56 (CASENT 2088819); 1 #m, Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m, 12–23 April 2003, 21° 15.99' S, 47° 25.21' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise, secondary tropical forest, MA-02-09C-58 (CASENT 2083276); 1 #m, Province Fianarantsoa, Ranomafana JIRAMA water works 10–14 January 2002, 21° 14.91' S, 47° 27.13' E, coll: M. Irwin, R. Harin'Hala, California Acad of Sciences, malaise trap near river elev 690 m, MA-02-09D-11 (CASENT 2088929).

**Comments.** This species is easily distinguished from other species because by having the head larger than long with vertex straight and the clypeus subtrapezoidal with large median tooth. The mesosoma of *Apenesia* #009 is similar to *A.* #002 by having the mesoscutum with incomplete notaulus. *Apenesia* #002 and *A.* #009 differ from each other especially by having the head trapezoidal and rectangular and the hypopygium posterior margin concave and straight, respectively.

**Distribution.** Afrotropical (Madagascar).

***Apenesia* #010 Alencar & Azevedo, sp. nov.**

(Figs. 3.B, 5.M, 8.A, 10.J, 13.J, 18.A-C)

**Description.** Holotype. Male. Length 2.8 mm. LFW 2.5 mm.

**Colors.** Body castaneus; wings hyaline, veins castaneus.

**Head.** Head as long as large, rounded. Frons polished and shining, sparsely punctulate; line on frons absent. Vertex convex. Clypeus broad with median lobe trapezoidal, median tooth absent, apical margin crenulate, median carina short in profile. Mandible with five apical teeth, teeth with different size, upper tooth mesad, three upper teeth equally sized. Eye strongly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc very short. Notaulus absent. Parapsidal signal weakly impressed. Scutellum longer than large, posterior margin convex; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, narrow, shallow. Axilla oval, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea drop-shaped; median region narrow, large, with posterior margin straight. Metapectal-propodeal complex long, posterior margin convex; metapostnotal median carina absent, metapostnotum almost entirely polished. Propodeal disc polished. Paraspicular sulcus polished; metapleural carina absent; lateral surface of propodeum polished, inferior region imbricate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate long, posterior margin almost straight, flap absent. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex convex. Cuspis with apical margin with two apical callus, dorsal larger than other, dorsal end very short. Aedeagus with two apical lobes, ventral lobe short; dorsal lobe short; subapical membrane short; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, BRAZIL, Bahia, Itajuípe, Faz. Trindade, 27.XI.2002, arm. malaise (UFES/CEPLAC) (Ibes n° 14220). Paratypes: BRAZIL: 1m#, Bahia, Itajuípe, Faz. Trindade, 27.XI.2002, arm. malaise, (UFES/CEPLAC) (Ibes n° 14280); ES: 1m#, Pancas, Faz.



Juliberto Stur, 19°13'10.5"S, 40°46'28.8"O, 24–31.i.2003, Armadilha Malaise, T3, M.T. Tavares, C.O. Azevedo e eq. col., (UFES) (UFES N° 11272); 2m#, Réserve Linhares, Brésil, Malaise, 15–30 novemb 2000, Bethylidae, (MNHN) (Ibes n° 14283, 14284).

**Comments.** This species is similar to *A. laevigata* because of the head rounded; the clypeus trapezoidal; the mandible with five teeth; the pronotum very short; the mesoscutellum long; the metapectal-propodeal complex long with posterior margin convex; the petiolo long; the hypopygium with plat long; the genitalia with basiparamere clearly divided and aedeagus narrow with ventral lobe very short. In the new species, however, the apical margin of the clypeous is crenulate, the notaulus is absent, the mesoscutum-mesoscutellar suture weakly arched and narrow, whereas *A. laevigata* presents the clypeus with smooth apical margin; the notaulus present; the mesoscutum-mesoscutellar suture strongly arched and wide.

**Distribution.** Neotropical (Brazil).

### *Apenesia conradti* Kieffer, 1910

(Figs. 24.C, G, I, 25.C)

*Apenesia conradti* Kieffer 1910, 3: 16. #f; Kieffer 1910, 3: 16; Kieffer 1912, 3: 106; Kieffer 1914, 41: 392, 393; Gordh & Móczár 1990, 46: 201 (catalog).

**Diagnosis.** Female.- Length 8.0 mm. **Color.** Body castaneous. Mandible with two apical teeth. Clypeus extending back frons, median lobe with apical margin concave, margin with few bristles, median carina absent. Eye dark, elliptical, with about 12 facets. Malar space slightly shorter than eye length. Frons weakly coriaceous, punctures small and very sparse. Head subquadrate,  $0.95 \times$  as long as wide, sides convex, vertex straight, occipital carina not visible in dorsal view. Pronotal disc with lateral margin parallel, sides diverging downward, anterior margin with median emargination. Maximum width of propodeal disc  $1.6 \times$  its minimum width, slope between propodeal disc and declivity rounded. Mesotibia strongly spinose. Metasoma much longer than head and mesosoma together, petiole long.

**Material examined.** Syntype #f: N Kamerun, L. Conradt S. (ZMHB).

**Remarks.** According to Gordh & Móczár (1990) *A. conradti* was described by “Kieffer, 1912, 3: 106”. The mistake related to the year of this publication is due to the fact that the article was published twice. The original description was published by in 1910 by Kieffer (pp. 1–29) and it was republished with the same title in 1912 (pp. 91–119). We were not able to see any other syntype of this species, so we did not propose lectotype.

**Distribution.** Afrotropical (Cameroon).

***Apenesia delicata* Evans, 1963**

(Figs. 25.J)

*Apenesia delicata* Evans 1963, 130: 268. 352. #f; Evans 1964, 132: 33; Gordh & Móczár 1990, 46: 202 (catalog).

**Diagnosis.** Female.- Length 2.56 mm. **Color.** Body castaneous. Mandible with two apical teeth. Clypeus truncate, median carina high, angled and produced beyond margin as tooth. Eye dark, subcircular. Malar space shorter than eye length. Frons polished, punctures small and very sparse, with dark line above clypeus. Head elongate with sides parallel and vertex straight, corner broadly rounded,  $1.33 \times$  as long as wide. Pronotal disc with sides parallel. Maximum width of propodeal disc  $1.77 \times$  its minimum width. Mesotibia strongly spinose. Metasoma as long as head and mesosoma together, with long petiole,  $0.5 \times$  length of metatibia.

**Material examined.** Holotype #f: JAMAICA, Gordontown, Sta 382, 4.II.1937, Chapin & Blackwelder col. (USNM, #66015).

**Distribution.** Neotropical (Jamaica).

***Apenesia dominica* Evans, 1963**

(Figs. 26.A)

*Apenesia dominica* Evans 1963. 130: 268, 352–353, figs. 129, 135. #f; Evans 1964, 132: 33; Evans 1969a, 3: 2; Gordh & Móczár 1990, 46: 202 (catalog).

**Diagnosis.** Female.- Length 3.1 mm. **Color.** Body castaneous. Mandible with three apical. Clypeus with median lobe short, subtrapezoidal, median carina high. Eye elliptical, with about six facet. Malar space shorter than eye length. Frons nearly polished, punctures small and very sparse. Head with sides parallel and almost straight. Vertex slightly convex,  $1.15 \times$  as long as wide. Pronotal disc with lateral margin parallel. Maximum width of propodeal disc  $1.33 \times$  its minimum width. Mesotibia strongly spinose. Metasoma nearly as long as head and mesosoma together, petiole short.

**Material examined.** Holotype #f: DOMINICA, W.I., Roseau, F. Lutz col. (MCZH, #30445).

**Distribution.** Neotropical (Dominica).

***Apenesia* #011 Alencar & Azevedo, sp. nov.**

(Figs. 3C, 6A, 8B, 11A, X–Y)

**Description.** Holotype. Male. Length 4 mm. LFW 3.2 mm.

**Colors.** Body dark castaneus; antenna gradually darker distally; metasoma castaneus; mandible and legs yellowish; wings ambar, veins dark castaneus.

**Head.** Head as long as large, trapezoidal. Frons coriaceous, densely puncticulate; line on frons absent. Vertex straight. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with three apical teeth, teeth with different size, upper tooth mesad, two upper teeth equally sized. Eye strongly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, complete, weakly converging posterad. Parapsidal signal well delimited. Scutellum as long as large, posterior margin convex; mesoscutum-scutellar sulcus strongly arched, with fovea on side edge, wide, deep. Axilla subtrapezoidal, deep, large. Metanotal trough foveolate, metanotal fovea drop-shaped; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin convex; metaposnotal median carina absent, metaposnotum rugulose, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina present; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity foveolate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin concave, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, almost equally sized, dorsal end long. Aedeagus with two apical lobes, ventral lobe short; dorsal lobe short; subapical membrane short; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, Central African Republic, Prefecture Sangha-Mbaéré, Parc National de Dzanga-Ndoki, 38.6km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 26–27.v.2001, Malaise trap, Lowland rainforest, 350m, CAR01-M231, S. van Noort (ISAM) (Ibes n° 14354). Paratypes: 2m#, same data as holotype (Ibes n° 14353, 14355).

**Comments.** This species is promptly recognized by having head larger than long; the mandible with their very small teeth; the notaulus complete; the mesoscutum-mesoscutellar suture strongly arched, deep and wide; the hypopygeal posterior margin concave and the genitalia with apical dorsal projection of basiparamere very large.

**Distribution.** Afrotropical (Central African Republic).

***Apenesia* #012 Alencar & Azevedo, sp. nov.**

(Figs. 3.D, 6.B, 8.C, 11.B, 13.L, 18.G-I)

**Description.** Holotype. Male. Length 3.4 mm. LFW 2.6 mm.

**Colors.** Body dark castaneus; antenna, clypeus and mandible castaneous; legs castaneous and yellowish; wings hyaline, veins castaneus.

**Head.** Head as long as large, quadrate. Frons coriaceous, densely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin smooth, median carina high in profile. Mandible with three apical teeth, teeth with different size, upper tooth mesad, two upper teeth equally sized. Eye weakly bulging. Ocelli small, triangle with distal edges.

**Mesosoma.** Pronotal disc long. Notaulus present, incomplete posteriorly, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum longer than large, posterior margin convex; mesoscutum-scutelar sulcus weakly arched, with fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea triangular; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina present, metaposnotum irregularly foveolate, and polished. Propodeal disc polished. Paraspicular sulcus weakly punctulate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity polished-punctulate.

**Metasoma.** Petiole short. Hypopygium with plate very short, posterior margin strongly concave, flap present. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex convex. Cuspis with apical margin serrate, dorsal end long. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane long; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype #m:Holotype m#, CENTRAL AFRICAN REPUBLICAN, Prefecture Sangha-Mbaéré, Parc National de Dzanga-Ndoki, Mabéa Bai, 21.4km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 3–4.vi.2001, Malaise trap, Lowland rainforest, marsh clearing, 510m, CAR01-M27, S. van Noort (ISAM) (Ibes n° 14357). Paratype: 1m#, CENTRAL AFRICAN REPUBLICAN, Prefecture Sangha-Mbaéré, Parc National de Dzanga-Ndoki, 38.6km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 22–23.V.2001, Malaise trap, Lowland rainforest, 350m, CAR01-M180, S. van Noort (ISAM) (ibes n° 14356).

**Comments.** This species is promptly recognized by having the head square; the ocelli small; the clypeus with median tooth large; the pronotum long; the notaulus incomplete posteriorly; the

mesoscutum-mesoscutellar suture weakly arched and narrow; the metapectal-propodeal complex short with posterior margin almost straight; the metaposnotum irregularly foveolate anteriorly; the hypopygium with plate short, with flap and posterior margin concave.

**Distribution.** Afrotropical (Central African Republic).

*Apenesia* #013 Alencar & Azevedo, sp. nov.

(Figs. 3.E, 6.C, 8.D, 11.C, 13.M, 19.A-C)

**Description.** Holotype. Male. Length 3.7 mm. LFW 3.5 mm.

**Colors.** Body dark castaneus; mandible and legs castaneus; wings ambar, veins dark castaneus.

**Head.** Head larger than long, rectangular. Frons weakly coriaceous, densely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye weakly bulging. Ocelli small, triangle with distal edges.

**Mesosoma.** Pronotal disc long. Notaulus present, complete, parallel. Parapsidal signal well delimited. Scutellum as long as large, posterior margin convex; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough foveolate, metanotal fovea oval; median region narrow, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum rugulose, and weakly coriaceous. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina present; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity foveolate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex convex. Cuspis with apical margin with three apical callus, almost equally sized, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane long; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, CENTRAL AFRICAN REPUBLICAN, Prefecture Sangha-Mbaéré, Parc National de Dzanga-Ndoki, Mabéa Bai, 21.4km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 1–2.v.2001, Malaise trap, Lowland rainforest, marsh clearing, 510m, CAR01-M02, S. van Noort (ISAM) (Ibes n° 14358). Paratype: 1m#, CENTRAL AFRICAN REPUBLICAN, Prefecture Sangha-Mbaéré, Parc national de Dzanga-Ndori, 38.6km, 173°S Lidjombo, 2°21.60'N, 16°03.20E, 22–23.v.2001, Malaise trap, Lowland rainforest, 350m, CAR01-M183, molecular A163, S. van Noort (ISAM) (ibes n° 14261).

**Comments.** This species is similar to *Apenesia* #014 by having the pronotum long; the notaulus complete and parallel; the hypopygium with flap and posterior margin strongly concave. Although, *Apenesia* #013 has the mesoscutum-mesoscutellar suture weakly narrow; the metaposnotum v-shaped and rugulose; the genitalia with cuspis with three apical callus, almost equally sized with dorsal end short, whereas *A.* #014 has the mesoscutum-mesoscutellar suture wide; the metaposnotum irregularly foveolate anteriorly; the genitalia with cuspis with two apical callus, ventral one larger than the dorsal with dorsal end short.

**Distribution.** Afrotropical (Central African Republic).

*Apenesia* #014 Alencar & Azevedo, sp. nov.

(Figs. 3.F, 6.D, 8.E, 11.D, 13.N, 19.D-F)

**Description.** Holotype. Male. Length 4.5 mm. LFW 4.3 mm.

**Colors.** Head dark castaneus; antenna gradually darker distally; clypeus and mandible yellowish.

**Head.** Head larger than long, rectangular. Frons weakly coriaceous, densely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye weakly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc long. Notaulus present, complete, parallel. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, wide, deep. Axilla subtrapezoidal, deep, large. Metanotal trough foveolate, metanotal fovea drop-shaped; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum irregularly foveolate, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity foveolate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex convex. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, CENTRAL AFRICAN REPUBLICAN, Prefecture Sangha-Mbaéré, Réserve Speciale de Fôret Dense de Dzanga-Sangha, 12.7km 326°NW Bayanga,

3°00.27'N, 16°11.55'E, 11–12.v.2001, Malaise trap, Lowland rainforest, marsh clearing, 420m, CAR01-M90, S. van Noort (ISAM) (Ibes n° 14359).

**Comments.** This species is similar to *Apenesia* #013 by having the pronotum long; the notaulus complete and parallel; the hypopygium with flap and posterior margin strongly concave. Although, *A.* #014 has the mesoscutum-mesoscutellar suture wide; the metaposnotum irregularly foveolate anteriorly; the genitalia with cuspis with two apical callus, ventral one larger than the dorsal with dorsal end short, whereas *A.* #013 has the mesoscutum-mesoscutellar suture weakly narrow; the metaposnotum v-shaped and rugulose; the genitalia with cuspis with three apical callus, almost equally sized with dorsal end short.

**Distribution.** Afrotropical (Central African Republic).

### *Apenesia flavipes* Cameron, 1888

(Fig. 26.B)

*Apenesia flavipes* Cameron 1888: 1: 449, tab. 19, fig. 11. #f; Kieffer 1908, 76: 25 (catalog); Kieffer 1914, 41: 392, 395; Evans 1963, 130: 269, 357–358; Evans 1964, 132: 32; Gordh & Móczár 1990, 46: 203 (catalog).

**Diagnosis.** Female.- Length 5.2 mm. **Color.** Body castaneous. Mandible with two apical teeth. Clypeus extending back frons, median lobe broadly trapezoidal, apical margin with bristles, median carina straight in profile. Eye dark, elliptical, with about 12 facets. Malar space shorter than eye length. Frons polished punctures sparse. Head quadrate with sides parallel and convex, vertex straight,  $1.03 \times$  as long as wide. Pronotal disc with sides nearly parallel. Maximum width of propodeal disc  $1.82 \times$  its minimum width. Mesotibia strongly spinose. Metasoma as long as head and mesosoma together, petiole short.

**Material examined.** Holotype #f: [PANAMA, *Chiriqui*], V[olcan] de Chiriqui, 2000–3000 f[ee]t, [G. C.] Champion col. (BMNH, 13255).

**Distribution.** Neotropical (Panama).

***Apenesia formosa* Vargas & Terayama, 2002**

(Fig. 26.C)

*Apenesia formosa* Vargas & Terayama 2002, 4: 29–30, figs. 9–12.

**Diagnosis.** Female.- Length 2.7 mm. **Color.** Body castaneous. Mandible with three apical teeth, uppermost small. Clypeus with subtrapezoidal median lobe, median carina high and straight, angled just before apical margin. Eye dark, elliptical, with about six facets. Malar space shorter than eye length. Frons polished, punctures small and very sparse. Head with sides subparallel, vertex slightly convex,  $1.3 \times$  as long as wide. Pronotal disc with sides parallel, posterior corner spotted. Maximum width of propodeal disc  $1.67 \times$  its minimum width. Mesotibia strongly spinose. Metasoma about as long as head and mesosoma together, petiole long.

**Material examined.** Holotype #f: COLOMBIA, *Antioquia*, Mun[icipio de] Urrao, P[arque] N[acional] N[atural] Orquideas, Cabaña Venados, 920m, 5.IV.1996, E. Palacios, J.M. Vargas R. col., VJIC 0150 (IAVH-E 86695).

**Distribution.** Neotropical (Colombia).

***Apenesia* #015 Alencar & Azevedo, sp. nov.**

(Figs. 3.G, 6.E, 8.F, 11.E, 13.O, 19.G-I)

**Description.** Holotype. Male. Length 5 mm. LFW 4.4 mm.

**Colors.** Body dark castaneous; clypeus, antenna, metasoma castaneous; mandible yellowish; legs castaneous and yellowish; wings ambar, veins castaneous.

**Head.** Head larger than long, rectangular. Frons coriaceous, densely puncticulate; line on frons sulcate. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye strongly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, complete, weakly converging posterad. Parapsidal signal well delimited. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutelar sulcus weakly arched, with fovea on side edge, wide, deep. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea drop-shaped; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum rugulose, and polished. Propodeal disc polished. Paraspicular sulcus puncticulate-foveolate;



metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity polished-foveolate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Apex convex. Cuspis with apical margin with two apical callus, almost equally sized, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, UGANDA, Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.859'N, 30°21.630'E, 31.vii–3.viii.2005, Malaise trap, primary mid-altitude Rainforest, 1505m, UG05-M08, S. van Noort, (ISAM) (Ibes n° 14360). Paratypes: 1m#, same data as holotype (Ibes n° 14361); UGANDA, Kibale National Park, Kanyawara, Makerere University Biological Field Station, Malaise trap, primary mid-altitude Rainforest, S. van Noort (ISAM): 2m#, 0°33.859'N, 30°21.630'E, 31.vii–3.viii.2005, 1505m, UG05-M07 (Ibes n° 14362, 14373); 12m#, 0°33.408'N, 30°22.603'E, 30.vii–5.viii.2005, 1587m, UG05-M10 (Ibes n° 14366, 14367, 14368, 14369, 14370, 14371, 14372, 14374, 14375, 14376, 14377, 14378).

**Comments.** This species is similar to *Apenesia* #016 by having the head larger than long; the notaulus complete; the mesoscutum-mesoscutellar suture weakly arched, wide and deep; the hypopygium with flap and posterior margin strongly concave and the genitalia with cuspis with two apical callus almost equally sized. However, *Apenesia* #015 has the frons without sulcus and the paraspicular punctulate-foveolate, whereas *A.* #016 has the frons with sulcus and the paraspicular sulcus weakly foveolate.

**Distribution.** Afrotropical (Uganda).

***Apenesia* #016 Alencar & Azevedo, sp. nov.**

(Figs. 3.H, 6.F, 8.G, 11.F, 14.A, 20.1-C)

**Description.** Holotype. Male. Length 3.9 mm. LFW 3.7 mm.

**Colors.** Body dark castaneus; clypeus, mandible, antenna and metasoma castaneus; legs castaneous and yellowish; wings light amber, veins castaneous.

**Head.** Head larger than long, rectangular. Frons coriaceous, densely punctulate; line on frons sulcate. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina high in profile. Mandible with one apical tooth. Eye strongly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, complete, strongly converging posterad. Parapsidal signal well delimited. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutellar sulcus weakly arched, with fovea on side edge, wide, deep. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea triangular; median region narrow, large, with posterior margin convex. Metapectal-propodeal complex short, posterior margin almost straight; metapostnotal median carina absent, metapostnotum rugulose, polished and weakly imbricate. Propodeal disc polished. Paraspicular sulcus weakly foveolate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity polished-foveolate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex convex. Cuspis with apical margin with two apical callus, dorsal larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype #m: Holotype m#, UGANDA, Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.996'N, 30°21.262'E, 29–31.vii.2005, Malaise trap, secondary mid-altitude Rainforest, 1495m, UG05-M02, S. van Noort (ISAM) (Ibes n° 14363). Paratypes: UGANDA, Kibale National Park, Kanyawara, Makerere University Biological Field Station, Malaise trap, primary mid-altitude Rainforest, S. van Noort (ISAM): 1m#, 0°33.408'N, 30°22.603'E, 30.vii–5.viii.2005, 1587m, UG05-M10 (Ibes n° 14379); 1m#, 0°33.859'N, 30°21.630'E, 12–18.viii.2005, 1505m, UG05-M21 (Ibes n° 14364); 1m#, 0°33.859'N, 30°21.630'E, 18–22.viii.2005, 1505m, UG05-M25 (Ibes n° 14365).

**Comments.** This species is similar to *Apenesia* #015 by having the head larger than long; the notaulus complete; the mesoscutum-mesoscutellar suture weakly arched, wide and deep; the hypopygium with flap and posterior margin strongly concave and the genitalia with cuspis with two apical callus almost equally sized. However, *Apenesia* #016 has the frons with sulcus and the paraspicular sulcus weakly foveolate, whereas *A.* #015 has the frons without sulcus and the paraspicular punctulate-foveolate.

**Distribution.** Afrotropical (Uganda).

***Apenesia* #017 Alencar & Azevedo, sp. nov.**

(Figs. 4.A, 6.G, 8.H, 11.G, 14.B, 20.D-F)

**Description.** Holotype. Male. Length 4.9 mm. LFW 4.3 mm.

**Colors.** Body dark castaneous; antenna, clypeus and mandible castaneous; legs castaneous and yellowish; wings ambar, veins castaneous.

**Head.** Head larger than long, rectangular. Frons coriaceous, densely punctulate; line on frons absent. Vertex straight. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin crenulate, median carina high in profile. Mandible with three apical teeth, teeth with different size, upper tooth mesad, uppermost much smaller than others. Eye weakly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, incomplete posteriorly, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum longer than large, posterior margin almost straight; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea triangular; median region wide, large, with posterior margin convex. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum row of anterior foveae, and polished. Propodeal disc weakly imbricate; Paraspicular sulcus weakly punctulate; metapleural carina present; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity polished-punctulate.

**Metasoma.** Petiole long. Hypopygium with plate very short, posterior margin concave, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, small, and acute. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with one callus, dorsal end long. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane absent; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined.** Holotype m#, UGANDA, Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.859'N, 30°21.630'E, 5–12.viii.2005, Malaise trap, primary mid-altitude Rainforest, 1505m, UG05-M17, S. van Noort (ISAM) (Ibes n° 14380).

**Comments.** This species is similar to *A. singularis* by having the pronotum short, the metaposnotum mostly polished with row of fovea anteriorly. However, #11 has the mandible with four teeth; the notaulus complete; the mesoscutum-mesoscutellar suture straight and shallow; the hypopygium with plate long and the genitalia with cuspis with three apical callus, whereas #017 has the mandible with three teeth; the notaulus incomplete posteriorly; the mesoscutum-mesoscutellar

suture weakly arched and deep; the hypopygium with plate short and the genitalia with cuspis with one apical callus.

**Distribution.** Afrotropical (Uganda).

***Apenesia* #018 Alencar & Azevedo, sp. nov.**

(Figs. 4.B, 6.H, 8.I, 11.H, 14.C, 20.G-I)

**Description.** Holotype. Male. Length 3.9 mm. LFW 3.8 mm.

**Colors.** Body dark castaneous; mandible yellowish; legs castaneous and yellowish; wings hyaline, veins castaneous.

**Head.** Head larger than long, trapezoidal. Frons coriaceous, sparsely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin crenulate, median carina short in profile. Mandible with four apical teeth, teeth with different size, upper tooth mesad, three upper teeth equally sized. Eye weakly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc very short. Notaulus present, complete, strongly converging posterad. Parapsidal signal weakly impressed. Scutellum longer than large, posterior margin almost straight; mesoscutum-scutellar sulcus almost straight, without fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea drop-shaped; median region wide, narrow, with posterior margin straight. Metapectal-propodeal complex long, posterior margin almost straight; metaposnotal median carina present, metaposnotum rugulose, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity foveolate.

**Metasoma.** Petiole short. Hypopygium with plate long, posterior margin almost straight, flap absent. **Genitalia:** paramere straight. Basivolsella apical inner margin projected mesad, large, and convex. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe long; subapical membrane absent; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, MALAYSIA, Pasoh Forest Res. Negri S., X.14.78, sec. for., P. & M. Becker (AEIC) (Ibes n° 14116).

**Comments.** This species is similar to *Apenesia* #004 by having the notaulus complete and the metaposnotum rugulose. However, *Apenesia* #004 has the mandible with five teeth; the mesoscutum-mesoscutellar suture strongly arched and deep; the hypopygium with flap and

posterior margin concave, whereas *A.* #018 has the mandible with four teeth; the mesoscutum-mesoscutellar suture straight and shallow; the hypopygium without flap and posterior margin almost straight.

**Distribution.** Oriental (Malaysia).

***Apenesia* #019 Alencar & Azevedo, sp. nov.**

(Figs. 4.C, 6.I, 9.A, 11.I, 14.D, 21.A-C)

**Description.** Holotype. Male. Length 3.2 mm. LFW 3.4 mm.

**Colors.** Body castaneus; antenna gradually darker distally; mandible castaneus; foreleg castaneous, others light yellowish; wings hyaline, veins castaneus.

**Head.** Head as long as large, trapezoidal. Frons coriaceous, densely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin crenulate, median carina short in profile. Mandible with three apical teeth, teeth with different size, upper tooth mesad, uppermost much smaller than others. Eye weakly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc long. Notaulus absent. Parapsidal signal well delimited. Scutellum longer than large, posterior margin convex; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea oval; median region narrow, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum row of anterior foveae, polished and weakly imbricate. Propodeal disc weakly imbricate; Paraspicular sulcus polished; metapleural carina absent; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate very short, posterior margin concave, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, small, and convex. Basiparamere with apical dorsal projection small, apex acute. Cuspis with apical margin with three apical callus, ventral larger than other, dorsal end long. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, NEW CALEDONIA, Col d'Amieu, Sarraméa, 21°34.407'S 165°45.674'E, 412m., 11–25.i.2008, Piège Malaise, T. Théry leg., (MNHN) (Ibes n° 14286). Paratypes: NEW CALEDONIA: Col des Roussetes, C. Yoshimoto & N. Krauss, Malaise Trap, 450–500m, J. L. Gressitt collector (BPBM): 5m#, 4–6.ii.63 (Ibes n° 14245, 14246, 14247, 14249,

14250); 1m#, Col de Ho, 11.ii.1963, C. Yoshimoto & N. Krauss, Malaise Trap (Ibes n° 14248); 1m#, Pic du Pin, site 2, 22°14'S, 166°50'E, 25nov–23dec2004, malaise, rainforest, 280m, Burwell, Wright (UQIC) (Ibes n° 14260); 1m#, NEW CALEDONIA, Col d'Amieu, Sarraméa, 21°34.407'S 165°45.674'E, 412m, 11–25.i.2008, Piège Malaise, T. Théry leg. (MNHN) (Ibes n° 14285).

**Comments.** The head trapezoidal and metaposnotum almost all polished with texture differentiate only anteriorly of *Apenesia* #019 are similar to those in *A.* #003. Although, *Apenesia* #019 has the clypeus with large median tooth; the mandible with three teeth and the genitalia with cuspis with three apical callus, whereas *A.* #003 has the clypeus with small median tooth; the mandible with four teeth and the genitalia with cuspis with two apical callus.

**Distribution.** Australian (New Caledonia).

***Apenesia* #020 Alencar & Azevedo, sp. nov.**

(Figs. 4.D, 6.J, 9.B, 11.J, 14.E, 21.D-E)

**Description.** Holotype. Male. Length 4.8 mm. LFW 4.1 mm.

**Colors.** Body reddish castaneous; metaposnotum-propodeal complex black; antenna, clypeus, mandible and legs castaneous; wings hyaline, veins castaneous.

**Head.** Head larger than long, trapezoidal. Frons weakly coriaceous, densely punctulate; line on frons sulcate. Vertex straight. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye strongly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, complete, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin convex; mesoscutum-scutelar sulcus weakly arched, without fovea on side edge, wide, deep. Axilla subtrapezoidal, deep, large. Metanotal trough mostly imbricate, with few foveae, metanotal fovea drop-shaped; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina present, metaposnotum irregularly strigate, and polished. Propodeal disc imbricate; Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum foveolate and imbricate, inferior region foveolate. Propodeal declivity foveolate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex acute. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end long. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, BRAZIL, Amazonas, Manaus, Reserva 1210, lateral oeste, 04.X. 1984, rede, Bert Klein col. (INPA) (Ibes n° 14345). Paratypes: COSTA RICA, Punctarenas, Golfito, VI.28.1987, J. Brambila (AEIC), (Ibes n° 14114). BRAZIL: 1m#, Amazonas, Manaus, Reserva 1210, 17.X.1985, Arm. Malaise, B. Klein col. (INPA) (Ibes n° 14346); Pará (MPEG): Juriti: 1m#, Ramal Mauari, Gaileia, 26–29.V.2008, Arm. Malaise, J. N. Santos & L. A. Quaresma col. (Ibes n° 14348), 1m# 15.VI.2009, Arm. Malaise, O. T. Silveira & equipe col. (Ibes n° 14349); 1m#, Vitória do Xingu, Rio Xingu, Igarapé Gaioso, 12–16.VIII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG), (Ibes n° 14350).

**Comments.** This species is similar to *Apenesia* #021 by having the head larger than long; the mandible with one tooth; the notaulus complete; the mesoscutum-mesoscutellar suture weakly arched, wide and deep; the hypopygium with flap and posterior margin concave. Although, *Apenesia* #020 has the metaposnotum irregularly strigate and the metaposnotal median carina present, whereas *A.* #021 has the metaposnotum almost all polished, being only strigate anteriorly and metaposnotal median carina absent.

**Distribution.** Neotropical (Costa Rica, Brazil).

***Apenesia* #021 Alencar & Azevedo, sp. nov.**

(Figs. 4.E, 6.K, 9.C, 12.A, 14.F, 21.G-I)

**Description.** Holotype. Male. Length 2.7 mm. LFW 2.5 mm.

**Colors.** Body redish castaneous; antenna, clypeus, mandible and legs castaneous; wings hyaline, veins castaneous.

**Head.** Head larger than long, rectangular. Frons weakly coriaceous, sparsely punctulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye strongly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc very short. Notaulus present, complete, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin convex; mesoscutum-scutellar sulcus weakly arched, without fovea on side edge, narrow, deep. Axilla oval, deep, large. Metanotal trough imbricate, metanotal fovea oval; median region narrow, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum strigate anteriorly, and polished. Propodeal disc polished. Paraspicular sulcus polished; metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex acute. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end long. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined.** Holotype m#, BRAZIL, Amazonas, Manaus, Reserva Ducke, Igarapé Ipiranga, 31.XII.2002, Arm. Malaise, J. Vidal & J. Vidal col. (INPA) (Ibes n° 14334). Paratypes: 1m#, TRINIDAD [AND TOBAGO], 8 km N Arima, Simla Res[erve] Sta[tion] {=William Beebe Tropical Research Station}, [10°40'N], [61°18'W], 14–24.VI.1993, M[alaise] T[rap], lower montane rain for[est], 260 m, S. & J. Peck [col.] (CNCI) (Ibes n° 4992). 1m#, TRINIDAD, Tunapuna, Mt. St. Benedict, 4–13.VI.1993, FIT, ravine for. Bottom, 230m, 93-3, S. & J. Peck (MPEG) (Ibes n° 14344). BRAZIL, Pará: 1m#, Belém, Dec. 1–4 1969, J. M. & B. A. Campbell (AEIC) (Ibes n° 14113); 1m#, Juriti, Propriedade Barroso, Arm. Malaise, J. N. Santos & L. A. Quaresma col. (MPEG) (Ibes n° 14338); 1m#, Anapu, Rio Xingu, Caracol, Barra do Vento, 07–10.VIII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14339); 3m#, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 12–16.VIII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14341, 14342, 14343); 1m#, Altamira, Rio Xingu, Itapuama, [03°13'16"S], [52°12'31"W], 19–23.VIII.2008, arm[adilha] Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 13012); 1m#, Altamira, Rio Xingu, Ilha Grande, 06–10.XI.2007, Arm. Malaise, O. T. Silveira & equipe col., (MPEG) (Ibes n° 14337); 1m#, Canaã dos Carajas, mata, 6.4°85'85"S, 49.8°98'56"W, 26.VII.2004, Arm. Malaise, R. M. Valente & E. M. Santos col. (MPEG) (Ibes n° 14340); 1m#, Bahia, S. J. da Vitória, Faz. São Roque, 15°04'S, 39°18'W, 12.III.2001, Arm. Malaise, J. A. Cardoso & J. R. Maia (UFES/CEPLAC) (Ibes n° 14335).

**Comments.** This species is similar to *Apenesia* #020 by having the head larger than long; the mandible with one tooth; the notaulus complete; the mesoscutum-mesoscutellar suture weakly arched, wide and deep; the hypopygium with flap and posterior margin concave. Although, *Apenesia* #021 has the metaposnotum almost all polished, being only strigate anteriorly and metaposnotal median carina absent, whereas *A.* #020 has the metaposnotum irregularly strigate and metaposnotal median carina present.

**Distribution.** Neotropical (Trinidad and Tobago, Brazil).



***Apenesia laevigata* (Evans, 1958)**

(Figs. 4.F, 6.L, 9.D, 12.B-C, 14.G, 22.A-C)

*Propristocera laevigata* Evans 1958, 59: 292–293, figs. 4–8. #f.

*Apenesia laevigata* (Evans, 1958): Evans 1963b, 130: 263, 302–303 (designation of combination), figs 44–47; Evans 1964, 132: 32; Lanes & Azevedo 2004, 679: 6; Gordh & Móczár 1990, 46: 205 (catalog).

**Description.** Holotype. Male. Length 2.9 mm. LFW 2.2 mm.

**Colors.** Head dark castaneous; antenna, clypeus and body castaneous; legs yellowish; wings hyaline, veins light castaneus.

**Head.** Head as long as large, rounded. Frons polished and shining, sparsely punctulate; line on frons absent. Vertex convex. Clypeus broad with median lobe trapezoidal, median tooth absent, apical margin smooth, median carina short in profile. Mandible with five apical teeth, teeth with similar size, upper tooth dorsad. Eye strongly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, incomplete posteriorly, weakly converging posterad. Parapsidal signal well delimited. Scutellum longer than large, posterior margin convex; mesoscutum-scutelar sulcus strongly arched, without fovea on side edge, wide, shallow. Axilla subtrapezoidal, deep, large. Metanotal trough imbricate, metanotal fovea oval; median region wide, narrow, with posterior margin straight. Metapectal-propodeal complex long, posterior margin convex; metaposnotal median carina absent, metaposnotum irregularly strigate, and polished. Propodeal disc polished. Paraspicular sulcus polished; metapleural carina present; lateral surface of propodeum polished, inferior region imbricate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate long, posterior margin almost straight, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection small, apex convex. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end very short. Aedeagus with two apical lobes, ventral lobe short; dorsal lobe short; subapical membrane absent; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined. Type:** Holotype male: MEX[ICO], [Veracruz], Cordoba, 21.V, A. Fenyes col. (USNM, #64114). **New material examined:** 1m#, TRINIDAD, 8KM n Arima Simla Res. Sta., lower montane rain for., 260m, 24.VI–8.VII.1993, FIT, S. & J. Peck, 93-57 (CNCI) (Ibes n° 14381). 1m#, FR. GUIANA, Regina Kaw Mountain, Patawa, 4°32'643"N, 52°9'153"W, Aug 2005, J. A. Cerda (AMNH) (Ibes n° 14231). 2m#, ECUADOR, Sucumbios, Rio Napo, Sacha Lodge, 0°30'S, 76°30'W, 3–16.VIII.1994, M[alaise] T[rap], P. [J.] Hibbs [col.], 225 m (CNCI) (Ibes n° 14230,

1222). BRAZIL: Amazonas: 1m#, 71°38'W, 4°33'S, IX.'79, Alvarenga (AEIC) (Ibes n° 14117); 1m#, Amazonas, Manaus, Reserva Ducke, Igarapé Uberê, vi.2003, arm. Malaise, J. M. G. Ribeiro & J. Vidal col. (INPA) (Ibes n° 14232); AM (INPA): 1m#, Manaus, Reserva 1208, 13.viii.1986, Malaise, B. Klein col. (Ibes n° 14233); 1m#, Tonantins, Igarapé Manaquinha, 02°50'15"S, 67°46'30"W, 16–20.ix.2005, Malaise, J. Rafael & F. Xavier col. (Ibes n° 14234); Pará, Juruti (MPEG): 1m#, Mineração Alcoa, Capiçanga, 29.x.2007, arm. Malaise, O. T. Silveira & equipe col. (Ibes n° 14235); 1m#, Estrada Mutum/Mauari, 07.xii.2008, arm. Malaise, O. T. Silveira & equipe col. (Ibes n° 14236).

**Comments.** This species is similar to *Apenesia* #010 because they have the head rounded; the clypeus trapezoidal; the mandible with five teeth; the pronotum very short; the mesoscutellum long; the metapectal-propodeal complex long with posterior margin convex; the petiolo long; the hypopygium with plat long; the genitalia with basiparamere clearly divided, aedeagus narrow with ventral lobe very short. Although, *Apenesia* #010 has the clypeus with crenulate apical margin; the notaulus absent; the mesoscutum-mesoscutellar suture weakly arched and narrow, whereas *A. laevigata* has the clypeus with smooth apical margin; the notaulus present; the mesoscutum-mesoscutellar suture strongly arched and wide. Beyond, *A. laevigata* is present in Amazon rainforest and upper places, whereas *A.* #010 is record from Atlantic rain forest. Here we first report *A. laevigata* to Trinidad and Tobago, French Guiana and Ecuador.

**Remarks.** Holotype genitalia in bad conditions and bad placed in the slide, useless to illustrate or describe it. Here the illustration of body, genitalia and hypopygium was done using a non type specimen in better conditions.

**Distribution.** Neotropical (Mexico, Trinidad and Tobago, French Guiana, Ecuador, Brazil).

### *Apenesia levis* Kieffer, 1904

(Fig. 26.D)

*Apenesia levis* Kieffer 1904, 41: 364–367. #f; Kieffer 1908, 76: 25 (catalog); Kieffer 1914, 41: 392, 393–394; Gordh & Móczár 1990, 46: 205 (catalog).

**Diagnosis.** Female.- Length 4.4 mm. **Color.** Body castaneous. Mandible with three apical teeth, uppermost small. Clypeus short with apical margin of median lobe concave, median carina absent. Eye gray, oval, with about 13 facets. Malar space longer than eye length. Frons polished, punctures small and very sparse. Head subquadrate with sides subparallel, vertex slightly convex, 1.1 × as long as wide. Pronotal disc with sides parallel, anterior margin with median emargination. Maximum width of propodeal disc 1.67 × its minimum width. Mesopleuron with carina dividing

dorsal and lateral faces. Mesotibia strongly spinose. Metasoma longer than head and mesosoma together, petiole short.

**Material examined.** Holotype #: [SÃO TOMÉ AND PRÍNCIPE], Is. Principe, Roca Inf. D. Henrique, I–IV.1901, 100–300m. L. Fea (MSNG).

**Comments.** Below locality labels there are other labels “Typus// *Apenesia laevis* K.// *laevis* Kieff.// Syntypus #f, *Apenesia, levis*, J. J. Kieffer, 1904// Museo Civico di Genova”. These labels were added to the specimen when Dr. Poggi organized Kieffer collection in MSNG (personal communication). Another apterous female of MSGN with identical data locality label of *Apenesia levis* got an extra label “Syntypus #f, *Apenesia, levis*, J. J. Kieffer, 1904// Museo Civico di Genova” when Dr. Poggi was carefully organizing Bethylidae’s Kieffer collection. Although we are able to check Kieffer (1904) described this species base on a unique specimen. In this paper, whenever Kieffer described species based on more than one specimens he let it explicit on material examined. Beyond, the second exemplar with a syntypus label of *A. levis* is actually a *Sclerodermus* with big developed eyes, although no ocelli. Here we conclude the holotype examined by Kieffer was clearly the *Apenesia* redescribed in this study. The other Bethylidae was accidentally labelled and both were wrongly typified as syntypus.

**Distribution.** Afrotropical (São Tomé and Príncipe).

### ***Apenesia leytensis* (Terayama, 1995)**

(Figs. 4.G, 6.M, 9.E, 12.D, 14.H, 22.D-F)

*Neoapenesia leytensis* Terayama 1995a, 63: 886–888, figs 11–15. #m

*Apenesia leytensis* (Terayama, 1995): Alencar, chapter 1, this volume (designation of combination).

**Description.** Holotype. Male. Length 3.8 mm. LFW 2.6 mm.

**Colors.** Head and body dark castaneous, except mesoscutum and metasoma castaneous; legs light castaneous; wings hyaline, veins dark castaneous.

**Head.** Head as long as large, trapezoidal. Frons polished and shining, sparsely punctulate; line on frons absent. Vertex convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin crenulate, median carina short in profile. Mandible with three apical teeth, teeth with different size, upper tooth mesad, two upper teeth equally sized. Eye weakly bulging. Ocelli large, triangle with proximal edges.

**Mesosoma.** Pronotal disc very short. Notaulus absent. Parapsidal signal well delimited. Scutellum longer than large, posterior margin almost straight; mesoscutum-scutelar sulcus weakly arched, with fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough

imbricate, metanotal fovea triangular; median region wide, large, with posterior margin straight. Metapectal-propodeal complex long, posterior margin convex; metaposnotal median carina present, metaposnotum rugulose, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate very short, posterior margin convex, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin projected mesad, small, and convex. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, ventral larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe short; dorsal lobe short; subapical membrane absent; aedeagal dorsal cover narrow.

**Female.** Unknown.

**Material examined. Types:** Holotype m#, PHILIPPINES, Baybay, Leyte, 6.II.1983, C.H. Starr & M. Tumilap leg. (PMAE). **New material examined:** 1m#, [PHILIPPINES], P. I., Albay Prov., Mt. Mayon, 16km NW of Lagaspi, 11.v.1962, H. M. Torrevillas collector, 900m, BPBM, (Ibes n° 14243). MALAYSIA, Pasoh Forest Res. Negeri S., P. & M. Becker (AEIC): 1m#, VI.28.78, forest (Ibes n° 14080); 1m#, VII.17.78, forest (Ibes n° 14079); 1m#, VIII.20.78, forest (Ibes n° 14081); 1m#, IX.26.78, prim. for. (Ibes n° 14075); 1m#, IX.9.78, for. gap (Ibes n° 14088); 1m#, VIII.17.79, for. gap, (Ibes n° 14074); 1m#, IX.15.79, prim. for. (Ibes n° 14085); 1m#, XII.31.79, forest, (Ibes n° 14078); 1m#, I.24.80, for. gap, (Ibes n° 14076); 1m#, I.31.80, forest, (Ibes n° 14077); 1m#, II.7.80, forest, (Ibes n° 14087); 1m#, II.29.80, prim. for. (Ibes n° 14089); 1m#, III.12.80, prim. for., (Ibes n° 14082); 1m#, III.12.80, for. gap (Ibes n° 14083); 1m#, III.10.80, for. gap, (Ibes n° 14084); 1m#, III.8.80, for. gap, (Ibes n° 14086). PENINSULA MALAYSIA, Pasoh Forest Reserve, Negeri Sembilan, Fine Malaise Trap, K. Konishi & K. Maeto (NIAES): 2m#, 25.iii–2.iv.1993 (Ibes n° 14131, 14132); 1m#, 2–8.iv.1993 (Ibes n° 14125); 1m#, 10–17.XII.1993 (Ibes n° 14128); 1m#, PENINSULA MALAYSIA, Air Hitam Forest Res., U.P..M., Selangor, 4–18.v.1992, Coarse Malaise Trap, NIAES, (Ibes n° 14127); 2m#, WEST MALAYSIA, Bukit Fraiser, 13–20.I.1992, Coarse Malaise Trap, T. Matsumura (NIAES) (Ibes n° 14126, 14134). INDONESIA: 1m#, Sumatra, N. Bengkulu, N.P. Kerincl Sebelat, 28.vii.1993, S. Kahono, c 50m, (RMNH'93) (Ibes n° 14149); 1m#, Borneo, Sarawak, Sadong, Kampong Tapuh, 10.vii.1958, T. C. Maa collector, 300–450, BPBM, (Ibes n° 14238); Sula Isl. Mangole, near Buya, C. V. Achterberg, RMNH'93: 1m#, 12.x.-2.xi.1993, Mal. trap 12, c 495m (Ibes n° 14135); 8M3, 12.x.-2.xi.1993, Mal. trap 11, c 460m, (Ibes n° 14137, 14138, 14139, 14224, 14222, 14227, 14229, 14382); 2m#, 12.x.-2.xi.1993, Mal. trap 9, c 480m (Ibes n° 14142, 14148); 8m#, 12.x.-2.xi.1993, Mal. trap 10, c 480m (Ibes n° 14136, 14140, 14141, 14144, 14145, 14146, 14147, 14386); 1m#, 13.x.-2.xi.1993, Mal. trap 15, c 445m (Ibes n°

14143); 4m#, 13.x.-2.xi.1993, Mal.trap 13, c 465m (Ibes n° 14221, 14223, 14225, 14226); 1m#, N Ceram, 9km E Wahai, nr PHPA-Q coastal rainforest, 28.ii.-21.iii.1997, Mal.trap 7, C. V. Acherberg (RMNH'97) (Ibes n° 14228). PAPUA NEW GUINEA, New Guinea: 2m#, Mt. Suckling 500m Mayu I, 13–16.vii.1972, Malaise Trap, J. L. Gressitt collector (BPBM) (Ibes n° 14240, 14241); 1m#, N[ew] Guinea, Lae-Zenag Road, XII.19.78–I.14.79, J. Sedlacek, 200m (AEIC) (Ibes n° 14042). Wanang, 1m#, 28/11/2012–29/11/2012, PNG MAL-WAN01-D11, P4910, 2113 (Ibes n° 14271); 1m#, 03/12/2012–04/12/2012, PNG MAL-WAN03-D16, P4947, 11077, (Ibes n° 14272); Mount Wilhelm, 1m#, 0700m, 30/10/2012–31/10/2012, PNG MAL-MW0700D-06/16-d06, P1441, 11252, (Ibes n° 14274); 1m#, MW0700-04, Malaise, 16/05/2013–17/05/2013, MAL-MW0700'D-04/16-d04, P4752, 20834, Coll. by Sam et al., understorey, (-5.731961,145.2522) 700m (Ibes n° 14288); 1m#, MW0700-03, Malaise, 23/05/2013–24/05/2013, MAL-MW0700'C-11/16-d11, P4743, 20618, Coll. by Sam et al., understorey, (-5.731961,145.2522) 700m (Ibes n° 14388); 1m#, 0700m, 25/10/2012–26/10/2012, PNG MAL-MW0700D-01/16-d01, P1436, 11978 (Ibes n° 14387); 1m# MW0700-04, Malaise, 27/05/2013–28/05/2013, MAL-MW0700'D-15/16-d15, P4763, 20564, Coll. by Sam et al., understorey, (-5.731961,145.2522) 700m (Ibes n° 14389). 1m#, MW0200-01, Malaise, 14/05/2013–15/05/2013, MAL-MW0200'A-04/16-d04, P4959 (Ibes n° 14290); 1m#, MW0200-03, Malaise, 17/05/2013–18/05/2013, MAL-MW0200'C-07/16-d07, P4994 (Ibes n° 14291), 1m#, MW0200-02, Malaise, 23/05/2013–24/05/2013, MAL-MW0200'B-13/16-d13, P4984, (Ibes n° 14289) (MNHN).

**Comments.** This is the type-species of *Neoapenesia*. It is clearly a male of *Apenesia* because it has all diagnostic features of the genus: clypeus subtrapezoidal with median tooth; mesoscutum gibbous; genitalia with paramere narrow and densely hairy, cuspis developed dorsad. This species is unique in having the head as long as large and trapezoidal, with long gena and vertex convex; the mandible with three teeth; the notaulus absent; the metaposnotum rugulose with metaposnotal median carina present; the hypopygium with plate very short with posterior margin convex and the cuspis with two apical callus. Some specimens seem to have notaulus incomplete posteriorly but it is so short that stays under posterior margin of pronotal disc so here we considered absent with this variation. The species was known only by one specimen recorded from Philippines (Terayama 1995a) and now it is record also from Malaysia, Indonesia and Papua New Guinea. This is the most abundant among the species of *Apenesia*.

**Remarks.** The illustration of body, genitalia and hypopygium was done using a non type specimen.

**Distribution.** Oriental (Philippines, Malaysia, Indonesia) and Australian (Papua New Guinea).

***Apenesia makiharai* (Sawada, Terayama & Mita, 2014)**

(Figs. 4.H, 6.N, 9.F, 12.E, 14.I, 22.G-I)

*Apenesia makiharai* Sawada, Terayama & Mita 2014, 17: 326–328, figs. 1–7. #f #m.

*Apenesia makiharai* (Sawada, Terayama & Mita, 2014): Alencar, chapter 1, this volume (designation of combination).

**Description.** Paratype. Male. Length 3.2 mm. LFW 2.3 mm.

**Colors.** Head black; mesosoma and metasoma redish castaneous; clypeus and mandible castaneous; antenna gradually darker distally; wings hyaline, veins light castaneus.

**Head.** Head as long as large, rounded. Frons coriaceous, sparsely punctulate; line on frons absent. Vertex convex. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin crenulate, median carina short in profile. Mandible with three apical teeth, teeth with different size, two upper teeth equally sized. Eye weakly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc short. Notaulus absent. Parapsidal signal well delimited. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutelar sulcus weakly arched, without fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, small. Metanotal trough imbricate, metanotal fovea linear; median region wide, narrow, with posterior margin straight. Metapectal-propodeal complex short, posterior margin convex; metaposnotal median carina absent, metaposnotum imbricate, and polished. Propodeal disc polished. Paraspicular sulcus weakly punctulate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity polished-imbricate.

**Metasoma.** Petiole short. Hypopygium with plate short, posterior margin strongly concave, flap absent. **Genitalia:** paramere slightly sinuous. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with three apical callus, ventral larger than other, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe short; subapical membrane long; aedeagal dorsal cover wide.

**Female.** Known.

**Diagnosis.** Paratype. Female.- Length 2.5 mm. **Color.** Body castaneous. Mandible with two apical teeth. Clypeus short with apical margin of median lobe concave, apical margin with bristles, median carina absent. Eye dark, oval, with facets indistinct. Malar space longer than eye length. Frons polished, punctures small and very sparse. Head subquadrate with sides subparallel, vertex slightly weakly concave,  $1.1 \times$  as long as wide. Pronotal disc with sides parallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.7 \times$  its minimum width.

Mesopleuron with carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma as long as head and mesosoma together, petiole short.

**Comments.** Holotype and allotype are deposited at TULE and were not examined. This species was first described from reared specimens in dead wood. It is easily recognized by having the head as long as large and rounded; the mandible with three teeth; the notaulus absent and the mesopostnotum imbricate anteriorly.

**Material examined.** Paratype #m #f, Japan, Ryukyus, /mt. Omoto-dake, Ishigakijima I., plant species unknown, Coll. 5.iii.2003, Emr. 11.xii.2011, H. Makihara leg (NIAES).

**Remarks.** The illustration of body, genitalia and hypopygium was done using a non type specimen.

**Distribution.** Oriental (Japan).

### ***Apenesia malaitensis* Brues, 1918**

*Apenesia malaitensis* Brues 1918, 62: 124–125. #f; Fouts 1936, 18: 8 (catalog); Gordh & Móczár 1990, 46: 206 (catalog).

**Diagnosis (extracted from literature).** Female.- Length 4.8 mm. **Color.** Body castaneous. Mandible with two apical teeth, apical tooth much larger than inner one. Clypeus sharply elevated medially. Eye small, oval. Malar space short. Frons aciculate, punctures small and sparse. Head elongate with sides subparallel, vertex slightly weakly concave,  $1/4 \times$  longer than wide. Pronotum  $1/2 \times$  longer than wide; neck visible from above disc with sides parallel, anterior margin with median emargination. Mesotibia strongly spinose. Metasoma as long as head and mesosoma together.

**Comments.** We were not able to analyze the type (MCZH). This diagnosis was based on Brues (1918). According to him, *A. malaitensis* is similar to *A. proxima* in color but the former has the head elongate, whereas the latter has the head subquadrate.

**Distribution.** Australian (Solomons Is.).

### ***Apenesia miki* (Terayama, 2004) comb. nov.**

*Archaeopristocera miki* Terayama 2004, 27: 44.

**Diagnosis (extracted from literature).** Female.- Head elongate, with parallel sides and vertex deeply concave; posterolateral corner acutely angulate; frons and vertex impunctate. Mandible with

four acute apical teeth. Anterior margin of clypeus convex, with pair of lateral teeth. Metasoma with very short petiole. Femora and tibiae wide and flat. Mesotibia spinose.

**Comments.** We were not able to analyze the type (NSMT). This diagnosed was based on Terayama (2004).

**Distribution.** Neotropical (Dominican Amber).

### ***Apenesia modesta* (Smith, 1864)**

*Scleroderma modesta* Smith 1864, 7: 27. #f.

*Apenesia modesta* (Smith, 1864): Westwood 1874, 171 (designation of combination); Westwood 1881, 125, 131, pl vn fig 4; Dalla Torre 1898, 5: 558 (catalog); Kieffer 1908, 76: 25 (catalog); Kieffer 1914, 41: 392, 396; Gordh & Móczár 1990, 46: 207 (catalog).

**Diagnosis (extracted from literature).** Female.- Length 2.0 mm. **Color.** Body light castaneous, metasoma dark castaneous. Head quadrate, vertex almost straight, corner rounded. Eye dark, rounded with six facets. Malar space short. Mesotibia strongly spinose. Metasoma elongate and laceolate as long as head and mesosoma together.

**Comments.** *Apenesia modesta* was first described as *Sclerodermus*. Since we were not able to access the type for this study, the descriptions here provided was based on the original description by Smith (1864) and Westwood (1874) redescription. Smith defined *A. modesta* especially by the color details. According to Westwood (1874), the mouth parts of *A. modesta* is similar to *A. amazonica*. The type material is supposed to be deposited at OXUM.

**Distribution.** Oriental (Indonesia).

### ***Apenesia nigra* Kieffer, 1904**

(Figs. 26.E)

*Apenesia nigra* Kieffer 1904, 41: 364-365; Kieffer 1908.76: 25 (catalog); Kieffer 1914, 41: 392-393; Gordh & Móczár 1990, 46: 207 (catalog).

**Diagnosis.** Female.- Length 8.0 mm. **Color.** Body black except mandible, scape, tibiae and claws redish, metasoma castaneous. Mandible with two apical teeth, uppermost small. Clypeus short with apical margin of median lobe rounded, median carina short. Eye gray, oval, with about 16 facets. Malar space very short. Frons coriaceous and shinnig, punctures small and very sparse. Head subquadrate with sides subparallel, vertex almost straight,  $0.95 \times$  as long as wide. Pronotal



disc with sides parallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.6 \times$  its minimum width. Mesopleuron without carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma longer than head and mesosoma together, petiole short.

**Material examined.** Holotype #: Is. S. Thomé, Aqua-Ize, XII.1900, 400–700m., L. Fea. (MSNG)

**Comments.** We analyzed the holotype in MSGN but we were not able to illustrate it.

**Distribution.** Afrotropical (São Tomé and Príncipe).

### *Apenesia parasitica* (Smith, 1865)

(Figs. 24.J, 25.D)

*Scleroderma parasitica* Smith 1865, 8: 79, #f.

*Apenesia parasitica* (Smith, 1865): Westwood 1881, 132 (designation of combination); Dalla Torre 1898, 5: 558 (catalog); Kieffer 1908, 76: 25 (catalog); Kieffer 1914, 41: 392, 394; Gordh & Móczár 1990, 46: 209 (catalog).

**Diagnosis.** Female.- Length 2.0 mm. **Color.** Body redish castaneous. Clypeus short with apical margin of median lobe slightly concave, median carina absent. Eye dark, oval. Malar space very short. Frons polished, punctures small and very sparse. Head weakly elongate with sides subparallel, vertex slightly concave,  $1.3 \times$  as long as wide, occipital carina visible in dorsal view. Pronotal disc short with sides subparallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.6 \times$  its minimum width. Mesopleuron without carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma longer than head and mesosoma together, petiole short.

**Material examined.** Holotype #: Is. S. Thomé, Aqua-Ize, XII.1900, 400–700m., L. Fea. (BMNH).

**Comments.** Gordh & Móczár (1990) assigned the authorship of this species as “Smith, 1864”. This literature exists but the correct year of publication is “Smith, 1865”. *Apenesia parasitica* was available to this study by the illustrations included in this paper. Our diagnosis is based on those illustrations and the description provided by Smith (1865) and Westwood (1881). Although there is a syntype label attached to the specimen, in the original description only one specimen was related on material examined.

**Distribution.** Oriental (Indonesia).

***Apenesia perlonga* Corrêa & Azevedo, 2006**

(Figs. 5.A, 6.O, 9.G, 12.F, 14.J, 23.A-C)

*Apenesia perlonga* Correa & Azevedo 2006, 50: 443, figs. 7–9.

**Description.** Holotype. Male. Length 4 mm. LFW 3.8 mm.

**Colors.** Body dark castaneus; mandible, antenna and legs castaneous; wings hyaline, veins dark castaneus.

**Head.** Head larger than long, rectangular. Frons weakly coriaceous, densely punctulate; line on frons absent. Vertex straight. Clypeus broad with median lobe subtrapezoidal, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with one apical tooth. Eye strongly bulging. Ocelli small, triangle with proximal edges.

**Mesosoma.** Pronotal disc short. Notaulus present, complete, weakly converging posterad. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutelar sulcus almost straight, without fovea on side edge, narrow, deep. Axilla subtrapezoidal, deep, large. Metanotal trough foveolate, metanotal fovea triangular; median region wide, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina present, metaposnotum rugulose, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region imbricate. Propodeal declivity foveolate.

**Metasoma.** Petiole short. Hypopygium with plate very short, posterior margin strongly concave, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin serrate, dorsal end short. Aedeagus with two apical lobes, ventral lobe large; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Material examined. Types:** Holotype #m, BRAZIL, Espírito Santo, Atílio Vivacqua, Fazenda José Carlos Lustroza, 20°55'57,6"S 41°11'22.1"W, 13–20.II.2003, armadilha Malaise, M.T. Tavares, C.O. Azevedo e eq. col. (UFES) (UFES n°37753). Paratype Espírito Santo, Pancas, Fazenda Juliberto Stur, 19°13'10,5"S 40°46'23,8"W, 24–31.I.2003, armadilha Malaise, M.T. Tavares, C.O. Azevedo e eq. col. (UFES). (UFES n° 10915). **New material examined:** ECUADOR, Napo, Limoncocha, [0°24'S], [76°37'W], 28-VI-1976, S. + J. Peck [col.] (PMAE) (Ibes n° 10007). BRAZIL: Amazonas, Manaus (INPA): 1m#, Reserva Ducke, Igarapé Ipiranga, V.2003, Arm. Malaise, J. M. G. Ribeiro col. (Ibes n° 14333); 1m#, Reserva 1501, km 41, 15–25.XI.1995, Arm. Suspensa (Ibes n° 14351); Pará, Arm. Malaise, O. T. Silveira & equipe col.

(MPEG): 1m#, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 12–16.VIII.2008 (Ibes n° 14336); 1m#, Anapu, Rio Xingu, Caracol, Barra do Vento, 07–10.VIII.2008 (Ibes n° 14352); 1m#, Bahia, Uruçuca, Faz. Brasil, 14°33'S, 39°21'W, 24.XI.2002, Arm. Malaise, (UFES/CEPLAC) (Ibes n° 14347); ES: Sooretama, ReBio Sooretama: 1m#, 11–19.XI.2011, malaise trap, C.O. Azevedo (UFES) (Ibes n° 14264); 3m#, (Ibes n° 14276, 14277, 14278); 1m#, Fragment Pasto Novo, Brésil, malaise II, 13–20.xi.2000, Bethylidae, (MNHN) (Ibes n° 14282); Santa Maria de Jetibá, Fazenda Paulo Seick, Arm. Malaise, Tavares, Azevedo e eq. col. (UFES): 1m#, 20°04'27.9"S, 40°44'51.3"W, 06–13.XII.2002, Arm. Malaise, Tavares, Azevedo e eq. col. (UFES n° 11275); 1m#, 20°02'31.1"S, 40°41'51.3"W, 29.XI–06.XII.2002 (UFES n° 11295); Atílio Vivacqua, Faz. José Carlos Lustoza, 20°55'57.6"S, 41°11'22.1"W, Arm. Malaise, Tavares, Azevedo e eq. col. (UFES): 2m#, 13–20.II.2003 (UFES n° 11376, 11377); 1m#, 20–27.II.2003 (UFES n° 11378).

**Comments.** *A. perlonga* is similar to *A.* #006 and *A.* #008 by having the head larger than long, rectangular; the mandible with one tooth; the pronotum short; the notaulus complete and convergent posteriorly and the hypopygium with flap and posterior margin concave. However, #006 has the head rectangular with vertex slightly convex as *A.* #008, whereas *A. perlonga* has the head rectangular with vertex straight.

**Remarks.** The illustration of body, genitalia and hypopygium draw was done using a non type specimen.

**Distribution.** Neotropical (Brazil, Ecuador).

### ***Apenesia proxima* Kieffer, 1904**

(Fig. 26.F)

*Apenesia proxima* Kieffer 1904, 41: 364, 367. #f; Kieffer 1908, 76: 25 (catalog); Kieffer 1914, 41: 392, 396; Gordh & Móczár 1990, 46: 210 (catalog).

**Diagnosis.** Female.- Length 5.0 mm. **Color.** Body castaneous, metasoma dark castaneous. Mandible with three apical teeth. Clypeus extending back frons, median lobe with apical margin almost straight, apical margin with bristles, median carina absent. Eye dark, oval, with about six facets. Malar space longer than eye size. Frons aciculate, punctures small and very sparse. Head subquadrate with sides subparallel, vertex slightly concave, 1.0 × as long as wide. Pronotal disc with sides nearly parallel, anterior margin with median emargination. Maximum width of propodeal disc 1.6 × its minimum width. Mesopleuron without longitudinal carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma slightly longer than head and mesosoma together, petiole long.

**Material examined.** Holotype #: [PAPUA NEW GUINEA], N. Guinea S. E. Hughibagu, V–IX.91, Loria [coll.] (MSNG).

**Comments.** The holotype was analyzed during the MSNG visit. According to Kieffer (1904), this species is similar to *A. nigra*.

**Distribution.** Australian (Papua New Guinea).

#### ***Apenesia punctata* Kieffer, 1904**

*Apenesia punctata* Kieffer 1904, 41: 364, 366. #f; Kieffer 1908, 76, 25 (catalog); Kieffer 1914, 41: 392, 393; Medler 1980, 30: 469 (list).

*Apenesia punctulata* Krombein 1989, 91: 620, 624 (replacement name for *Epyris punctatus* Cameron, 1888); Gordh & Móczár 1990, 46: 210 (catalog).

**Diagnosis.** Female.- Length 6.0 mm. **Color.** Body castaneous, metasoma dark castaneous. Mandible with two apical teeth. Clypeus extending back frons, median lobe with apical margin almost straight, apical margin with bristles, median carina absent. Eye dark, elliptical, with about 11 facets. Malar space short. Frons aciculate, punctures small and very sparse. Head subquadrate with sides subparallel, vertex slightly concave, 1.0 × as long as wide. Pronotal disc with sides nearly parallel, anterior margin with median emargination. Maximum width of propodeal disc 1.6 × its minimum width. Mesopleuron without longitudinal carina dividing dorsal and lateral faces. Mesotibia strongly spinose. Metasoma slightly longer than head and mesosoma together, petiole long.

**Material examined.** Holotype #: Mte. Camerun, Buea, 800–1200m. s. m., VI–VII.1902, L. Fea. (MSNG)

**Comments.** The holotype was analyzed at MSNG but it was not possible to illustrate it. According to Kieffer (1904) *A. punctata* is similar to *A. nigra* and *A. amazonica*.

**Distribution.** Afrotropical (Cameroon).

#### ***Apenesia sahyadrica* Azevedo & Waichert, 2006**

(Figs. 5.B, 6.P, 9.H, 12.E, 14.K, 23.D-F, 24.D, H, 25.E)

*Apenesia sahyadrica* Azevedo & Waichert, 2006, 1174: 64–67, figs. 1–6.

**Description.** Holotype. Male. Length 5.7 mm. LFW 4.6 mm.

**Colors.** Body black; metasoma dark castaneous; legs castaneous; wings hyaline, veins castaneous.

**Head.** Head as long as large, quadrate. Frons weakly coriaceous, densely puncticulate; line on frons absent. Vertex slightly convex. Clypeus broad with median lobe rounded, median tooth present, and small, apical margin smooth, median carina short in profile. Mandible with three apical teeth, teeth with different size, upper tooth mesad, uppermost much smaller than others. Eye strongly bulging. Ocelli large, triangle with distal edges.

**Mesosoma.** Pronotal disc long. Notaulus present, complete, strongly converging posterad. Parapsidal signal well delimited. Scutellum as long as large, posterior margin convex; mesoscutum-scutelar sulcus weakly arched, without fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, small. Metanotal trough mostly imbricate, with few foveae, metanotal fovea oval; median region wide, narrow, with posterior margin straight. Metapectal-propodeal complex short, posterior margin convex; metaposnotal median carina absent, metaposnotum irregularly foveolate. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina absent; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity foveolate.

**Metasoma.** Petiole short. Hypopygium with plate long, posterior margin almost straight, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Basiparamere with apical dorsal projection large, apex convex. Cuspis with apical margin with two apical callus, dorsal larger than other, dorsal end long. Aedeagus with two apical lobes, ventral lobe large; dorsal lobe long; subapical membrane absent; aedeagal dorsal cover wide.

**Female.** Known.

**Diagnosis.** Allotype. Female.- Length 5.9 mm. **Color.** Body castaneous, metasoma dark castaneous. Mandible with two apical teeth. Clypeus extending back frons, median lobe with apical margin slightly concave, apical margin with bristles, median carina present and short, angled just before apical margin. Eye dark, elliptical, with about 13 facets. Malar space shorter than eye length. Frons aciculate, punctures sparse. Head quadrate with sides parallel, vertex slightly concave,  $1.07 \times$  as long as wide. Pronotal disc with sides nearly parallel, anterior margin with median emargination. Maximum width of propodeal disc  $1.27 \times$  its minimum width. Mesopleuron without longitudinal carina dividing dorsal and lateral faces. Midtibia strongly spinose. Metasoma slightly longer than head and mesosoma together, petiole short.

**Material examined. Types:** Holotype 1m#, INDIA, Karnataka, Chikmagalur, Farm of Coffee Research Station, 12.I.2000, extracted from stem borer larvae of *Xylotrechus quadripes* from tunnels of infested coffee stems, H.G. Seetharama col. (UFES) (UFES n° 11128). Allotype 1f#, same data as holotype (UFES n° 11129). Paratypes: 6f#, 6m#, same data as holotype (UFES n° 11116, 11117, 11118, 11119, 11120, 11121, 11122, 11123, 11124, 11125, 11126, 11127). Holotype

m#. **New material examined:** 1m#, THAILAND, Petchaburi Kaeng Krachan NP Panernthung/km27, 12°49.302'N, 99°22.263'E, 28.xii.2008–4.i.2009, Malaise trap, Sirichai leg., (QSBG) (Ibes n° 14383).

**Comments.** This species was first described based on specimens from Arabic coffee infested with the white stem borer *Xylotrechus quadripes* Chevrolat. This species is promptly recognized by having the clypeus rounded; the notaulus complete; the metaposnotum irregularly foveolate; the hypopygium with plate long, with flap and posterior margin almost straight.

**Remarks.** The illustration of body, genitalia and hypopygium was done using paratypes.

**Distribution.** Oriental (India).

### ***Apenesia singularis* Lanes & Azevedo, 2004**

(Figs. 5.C, 6.Q, 9.I, 12.H, 14.L, 23.G-I)

*Apenesia singularis* Lanes & Azevedo, 2004, 679: 6–8, figs. 8–10.

**Description.** Holotype. Male. Length 5.1 mm. LFW 4.1 mm.

**Colors.** Head and body black; antenna, mandible and clypeus dark castaneus; legs castaneus; wings hyaline, veins castaneous.

**Head.** Head larger than long, rectangular. Frons weakly coriaceous, densely punctulate; line on frons absent. Vertex straight. Clypeus broad with median lobe subtrapezoidal, median tooth present, and large, apical margin smooth, median carina short in profile. Mandible with four apical teeth, teeth with different size, upper tooth mesad, two upper teeth equally sized. Eye weakly bulging. Ocelli small, triangle with proximal edges.

**Mesosoma.** Pronotal disc very short. Notaulus present, complete, strongly converging posterad. Parapsidal signal weakly impressed. Scutellum as long as large, posterior margin almost straight; mesoscutum-scutellar sulcus almost straight, without fovea on side edge, narrow, shallow. Axilla subtrapezoidal, deep, small. Metanotal trough mostly imbricate, with few foveae, metanotal fovea oval; median region wide, large, with posterior margin straight. Metapectal-propodeal complex short, posterior margin almost straight; metaposnotal median carina absent, metaposnotum row of anterior foveae, and polished. Propodeal disc polished. Paraspicular sulcus irregularly foveolate; metapleural carina present; lateral surface of propodeum imbricate, inferior region foveolate. Propodeal declivity polished-foveolate.

**Metasoma.** Petiole short. Hypopygium with plate long, posterior margin almost straight, flap present. **Genitalia:** paramere straight. Basivolsella apical inner margin smooth. Apex convex. Cuspis with apical margin with three apical callus, ventral larger than other, dorsal end short.

Aedeagus with two apical lobes, ventral lobe large; dorsal lobe long; subapical membrane short; aedeagal dorsal cover wide.

**Female.** Unknown.

**Comments.** This species is similar to *Apenesia* #017 by having the pronotum short, the metapostnotum mostly polished with row of fovea anteriorly. However, *A. singularis* has the mandible with four teeth; the notauli complete; the mesoscutum-mesoscutellar suture straight and shallow; the hypopygium with plate long and the genitalia with cuspis with three apical callus, whereas *A.* #017 has the mandible with three teeth; the notauli incomplete posteriorly; the mesoscutum-mesoscutellar suture weakly arched and deep; the hypopygium with plate short and the genitalia with cuspis with one apical callus.

**Material examined. Types:** Holotype m#, BRAZIL, Rondônia, Ouro Preto do Oeste, Linha 2/2, lote 36, gleba 21-b, 03–05.IX.1986, Malaise trap, F. F. Ramos col. (MPEG). Paratypes: BRAZIL, Amazonas: 1m# Reserve Ducke, 06–17.VII.1992, Stick trap 10–20 m, J. Vidal & J. Vidal col. (UFES n° 11133), 1 m#, Reserve 1113, 31.X.1985, Malaise trap, B. Klein col. (UFES n° 11132); 1m# Maranhão, Imperatriz, Ribeirãozinho, 02–05.VIII.1989, Malaise trap, F. F. Ramos col. (UFES n° 11134); Pará: 1m#, Serra dos Carajás, Estrada Manganês, 07.VI.1983–12.VI.1993, Malaise trap, T. Pimentel & equipe col. (UFES n° 11135); 2m#, Serra Norte, Estrada Manganês, 16.VI.1983–08.VI.1993, Malaise trap (UFES n° 11136, 11137). **New material examined:** COSTA RICA (PMAE): 2m#, La Selva, CC100, 8–15-v-1989, MT, Tree fall gap, Brown and Feener, (PMAE) (Ibes n° 14214, 14215); 1m#, Alajuela, Chiles de Aguas Zarcas, xi-1989–i-1990, R. Cespedes, coffee, 300m, (Ibes n° 14216). 1m#, PANAMÁ, Comarca Kuna Yala, Ustupu, Rio Abudi, [09°07'57"N], [77°55'36"W], 6–12 dic. 1999, Malaise, P. González [col.], (MIUP) (Ibes n° 12020). ECUADOR: 1m#, Sucumbios, Rio Napo, Sacha Lodge, 0°30'S, 76°30'W, 3–13.VIII.1994, M[alaise] T[rap], P. [J.] Hibbs [col.], 225 m, (CNCI) (Ibes n° 1208); 1m#, Sucumbios, Sacha Lodge, 0.5°S, 76.5°W, 3–13.iv.1994, Malaise trap, P. Hibbs [col.], 290 m, (LACM) (Ibes n° 9084); 1m#, Napo, Yasuni Biol. Sta., 0.67°S, 76.39°W, 18–26.v.1996, Malaise trap, P. Hibbs, 220m, Cephalotes site, (AEIC) (Ibes n° 14115). 1m#, PERU, SM, Tarapoto-Yurimaguas rd, km 20, "Biodiversidad", 0634S, 7620W, 7–8.vii.04, Bbrown, Crasmussen, Ecorona, 950m, (MUSM) (Ibes n° 14219). BRAZIL: 1m#, AC, Brasília, ramal 13 (km 13) da estrada que liga Brasília a Assis Brasil, mata, S 10° 54' 30.9", W 68° 49' 27.1", 12–19.i.2014, coleta manual em barraca de shannon, (Ibes n° 14265); 1m#, Amazonas, Novo Aripuanã, Reserva Soka, 01°15'53"S, 60°07'08"W, 17–25.VIII.1999, arm[adilha] Suspensa, J. F. Vidal & A. L. Henriques col., Igarapé, (INPA) (Ibes n° 10408); 2m#, AM, Novo Aripuanã, Reserva Soka, 05°15'53"S, 60°07'08"W, 17–25.VIII.1999, Arm. Malaise, J.F. Vidal & A.L. Henriques col. (INPA) (Ibes n° 14281, 14292); 1m#, Novo Aripuanã, Reserva Soka, 05°15'53"S, 60°07'08"W, 17–25.VIII.1999, arm[adilha] Suspensa, J. F. Vidal & A. L.

Henriques col., Igarapé (INPA) (Ibes n° 14293); 1m#, AM, Novo Aripuanã, Reserva Soka, 01°15'53"S, 60°07'08"W, 17–25.VIII.1999, arm[adilha] Suspensa, J. F. Vidal & A. L. Henriques col., Igarapé (INPA) (Ibes n° 14294); 1m#, AM, Novo Aripuanã, Reserva Soka, 06–10.xii.1999, Arm. Malaise, J. F. Vidal col., Área aberta (INPA) (Ibes n° 14295); 1m#, AM, Novo Aripuanã, Lago Xadá, C. Bela Vista, 17.IV.2005, Arm. Malaise, T. Flane col. (INPA) (Ibes n° 14296); 1m#, AM, Parc. Nac. Do Jaú, Rio Jaú, Igarapé Patauí, 23–28.Vii.1995, Arm. Malaise, J. A. Rafael & J. F. Vidal col. (INPA) (Ibes n° 14297); 1m#, Amazonas, Manaus, Reserva 1110, Lateral leste, 11.X.1984, rede, Bert Klein col. (INPA) (Ibes n° 14298); 1m#, Amazonas, Manaus, Reserva 1112, Lateral oeste, 24.X.1984, rede, Bert Klein col. (INPA), (Ibes n° 14299), 1m#, Amazonas, Manaus, Reserva 1501, km 41, Lateral oeste, 15–30.III.1996, arm. Suspensa (INPA) (Ibes n° 14300); 1m#, AM, Itacoatiara, Mil Madereira, 16.XII.1999, Arm. Malaise, J. F. Vidal col. (INPA) (Ibes n° 14301); 1m#, Amazonas, Presidente Figueredo, 02°01'05"S, 59°49'59"W, 04–08.IX.2008, Arm. Malaise, T.R. Krobow & F. F. Xavier Fo col. (INPA), (Ibes n° 14302); 1m#, Amazonas, Manaus, Reserva Ducke, Rod. AM 010 km 26, Igarapé Acará, X. 2001, Arm. Malaise, J. F. Vidal col. (INPA) (Ibes n° 14303); 1m#, Amazonas, Manaus, Reserva Ducke, Rod. AM 010 km 26, Igarapé Acará, X. 2001, Arm. Malaise, J. F. Vidal col. (INPA) (Ibes n° 14304); 1m#, Amazonas, Manaus, Reserva Ducke, Rod. AM 010 km 26, Igarapé Bolívia, 10.II.2003, Arm. Malaise, J.M.G. Ribeiro col. (INPA) (Ibes n° 14305); 1m#, Amazonas, Manaus, Reserva Ducke, 31.ix.1986, Ulisses, L. col. (INPA) (Ibes n° 14306); 1m#, Pará, Parauapebas, Serra do Norte, Carajás Igarapé do Pajuca, [05°54'S], [49°53'W], 20–22.V.1984, arm[adilha] Suspensa (2m), O. T. Silveira & equipe col. (MPEG) (Ibes n° 13189); 1m#, Pará, Vitória do Xingu, Rio Xingu, Bacajá, Bom Jardim, 20–24.XI.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14307); 1m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 13–17.XI.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14308); 1m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 13–17.XI.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14309); 1m#, Pará, Vitória do Xingu, Rio Xingu, Bacajá, Bom Jardim, 20–24.XI.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) 14310; 1m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 07–11.II.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14311); 1m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 2–16.VII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14312); 1m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 2–16.VII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14313); 2m#, Pará, Vitória do Xingu, Rio Xingu, Bacajá, Bom Jardim, 07–10.VII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14314, 14315); 3m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Di Maria, 12–16.VIII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14316, 14317, 14318); 1m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Gaioso, 12–16.VIII.2008, Arm.



Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14319); 1m#, Pará, Vitória do Xingu, Rio Xingu, Igarapé Gaioso, 07–10.VII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14320); 1m#, Pará, Anapu, Rio Xingu, Caracol, Barra do Vento, 24–25.IV.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14321); 1m#, Anapu, Rio Xingu, Caracol, Barra do Vento, 20–23.IX.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14322); 2m#, Pará, Altamira, Rio Xingu, Ilha Bela Vista, 07–10.VIII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14323, 14324); 1m#, Pará, Altamira, Rio Xingu, Ilha Grande, 06–10.XI.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14325); 3m#, Pará, Altamira, Rio Xingu, Itapuama, 06–11.XI.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14326, 14327, 14328); 1m#, Pará, Juriti, Propriedade Barroso, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14329); 1m#, Pará, Juriti, Mauari, 01.XII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14330); 1m#, Pará, Juriti, Mineração Alcoa, Capiranga, 29.x.2007, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 143310); 1m#, Pará, Vitória do Xingu, Rio Xingu, Bacajá, Bom Jardim, 07–10.VIII.2008, Arm. Malaise, O. T. Silveira & equipe col. (MPEG) (Ibes n° 14332); 1m#, Pará, Óbidos, Sitio Curió, 01°47'03"S, 55°07'05"W, 29.viii–08.ix.2001, arm. Malaise, J. A. Rafael & J. F. Vidal (INPA) (Ibes n° 14218); 1m#, Pernambuco, Caruaru, v-1972, J. Lima (PMAE) (Ibes n° 14217); 1m#, Caruaru, Apr. 1972, M. Alvarenga (AEIC) (Ibes n° 14119).

**Remarks.** The illustration of body, genitalia and hypopygium was done using a non type specimen.

**Distribution.** Neotropical (Brazil).

### ***Apenesia sjostedti* (Tullgren, 1904)**

*Aleurodes sjostedti* Tullgren 1904, 1: 429–430, figs. 1, 2, 3. #f.

*Apenesia sjostedti* (Tullgren, 1904): Kieffer 1914, 41: 391, 392, 394 (designation of combination), fig 145; Gordh & Móczár 1990, 46: 211 (catalog).

**Diagnosis (extracted from literature).** Female.- Length 6.5 mm. **Color.** Body light castaneous, metasoma dark castaneous. Mandible with two apical teeth. Clypeus very short, median lobe trapezoidal, median margin concave, and high medially so that it is triangular in frontal view, margin with bristles, clypeus strongly projected backward between up to top eye level. Eye dark, elliptical, with about eight facets. Malar space longer than eye length. Frons polished, punctures small and sparse. Head subquadrate with sides parallel and vertex barely concave, 1.1 × as long as wide. Pronotal disc with sides diverging posteriorly. Maximum width of propodeal disc 1.6 × its

minimum width. Mesopleuron with longitudinal carina dividing dorsal and lateral faces. Mesotibia strongly spinose, spines wide. Metasoma longer than head and mesosoma together, petiole long.

**Comments.** This redescription was made base on Tullgren (1904). The type material was not available to this study (NHRS). *Aleurodes* (today synonymous under *Apenesia*) was originally described as a genus in Thynnidae.

**Distribution.** Afrotropical (Cameroon).

### ***Apenesia substriata* Kieffer, 1904**

(Fig. 26.G)

*Apenesia substriata* Kieffer 1904, 41: 364, 365–366. #f; Kieffer 1908, 76: 25 (catalog); Kieffer 1914, 41: 392, 395; Evans 1963, 130: 269, 355; Evans 1964, 132: 34; Gordh & Móczár 1990, 46: 212 (catalog).

**Diagnosis.** Female.- Length 4.92 mm. **Color.** Body light castaneous, metasoma castaneous. Mandible with two apical teeth. Clypeus very short, median lobe trapezoidal, median margin concave, and high medially so that it is triangular in frontal view, margin with bristles, clypeus strongly projected backward between up to top eye level. Eye dark, elliptical, with about eight facets. Malar space shorter than eye length. Frons with very fine striations, punctures small and sparse. Head quadrate with sides parallel and vertex nearly straight (barely concave),  $1.17 \times$  as long as wide. Pronotal disc with sides diverging posteriorly. Maximum width of propodeal disc  $2.0 \times$  its minimum width. Mesotibia strongly spinose, spines wide. Metasoma subpetiolate, as long as head and mesosoma together.

**Comments.** This species is very similar to *A. amoena* Evans, 1963 by having similar size, head quadrate and mandible with two teeth. However *A. substriata* has the clypeus with median lobe trapezoidal and median margin concave, whereas *A. amoena* has the clypeus emarginated.

**Material examined.** Syntype #f: BOLIVIA, [Rio Beni, Salinas], Balzan col. (MSNG). Here designated as lectotype. Syntypes 4 #f pinned together: BOLIVIA, Rio Beni, Salinas, Balzan col. (MSNG). Here designated as paralectotypes.

**Distribution.** Neotropical (Bolivia).

### ***Apenesia unicolor* Kieffer, 1904**

(Fig. 26.H)

*Apenesia unicolor* Kieffer 1904, 41: 364, 366–367. #f; Kieffer 1908, 76: 25 (catalog); Kieffer 1914,

41: 392, 394; Kieffer 1922, 20: 80; Kurian 1954, 3: 274 (catalog); Baltazar 1966, 8: 198–199 (catalog); Gordh & Móczár 1990, 46: 213 (catalog).

**Diagnosis.** Female.- Length 5.0 mm. **Color.** Body light castaneous, metasoma castaneous. Mandible with two apical teeth. Clypeus very short, median lobe with apical median margin concave, apical margin with bristles, clypeus strongly projected backward between up to top eye level, median carina absent. Eye dark, elliptical, with about eight facets. Malar space shorter than eye length. Frons aciculate, punctures small and sparse. Head elongate with sides parallel and vertex barely concave,  $1.27 \times$  as long as wide. Pronotal disc with sides diverging posteriorly. Maximum width of propodeal disc  $1.8 \times$  its minimum width. Mesopleuron with longitudinal carina dividing dorsal and lateral faces Mesotibia strongly spinose, spines wide. Metasoma longer than head and mesosoma together, petiole long.

**Comments.** This species is very similar to *A. substriata* by having mandible with two apical teeth, clypeus very short, median lobe with apical median margin concave, eye dark, elliptical, with about eight facets. However *A. unicolor* has the head elongate, whereas *A. substriata* has the head quadrate.

**Material examined.** Holotype #f: Is. Fernando Poo, Basile, 400–600 m. S. M., VIII–IX.1901, L. Fea (MSNG).

**Distribution.** Oriental (Philippines) and Afrotropical (Equatorial Guinea).

### *Apenesia vaurieorum* Evans, 1969

(Fig. 26.I)

*Apenesia vaurieorum* Evans 1969a: 71: 519. #f.

*Apenesia vauricorum* [lapsus] in Gordh & Móczár 1990, 46: 213 (catalog).

**Diagnosis.** Female.- Length 6.5 mm. **Color.** Body castaneous. Mandible with two large sharpened apical teeth. Clypeus extending backward into frons, with short, broad trapezoidal median lobe, apical margin straight. Eye subcircular, with eight facets. Malar space as long as eye length. Frons weakly coriaceous, punctures small and very sparse. Head quadrate with sides straight and parallel anteriorly, convex posteriorly,  $1.08 \times$  as long as wide. Vertex straight. Occipital carinae visible in dorsal view. Pronotal disc with lateral margin parallel, sides diverging downward. Maximum width of propodeal disc  $1.65 \times$  its minimum width, spiracles placed at lateral of propodeum, below constriction. Mesotibia strongly spinose. Tarsi spinose, claws simple. Metasoma as long as head and mesosoma together, petiole very short.

**Material examined.** Holotype #f: Antilles: JAMAICA, *Hardwar Gap*, 4800', 13–15.VII.1960, P. & C. Vaurie col. (AMNH).

**Distribution.** Neotropical (Jamaica).

## Biology

The life history of *Apenesia* is poorly known. Females of *Apenesia* present a set of characteristics which allow to explore cryptic environment such as wood gallery or tunnels of stem borer, such as the body depressed, the mandibles robust and strong, the absent of wings and ocelli, the eyes very small with only few facets covered to wide chitin exoskeleton (Alencar, chapter 1, this volume ) and the legs spinose. Only three species have records about their biology: *Apenesia* #007; *A. makiharai* and *A. sahyadrica* attacking beetle larvae.

*Apenesia makiharai* was obtained from several dead wood plants in Japan. Sawada *et al.* (2014) got 16 coleopteran wood-borers species and two predators were obtained together with *A. makiharai*. Since many *A. makiharai* specimens were reared from dead wood severely affected by *Cerecium longicorne* Pic, 1926 and this was the most common beetle species obtained from all wood samples, Sawada *et al.* (2014) inferred this cerambycid species the potential host species to *A. makiharai*. They also observed *A. makiharai* females active at night and males during the day. However copulation was only observed only during the daytime.

Azevedo & Waichert (2006) described *Apenesia sahyadrica* as a natural parasitoid of the coffee white stem borer *Xylotrechus quadripes* Chevrolat (Coleoptera, Cerambycidae) larvae. *Apenesia sahyadrica* has been used as an important natural enemy of this stem borer in coffee crop in India (Azevedo & Waichert, 2006) before it had its description made. Seetharama *et al.* (2007) studied this species in laboratorial condition. They record informations about eggs, all laval instars, pupation sex ratio and mate.

The specimens of *Apenesia* #007 borrowed from BMNH are labeled “*ex larva of Pantorhytes plutus*”, including the holotype and allotype of its species. That means these specimens were rearing from Curculionidae larvae *Pantorhytes plutus* Faust, 1892. They were reared in 1946 and since then they were pinned and deposited at BMNH collection with no identification. The weevil larvae of *Pantorhytes plutus* (Oberthür) live in cryptical gallery as Cerambycidae *Cerecium longicorne* (related to *A. makiharai*) and *Xylotrechus quadripes* (related to *A. sahyadrica*). According to Gressit (1966), *Pantorhytes plutus* is one of the major pests of cacao trees, particularly in Papua New Guine where many specimens of *A.* #007 were found.

## Discussion

The conception of *Apenesia* sensu Alencar (chapter 1, this volume) adopted here is an extended view of Terayama (1995a) for *Neoapenesia* adding some *Apenesia* species sensu Evans (1963) such as (1) part of *laevigata* species group (*A. laevigata*, *A. perlonga* and *A. singularis*) and *A. sahyadrica* for males and (2) females of *Apenesia* core.

The current concept of *Apenesia* was established only because we were able to figure out its males and females (see Alencar, chapter 1, this volume). The type species of the genus, *Apenesia amazonica*, is known from few females only. This species is remarkable distinct from other Pristocerinae females by having the head larger than mesosoma, the clypeus not prominent and extended back frons, the antennae very short. All these features are also present in females of *A. sahyadrica* reared from Cerambicidae larvae, which males and females are quite similar to those in *A. makiharai*. When Sawada *et al.* (2014) described the species as *Neoapenesia makiharai*, which was reared from dead wood, they pointed out that “*morphological characteristics* [of its female] *closely resemble those of Apenesia*”. Sawada *et al.* (2014) confirmed the male-female association between of *Neoapenesia makiharai* because of the partial mitochondrial COI gene sequences is identical and the mating behavior was often observed. Alencar (chapter 1, this volume) delimited *Apenesia* cladistically and proposed *Neoapenesia* as synonymous junior to the genus.

Although the knowledge of morphological pattern of female is highly important to delimit *Apenesia*, species known only by females are hardly to be identified or distinguished from the females of other species. Thus proposing a new species based exclusively on females is a risky task. Females of *Apenesia* are very similar one to another and hardly separable, because there is little variation among the species. Because of that, it is tough to build a key for females. We tried to include a set diagnose features for each species known from females but we did not propose any synonym, even when they are quite similar, because they may be cryptical. Female body may be so specialized to live exclusively in a cryptical enviroment, such as wood gallery or tunnels, that different species are convergent morphologically. They are all apterous, have large head, badly developed eyes with few facets, ocelli absent, strong anterior legs, mesotibia spinose. The restricted range of variation of the body design of females is probably because this pattern somehow increases female fitness to survive in those cryptical enviroments. The convergence pattern can be seen as a result to pressure selection found in those kinds of similar adverse enviroments.

Since they live in cryptical enviroment, females are very rare in collections. That happens because Malaise trap has been the most commom method to collect Bethylidae (see Mugrabi *et al.* 2008; Azevedo *et al.* 2003; Noyes 1989), which intercept insects during their flight. Thus it seems hard to propose hypotheses based only on females applying the traditional methods for taxonomy.

Today, the female species delimitation needs to explore new frontiers such as biological experiments in field and/or laboratory experiments and molecular assessment. For the same reasons, the male-female association should be done carefully and may be supported by molecular analyzes or rearing data since morphological correspondance is non-existent.

Analyzes based on males of *Apenesia* are easier when compared with those of females because males present an extended range of variation. In fact, this is also found in other genera of Pristocerinae with males and females known as in *Acrepyris* Kieffer, *P1*, *Dissomphalus* Ashmead, *Parascleroderma* Kieffer, *Pristocera* Klug, and *Pseudisobrachium* Kieffer.

The main phenotypic variations in males of *Apenesia* occur in the following features: width of the head and the vertex shape of the head; presence of median clypeal tooth; length of pronotal disc; presence, length and shape of the notauli; shape of mesoscutum-mesoscutellar suture; length of metapectal-propodeal complex and its posterior margin; presence of median metaposnotal carina; texture of metaposnotum and the lateral of propodeum.

Most of males of *Apenesia* present the head larger than long, trapezoidal (Figs. 2A) or rectangular (Figs. 3A) because the vertex is straight or nearly straight such as *A.* #001; *A.* #002, *A.* #003, *A. sahyadrica*. On the other hand, *A.* #010 (Fig. 3B), *Apenesia laevigata* (Fig. 4F), and *A. leytensis* (Fig. 4G) have the head almost as large as long with rounded aspect and vertex short and strongly convex.

Many species of *Apenesia* present the clypeus with subtrapezoidal median lobe and a median tooth, for instance: *A.* #001 (Fig. 2A), *A.* #002 (Fig. 2B), *A.* #003 (Fig. 2C). Sometimes the median clypeal lobe has rounded apical margin such as described for *A. sahyadrica* in Azevedo & Waichert (2006) (Fig. 5B). In *Apenesia* #009 (Fig. 3A), the median clypeal tooth is larger than in other species. *Apenesia* #010 (Fig. 3B) and *A. laevigata* (Fig. 4F) are unique in lacking the median clypeal tooth.

In comparison to other Pristocerinae genera, the pronotum in males of *Apenesia* is short and similar to *Dissomphalus*. Although, among *Apenesia* species there is a wide range of variation in the length of pronotal disc, in *A.* #003 (Fig. 7C), *A.* #006 (Fig. 7F), *A.* #008 (Fig. 7H) the pronotum is long, whereas in *A.* #001 (Fig. 7A), *A.* #002 (Fig. 7B), *A.* #M5 (Fig. 7D) the pronotum is short.

Another remarkable structure that varies in males of *Apenesia* is the notauli, their orientation, length, shape and presence or absence is highly variable. When notauli is present, it may be complete as in *A. sahyadrica* (Fig. 9H) or incomplete posteriorly as in #009 (Fig. 7I). They also may be almost paralel as in *A. sahyadrica* (Fig. 9H) or convergent posteriorly as in *A. singularis* (Fig. 9I). The absence of notauli is reported to *A.* #003 (Fig. 7C), *A.* #007 (Fig. 7G), *A.* #010 (Fig. 8A), *A.* #019 (Fig. 9A), *A. leytensis* (Fig. 9E), *A. makiharai* (Fig. 9F). According to Terayama (1996), *Protisobrachium*, *Pseudisobrachium* and *Neoapenesia* (now synonymous of

*Apenesia*) constituted a monophyletic assemblage by having the notauli lacking or indistinct. However, *Protisobrachium* and *Pseudisobrachium* have species with or without notauli, as for instance, *Protisobrachium asianum* Terayama, 1995b and *Pseudisobrachium angulatum* Evans, 1964 with notauli, and *Protisobrachium gracile* Benoît, 1957 and *Pseudisobrachium laisum* Gobbi & Azevedo, 2010 without notauli. Beyond, Alencar (chapter 1, this volume) retrieved *Pseudisobrachium* as sister group of all other Pristocerinae.

The mesoscutum-scutelar sulcus also varies among males of *Apenesia*. Most species has the mesoscutum-scutelar sulcus weakly arched, narrow and deep as in A. #008 (Fig. 7H). However, some species present the mesoscutum-scutelar sulcus arched, wide and deep as in A. #011 (Fig. 8B).

The texture of metaposnotum helps to delimit the species easier than genitalia characters in *Apenesia*. The texture of metaposnotum in the males of varies from completely polished and shiny to strongly rugulose, imbricate or irregularly foveolate. In *Apenesia*, it is also remarkable the presence or absence of a complete median metaposnotal carina. This is not typical for Pristocerinae, which generally present the metaposnotum rugulose (Kawada *et al.* 2015). In macropterous forms, the metapectal-propodeal complex usually presents a distinguished texture on median surface, which is the metaposnotum (Lanes, pers. comm.). This median surface may be coincident to the extension of mesophragma where the flight muscles are attached. As the texture in metaposnotum appears not having a physiological function, it is probable the wide extended variation found in males of *Apenesia* is randomly selected by genetic drift.

According to Alencar (chapter 1, this volume), the hypopygium is helpful in delimiting pristocerine genera. In *Apenesia*, the hypopygeal plate is usually short and has with three stalks. Terayama (1995a) considered the median stalk long in *Neoapenesia* but Sawada *et al.* (2014) pointed out Terayama missinterpreted an adjacent sclerite of hypopygium as the median stalk. Here we observed that the hypopygium has a membrane, which is attached to it. Alencar (chapter 1, this volume) also observed this membrane occurring in several ways in all Pristocerinae genera. This membrane is hardly detachable from the hypopygium because they are completely fused at apical margin in *Apenesia*. In *Apenesia*, this membrane has a long stalk, which we considered as a part of the hypopygium because it fixes at the genital ring as any other median stalk in Bethyridae. Despite the long median stalk always present, the apical margin and the length of hypopygeal plate vary among *Apenesia* species. The hypopygeal plate may be long as in A. *sahyadrica* (Fig.14.K) or very short as in A. #012 (Fig. 13.L) and A. #017 (Fig. 14.B). In *Apenesia* species, it is common the hypopygium with apical margin straight as in A. #001 (Fig. 13.A), slightly concave as in A. #004 (Fig. 13.D) or strongly concave such as in A. #013 (Fig. 13.M). However, A. *leytensis* (Fig. 14.H) presents the apical margin of hypopygium convex.

In the majority Pristocerinae, the genitalia are completely different for each species and it provide the mainly diagnostic features to identify species. For instance, in *Dissomphalus* it is possible to rescue the species identity only by the genitalia characters (see for instance Redighieri & Azevedo 2006, Mugrabi & Azevedo 2013). However although the male genitalia of *Apenesia*, present a remarkable set of characters, which help to delimit the genus identity, they are quite similar among the species. The main diagnostic features in the male genitalia are the paramere narrow and long with surface densely pilose, the cuspis projected dorsad, the presence of an apical projection on basiparameral apex in dorsal view, the aedeagus with ventral apical lobe with warts and slender dorsal cover.

The paramere in *Apenesia* is narrow when compared to the other Pristocerinae genera. It is usually narrow, straight and pilose (see Figs. 1.E-F) or very narrow as in *A. laevigata* (Figs. 22.A-B) and *A. #010* (Figs. 18.A-B). When the paramere is very narrow as in *A. laevigata* it is always straight and pilose, differing from the very narrow, curved and not densely pilose paramere which is diagnostic for P7 (Alencar chapter 1, this volume). The paramere long and setose probably is sensory and interprets information provided by the subapical sternum of the female, according to Gordh (1990).

The basiparamere of *Apenesia* probably plays an important role during the copulation. It is very developed and subdivided into different plates in ventral part (Fig. 15.D). This was first attempted by Alencar (chapter 1, this volume) but it is noted in illustrations of male genitalia such as in *A. laevigata* (Evans 1958, Fig. 8), *A. singularis* (Lanes & Azevedo 2004, Fig. 10), *A. sahyadrica* (Azevedo & Waichert 2006, Fig. 3), *A. perlonga* (Corrêa & Azevedo 2006, Fig. 9) and *A. makiharai* (Sawada *et al.* 2014, Fig. 6). Those plates may allow twisting, opening and closing movements that could help fitting male and female genitalia during the copulation. The basivolsella is clearly delimited and articulated to a small ventral portion and a latero-dorsal portion of basiparamere.

The volsellar process in *Apenesia* is also peculiar to this genus. The digitus is always short, whereas the cuspis is long (Fig. 1E), usually articulate on basivolsellar base, its apex is developed dorsad with projections, callus and setae. We also observed that the inner margin of the base of digitus is an important structure to identify *Apenesia* species. It can be much projected inward with deep concave surface (Fig. 15.G) or little projected inward without differentiation on its surface (Fig. 16.G). It can also be straight (Fig. 18.D), slightly concave (Fig. 17.D) or convex, resembling an elbow (Fig. 17.A). This inner margin of digitus is usually densely pilose.

The cuspis developed dorsad was first observed by Sawada *et al.* (2014) for *A. makiharai*. According to Evans (1969b), the volsellae grasped the edge of the apical sternite of females like a pair of small pincers, being of much importance during copulation. In *Apenesia*, the exclusive



cuspid developed with dorsad projections is remarkable observed in lateral view (e.g. Figs. 15. C, F, I). When the cuspid is observed only in ventral view, its projections and callus seem to be separated structures as cuspid divided into dorsal and ventral arms, just as it is diagnostic for *Cleistopyris*. The cuspid divided into dorsal and ventral arm was considered synapomorphic for *Apenesia* by Terayama (1996). However, he used *Apenesia* sensu Evans (1963) conception, which included *Cleistopyris* species. Thus he might misinterpreted the cuspid of *P3* species, which were analyzed under *Apenesia* concept. Alencar (chapter 1, this volume) pointed out that the cuspid with ventral arm is present in *P1*, *P4*, *P6* and *P5*, whereas in *Apenesia* it is developed dorsad. The cuspid developed dorsad is the main variable feature in genitalia of *Apenesia*. Whenever similar body and general genitalia patterns were found such as in *A.* #020 and *A.* #021, the cuspid shape in lateral view helped to delimit the species (see Figs. 21.F, I). The articulate base of cuspid in *Apenesia* may be related to the need of movement to grasp female sternite during the copulation. Since the digitus is short and there is an apical projection on basiparamere apex in dorsal view, probably the ventral callus of cuspid grasps the sternite apex of females either with digitus or the apical projection on basiparamere dorsally.

The apical projection on basiparameral apex in dorsal view is an exclusive feature of *Apenesia*. Similar projection is also found in *P6* and *P5*. However, in *Apenesia* this projection has a dorsal surface continuous to basiparamere near the genital ring, whereas in *P6* and *P5* the projection is only an extension of parameral apical margin (see Figs.1.F-G). The texture of this projection is also different. The lateral and ventral surfaces of basiparamere in *P6* and *P5*, including the projection, are sclerotized, whereas in *Apenesia* the apical projection and part of basiparamere dorsal area are membranous. This feature is realized on optical microscope. Actually, it was illustrated by Sawada *et al.* (2014, Fig. 6), when they traced a line in basiparamere of *A. makiharai*. However, under SEM analyzes the dorsal surface of basiparamere is a soft imbricate membranous with quitinous filaments as reported already by Alencar (chapter 1, Fig. 9.G, this volume).

The aedeagus in *Apenesia* are quite similar in its entire species. It is wide and has an apex narrower than its base. There are two pairs of apical lobes, the ventral pair is elliptical with remarkable warts on its surface (for exemple see Figs. 15.A, D, G) and a dorsal pair that covers the ventral one. The ventral pair is usually large and developed (as in Fig. 15.A) but it can be very small as in *A. laevigata* (Fig.22.A) and *A.* #010 (Fig. 18.A). The dorsal pair can be slender (Fig. 20.H) or wide (Fig. 15.B). A ventral projection in the aedeagus below the ventral pair of lobe is also observed in many species such as #001 (Fig. 15.A), #002 (Fig. 15.D), #003 (Fig.15.G), #006 (Fig. 16.G), #007 (Fig. 17.A), and #008 (Fig. 17.D). It is hard to observe this ventral projection if the genitalia is not properly diafanized.

Another feature recorded to *Apenesia* is the dorsal cover of aedeagus. It is also common in *Foenobethylus* Kieffer, *Parascleroderma*, *P3* and *Pseudisobrachium*. However this cover is always narrow, long and with acute apex in *Apenesia*, *P3* and *Pseudisobrachium*, whereas is very wide, long and with acute apex in *Foenobethylus* (Várkonyi & Polaszek 2007, Figs. 20; 23; 26 and 29) and very wide and truncate in *Parascleroderma*.

Phoretic copulation was not reported to *Apenesia* sensu Alencar (chapter 1, this volume). According to the hypotheses of Sawada *et al.* (2014), the phoretic copulation may not occur in *Apenesia* because females are cryptical and larger than their conespecific males, which would be difficult to sustain the flight. In *Pristocerinae*, phoretic copulation is commonly reported for *Dissomphalus* (Azevedo 1999, Alencar & Azevedo 2008, Azevedo *et al.* 2016) but it also recorded for *P1* (Evans 1969b; Ramos *et al.* 2010), *P4* (Corrêa & Azevedo 2006), *P6* (Gordh 1990). These genera present a wide range of variation in the genitalia structures. In these cases, the male genitalia should be specific to attached in female genitalia and support it during the flight. But interestingly the genitalia of *Apenesia* is little variable when we compare the amount of variation found for the head, mesosoma and hypopygium.

Most *Apenesia* males have the body robust and clypeus with a median tooth prominent, which may lead misidentification of them as *Dissomphalus*. Indeed, some males of *Apenesia* resemble the general ground plan of *Dissomphalus*, so that they are sometimes sorted out among as those *Dissomphalus* big with median lobe of clypeus with long median tooth, without lateral projections or teeth (similar to *D. rettenmeyeri* Evans, 1964 and *D. bispinulatus* Evans, 1969b) and without tergal process. Although the clypeus may be similar, the metasoma of *Apenesia* males are thin in profile view, whereas in *Dissomphalus* it is thick. Despite that, genitalia of both genera are completely different: in *Apenesia*, the paramere is densely pilose, narrow and almost straight; the aedeagus is simple with dorsal cover; the basivolsella is divided; the cuspis is developed dorsad, its base is articulate and there is a lateral remaining basal ring, whereas in *Dissomphalus* the paramere is glabrous, wide and curved mesad; the aedeagus is divided without dorsal cover; the basivolsella is completely fused; the cuspis is not developed dorsad, its base is fixed and there is not any remaining basal ring. The clypeus of male *Apenesia* can be also confused to *P10*. Although in *Apenesia* the clypeus has a median lobe easily recognized and trapezoidal, in *P10* the median clypeal lobe is almost indistinguishable. Both taxa also differ by having the distinct features in the hypopygium and genitalia: in *Apenesia* the hypopygium has the apical margin straight or concave and the aedeagus has ventral lobe with warts, whereas in *P10* the hypopygium has the apical margin strongly concave medially and the aedeagus has ventral lobe with long setae.

Males of *Apenesia* also resemble some alate Formicidae because of mesoscutum large and high in profile and with thin metasoma also seen in lateral view. However, *Apenesia* is a bethylid

flat wasp because the head is prognathous; the antennae are not geniculate; the wings have Chrysoidea pattern of veins and absence of nodular process in the metasoma.

*Apenesia* sensu Alencar (chapter 1, this volume) is a wide spread genus. Many species are restricted to single or few sites as *A.* #002, *A.* #003, *A.* #005, *A.* #008, *A.* #009. However, *A. leytensis*, *A.* #004, #, *A. singularis* have a more wide range of distribution. Despite the genus is recorded from all zoogeographic regions (except in Antarctica), *Apenesia* is not abundantly collected by the regular field methods especially Malaise trap. Although males fly as most bethylid, the few biological data we have reported for males also keep near to female gallery and tunnels to copulate. Sawada *et al.* (2014) collected several males and females from dead wood rearing. It may indicate the collection methods to Bethylidae probably undersampled *Apenesia*. To gether all material studied in this revision, it got many year of visiting and sorting material in several museums in the world. Our effort represents almost all *Apenesia* material we found in several years researching Bethylidae.

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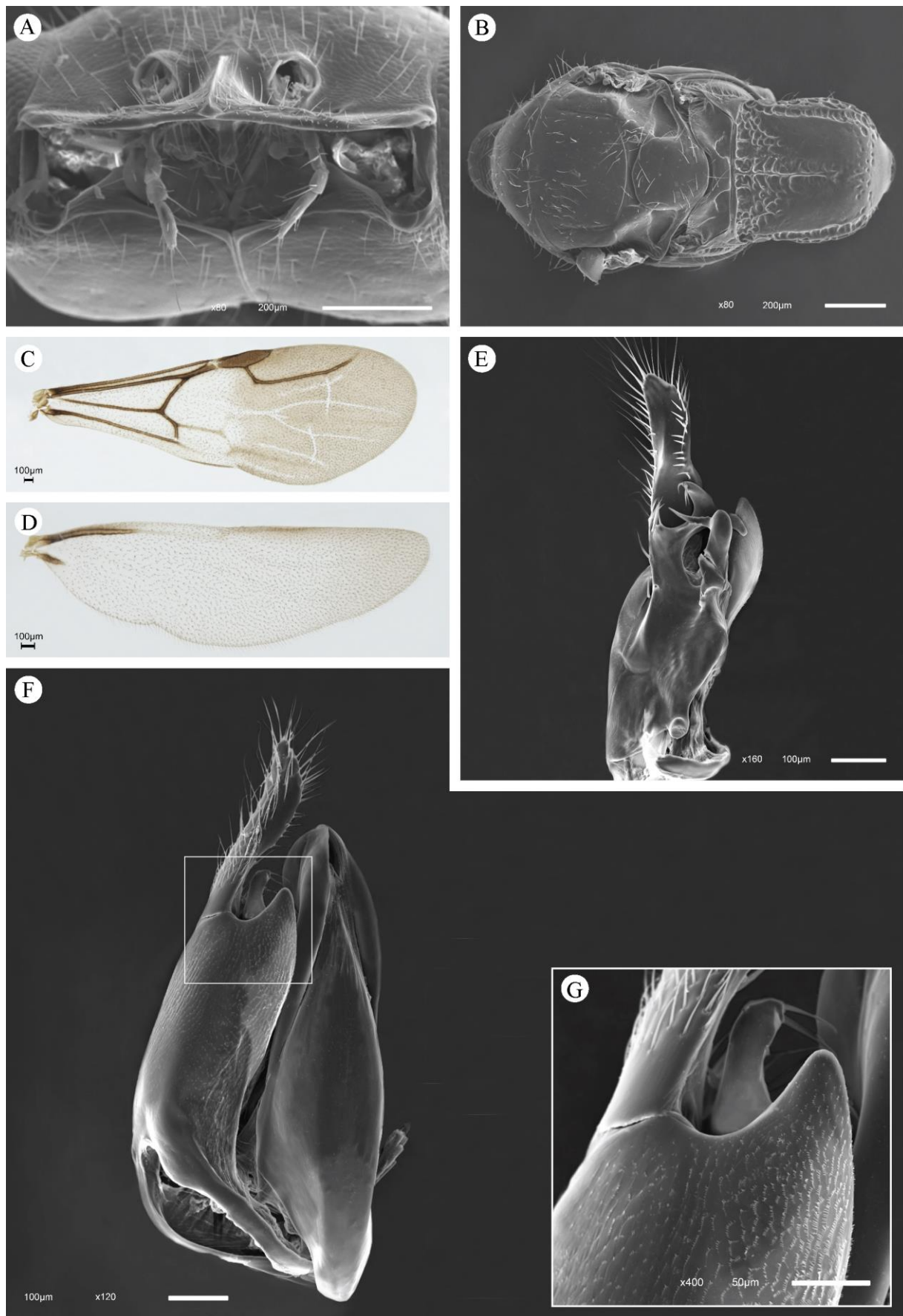
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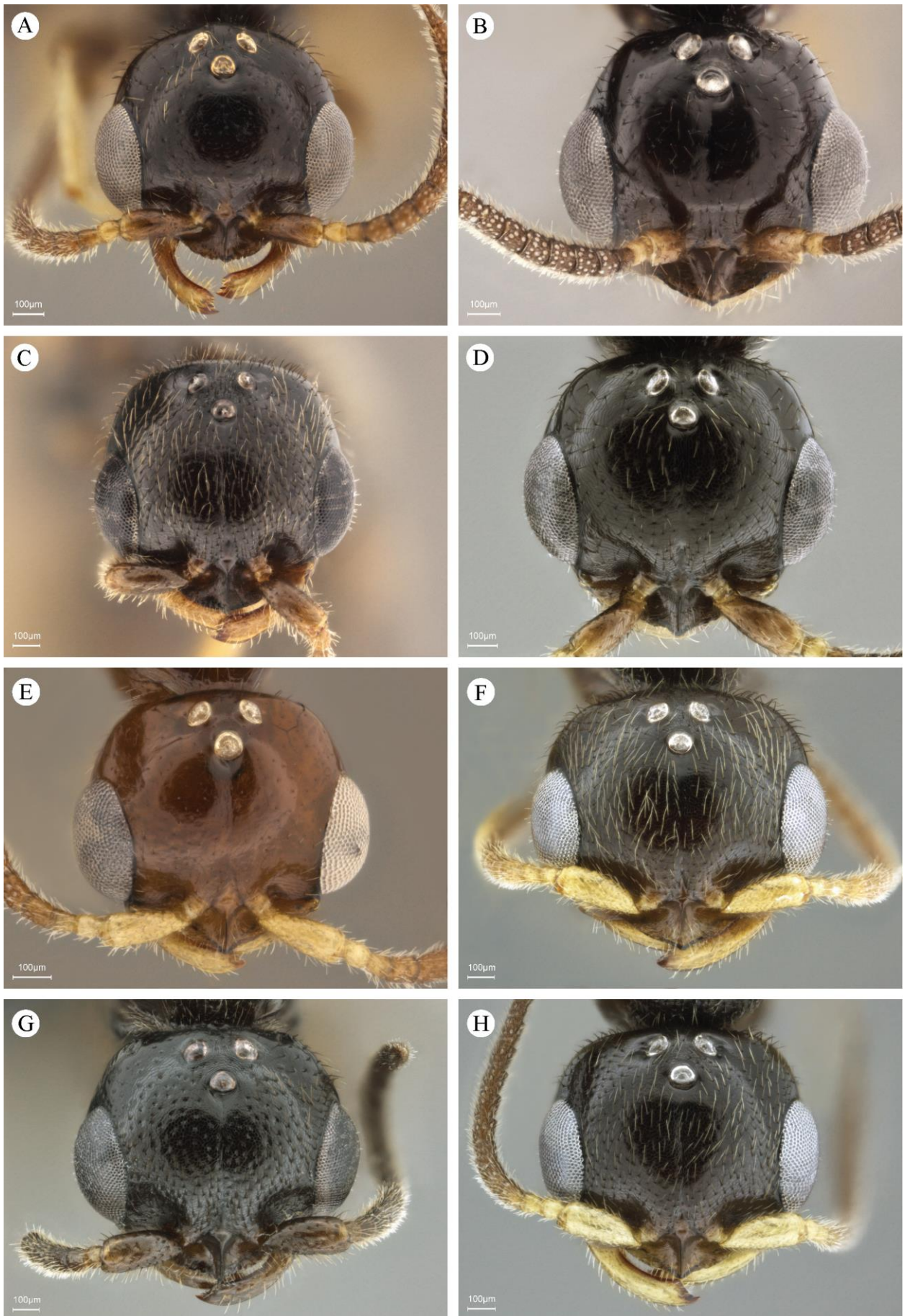
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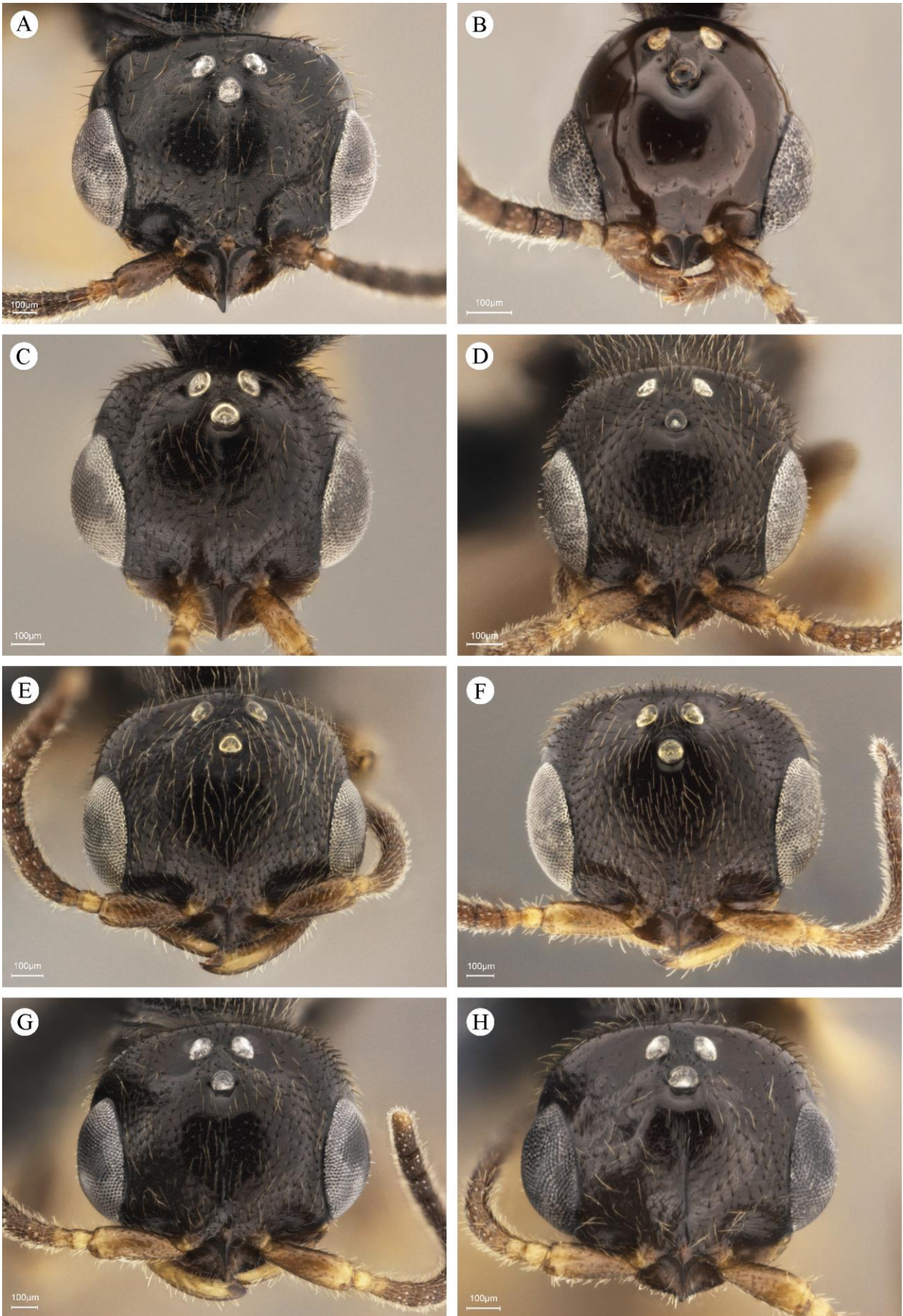


**Figure 1.** General characteristics of *Apenesia*. **A.** Palpi; **B.** Mesosoma, dorsal view, **C.** Forewing; **D.** Hindwing; **E-G.** Genitalia: **E.** Basivolsella, internal view; **F.** Genitalia, dorsal view; **G.** Detail at higher magnifications of apical projection on basiparamere apex, dorsal view.



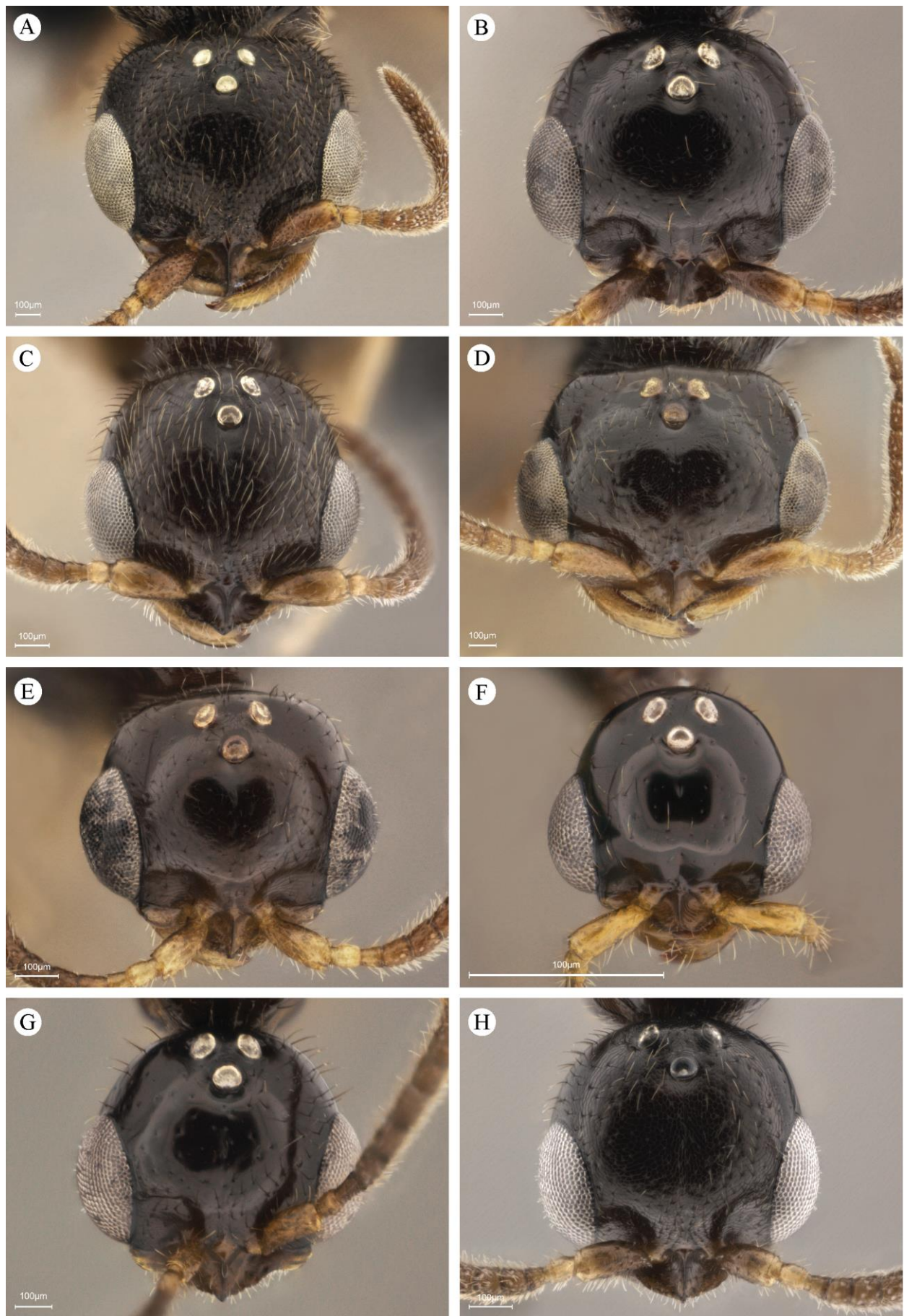
**Figure 2.** Head. **A.** *Apenesia* #001; **B.** *Apenesia* #002; **C.** *Apenesia* #003; **D.** *Apenesia* #004; **E.** *Apenesia* #005, **F.** *Apenesia* #006; **G.** *Apenesia* #007; **H.** *Apenesia* #008.





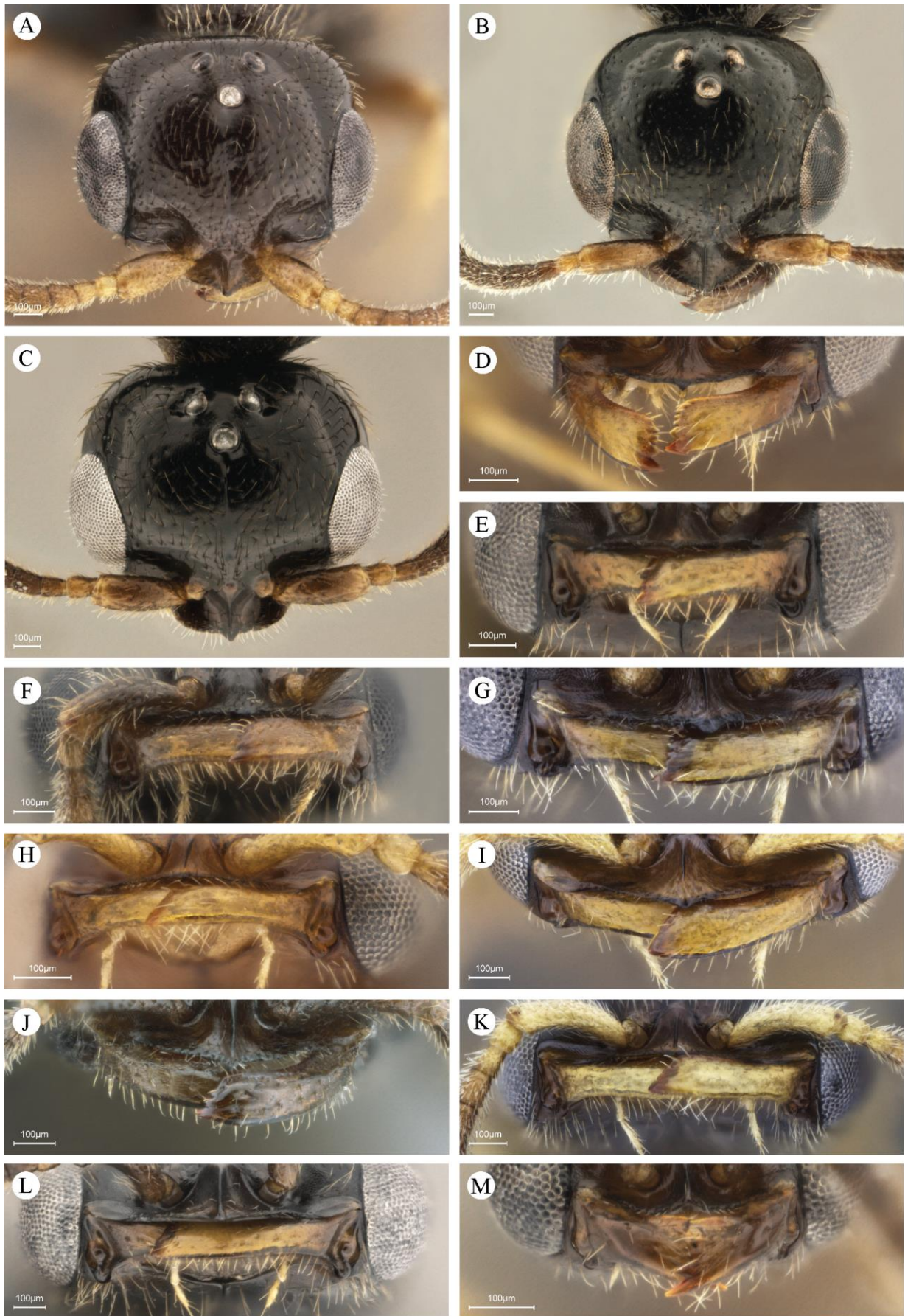
**Figure 3.** Head. **A.** *Apenesia* #009; **B.** *Apenesia* #010; **C.** *Apenesia* #011; **D.** *Apenesia* #012; **E.** *Apenesia* #013, **F.** *Apenesia* #014; **G.** *Apenesia* #015; **H.** *Apenesia* #016.





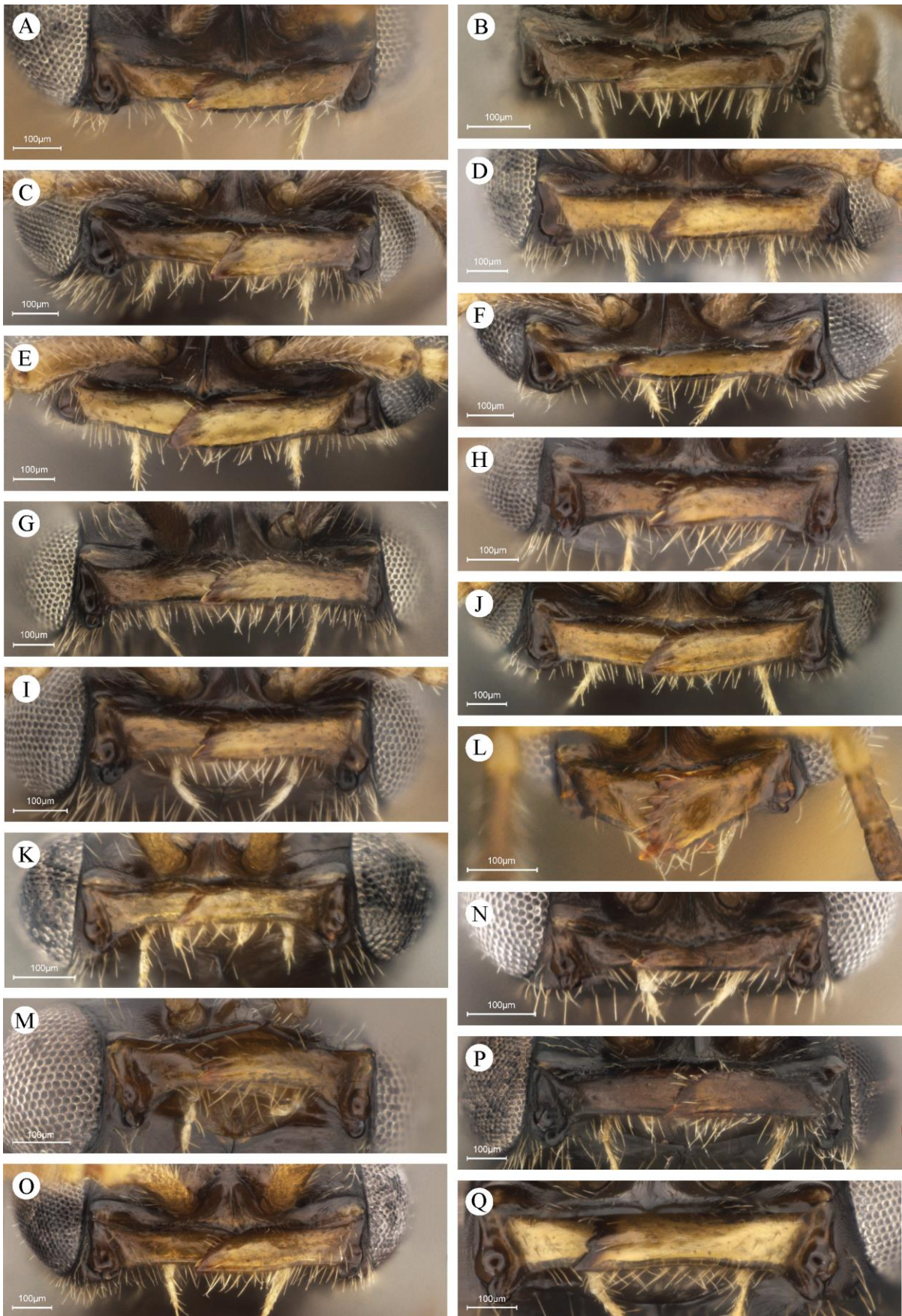
**Figure 4.** Head. **A.** *Apenesia* #017; **B.** *Apenesia* #018; **C.** *Apenesia* #019; **D.** *Apenesia* #020; **E.** *Apenesia* #021, **F.** *Apenesia laevigata*; **G.** *Apenesia leytenensis*; **H.** *Apenesia makihari*.





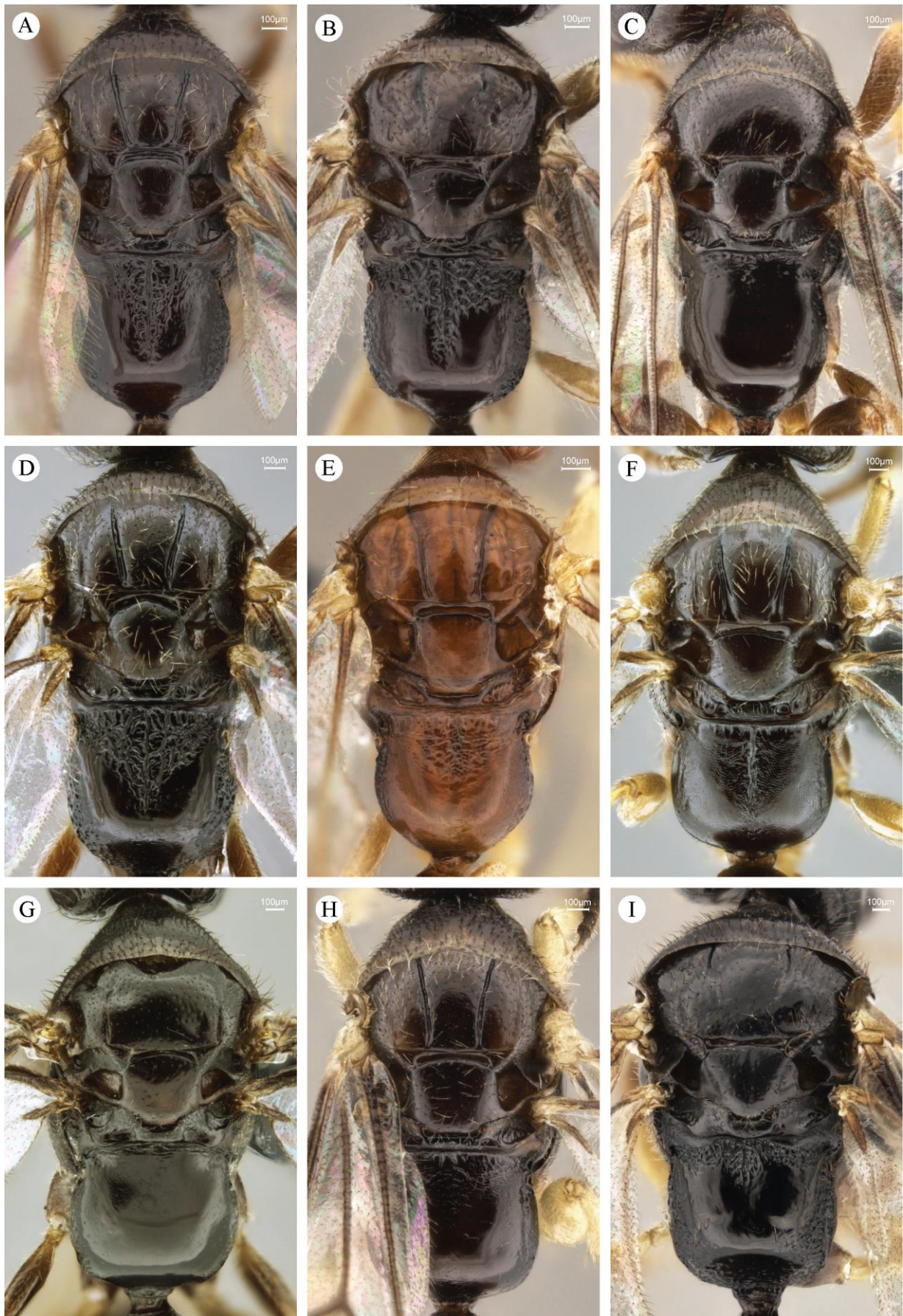
**Figure 5.** Head. **A.** *Apenesia perlonga*; **B.** *Apenesia sahyadrica*; **C.** *Apenesia singularis*. Mandible. **D.** *Apenesia* #001; **E.** *Apenesia* #002, **F.** *Apenesia* #003; **G.** *Apenesia* #004; **H.** *Apenesia* #005; **I.** *Apenesia* #006; **J.** *Apenesia* #007, **K.** *Apenesia* #008; **L.** *Apenesia* #009; **M.** *Apenesia* #010.





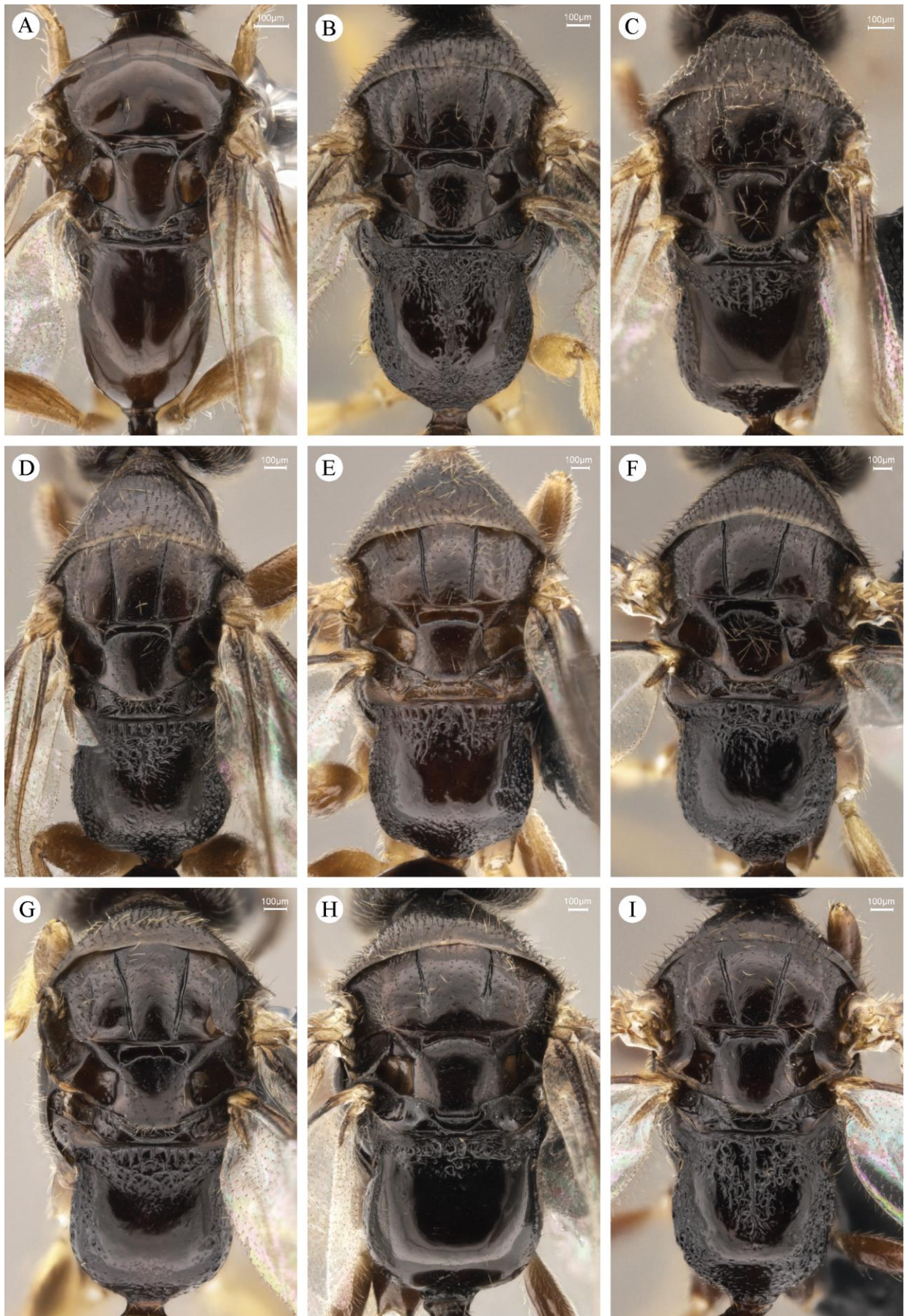
**Figure 6.** Mandible. **A.** *Apenesia* #011; **B.** *Apenesia* #012; **C.** *Apenesia* #013; **D.** *Apenesia* #014; **E.** *Apenesia* #015, **F.** *Apenesia* #016; **G.** *Apenesia* #017; **H.** *Apenesia* #018; **I.** *Apenesia* #019; **J.** *Apenesia* #020, **K.** *Apenesia* #021; **L.** *Apenesia laevigata*; **M.** *Apenesia leytenensis*; **N.** *Apenesia makihari*; **O.** *Apenesia perlonga*; **P.** *Apenesia sahyadrica*; **Q.** *Apenesia singularis*.





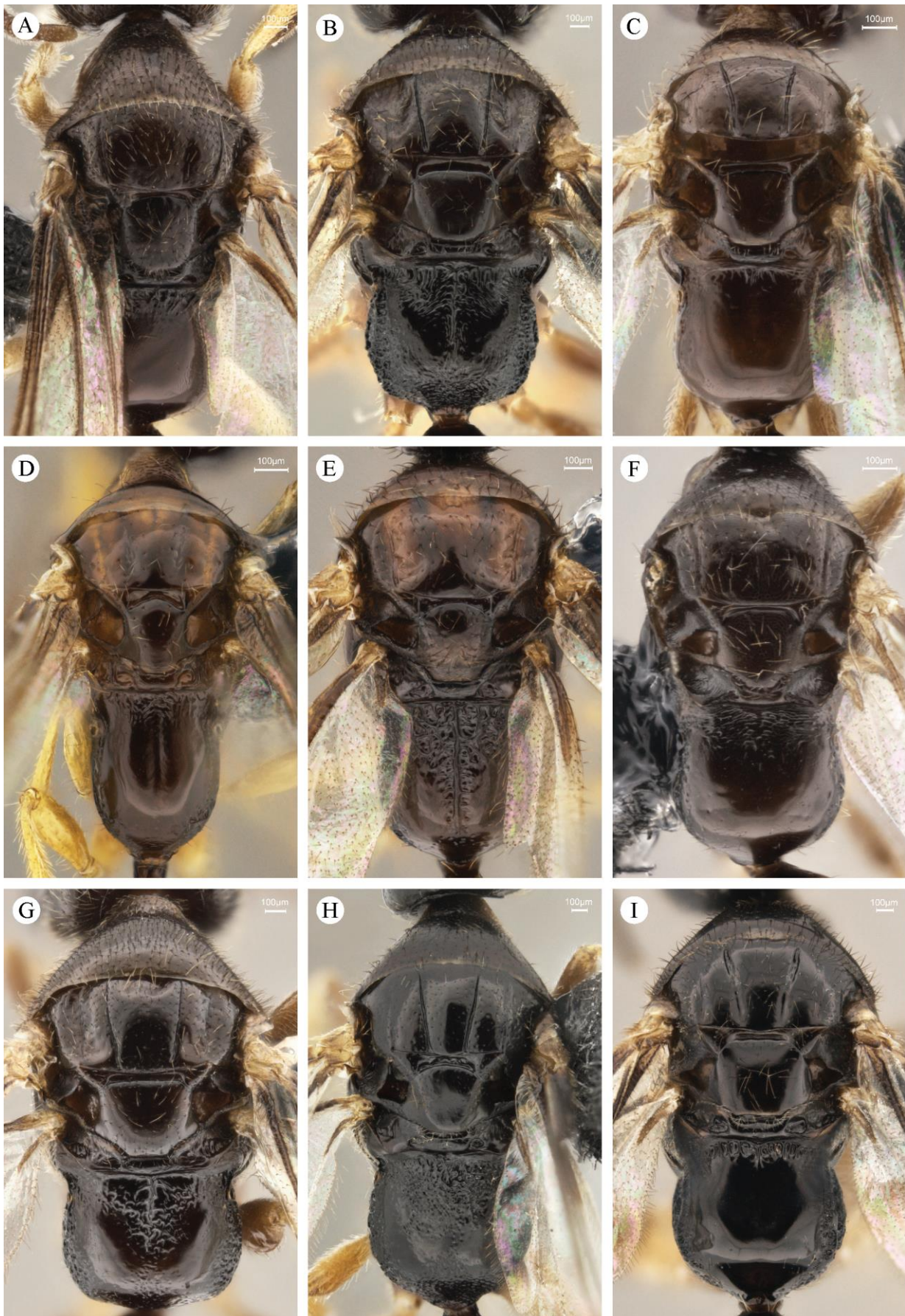
**Figure 7.** Dorsal mesosoma. **A.** *Apenesia* #001; **B.** *Apenesia* #002; **C.** *Apenesia* #003; **D.** *Apenesia* #004; **E.** *Apenesia* #005, **F.** *Apenesia* #006; **G.** *Apenesia* #007; **H.** *Apenesia* #008; **I.** *Apenesia* #009.





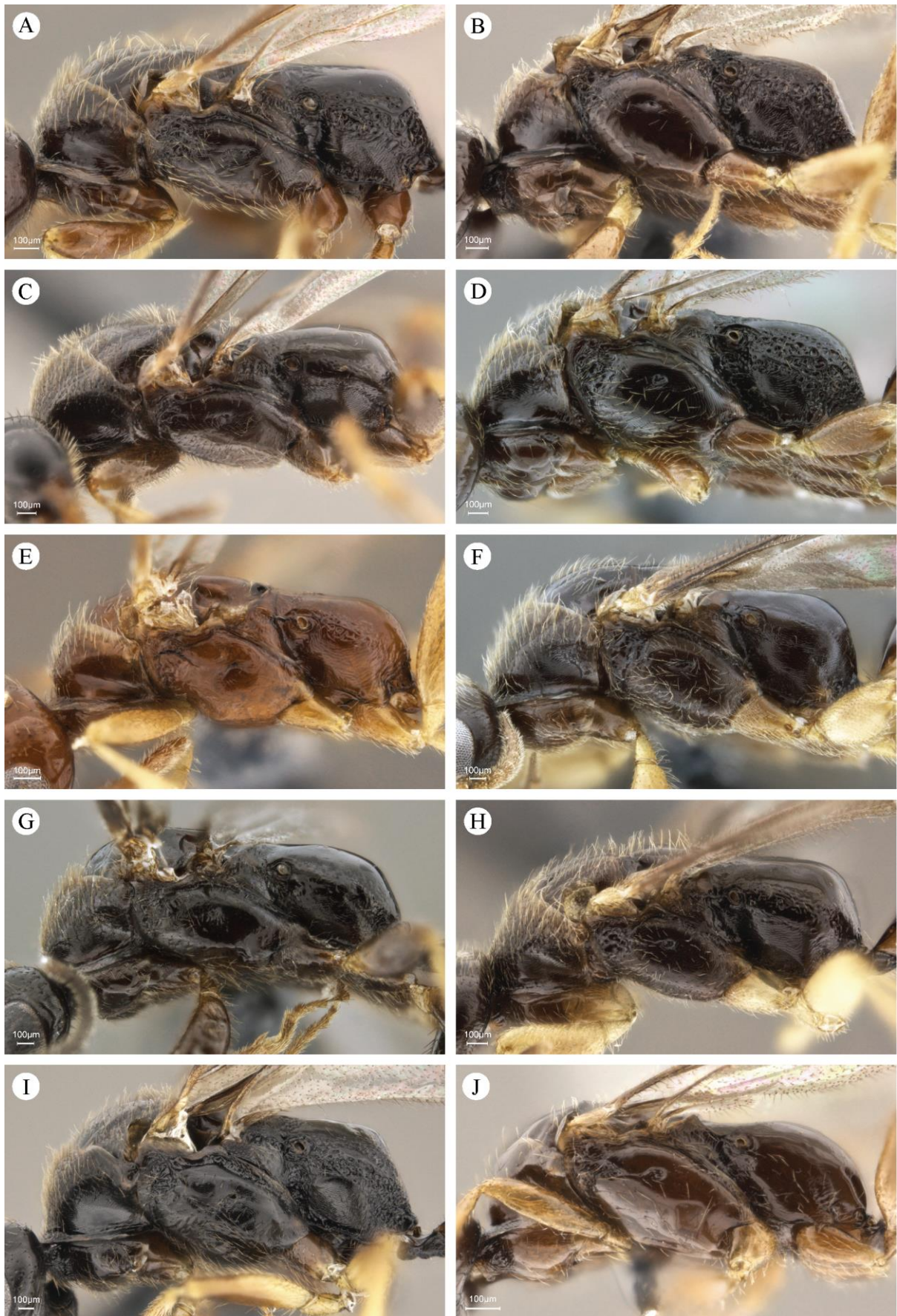
**Figure 8.** Dorsal mesosoma. **A.** *Apenesia* #010; **B.** *Apenesia* #011; **C.** *Apenesia* #012; **D.** *Apenesia* #013; **E.** *Apenesia* #014, **F.** *Apenesia* #015; **G.** *Apenesia* #016; **H.** *Apenesia* #017; **I.** *Apenesia* #018.





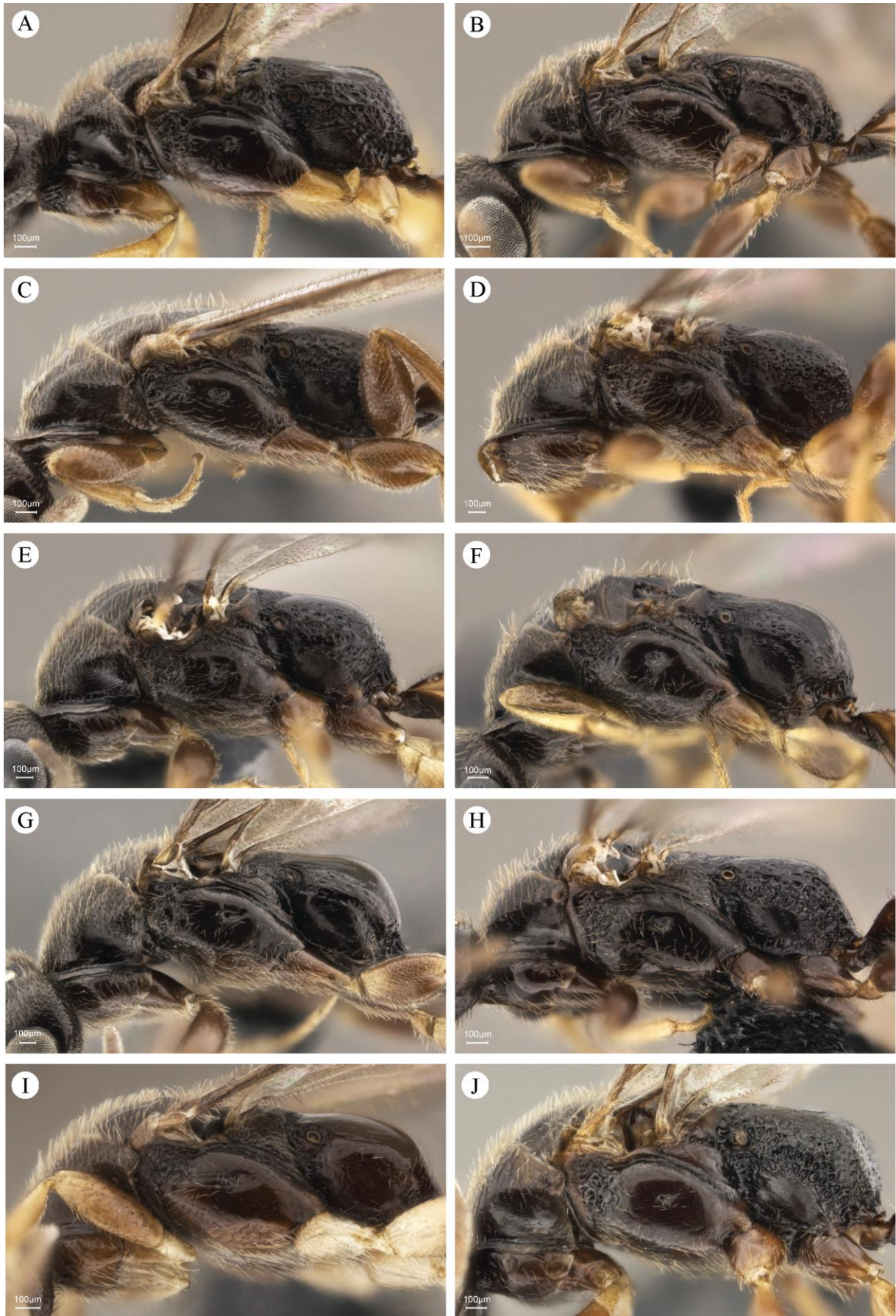
**Figure 9.** Dorsal mesosoma. **A.** *Apenesia* #019; **B.** *Apenesia* #020; **C.** *Apenesia* #021; **D.** *Apenesia laevigata*; **E.** *Apenesia leytensis*, **F.** *Apenesia makihari*; **G.** *Apenesia perlonga*; **H.** *Apenesia sahyadrica*; **I.** *Apenesia singularis*.





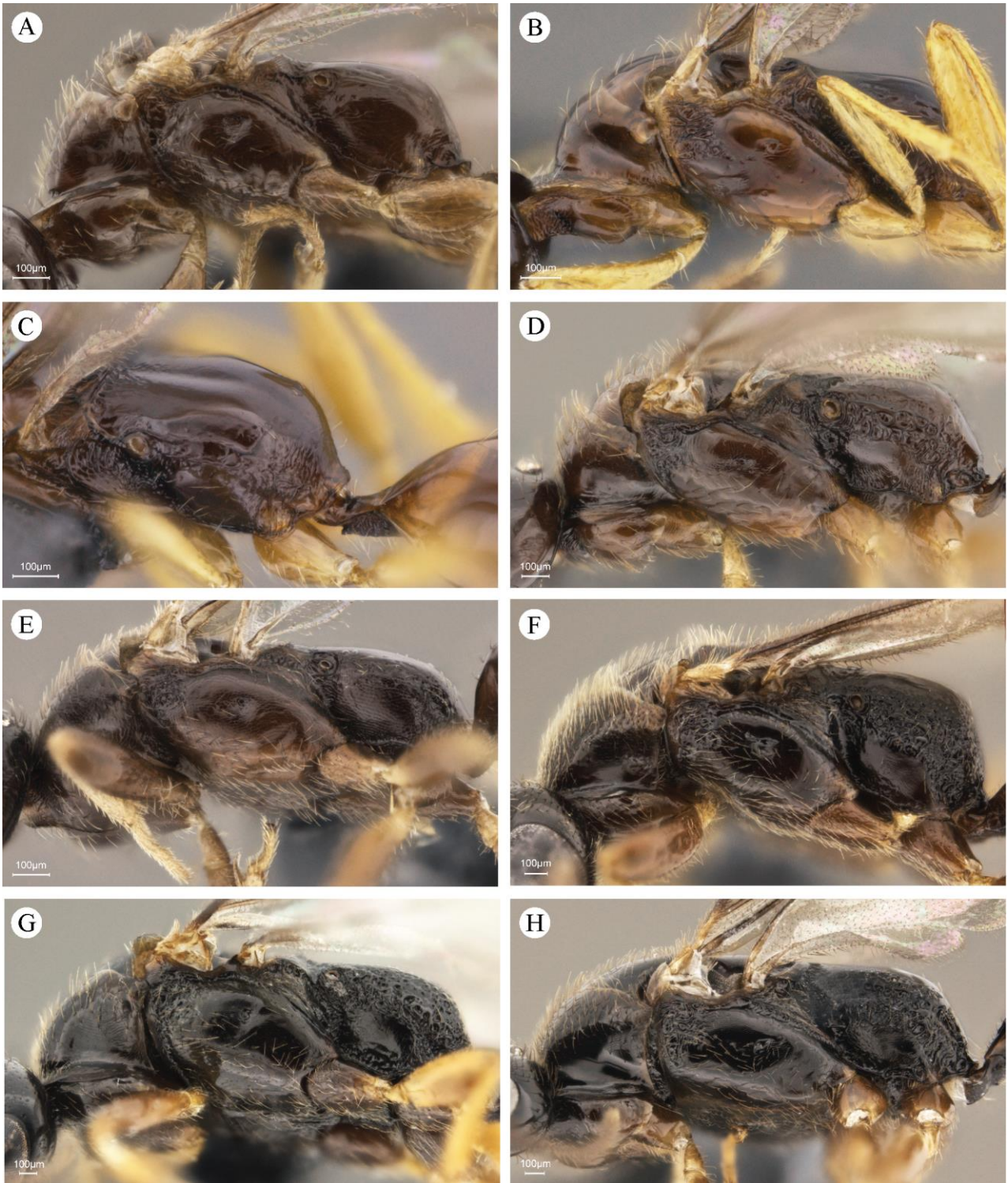
**Figure 10.** Lateral mesosoma. **A.** *Apenesia* #001; **B.** *Apenesia* #002; **C.** *Apenesia* #003; **D.** *Apenesia* #004; **E.** *Apenesia* #005, **F.** *Apenesia* #006; **G.** *Apenesia* #007; **H.** *Apenesia* #008; **I.** *Apenesia* #009; **J.** *Apenesia* #010.



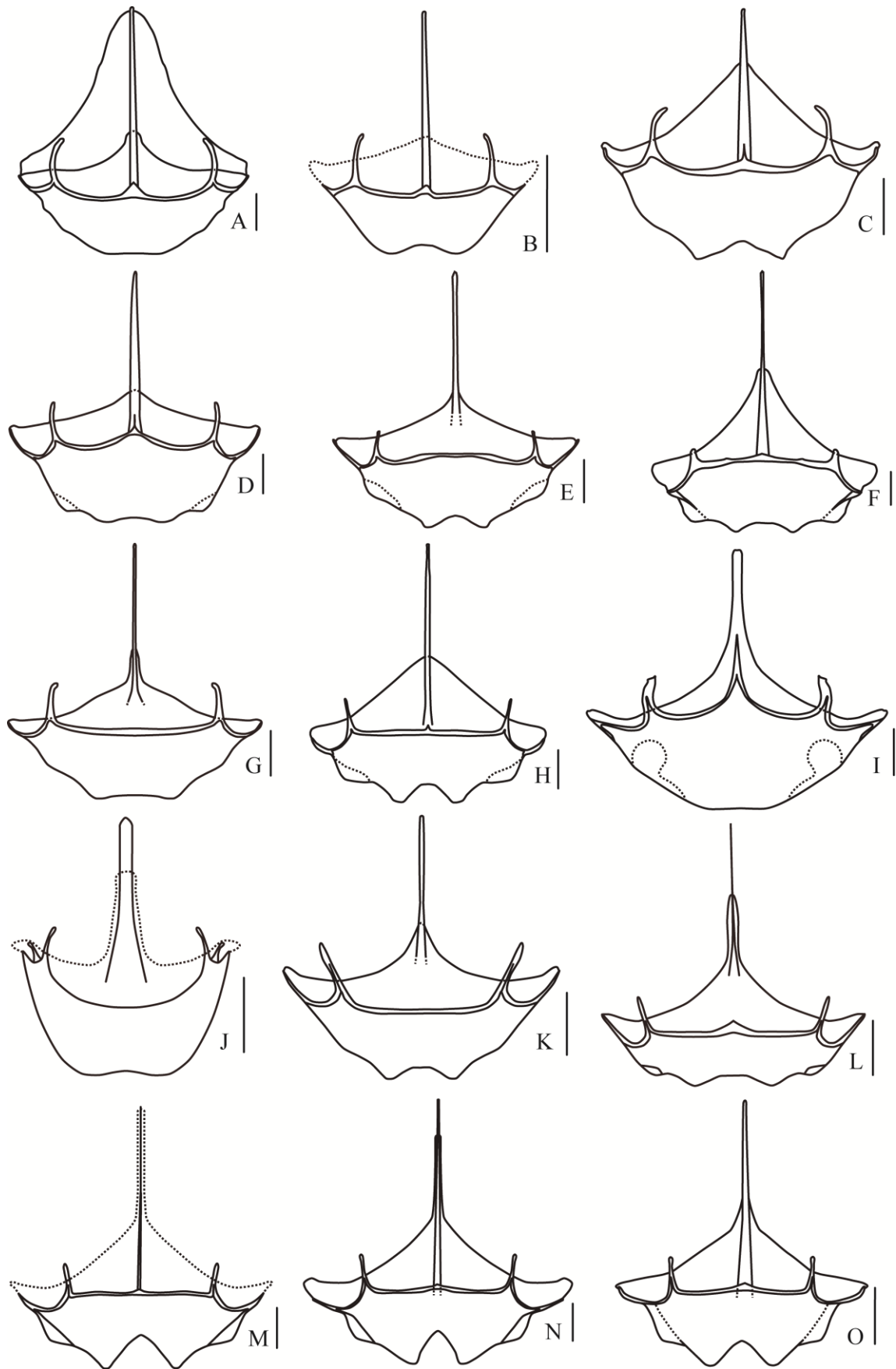


**Figure 11.** Lateral mesosoma. **A.** *Apenesia* #011; **B.** *Apenesia* #012; **C.** *Apenesia* #013; **D.** *Apenesia* #014, **E.** *Apenesia* #015; **F.** *Apenesia* #016; **G.** *Apenesia* #017; **H.** *Apenesia* #018; **I.** *Apenesia* #019; **J.** *Apenesia* #020.

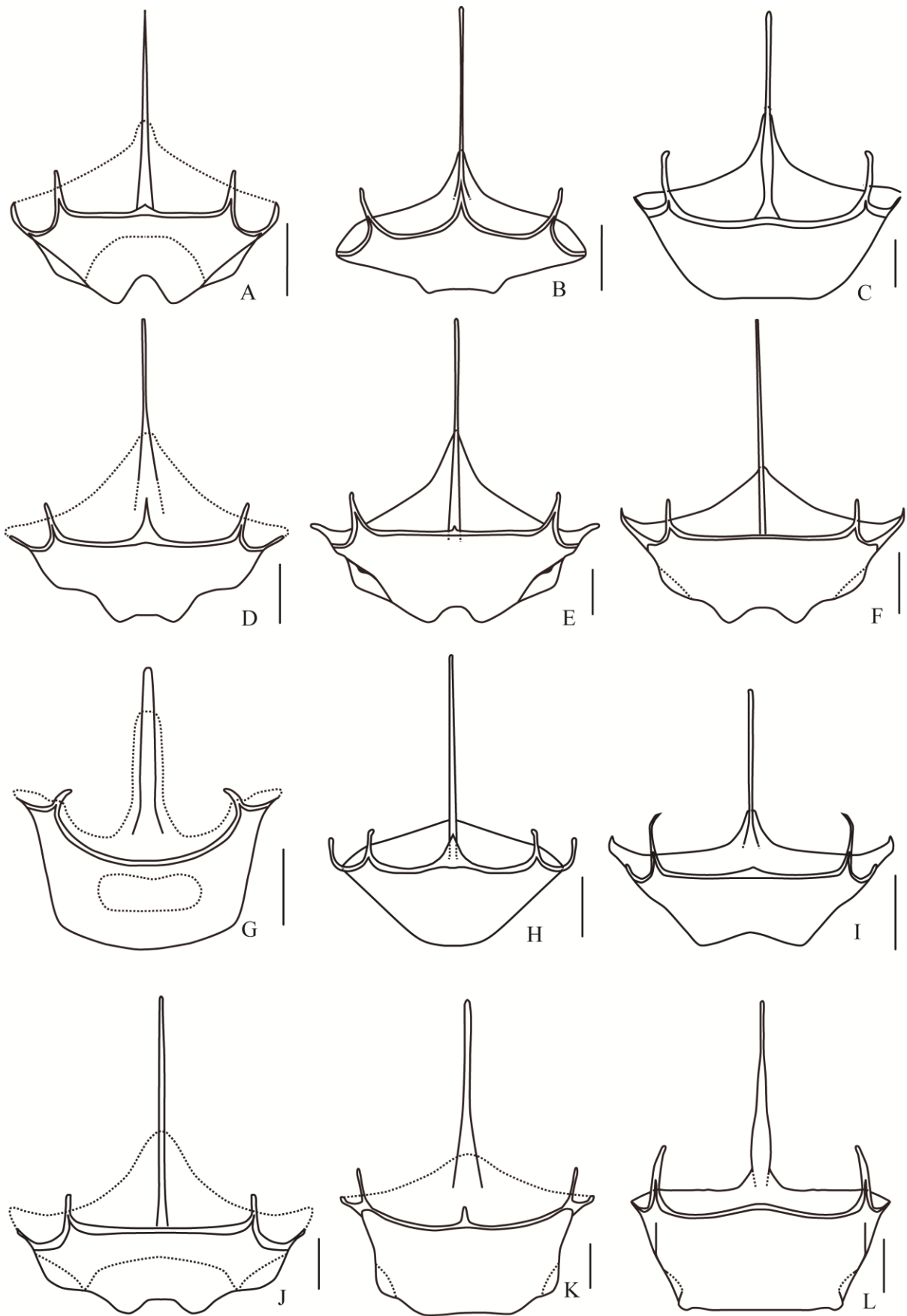




**Figure 12.** Lateral mesosoma. **A.** *Apenesia* #021; **B.** *Apenesia laevigata*; **C.** *Apenesia leytenis*, **D.** *Apenesia makihari*; **E.** *Apenesia perlonga*; **F.** *Apenesia sahyadrica*; **G.** *Apenesia singularis*.

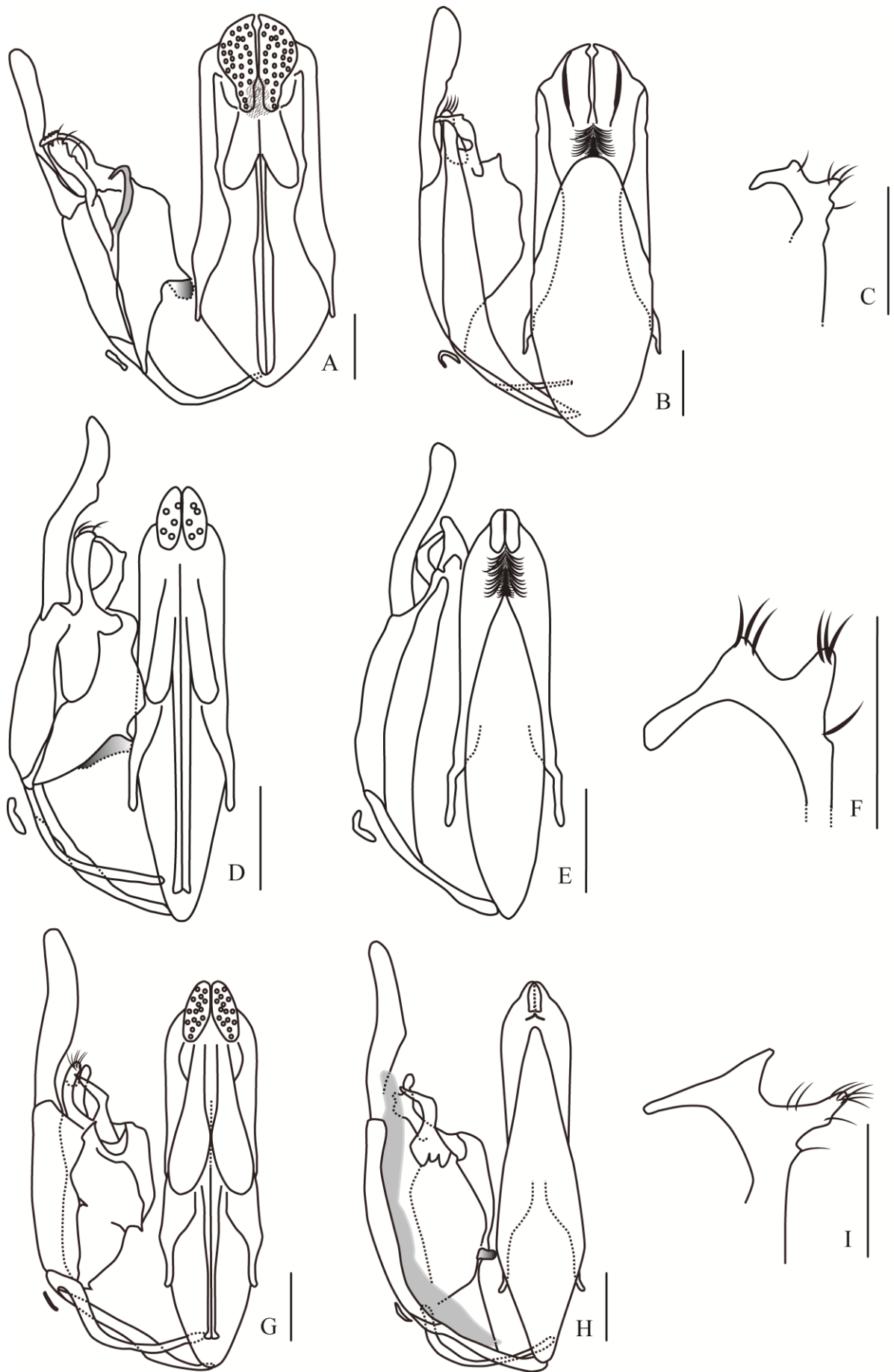


**Figure 13.** Hypopygium. **A.** *Apenesia* #001; **B.** *Apenesia* #002; **C.** *Apenesia* #003; **D.** *Apenesia* #004; **E.** *Apenesia* #005; **F.** *Apenesia* #006; **G.** *Apenesia* #007; **H.** *Apenesia* #008; **I.** *Apenesia* #009; **J.** *Apenesia* #010; **K.** *Apenesia* #011; **L.** *Apenesia* #012; **M.** *Apenesia* #013; **N.** *Apenesia* #014; **O.** *Apenesia* #015. (Scale bar 125 $\mu$ m)

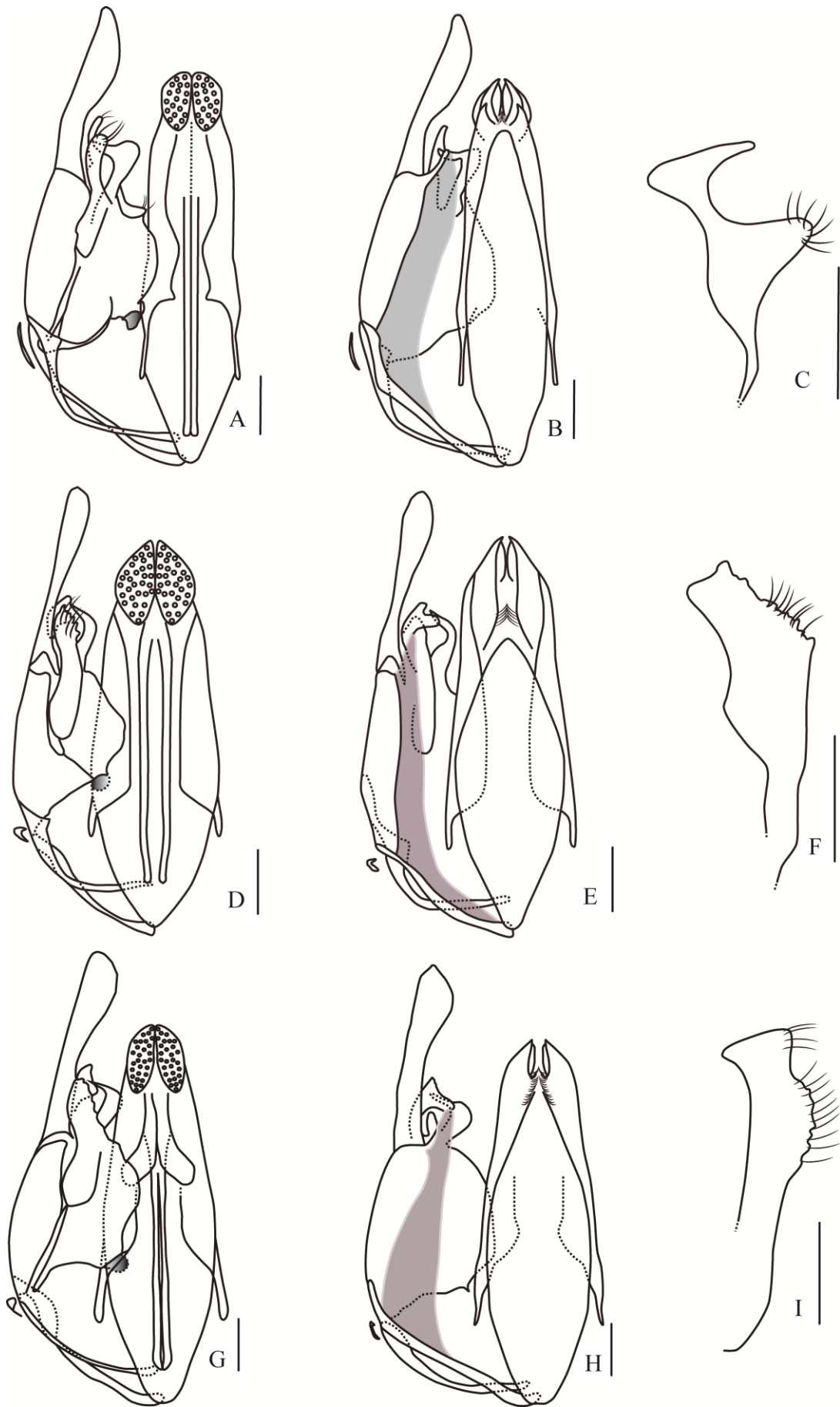


**Figure 14.** Hypopygium. **A.** *Apenesia* #016; **B.** *Apenesia* #017; **C.** *Apenesia* #018; **D.** *Apenesia* #019; **E.** *Apenesia* #020; **F.** *Apenesia* #021; **G.** *Apenesia laevigata*; **H.** *Apenesia leytensis*; **I.** *Apenesia makihari*; **J.** *Apenesia perlonga*; **K.** *Apenesia sahyadrica*; **L.** *Apenesia singularis*. (Scale bar 125 $\mu$ m)



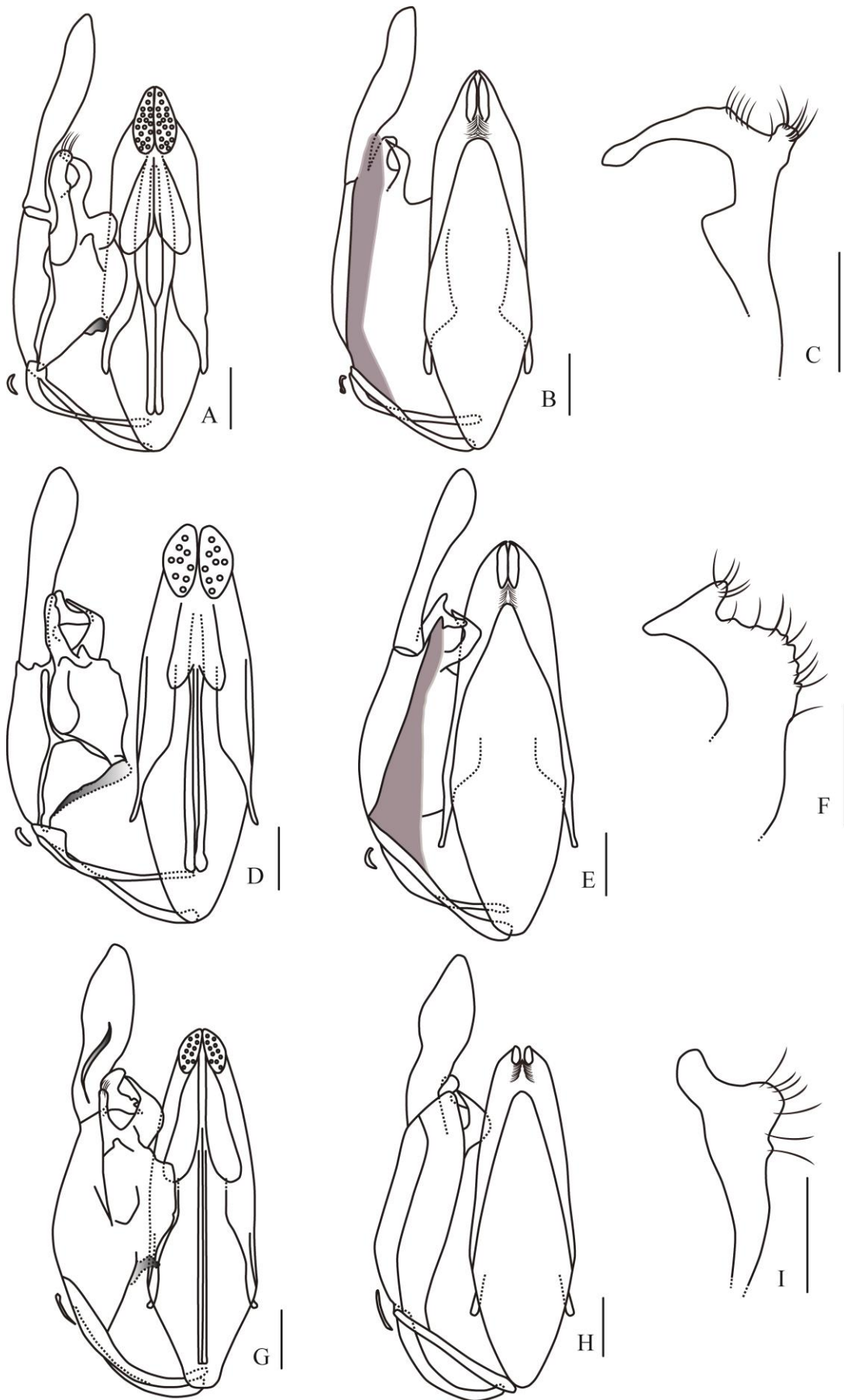


**Figure 15.** Genitalia. **A-C.** *Apenesia* #001; **D-F.** *Apenesia* #002; **G-I.** *Apenesia* #003; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)

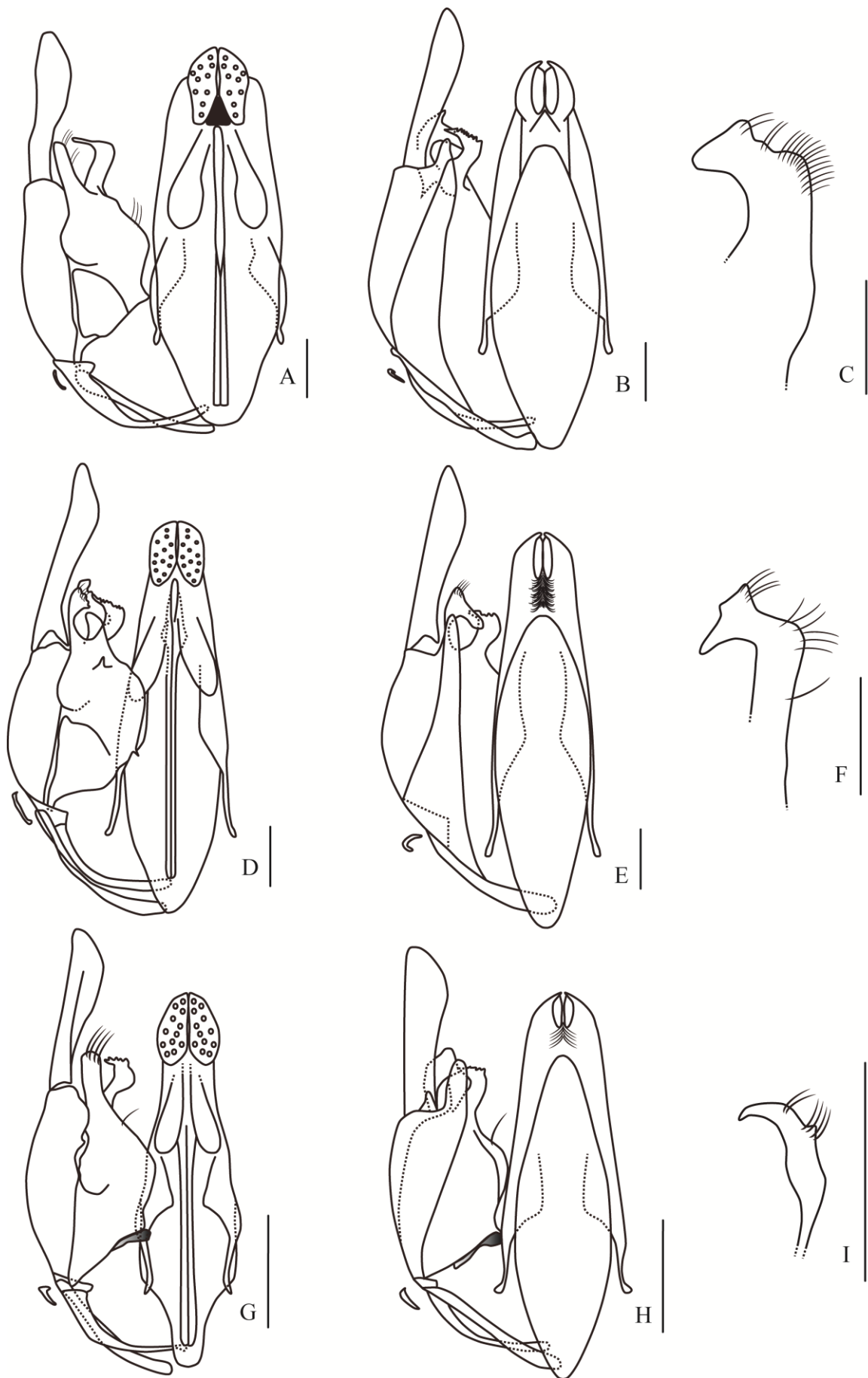


**Figure 16.** Genitalia. **A-C.** *Apenesia* #004; **D-F.** *Apenesia* #005; **G-I.** *Apenesia* #006; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)

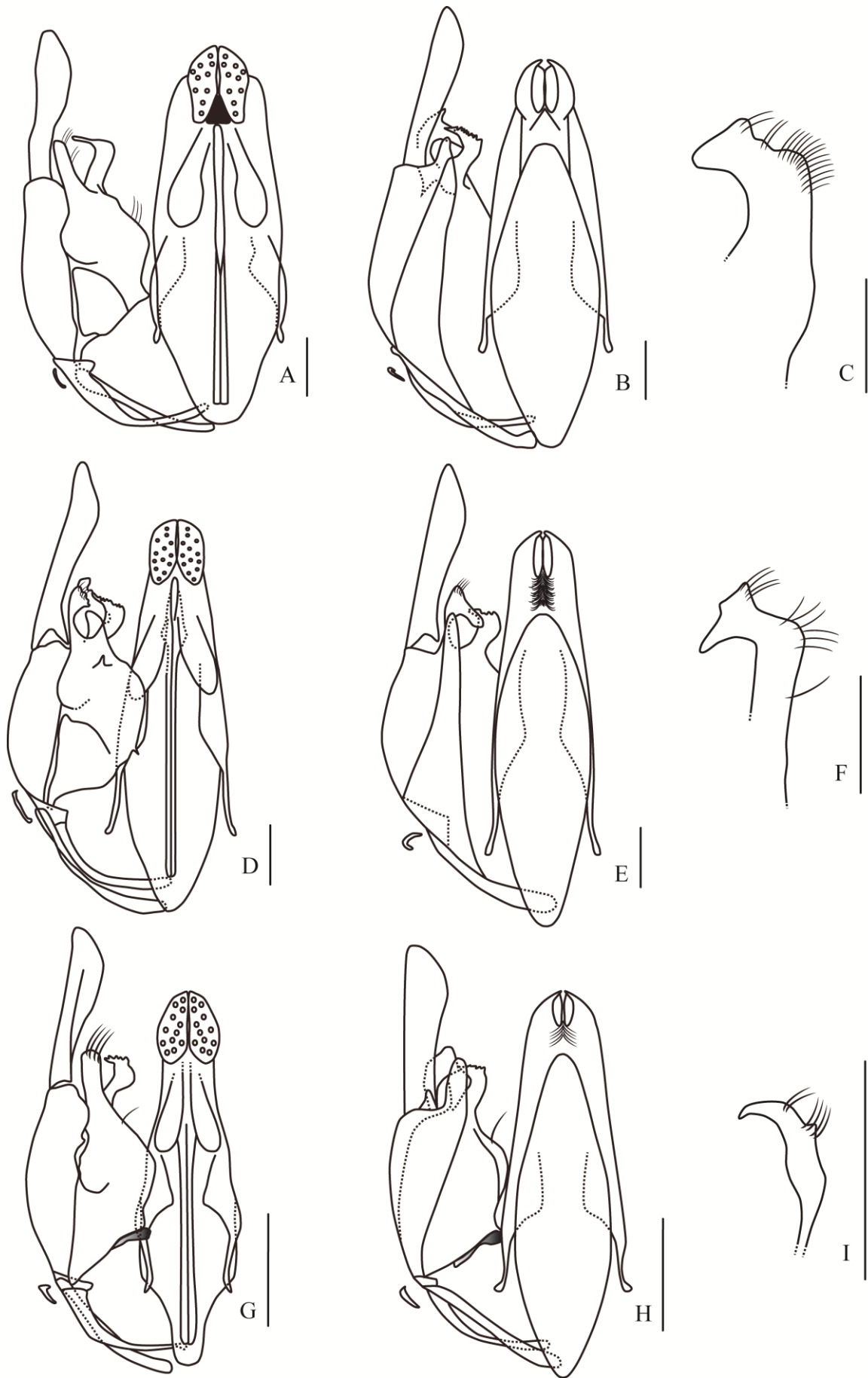




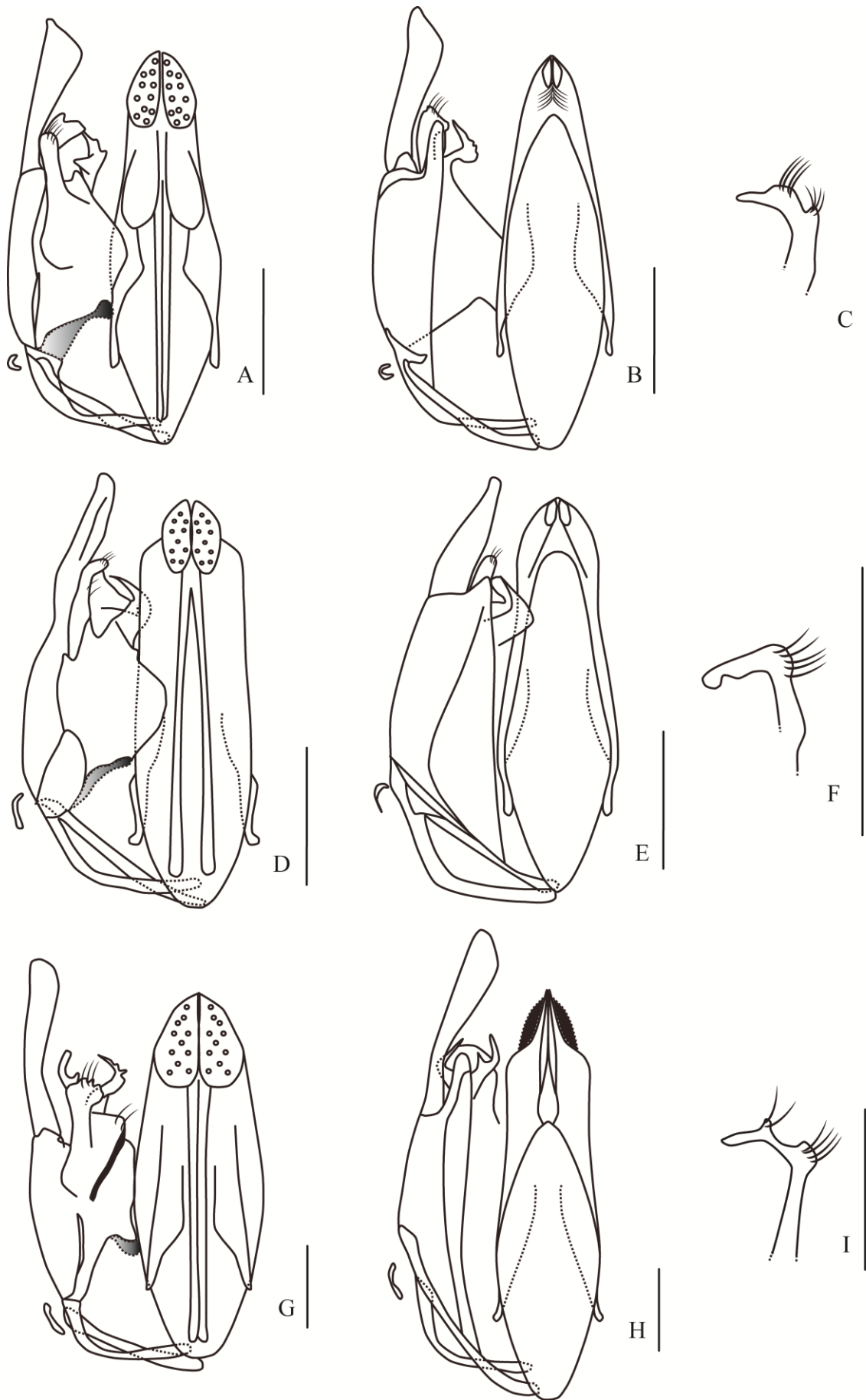
**Figure 17.** Genitalia. **A-C.** *Apenesia* #007; **D-F.** *Apenesia* #008; **G-I.** *Apenesia* #009; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)



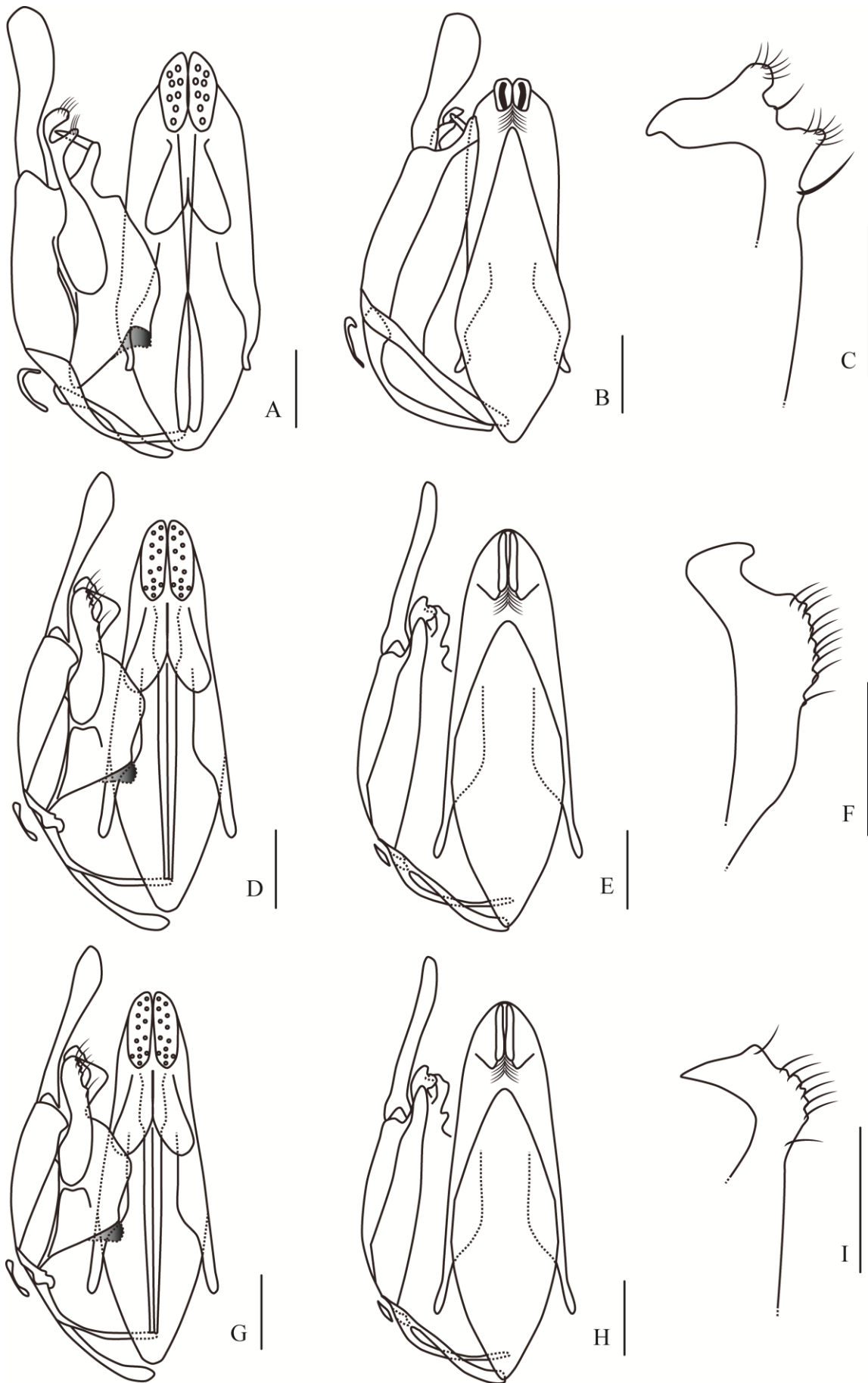
**Figure 18.** Genitalia. **A-C.** *Apenesia* #010; **D-F.** *Apenesia* #011; **G-I.** *Apenesia* #012; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)



**Figure 19.** Genitalia. **A-C.** *Apenesia* #013; **D-F.** *Apenesia* #014; **G-I.** *Apenesia* #015; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)

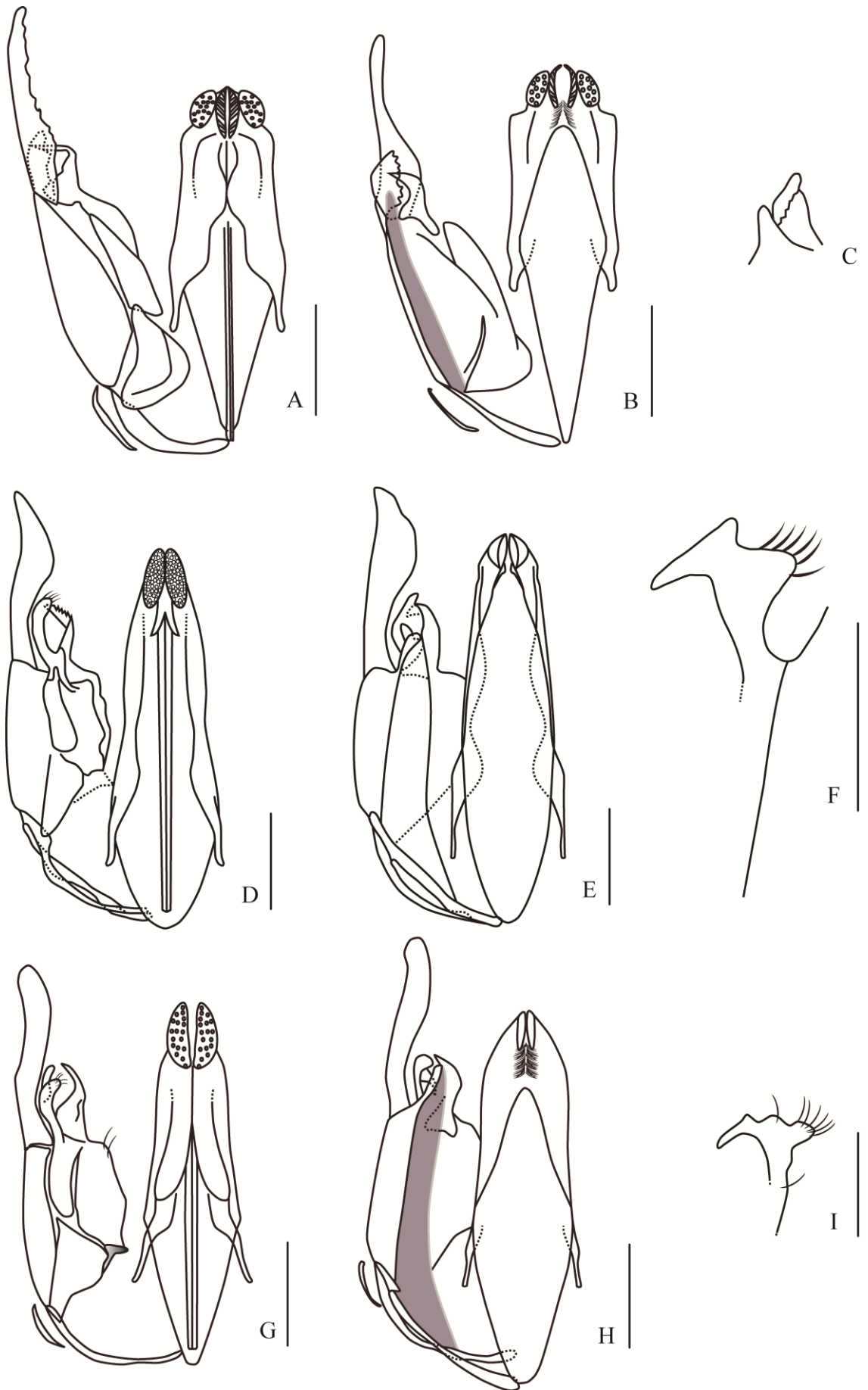


**Figure 20.** Genitalia. **A-C.** *Apenesia* #016; **D-F.** *Apenesia* #017; **G-I.** *Apenesia* #018; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)

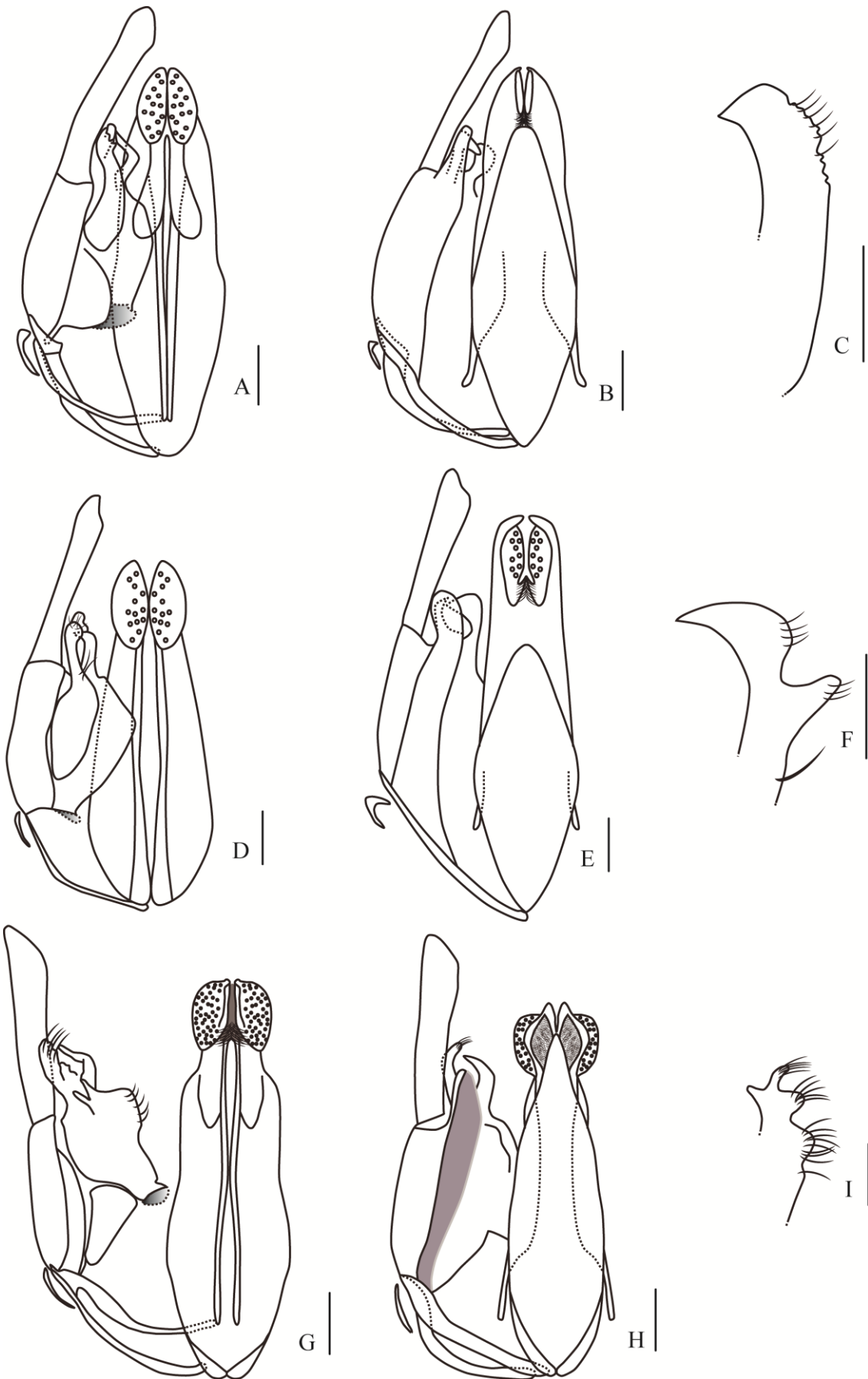


**Figure 21.** Genitalia. **A-C.** *Apenesia* #019; **D-F.** *Apenesia* #020; **G-I.** *Apenesia* #021; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)

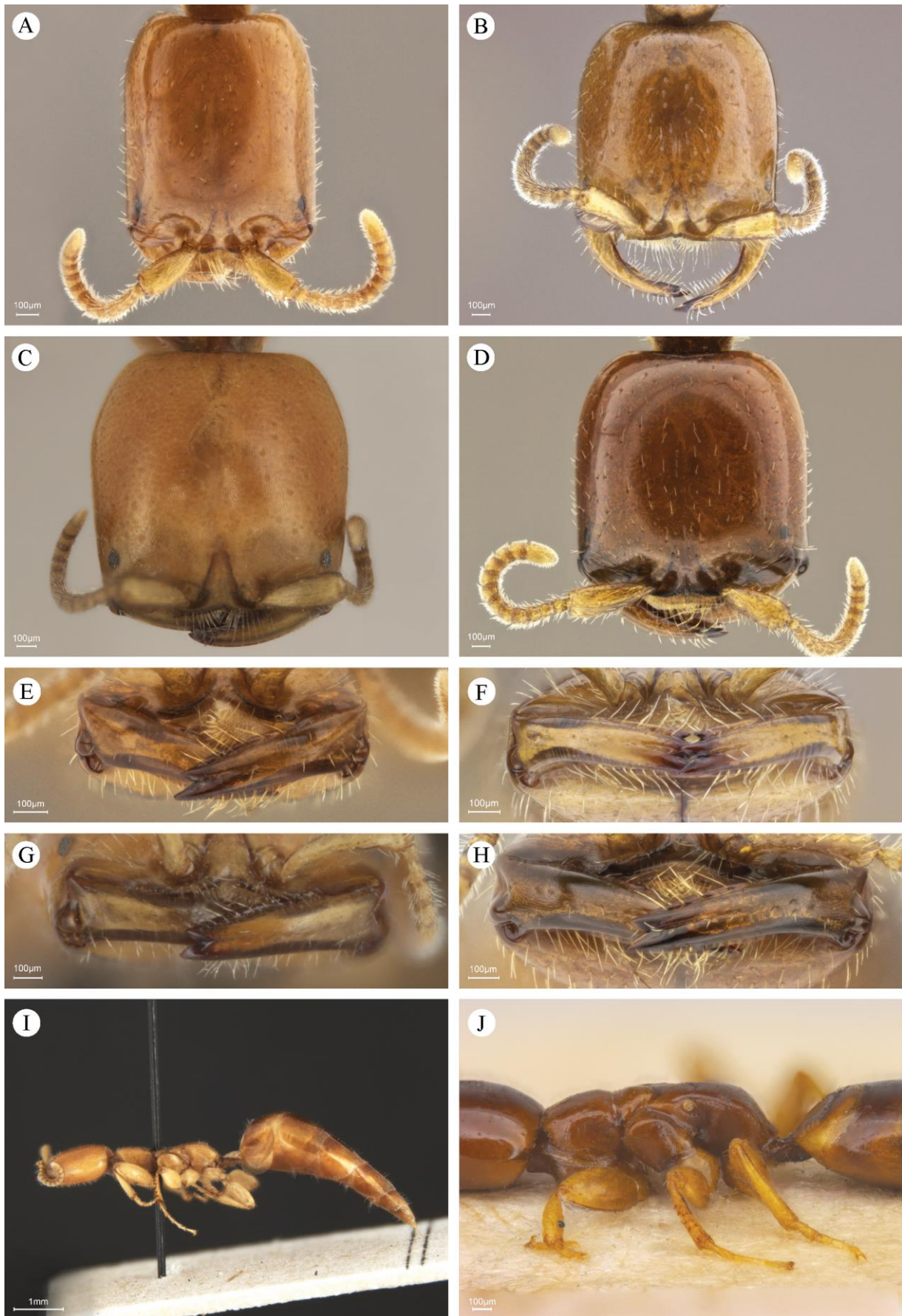




**Figure 22.** Genitalia. **A-C.** *Apenesia laevigata*; **D-F.** *Apenesia leytensis*; **G-I.** *Apenesia makihari*; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)

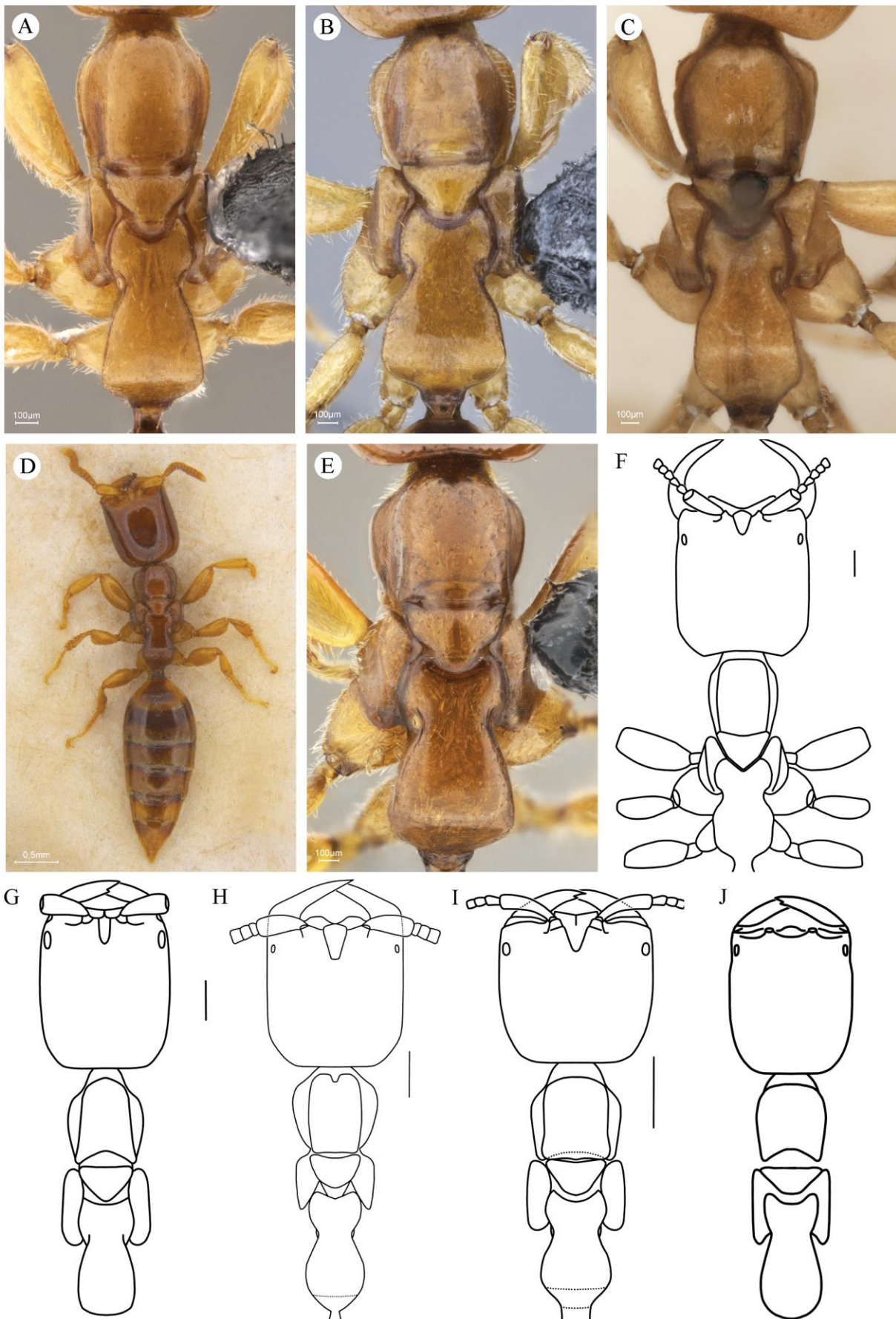


**Figure 23.** Genitalia. **A-C.** *Apenesia perlonga*; **D-F.** *Apenesia sahyadrica*; **G-I.** *Apenesia singularis*; **A, D, G.** ventral view; **B, E, F.** dorsal view; **C, F, G.** cuspis, lateral view. (Scale bar 125 $\mu$ m)

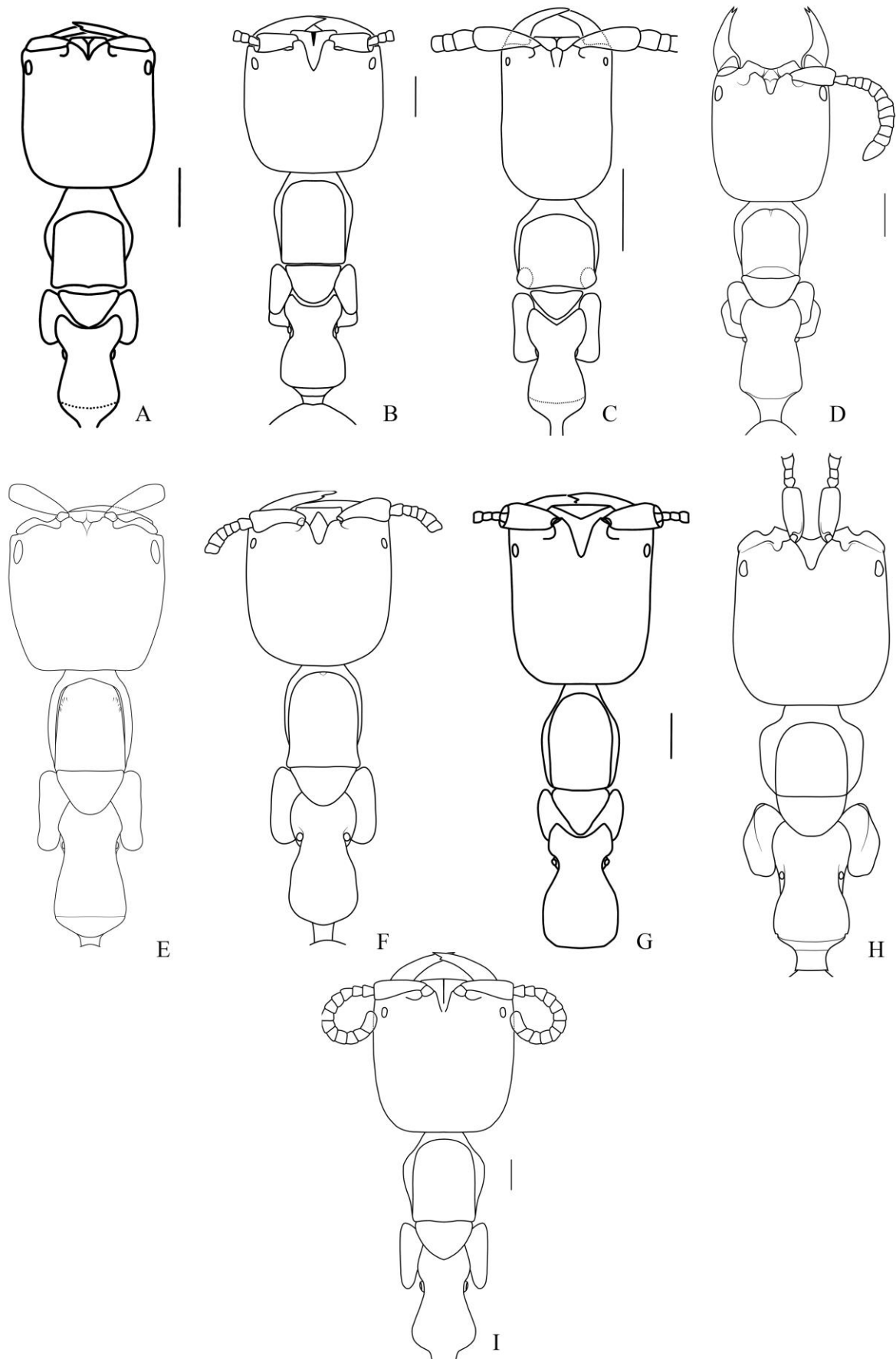


**Figure 24.** Head. **A.** *Apenesia* #003; **B.** *Apenesia* #007; **C.** *Apenesia conradti*; **D.** *Apenesia sahyadraca*. Mandible. **E.** *Apenesia* #003; **F.** *Apenesia* #007; **G.** *Apenesia conradti*; **H.** *Apenesia sahyadraca*. Lateral mesosoma. **I.** *Apenesia conradti*; **J.** *Apenesia parasitica*.





**Fig. 25.** Dorsal mesosoma. **A.** *Apenesia* #003; **B.** *Apenesia* #007; **C.** *Apenesia conradti*; **D.** *Apenesia parasitica*, **E.** *Apenesia sahyadrica*. Body. **F.** *Apenesia amazonica*; **G.** *Apenesia amoena*; **H.** *Apenesia bicolor*; **I.** *Apenesia chontaica*; **J.** *Apenesia delicata*. (Scale bar F-J 250µm)



**Fig. 26.** Body. **A.** *Apenesia dominica*; **B.** *Apenesia flavipes*; **C.** *Apenesia formosa*; **D.** *Apenesia levis*, **E.** *Apenesia nigra*; **F.** *Apenesia proxima*; **G.** *Apenesia substriata*; **H.** *Apenesia unicolor*; **I.** *Apenesia vaurieorum*. (Scale 250 $\mu$ m)

## CAPÍTULO III

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[http://www.nbair.res.in/Featured\\_insects/Apenesia-sahyadrica.php](http://www.nbair.res.in/Featured_insects/Apenesia-sahyadrica.php)

# Global Guide of the Flat Wasps *Pristocerinae* (Hymenoptera, Bethylidae)

## Abstract.

The flat wasps *Pristocerinae* lack global scale literature on their alpha taxonomy. The only world revision for *Bethylidae* of 1914 by Kieffer is outdated; the only catalog of 1990 by Gordh & Móczár is out of dated; and the most recent world genera key of 2003 by Terayama does not reflect the current knowledge we have for the family. Given the scenario we propose a global guide for *Pristocerinae* with diagnoses, taxonomic evaluation, key, and checklist of all genera included. We visited the main collections around the world, analyzed about 2,000 holotypes, and examined at least 400,000 specimens. All *Pristocerinae* species were analyzed to produce a check list by genus. Most of species had their holotypes directly analyzed. We studied some types by combination of pictures or draws. Few other species were analyzed only by the literature. To eliminate homonymies, we add the prefix “neo” to the original specific epithet when possible. To standardize the morphostructural terminology and propose primary homologies, we dissected various specimens and made a comparative analysis with papers and glossaries about morphostructure of Hymenoptera and other insect orders. We confirm *Pristepyris* as syn senior of *Acrepyris*. We proposed three new genus-group synonyms within *Pristocerinae*: *Apristocera* Kieffer and *Parapristocera* Brues **syn. nov.** of *Pristocera* Klug; *Usakosia* Kieffer **syn. nov.** of *Prosapenesia* Kieffer. One *Pristocerinae* genus is transferred to *Scleroderminae*: *Anisobrachium* Kieffer **syn. nov.** of *Sclerodermus* Latreille. Forty seven new combinations are proposed: four in *Dissomphalus*, two in *Parascleroderma*, 35 in *Pristepyris*, one in *Prosapenesia*, two in *Pristocera*, one in *Protisobrachium*, two in *Pseudisobrachium*. Three revalidated combinations are proposed: one in *Pristocera*, two in *Pristepyris*. Four new names are proposed to avoid secondary homonyms. The subfamily will be composed by 1,040 species allocated in 22 genera. A new key to the genera are provided. The text is followed by 229 illustrations organized in 26 plates.

**Keywords.** Sexual dimorphism; Chrysidoidea, Aculeata.

# Subfamily *Pristocerinae* Mocsáry, 1881

(Type-genus: *Pristocera* Klug, 1808)

*Pristocerinae*: Mocsáry 1881, 17: 86; Dalla Torre 1898, 5: 561.

*Pristocerini*: Kieffer 1914d, 41: 451.

*Pristocerinae*: Berland 1928, 19: 208; Evans 1964, 132: 19; Terayama 2006, 1: 25.

## **Synonymous.**

*Afgoiogfinae* Argaman 1988, 120: 140. Synonymy by Gordh & Móczár 1990, 46: 198.

**Original description**— Argaman 1988, 120: 140.

**Type-genus**— *Afgoiogfa* Argaman, 1988.

## **Diagnosis (♂♀)**

- Strong sexual dimorphism: males winged with ocelli; females apterous without ocelli or tegula
- Antenna with 11 flagellomeres
- Male palpal formula usually 6:3 except *Afgoiogfa*, *Foenobethylus*, *Parascleroderma* and *Protisobrachium* 5:2; *Calobrachium* 1:1; *Dissomphalus* 5:3 and *Apenesia* 4:3
- Male median clypeal lobe usually well developed angled, rounded, quadrangular or trapezoidal except *Prosapenesia* which is usually very reduced; lateral clypeal lobe reduced in most genera, except for *Dissomphalus*, *Trichiscus* and *Protisobrachium* in which clypeus are wholly prominent forward, its median lobe not well outlined
- Male mesoscutum with notauli usually well impressed, except in *Pseudisobrachium* and *Protisobrachium* that can be absent or weakly impressed
- Male protrochanter conical and long
- Male mesoscutellum never surpassing metanotum medially
- Male mesoscutellum with strong basal groove

- Male metanotum medial profile depressed only half anterior, half posterior continuous at the same plane
- Male metapostnotal-propodeal complex usually long and with posterolateral area round
- Male metapostnotum usually rugulose
- Male forewing with three closed cells: costal, radial, first cubital
- Male costal cell very narrow at least in the first part
- Phoretic copulation reported to some genera
- Male genitalia megadiverse
- Female with ant-like body
- Female with eye absent or with few ommatidia
- Female ocelli absent
- Female mesoscutum never subdivided
- Female metapostnotal-propodeal complex usually long
- Female profemur large

**Taxonomy.** Pristocerinae have been cited as Dalla Torre (1898) authorship (see Costa Lima 1962; Vargas and Terayama 2002; Terayama 2003a; Terayama 2006; Macek *et al.* 2007). In Dalla Torre (1898, p. 561) catalogue there is a line that cite: “*Mocsáry, Magy. Tud. Akad. Termész. Közlem. XVII. 1881 p. 86 n. 2.*” However, Dalla Torre (1898) did not provided a reference list for the catalogue even Mocsáry (1881) is cited on that quote. Even though, many authors who studied Pristocerinae propagated this wrong authorship for the subfamily. Now we got Mocsáry (1881) original paper and we confirmed his authorship for Pristocerinae.

The subfamily Afgoiogfinae was proposed by Argaman (1988) as a subfamily close to Pristocerinae. Gordh & Móczár (1990) considered their genera *Afgoiogfa* and *Parascleroderma* as belonging to Pristocerinae but they did not make explicit mention to the subfamily synonym. Finnamore and Brothers (1993 in Goulet and Huber 1993) also considered Afgoioginae as Pristocerinae following Gordh & Móczár (1990). This was confirmed by phylogenetic hypothesis proposed by Terayama (1996c) who considered the subfamilies provisionally as synonymies (see Terayama 2003a and Terayama 2006). In 2003a, Terayama explained that both subfamilies are clearly

synonymies since he proposed the nomenclatural act adding “**Syn. Nov.**” (see Terayama 2003a, page 7). Following the rules of ICZN (1999), Gordh & Móczár (1990) is considered as first valid for nomenclatural purposes.

Pristocerinae are one of the most diverse group in Bethylidae. Most species of this subfamily are known only by males or females. The strong sexual dimorphism is unique among Bethylidae subfamilies although there are some genera in other subfamilies which sex correspondence it is not possible by morphostructural characters. The male-female association become possible in Pristocerinae by (1) couples take in phoretic copulation; (2) when mating behavior are observed or (3) they are reared from parasitized larvae. Nowadays the (4) molecular advances will probably help Pristocerinae taxonomists to point a new scientific way for sex association in species level. Any other try to make sex association in Pristocerinae will fail by scientific arguments.

Beyond the high strong sexual dimorphism, males of Pristocerinae are easy to distinguish of other subfamilies because metanotum medially is well developed, always higher than scutellum, and females of Pristocerinae have no ocelli and eyes, when present, are always small. Pristocerinae females are barely known and few specimens are in collections, when comparing to the number of males available. Female taxonomic knowledge is poor what makes difficult to identify them even in generic level. Males, however, are better understood.

**Genera included (22).** P4 Alencar, chapter 1; *Afgoiogfa* Argaman, 1988; *Apenesia* Westwood, 1874; P6 Alencar, chapter 1; *Caloapenesia* Terayama, 1995; *Calobrachium* Gobbi & Azevedo 2016; *Cleistepyris* Kieffer, 1910; *Dissomphalus* Ashmead, 1893; P5 Alencar, chapter 1; P7 Alencar, chapter 1; P9 Alencar, chapter 1; *Foenobethylus* Kieffer, 1913; *Parascleroderma* Kieffer, 1904; *Pristepyris* Kieffer, 1905; *Pristocera* Klug, 1808; P10 Alencar, chapter 1; *Propristocera* Kieffer, 1905; *Prosapenesia* Kieffer, 1910; *Protisobrachium* Benoît, 1957; *Pseudisobrachium* Kieffer, 1904; *Scaphepyris* Kieffer, 1905; *Trichiscus* Benoît, 1956.

**Species included (1,040).** See the list genus by genus above.

## Key to the extant genera of *Pristocerinae* (♂)

1. Body size usually large (10–30 mm), with some exceptions; antennae short; hypopygium deeply divided into two lobes; median stalk of hypopygium strongly reduced and triangular shaped; lateral hypopygeal stalk absent or indistinct (Figs. 40.H, 48.O)... *Pristocera*
- 1'. Body size usually smaller than 1.5 mm, with some exceptions; antennae long or short; hypopygium not deeply divided into two lobes, posterior margin at most concave; median stalk of hypopygium usually long or at least well defined and narrow; lateral hypopygeal stalk usually present (Figs. 48.S)... 2
2. Outer hypopygeal median ventral surface lamellar or strongly concave; stalks of hypopygium almost equally short (Fig. 42.H)... 4
- 2'. Hypopygium simple, outer surface flat; stalks of hypopygium varying in size (Fig. 48.R)... 5
3. Head usually truncated anteriorly; median clypeal lobe usually very reduced and with apical margin concave; stigma usually exceptionally large; hypopygeal apical margin of outer surface with a lamellar lobe (Fig. 43)... *Prosapenesia*
- 3'. Head never truncated anteriorly; median clypeal lobe usually triangular; pterostigma small to large; hypopygeal outer surface lamellar to strongly concave, sometimes resembling those deeply divided into two lobes as in *Pristocera* when not dissected (Fig. 42)... *Propristocera*
4. Clypeus wholly prominent forward, its median lobe not well outlined (Fig. 32.A) ... 6
- 4'. Clypeus with median lobe clearly defined, varying shapes... 8
5. Body usually robust; pronotum short; mesoscutum with notauli well developed, complete or nearly so (Fig. 32.C); metasoma with tergal process usually present (Fig. 32.H)... 7
- 5'. Body long and narrow; pronotum long; mesoscutum with notauli absent or weakly impressed (Fig. 44.C); metasoma simple... *Protisobrachium*



6. Clypeus with median region usually bidentate or straight; metasomal tergite I longer than II (Fig. 46.A); metasomal tergite II with posterolateral margin strongly concave; third metasomal with tergal process usually strongly hairy (Fig. 46.F); hypopygeal median stalk very wide (Fig. 48.S)... *Trichiscus*
- 6'. Clypeus with median region usually unidentate or tridentate (Fig. 32.A); metasomal tergite II longer than I; metasomal tergite II simple or with tergal process as a pair of spots, pits or depressions; third metasomal never with tergal process... *Dissomphalus*
7. Pronotal disc short, with lateral margin much longer than anterior one, sometimes margins badly distinct (Fig. 27.C)... 9
- 7'. Pronotal disc long, with lateral and anterior margin almost same size, but always distinct (Fig. 39.D)... 12
8. Body robust; propleuron simple, short; prepectus reduced; anterior wing with R<sub>12v(a)</sub> near to stigma (Fig. 27.F); basiparamere with small projection dorsally (Fig. 49.E)... *Apenesia*
- 8'. Body flattened and slightly elongate (Fig. 36.C-E); propleuron usually long, neck-shaped; prepectus very large; anterior wing with R<sub>12v(a)</sub> very far from stigma (Fig. 36.G); basiparamere without such projection... 10
9. Profemur swollen; metafemur usually with spine or small teeth (Fig. 36.F); hypopygium with apical margin strongly v-concave; lateral stalks present almost as long as median stalk (Fig. 48.L)... *Foenobethylus*
- 9'. Profemur narrow; metafemur without spine or small teeth; hypopygium with apical margin at most slightly concave; lateral stalks absent; hypopygium corner very developed, almost as long as median stalk (Fig. 48.M)... 11
10. Anterior margin of clypeus with single median projection (Fig. 37.A)... *Parascleroderma*
- 10'. Anterior margin of clypeus with three small projections... *Afgoiogfa*

11. Eyes very hairy; clypeus usually trapezoidal (Fig. 30.A); paramere double (Figs. 49.H-I)... 13
- 11'. Eyes usually glabrous; clypeus diverse; paramere simple... 15
12. Pterostigma obscure or absent (Fig. 29.F)... *Caloapenesia*
- 12'. Pterostigma always present... 14
13. Head usually as long as large; eye sometimes bulging; palpal formula 6:3; hind wing with jugal lobe very reduced; Sc+R<sub>3v</sub> of hind wing short (Fig. 45.G); dorsal paramere with lateral insertion, apex hairy, strongly narrower than ventral paramere (Fig. 51.I)... *Pseudisobrachium*
- 13'. Head usually long; eyes usually hairy and bulging; palpal formula 1:1; hind wing with jugal lobe reduced; Sc+R<sub>3v</sub> of hind wing long (Fig. 30.G); dorsal paramere with frontal insertion, apex glabrous, as large as ventral paramere (Fig. 49.J)... *Calobrachium*
14. Cuspis divided into two arms... 16
- 14'. Cuspis simple... 20
15. Basivolvella with small spine medially (Fig. 49.F); paramere narrow and curved mesad; inner surface of paramere with a well-developed projection... 17
- 15'. Basivolvella without such modification; paramere usually large; inner surface of paramere without such projection... 18
16. Hypopygium with base large, inner hypopygeal surface with spots less sclerotized (Fig. 48.D); paramere apex rounded... **P6** (chapter 1=*new genus*)
- 16'. Hypopygium normal sized, inner hypopygeal surface without spots; paramere apex beveled (Fig. 50.D)... **P5** (chapter 1=*new genus*)
17. Basiparamere long and narrow... 19
- 17'. Basiparamere short and wide (Fig. 49.A)... **P4** (chapter 1=*new genus*)

18. Hypopygium with inner membrane very developed, forming thick apical margin; paramere very narrow and curved c-shaped (Fig. 48.J)... **P7** (chapter 1=*new genus*)
- 18'. Hypopygium with inner membrane poorly developed; paramere axe-shaped (Fig. 50.A)... *Cleistepyris*
19. Antenna very long, antenomere gradually longer and narrower distally (Fig. 39.B); aedeagus with three valve (Fig. 51.A)... *Pristepyris*
- 19'. Antenna long, antenomere usually same sized; aedeagus with one valva... 21
20. Paramere fused to basiparamere; basivolsella long; apical lobes of aedeagus without long setae (Fig. 35.E)... **P9** (chapter 1=*new genus*)
- 20'. Paramere distinct to basiparamere; basivolsella very short; apical lobes of aedeagus with long setae (Fig. 41.G)... **P10** (chapter 1=*new genus*)

#### **Key to the extant genera of Pristocerinae (♀)**

1. Mesonotum very elongate; mesopleuron not reaching lateral of metapectal-propodeal complex in dorsal view (Fig. 42.K)... 2
- 1'. Mesonotum short, mesopleuron reaching at least anterior third of lateral of metapectal-propodeal complex in dorsal view (Fig. 26.I)... 3
2. Mesonotum triangular in dorsal view; mesopleura converging posterad in dorsal view (Fig. 42.K)... *Propristocera*
- 2'. Mesonotum almost trapezoidal in dorsal view, posterior dorsal surface elevate medially; mesopleura parallel in dorsal view (Fig. 45.I)... *Pseudisobrachium*
3. Mesopleuron, seen in dorsal view, very narrow with only small callus; mesonotum surface bellow pronotum and metapectal-propodeal complex; metapectal-propodeal complex without evident constriction at or near spiracles; sides of metapectal-propodeal complex almost parallel in dorsal view (Fig. 32.J)... *Dissomphalus*
- 3'. Mesopleuron, seen in dorsal view, quite large; mesonotum surface bellow pronotum and metapectal-propodeal complex; metapectal-propodeal complex with evident constriction at or near spiracles; sides of metapectal-propodeal complex sinuous in

dorsal view (Fig. 27.I)... 4

4. Body strongly flattened; lateral of pronotum strongly arched, broadly visible in dorsal view; mesonotum somewhat diamond-shaped; metapectal-propodeal complex wider anteriorly (Fig. 37.G)... 5

4'. Body at most only weakly flat dorsoventrally; lateral of pronotum weak to moderately arched, moderately visible in dorsal view; mesonotum triangular, metapectal-propodeal complex not wider anteriorly (Fig. 26.A)... 6

5. Base of pronotum not in contact with mesonotum in dorsal view; mesonotum divided into scutum and scutellum ... *Afgoiogfa*

5'. Base of pronotum in contact with base of mesonotum in dorsal view; mesonotum not divided (Fig. 37.G)... *Parascleroderma*

6. Clypeus strongly produced medially, apical margin subangulate (Fig. 47.B); mesopleuron with large and long upper groove (Fig. 47.D)... *Scaphepyris* Kieffer

6'. Clypeus emarginated, truncate or somewhat produced medially (trapezoidal in some species); mesopleuron smooth ... 7

7. Composed eye usually with one facet or even absent...8

7'. Composed eye with uncountable facets...9

8. Metasoma with long petiole, distinctly longer than wide... *Cleistepyris*

8'. Metasoma with indistinct petiole... **P6** (chapter 1=*new genus*)

9. Anterior portion of metapectal-propodeal complex with dorsal fovea (Fig. 40.J); abdominal sternite II petiolar flap expanded laterally... *Pristocera*

9'. Anterior portion of metapectal-propodeal complex smooth; abdominal sternite II petiolar flap not expanded laterally...10

10. Head distinctly wider than maximum pronotal width; clypeus short and continuous to frons (Fig. 27.H); anterior corner of prosternum uncovered by pronotal collar; mesopleuron with lateral surface concave (Fig. 27.I)... *Apenesia*

10'. Head less or as large as pronotal width and oval shaped; clypeus produced and not continuous to frons (Fig. 26.H); anterior corner of prosternum completely covered by pronotal collar in dorsal view; mesopleuron with lateral surface convex (Fig. 26.I)...11

11. Anterior portion of metapectal-propodeal complex slightly narrower than posteriorly (Fig. 26.I)... **P4** (chapter 1=*new genus*)

11'. Anterior portion of metapectal-propodeal complex much constricted, at most half wide as posterior width... 9

12. Palpal formula 6:3... *Pristepyris*

12. Palpal formula 5:3... *Caloapenesia*

## ***P4***

new genus to be proposed as in chapter 1, this volume

(Figs. 26, 48.A, 49.A)

**Original description**— Alencar, chapter 1, this volume.

**Type-species**— *Apenesia elongata* Evans, 1963.

**Kind of designation**— original designation.

**Designator**— Alencar, chapter 1, this volume.

**Synonymous.** None.

### **Diagnosis** ♂

- Clypeus rectangular or trapezoidal, always very projected forward
- Anteromesoscutum long
- Notaulus badly impressed
- Metaposnotal median carina presente, incomplete
- Metaposnotal area with divergente carinae
- Forewing:

- Pterostigma laceolate
- R<sub>12v</sub>(b) long
- R<sub>S2v</sub> very long with distal end spectral
- r-rs<sub>2v</sub>&R<sub>S2v</sub> junction distinct and angled
- Hypopigium with median stalk long
- Genitalia with:
  - Paramere with apex beveled
  - Basiparamere short and wide
  - Cuspis and digitus long
  - Basal ring narrow and ventrad

#### **Diagnosis** ♀

- Head elongate
- Antenna long
- Scape with same width along its length
- Eye small and distinct
- Pronotum long
- Mesoscutum triangular, with anterior margin concave and posterior one convex
- Metapectal-propodeal complex with an inconspicuous constriction
- Spiracle small and oval, placed latero-dorsally
- Petiole short

**Taxonomy.** This genus was proposed by Alencar (chapter 1, this volume) to include some large specimens which have a distinct median clypeal lobe rectangular; genitalia with beveled paramere apex; volsella well developed and large at base; basal ring reduced and placed ventrally. They used to be placed in the *columbana* and *pilicornis* groups of *Apenesia*, according to Evans (1963b).

**Starting point.** Alencar (chapter 1, this volume) and Evans (1963b).

**Distribution.** Neotropical, 14 species.

**Hosts.** Unknown.

**Check list.**

*angusticeps* (Evans, 1963)  
*coarctata* (Kieffer, 1909)  
*elongata* (Evans, 1963)  
*exilis* (Evans, 1963)  
*fusilis* (Corrêa & Azevedo, 2001)  
*guatemalensis* (Evans, 1963)  
*luteola* (Evans, 1969)  
*martini* (Evans, 1963)  
*ornata* (Evans, 1963)  
*pilicornis* (Evans, 1963)  
*punctata* (Cameron, 1888)  
*reducta* (Evans, 1963)  
*tenebrosa* (Evans, 1963)  
*venezuelana* (Evans, 1963)

## ***Afgoiogfa* Argaman, 1988**

(Fig. 48.B, 49.B)

**Original description**— Argaman 1988, 120: 141, 143.

**Type-species**— *Afgoiogfa olmiana* Argaman, 1988.

**Kind of designation**— original monotypy.

**Designator**— Argaman 1988, 120: 141, 143.

**Diagnosis** ♂

- Clypeus short, tridentate with median tooth longer than lateral ones
- Palpal formula 5:2
- Malar space absent
- Pronotal collar large and well projected medially
- Pronotum short with anterior margin arched



- Propleuron elongated and exposed
- Forewing with:
  - R<sub>12</sub>v(a) vein long and oblique
  - Pterostigma comma-like
- Hypopygium with:
  - Posterior margin slightly emarginate
  - Three long stalks, median one slightly longer than lateral ones
- Genitalia with:
  - Paramere wide, apex larger than base, with two lobes, both with three spines
  - Aedeagus cylindrical, apex bilobed

**Diagnosis** ♀

- Head longer than wide, ovoid
- Eye large
- Metapectal-propodeal complex 2 × as long as wide
- Metasoma broader than head, strongly flattened
- Apical tarsal segment setulose

**Taxonomy.** *Afgoiogfa* is closely related to *Parascleroderma* and *Foenobethylus* by having propleuron elongated and exposed dorsally, R<sub>12</sub>v(a) long; genitalia with aedeagus cylindrical and large according to Azevedo & Lanes (2007).

**Starting point.** Argaman (1988) described *Afgoiogfa* as a monotypic genus which is known from a couple and few male specimens of *A. olmiana*.

**Distribution.** Afrotropical region, 01 species.

**Hosts.** Unknown.

**Check list.**

*olmiana* Argaman, 1988

# *Apenesia* Westwood, 1874

(Figs. 27, 48.C, 49.C-E)

**Original description**— Westwood 1874, 170.

**Type-species**— *Apenesia amazonica* Westwood, 1874.

**Kind of designation**— subsequent designation.

**Designator**— Westwood 1881, 130.

**Synonymous.**

*Aeluroides* Tullgren, 1904. Synonymy by Kieffer 1914d, 41: 391.

**Original description**— Tullgren 1904, 1: 429-428.

**Type-species**— *Aeluroides sjostedti* Tullgren, 1904.

**Kind of Designation**— original monotypy.

**Designator**— Tullgren 1904, 1: 429-430.

*Archaeopristocera* Terayama, 2004b. Synonymy to be proposed as in Alencar, chapter 2, this volume.

**Original description**— Terayama 2004b, 27: 44.

**Type-species**— *Archaeopristocera miki* Terayama, 2004b.

**Kind of designation**— original monotypy.

**Designator**— Terayama 2004b, 27: 44.

*Neoapenesia* Terayama, 1995. Synonymy to be proposed as in Alencar, chapter 1, this volume.

**Original description**— Terayama 1995c, 63: 886.

**Type-species**— *Neoapenesia leytensis* Terayama, 1995c.

**Kind of designation**— original monotypy.

**Designator**— Terayama 1995c, 63: 886.

### Diagnosis ♂

- Head usually wider than long
- Mandible narrow
- Maxillar palpus short
- Palpal formula 4:3
- Clypeus with median lobe projected and usually with median small tooth
- Flagellomere short
- Thorax very high
- Pronotal disc very short
- Prosternum triangular
- Mesoscutum gibbous
- Forewing with:
  - R<sub>12v(a)</sub> long
  - R<sub>12v(b)</sub> absent
  - Cu<sub>2v</sub> spectral and long, usually subdivided
- Hypopygium short, with:
  - Three anterior stalks
  - Median stalk very long
  - Anterior corner stalk-shaped
- Genitalia with:
  - Paramere narrow and long
  - Cuspis developed dorsad
  - Apical projection on basiparamere with membranous area with chitinous projections

### Diagnosis ♀

- Head quadrate and distinctly larger than pronotal width
- Clypeus short, with basal margin surpassing posterior margin of torulus
- Mandible long and narrow
- Palpal formula 4:3
- Antenna short, not reaching posterior margin of head
- Mesopleuron with lateral surface concave
- Mesocoxa very developed

- Metapectal-propodeal complex with strong anterior constriction
- Anterior region of metapectal-propodeal complex with lateral margin bulging

**Taxonomy.** *Apenesia* is a widespread genus, occurring all over the world except in Palearctic region. The genus was recently redefined by Alencar (chapter 1, this volume) and revised (Alencar, chapter 2, this volume). The new conception of *Apenesia* is an extended view of Terayama (1995a) for *Neoapenesia* adding some *Apenesia* species sensu Evans (1963) such as (1) part of *laevigata* species group (*A. laevigata*, *A. perlonga* and *A. singularis*) and *A. sahyadrica* for males and (2) females of *Apenesia* core (Alencar, chapter 2, this volume).

*Apenesia* males may misidentify as some large species of *Dissomphalus* especially by having the clypeus broad with a small tooth and mesoscutum gibbous. However, both genera can be easily separated by the metasoma very narrow in a transversal section, the paramere narrow, the basiparamere with apical projection, the cuspis developed dorsad and the aedeagus simple in *Apenesia*, whereas in *Dissomphalus* the metasoma is large medially in a transversal section, the paramere very large, the basiparamere and the cuspis simple and the aedeagus complex and divided in ventral ramus and dorsal body.

**Starting point.** Alencar (chapter 2, this volume); Evans (1963b), Terayama (1995c) and Sawada *et al.* (2014).

**Distribution.** Neotropical, Afrotropical, Oriental and Australian regions, 48 species.

**Hosts.** *Apenesia sahyadrica* Azevedo & Waichert was extracted from the tunnels of the coffee white stem borer, *Xylotrechus quadripes* Chevrolat (Coleoptera, Cerambycidae) (Azevedo & Waichert 2006). The life cycle of *Apenesia sahyadrica* is detailed in Seetharama *et al.* (2007). *Apenesia* #007 Alencar & Azevedo were reared from Curculionidae beetle larvae *Pantorhytes plutus* Faust, 1892. According to Sawada *et al.* (2014), many individuals of *A. makiharai* (Sawada, Terayama & Mita) were reared from dead wood severely affected by *Cerecium longicornis* Pic, 1926 that was considered a potential host species.

**Check list.**

#001 Alencar &Azevedo

#002 Alencar &Azevedo

#003 Alencar &Azevedo

#004 Alencar &Azevedo

#005 Alencar &Azevedo

#006 Alencar &Azevedo

#007 Alencar &Azevedo

#008 Alencar &Azevedo

#009 Alencar &Azevedo

#010 Alencar &Azevedo

#011 Alencar &Azevedo

#012 Alencar &Azevedo

#013 Alencar &Azevedo

#014 Alencar &Azevedo

#015 Alencar &Azevedo

#016 Alencar &Azevedo

#017 Alencar &Azevedo

#018 Alencar &Azevedo

#019 Alencar &Azevedo

#020 Alencar &Azevedo

#021 Alencar &Azevedo

*amazonica* Westwood, 1874

*amoena* Evans, 1963

*bicolor* Vargas & Terayama, 2002

*chontalica* Westwood, 1881

*conradti* Kieffer, 1910

*delicata* Evans, 1963

*dominica* Evans, 1963

*flavipes* Cameron, 1888

*formosa* Vargas & Terayama, 2002

*laevigata* (Evans, 1958)

*leytensis* (Terayama, 1995)

*levis* Kieffer, 1904  
*makiharai* (Sawada, Terayama & Mita, 2014)  
*malaitensis* Brues, 1918  
*miki* (Terayama, 2004)  
*modesta* (Smith, 1864)  
*nigra* Kieffer, 1904  
*parasitica* (Smith, 1864)  
*perlonga* Correa & Azevedo, 2006  
*proxima* Kieffer, 1904  
*punctalata* Krombein, 1989  
*sahyadrica* Azevedo & Waichert, 2006  
*singularis* Lanes & Azevedo, 2004  
*sjostedti* (Tulgren, 1904)  
*substriata* Kieffer, 1904  
*unicolor* Kieffer, 1904  
*vaurieorum* Evans, 1969

## ***P6***

new genus to be proposed as in chapter 1, this volume  
(Figs. 28, 48.D, 49.F-G)

**Original description**— Alencar, chapter 1, this volume.

**Type-species**— *Apenesia evansi* Gordh, 1990.

**Kind of designation**— original designation.

**Designator**— Alencar, chapter 1, this volume.

**Synonymous.** None.

### Diagnosis ♂

- Body size small
- Clypeus short, with apical slightly convex or straight
- Prepectus divided and large
- Forewing:
  - Pterostigma short and oval
  - $R_{1+2v}(b)$  short
  - $Rs_{2v}$  very long
  - $r-rs_{2v}$  &  $Rs_{2v}$  junction smooth
- Hypopigium with:
  - Three stalks
  - Median stalk long with base very large
  - Median surface with light spots
- Genitalia with:
  - Paramere very narrow and curved mesad
  - Paramere usually with a median spine projection at inner surface
  - Dorsal base of paramere with a hard projection variable in size and position
  - Basivolsella long with an apical spine
  - Basiparamere apical margin without distinction to paramere
  - Basal ring large and placed laterally on genital ring

### Diagnosis ♀

- Head elongate
- Clypeus produced and not continuous to frons
- Antenna long
- Eye absent
- Mesoscutelum triangular, with anterior margin slightly concave and posterior one convex
- Metapectal-propodeal complex constriction weak
- Petiole short

**Taxonomy.** Alencar (chapter 1, this volume) proposed this genus to include some Australian species which were placed at *Apenesia*. They resemble *Pristepyris* when



rectangular median clypeal lobe is present but they are much smaller in body size. They are diagnosed by features in genitalia such as: the basivolsellar apical spine, the paramere narrow and curved mesad with a projection inside. The female are quite similar to those found in *Cleistepyris*. Although females of P6 are diagnosed by the head elongate and those in *Cleistepyris* have the head globoid. According to Alencar (chapter 1, this volume), there are many new species to be described including some record from Chile.

**Starting point.** Alencar (chapter 1, this volume); Gordh (1990).

**Distribution.** Neotropical (Chile) and Australian regions, 4 species.

**Hosts.** Unknown.

**Check list.**

*australiense* (Kieffer, 1906)

*chilena* (Evans, 1967)

*evansi* (Gordh, 1990)

*tofti* (Ward, 2013)

## *Caloapenesia* Terayama, 1995

(Figs. 29, 48.R, 49.H-I)

**Original description**— Terayama 1995c, 63(4): 882-883.

**Type-species**— *Caloapenesia thailandiana* Terayama, 1995c.

**Kind of designation**— original designation.

**Designator**— Terayama 1995c, 63(4): 882.

**Synonymous.** None.

### Diagnosis ♂

- Body usually strongly punctuate
- Palpal formula 5:3
- Eye usually prominent, with long erect hairs
- Prepectus fused
- Forewing with:
  - Pterostigma absent
  - C<sub>2v</sub> obscure
  - C<sub>2c</sub> wide
- Hypopygium with:
  - Simple with median stalk long and lateral one reduced or absent
  - Posterior margin slightly to strongly trilobate
- Genitalia with:
  - Paramere deeply divided into separate arms
  - Dorsal paramere is straight, slightly sclerotized and glabrous
  - Aedeagus with small diamond-shaped sclerite on basis
  - Basis of volsella with small tubular sclerite, below cuspis and digitus
  - Basal ring ventrad

### Diagnosis ♀

- Mandible with four apical teeth
- Palpal formula 5:3
- Clypeus with median lobe trapezoidal
- Median carina of clypeus divided in two apically
- Mesoscutum triangular
- Mesopleuron large in dorsal view, projected anteriorly
- Metapectal-propodeal complex strongly constricted anteriorly
- Forebasitarsus strongly curved
- Mesotibia strongly spinose

**Taxonomy.** *Caloapenesia* is unique among Bethyridae by the absence of pterostigma in the forewings. Other peculiar diagnostic character of *Caloapenesia* is the genitalia with paramere deeply divided into separate arms, which is similar to *Pseudisobrachium*.

However *Pseudisobrachium* the dorsal paramere is curved, strongly sclerotized and hairy, whereas *Caloapenesia* the dorsal paramere is straight, slightly sclerotized and glabrous. Among Pristocerinae genera, the complete basal ring is present only in both genera. Those genitalia conditions are present only in the *Pseudisobrachium* and *Caloapenesia*.

This genus has only one species with female described for *Caloapenesia brevis* Azevedo which was described based on both sexes by Azevedo (2004).

**Starting point.** Gobbi & Azevedo (2014) revised *Caloapenesia*, presenting a key to all known male species.

**Distribution.** Oriental region, 19 species.

**Hosts.** Unknown.

**Check list.**

*ana* Gobbi & Azevedo, 2014

*arbeni* Gobbi & Azevedo, 2014

*brevis* Azevedo, 2004

*diba* Gobbi & Azevedo, 2014

*edas* Gobbi & Azevedo, 2014

*heira* Gobbi & Azevedo, 2014

*inyara* Gobbi & Azevedo, 2014

*jailuna* Gobbi & Azevedo, 2014

*lani* Gobbi & Azevedo, 2014

*launeci* Gobbi & Azevedo, 2014

*leptata* Gobbi & Azevedo, 2014

*mugra* Gobbi & Azevedo, 2014

*nadaili* Gobbi & Azevedo, 2014

*paruwa* Gobbi & Azevedo, 2014

*philippinensis* Terayama, 1995

*rikawa* Gobbi & Azevedo, 2014

*sabeli* Gobbi & Azevedo, 2014

*supra* Gobbi & Azevedo, 2014

*thailandiana* Terayama, 1995

## ***Calobrachium* Gobbi & Azevedo, 2016**

(Figs. 30, 48.F, 49.J-K)

**Original description**— Gobbi & Azevedo 2016, 4083: 222.

**Type-species**— *Calobrachium salum* Gobbi & Azevedo, 2016.

**Kind of designation**— original designation.

**Designator**— Gobbi & Azevedo 2016, 4083: 222.

**Diagnosis** ♂ (♀ unknown)

- Body elongated
- Palpal formula 1:1
- Mandible with four angulate apical teeth
- Clypeus with trapezoidal median lobe
- Eye bulging, densely hairy
- Mesopleuron with transversal furrow; without callus and foveae
- Forewing with stigma very slender
- Hind wing with:
  - Vannus reduced
  - Sc+R<sub>3v</sub> very long
- Male hypopygium with:
  - Posterior margin slightly to strongly trilobate, with ventral posterior projection convex and drop-shaped
  - Median stalk short, lateral stalk inconspicuous or absent
- Male genitalia with:
  - Paramere double
  - Dorsal paramere apparently with frontal insertion, slightly sclerotized, glabrous
  - Ventral paramere subangulate

- o Cuspis very long and convex
- o Aedeagus mesoconvex
- o Basal ring present, usually quadrangular

**Taxonomy.** *Calobrachium* is defined in the context of its resemblance to *Caloapenesia* and *Pseudisobrachium*. It is similar to *Caloapenesia* because both have the epipygium with posterior margin trilobite, the posterior hypopygeal margin trilobate and lateral hypopygeal stalk very small or even absent. It shares the median clypeal lobe trapezoidal as a diagnostic feature as *Pseudisobrachium*. *Calobrachium*, *Caloapenesia* and *Pseudisobrachium* are unique among Pristocerinae with paramere double, although this feature also occurs in Mesitiinae, Bethylinae and Scleroderminae.

*Calobrachium* differs from all other genera in Bethylinidae by the presence of palpal formula 1:1; the forewing with stigma very narrow; the hind wing with vannus very reduced and subcostal vein long; drop-shaped projection in the base of aedeagus and the basal ring quadrangular and basad.

**Starting point.** Gobbi & Azevedo (2016) is the unique reference to this genus and included the genus and species description, with key and illustrations for all species.

**Distribution.** Oriental region (Thailand), 08 species.

**Hosts.** Unknown.

**Check list.**

*lepidum* (Terayama, 2004)

*luangum* Gobbi & Azevedo, 2016

*miticum* Gobbi & Azevedo, 2016

*pongum* Gobbi & Azevedo, 2016

*salum* Gobbi & Azevedo, 2016

*thanum* Gobbi & Azevedo, 2016

*trilinum* Gobbi & Azevedo, 2016

*vancum* Gobbi & Azevedo, 2016

# *Cleistepyris* Kieffer, 1910

*Stat. rev.* to be proposed as in chapter 1, this volume

(Figs. 31, 48.G, 50.A)

**Original description**— Kieffer 1910b, 79: 48.

**Type-species**— *Cleistepyris punctatus* Kieffer, 1910b = *Apensia peruana* new name Evans 1963b and syn. jr. of *Cleistepyris brasiliensis* **nec** *Apenesia punctata* (Cameron 1888)

**Kind of designation**— subsequent designation.

**Designator**— Kieffer 1914d, 41: 490.

## **Synonymous.**

*Dipristocera* Kieffer, 1914d. Synonym to be proposed as in Alencar, chapter 1, this volume.

**Original description**— Kieffer 1914d, 41: 471.

**Type-species**— *Pristocera microchela* Kieffer, 1911b.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1914d, 41: 471.

## **Diagnosis** ♂

- Median clypeal lobe with variable shape but usually triangular and short
- Eye glabrous
- Antenna long, first antennomeres larger than distal ones
- Palpal formula 6:3
- Forewing:
  - Pterostigma short and triangular
  - R<sub>1</sub><sub>2</sub>v(*b*) short
  - R<sub>S</sub><sub>2</sub>v very long with distal end spectral and almost touching the wing margin
  - r-rs<sub>2</sub>v&R<sub>s</sub><sub>2</sub>v junction almost smooth
- Genitalia with:

- Paramere with base narrow and apex very expanded
- Cuspis divided into ventral and dorsal arms, ventral one usually large

**Diagnosis** ♀

- Head slightly globoid
- Antenna reaching pronotum
- Mandibles with from two to four teeth
- Clypeus usually short
- Eye absent or very small, indistinct
- Mesonotum caliciform with anterior margin strongly concave and rounded behind
- Mesopleuron conspicuous dorsally, lateral surface convex
- Metapectal-propodeal complex weakly to moderately constricted near spiracles
- Petiole long

**Taxonomy.** *Cleistepyris* and *Dipristocera* were synonymized together under *Apenesia* by Evans (1963b, 130: 257). Their species represented some *Apenesia* included in the *brasiliensis* species group and some other related species included in *exilis*, *laevigata*, *mexicana* and *nitida* groups of *Apenesia*. Alencar (chapter 1, this volume) proposed to revalidate the generic status of *Cleistepyris* and included most of the species of *Apenesia*. Since the conception of *Cleistepyris* and *Dipristocera* fits into the same corn, Alencar (chapter 1, this volume) synonymized the later to the first one to follow the ICZN rules. *Cleistepyris* is specially diagnosed by genitalia pattern with paramere axe-shaped. There are few sex association by phoretic copulation and females of this group have head oval or rounded, scutellum triangular, mesopleuron developed in dorsal view reaching the anterior constriction at the metapectal-propodeal complex.

**Starting point.** Alencar (chapter 1, this volume) and Evans (1963b).

**Distribution.** Neotropical and Nearctic regions, 76 species.

**Hosts.** Unknown.

**Check list.**

*acia* (Lanes & Azevedo, 2004)  
*alutaceus* (Evans, 1963)  
*angustatus* (Evans, 1958)  
*apicilatus* (Azevedo & Batista, 2002)  
*atlantica* (Correa & Azevedo, 2006)  
*auricula* (Lanes & Azevedo, 2004)  
*auritus* (Waichert & Azevedo, 2003)  
*brasiliensis* (Kieffer, 1909)  
*bugabensis* (Cameron, 1888)  
*chiricahua* (Evans, 1963)  
*clypeatus* (Leal & Azevedo, 2001)  
*cochise* (Evans, 1963)  
*columbanus* (Westwood, 1874)  
*conconvexus* (Corrêa & Azevedo, 2001)  
*crenulatus* (Kieffer, 1909)  
*cubensis* (Evans, 1963)  
*curvatus* (Lanes & Azevedo, 2004)  
*distinctus* (Corrêa & Azevedo, 2001)  
*exigua* (Correa & Azevedo, 2006)  
*fulvicollis* (Westwood, 1874)  
*hepaticus* (Correa & Azevedo, 2006)  
*inca* (Evans, 1963)  
*jamaica* (Evans, 1969)  
*laceratus* (Evans, 1969)  
*laevicornis* (Evans, 1969)  
*lapsus* (Lanes & Azevedo, 2004)  
*leucophthalmus* (Evans, 1964)  
*lobatus* (Azevedo & Batista, 2002)  
*longus* (Ramos & Azevedo, 2010)  
*magnus* (Ramos & Azevedo, 2010)  
*malinche* (Evans, 1963)  
*maya* (Evans, 1963)



*megaventris* (Azevedo & Batista, 2002)  
*membranaceus* (Lanes & Azevedo, 2004)  
*mexicana* (Cameron, 1904)  
*microchelus* (Kieffer, 1911)  
*mohave* (Evans, 1963)  
*neotropica* Kieffer, 1910  
*nitidus* Kieffer, 1910  
*ocullatus* (Azevedo & Batista, 2002)  
*olmeca* (Evans, 1963)  
*percurrrens* (Kieffer, 1910)  
*paradoxus* (Evans, 1963)  
*paraensis* (Kieffer, 1910)  
*patens* (Correa & Azevedo, 2006)  
*peccatus* (Ramos & Azevedo, 2010)  
*pectinatus* (Correa & Azevedo, 2006)  
*peculiaris* (Evans, 1963)  
*perconcausus* (Ramos & Azevedo, 2010)  
*permaximus* (Ramos & Azevedo, 2010)  
*quadratus* (Evans, 1963)  
*quadrimerus* (Leal & Azevedo, 2001)  
*quelatus* (Ramos, Araújo & Azevedo, 2010)  
*rectus* (Ramos & Azevedo, 2010)  
*rostrum* (Azevedo & Batista, 2002)  
*rotundum* (Leal & Azevedo, 2001)  
*santaecatarinae* (Evans, 1964)  
*serrulatus* (Azevedo & Batista, 2002)  
*simplex* (Correa & Azevedo, 2006)  
*spatulatus* (Evans, 1969)  
*spinipes* (Evans, 1969)  
*striatulus* (Evans, 1963)  
*strictus* (Corrêa & Azevedo, 2001)  
*strigulatus* (Lanes & Azevedo, 2004)  
*sulcatus* (Evans, 1963)

*tarascana* (Evans, 1963)  
*testaceipes* (Cameron, 1888)  
*tlahuicana* (Evans, 1963)  
*transversus* (Evans, 1963)  
*triangulum* (Azevedo & Batista, 2002)  
*triapicalis* (Azevedo & Batista, 2002)  
*trivisum* (Ramos, Araújo & Azevedo, 2010)  
*unipilosus* (Corrêa & Azevedo, 2001)  
*ventosus* (Azevedo & Batista, 2002)  
*williamsi* (Evans, 1966)  
*zamorum* (Evans, 1963)

## ***Dissomphalus* Ashmead, 1893**

(Figs. 32, 48.H, 50.B-C)

**Original description**— Ashmead 1893, 45: 41-42.

**Type-species**— *Dissomphalus xanthopus* Ashmead, 1893.

**Kind of designation**— original designation.

**Designator**— Ashmead 1893, 45: 41.

**Synonymous.**

*Ecitopria* Wasmann, 1899. Synonymy by Evans 1955(1954), 56: 290.

**Original description**— Wasmann 1899, 11: 55.

**Type-species**— *Ecitopria crassicornis* Wasmann, 1899.

**Kind of Designation**— original monotypy.

**Designator**— *Ecitopria crassicornis* Wasmann 1899, 26: 55.

*Dissemphalus* (sic): Ashmead 1902, 9: 271 [*laspus*].

*Psilobethylus* Kieffer, 1906. Synonymy by Terayama 1995c, 63: 888.

**Original description**— Kieffer 1906 in Kieffer & Marshall 1904–1906, 9: 461–462.

**Type-species**— *Psilobethylus luteus* Kieffer, 1906 in Kieffer & Marshall 1904–1906.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1906 in Kieffer & Marshall 1904–1906, 9: 462-463.

*Glenobethylus* Kieffer, 1910b. Synonymy by Evans 1964, 132: 41.

**Original description**— Kieffer 1910b, 79: 50.

**Type-species**— *Glenobethylus montanus* Kieffer, 1910b.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1910b, 79: 50.

*Thaumatepyris* Kieffer, 1910b. Synonymy by Evans 1964, 132: 41.

**Original description**— Kieffer 1910b, 79: 47.

**Type-species**— *Thaumatepyris punctatus* Kieffer, 1910b.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1910b, 79: 47.

*Parisobrachium* Kieffer, 1914d. Synonymy by Azevedo 2008a, 25: 784.

**Original description**— Kieffer 1914d, 41: 424.

**Type-species**— *Rhabdepyris ? albipes* Kieffer, 1904.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1914d, 41: 424.

*Parecitopria* Ogloblin, 1930. Synonymy by Evans 1964, 132: 41.

**Original description**— Ogloblin 1930, 3: 15.

**Type-species**— *Parecitopria azarai* Ogloblin, 1930.

**Kind of Designation**— original monotypy.

**Designator**— Ogloblin 1930, 3: 15.

### Diagnosis ♂

- Body robust
- Clypeus broad, its median lobe usually not delimited by groove
- Pronotum short
- Metasoma relatively broad and short, oval in dorsal view
- Second tergite usually with tergal process (spots, depressions, pits, tufts of setae or tubercles)
- Hypopygium usually with three stalks, median one longer than lateral ones
- Genitalia short and wide with:
  - Paramere usually mitten-like
  - Basivolsella completely fused to basiparamere
  - Volsella G-like; cuspis long and digitus very short
  - Aedeagus very complex, composed by ventral ramus and dorsal body.

### Diagnosis ♀

- Head longer than wide
- Eye small, with from one to about 25 facets
- Clypeus continuous to frons
- Mesonotum short, transverse, slightly depressed medially, its posterior margin gently convex at its broad junction with metapectal-propodeal complex
- Anterior margin of metapectal-propodeal complex not embracing sides of mesonotum to any appreciable extent
- Metapectal-propodeal complex elongate, more or less parallel-sided; constriction absent
- Mesopleuron slightly prominent in dorsal view.

**Taxonomy.** Taxonomy of *Dissomphalus* is strongly based on males. Females of different species of *Dissomphalus* are very similar and hardly separable, because there is little variation, and they are also highly modified, without ocelli, notauli, parapsidal furrows, mesoscutum, pronotal and propodeal carinae, mesepisternal and subalar grooves and tergal processes (Azevedo 1999a). Females are very rare in collections and sex association is virtually impossible unless couples are taken in copula (Azevedo 2003).

*Dissomphalus* was described based on some Pristocerinae species possessing two pubescent tubercles on the second metasomal tergite in the males (Evans 1955 [1954]). The tergal processes can vary within *Dissomphalus* species as spots, depressions, pits, tufts of setae or tubercles (see Azevedo 1999a; 2003; Mugrabi & Azevedo 2013). These tergal processes seem to be an ornamented opening of a gland on the surface of this tergite (Evans 1979c). Although the tergal processes are an apomorphic character of the genus which make the genus easily recognized among Pristocerinae (Azevedo 2003; Terayama 1996c), it seems some species have lost the processes during the evolution of different monophyletic groups (Azevedo 2003). Since *Dissomphalus* was described, the main diagnostic character for species in this genus was the tergal process. However, according to Azevedo (2003), the main synapomorphy shared by all species of *Dissomphalus*, both with or without tergal processes, is the aedeagus divided into two distinct structures, a pair of ventral rami and a dorsal body.

Until Azevedo (2003) stated some aedeagus features to diagnose *Dissomphalus*, Pristocerinae species similar to the genus that lack the tergal processes usually run to *Apenesia*. These species were accommodated on *dissomphaloides* species group proposed by Evans (1963b) in his revision of the genus *Apenesia*. The *dissomphaloides* species group has all listed here as diagnostic features present in *Dissomphalus* except the tergal process. Recently, some *Dissomphalus* species have been described with notes on the tergal process varying from absent to conspicuous (e.g. *D. microstictus* in Alencar & Azevedo 2008), obsolescent or completely absent (e.g. species of *incomptus* species-group in Azevedo 2003).

Alencar (chapter 1, this volume) transfer 15 *Apenesia* species to *Dissomphalus*, almost all from *dissomphaloides* species group. These species were analyzed, including their holotypes and genitalia. They all share the robust body; the clypeus broad; the pronotum short; the metasoma lacking tergal process but short and oval in dorsal view; the genitalia wide with aedeagus divided into ventral ramus and dorsal body; the paramere mitten-shaped; the basivolsella fused to basiparamere; the volsella G-shaped; cuspis long and arched; digitus short.

**Starting point.** Azevedo (2003) and Azevedo (1999a) are both equally first recommended references to *Dissomphalus* taxonomy. Recently, a revision of

*Dissomphalus* from Thai added many new species and discussed new features to identify its species (see Mugarabi & Azevedo 2013).

**Distribution.** Cosmopolitan, 393 species

**Hosts.** According to Evans (1954; 1978b), *Dissomphalus apertus* was associated to *Bruchus brachialis* Fahraeus, 1839 (Bruchidae, Coleoptera), *Dissomphalus xanthopus* was associated to Micromalthidae (Coleoptera) and Cecidomyiidae (Diptera).

**Check list.**

*abababa* Mugarabi & Azevedo, 2016

*abruptus* Azevedo, 2001

*aculeatus* Alencar & Azevedo, 2006

*adscitus* Benoît, 1956

*ailan* Mugarabi & Azevedo, 2016

*ais* Mugarabi & Azevedo, 2016

*aiskrim* Mugarabi & Azevedo, 2016

*alberti* Benoît, 1957

*albipes* (Kieffer, 1904)

*alticarinatus* Azevedo, 2001

*alticlypeatus* Azevedo, 2003

*altivolans* Evans, 1954

*amana* Colombo & Azevedo, 2016

*ambrela* Mugarabi & Azevedo, 2016

*amplexos* Redighieri & Azevedo, 2006

*amplifoveatus* Redighieri & Azevedo, 2006

*amplus* Redighieri & Azevedo, 2006

*ananas* Mugarabi & Azevedo, 2016

*angulatus* Azevedo, 1999

*anien* Mugarabi & Azevedo, 2016

*anka* Mugarabi & Azevedo, 2016

*apertus* Kieffer, 1914

*archboldi* Evans, 1969

*archeatus* Azevedo, 2001  
*arizonicus* Evans, 1962  
*attaphilus* (Bruch, 1916)  
*auritus* Alencar & Azevedo, 2006  
*azarai* (Ogloblin, 1930)  
*babaeculum* Benoît, 1957 **comb. to be proposed** from *Pseudisobrachium*  
*bahiensis* Redighieri & Azevedo, 2006  
*balteus* Alencar & Azevedo, 2008  
*balus* Muğrabi & Azevedo, 2016  
*barberi* Evans, 1954  
*barbus* Muğrabi & Azevedo, 2013  
*basidentatus* Azevedo, 1999  
*basivolsellus* Azevedo, 2001  
*bicarenatus* Azevedo, 1999  
*bicavatus* Evans, 1979  
*bicerutus* Azevedo, 2003  
*bifoveatus* Kieffer, 1906  
*bifurcatus* Azevedo, 1999  
*biknait* Muğrabi & Azevedo, 2016  
*bilas* Muğrabi & Azevedo, 2016  
*bilobatus* Azevedo, 1999  
*binatang* Muğrabi & Azevedo, 2016  
*bisket* Muğrabi & Azevedo, 2016  
*bisserratus* Azevedo, 1999  
*bisulcus* Ashmead, 1894  
*bivolsellus* Azevedo, 2001  
*blakbokis* Muğrabi & Azevedo, 2016  
*blut* Muğrabi & Azevedo, 2016  
*botocudus* Colombo & Azevedo, 2016  
*brasiliensis* Kieffer, 1910  
*bratasusa* Muğrabi & Azevedo, 2016  
*brevinervis* Kieffer, 1904  
*browni* (Evans, 1964)

*bun* Mugrabi & Azevedo, 2016  
*cacirus* Colombo & Azevedo, 2016  
*californicus* Ashmead, 1893  
*caparao* Colombo & Azevedo, 2016  
*capixaba* Colombo & Azevedo, 2016  
*caribbeanus* (Evans, 1969)  
*catalinae* Vargas & Terayama, 2002  
*caviclepeus* Evans, 1969  
*cerutus* Azevedo, 1999  
*cervoides* Azevedo, 2003  
*cherrus* Mugrabi & Azevedo, 2013  
*chiangmaiensis* Terayama, 2001  
*chiapanus* Evans, 1962  
*chipenensis* Terayama, 1995  
*claudivani* Argaman, 1989  
*clausus* Kieffer, 1908  
*claviger* Evans, 1954  
*clibanarius* Benoît, 1957  
*clovisi* Colombo & Azevedo, 2016  
*clypeatus* Evans, 1954  
*collaris* Evans, 1962  
*completus* Azevedo, 1999  
*concevatus* Azevedo, 1999  
*confusus* Ashmead, 1894  
*congo* Colombo & Azevedo, 2016  
*conicus* Azevedo, 2003  
*connubialis* Evans, 1966  
*contractus* Azevedo, 2003  
*cornutus* Evans, 1964  
*coronatus* Alencar & Azevedo, 2006  
*crassicornis* (Wasmann, 1899)  
*crassus* Redighieri & Azevedo, 2006  
*cristatus* Redighieri & Azevedo, 2004



*crucialis* Benoît, 1957  
*culteratus* Alencar & Azevedo, 2006  
*curvifoveatus* Azevedo, 1999  
*curvilongus* Azevedo, 2001  
*curviventris* Azevedo, 2003  
*daimen* Mugrabi & Azevedo, 2016  
*daneus* Mugrabi & Azevedo, 2013  
*davus* Mugrabi & Azevedo, 2013  
*declinatus* Alencar & Azevedo, 2006  
*decussatus* Alencar & Azevedo, 2006  
*deformis* Evans, 1969  
*delgatus* Azevedo, 1999  
*denticulatus* (Evans, 1963)  
*dentiformis* Azevedo, 1999  
*dewel* Mugrabi & Azevedo, 2016  
*differens* Redighieri & Azevedo, 2006  
*digitatus* Azevedo, 1999  
*dilatatus* Azevedo, 1999  
*dissomphaloides* (Evans, 1963)  
*distans* Redighieri & Azevedo, 2006  
*divaricatus* Alencar & Azevedo, 2008  
*divisus* Redighieri & Azevedo, 2006  
*diwai* Mugrabi & Azevedo, 2016  
*dumosus* Evans, 1966  
*eksospaip* Mugrabi & Azevedo, 2016  
*elegans* Redighieri & Azevedo, 2006  
*ellipticus* Evans, 1969  
*elongatus* Azevedo, 2001  
*ensel* Mugrabi & Azevedo, 2016  
*epitus* Mugrabi & Azevedo, 2013  
*evansi* Azevedo, 1999  
*excellens* Redighieri & Azevedo, 2006  
*excisicrus* Kieffer, 1912

*extrarramis* Azevedo, 1999  
*falcatus* Evans, 1962  
*falciformis* Azevedo, 2001  
*ferocus* Azevedo, 2003  
*ferrurus* Mugrabi & Azevedo, 2013  
*filiformis* Redighieri & Azevedo, 2006  
*filus* Azevedo, 2003  
*fimbriatus* Redighieri & Azevedo, 2006  
*firmus* Redighieri & Azevedo, 2006  
*flagellatus* Azevedo, 2001  
*flavipes* Kieffer, 1910  
*flaviscapus* (Evans, 1969)  
*flexuosus* Alencar & Azevedo, 2006  
*forceps* Alencar & Azevedo, 2008  
*forchhammeri* (Krombein, 1989)  
*fredi* Colombo & Azevedo, 2016  
*fungosus* Evans, 1979  
*fuscus* (Kieffer, 1904)  
*gabrus* Mugrabi & Azevedo, 2013  
*galeatus* Alencar & Azevedo, 2006  
*gamtri* Mugrabi & Azevedo, 2016  
*geanus* Mugrabi & Azevedo, 2013  
*geniculatus* Azevedo, 2001  
*gigantus* Azevedo, 1999  
*gilvipes* Evans, 1979  
*gionus* Mugrabi & Azevedo, 2013  
*gladius* Azevedo, 2001  
*globiceps* Benoît, 1957  
*gordus* Azevedo, 2003  
*gorgor* Mugrabi & Azevedo, 2016  
*graun* Mugrabi & Azevedo, 2016  
*guarani* Colombo & Azevedo, 2016  
*guttus* Azevedo, 2003

*hama* Muğrabi & Azevedo, 2016  
*han* Muğrabi & Azevedo, 2016  
*hemisphaericus* Azevedo, 2003  
*hetus* Muğrabi & Azevedo, 2013  
*hirtus* Alencar & Azevedo, 2006  
*horizontalis* Azevedo, 1999  
*h-ramus* Redighieri & Azevedo, 2004  
*ibirapitanga* Colombo & Azevedo, 2016  
*inclinatus* Redighieri & Azevedo, 2006  
*incompletus* Azevedo, 1999  
*incomptus* Evans, 1964  
*incurvatus* Alencar & Azevedo, 2008  
*indeceptibilis* Benoît, 1957  
*infissus* Evans, 1969  
*inflexus* Redighieri & Azevedo, 2006  
*insulanus* (Evans, 1969)  
*intradentatus* Azevedo, 2001  
*joelus* Muğrabi & Azevedo, 2013  
*jubus* Muğrabi & Azevedo, 2013  
*julius* Muğrabi & Azevedo, 2013  
*kakaruk* Muğrabi & Azevedo, 2016  
*kansanus* Evans, 1955  
*kas* Muğrabi & Azevedo, 2016  
*kasang* Muğrabi & Azevedo, 2016  
*kelsus* Muğrabi & Azevedo, 2013  
*khaoyaiensis* Terayama, 1995  
*kiau* Muğrabi & Azevedo, 2016  
*kiefferi* (Benoît, 1957) **comb. to be proposed** from *Pseudisobrachium*  
*kina* Muğrabi & Azevedo, 2016  
*kinabarensis* Terayama, 1995  
*klok* Muğrabi & Azevedo, 2016  
*koki* Muğrabi & Azevedo, 2016  
*krombeini* Azevedo, 1999

*kuara* Colombo & Azevedo, 2016  
*kuka* Mugrabi & Azevedo, 2016  
*kukamba* Mugrabi & Azevedo, 2016  
*kyushuensis* Terayama, 1999  
*lamellatus* Redighieri & Azevedo, 2006  
*laminaris* Redighieri & Azevedo, 2004  
*lanceolatus* Azevedo, 1999  
*lang* Mugrabi & Azevedo, 2016  
*largidentatus* Azevedo, 1999  
*largimanus* Azevedo, 2001  
*laticephalus* Azevedo, 2003  
*latimerus* Azevedo, 2003  
*latus* Azevedo, 2001  
*lewa* Mugrabi & Azevedo, 2016  
*lidinus* Mugrabi & Azevedo, 2013  
*lilloanus* (Evans, 1969)  
*linearis* Azevedo, 1999  
*lobicephalus* Azevedo, 2003  
*lobisserratus* Azevedo, 2001  
*loliwara* Mugrabi & Azevedo, 2016  
*longicephalus* Azevedo, 2000  
*longiclypeus* Azevedo, 1999  
*longimerus* Azevedo, 2001  
*longipilosus* Azevedo, 2001  
*luscus* Evans, 1964  
*luteus* (Kieffer, 1906)  
*magnetus* Mugrabi & Azevedo, 2013  
*magnus* Redighieri & Azevedo, 2006  
*malaysianus* Terayama, 2001  
*maleo* Mugrabi & Azevedo, 2016  
*mama* Mugrabi & Azevedo, 2016  
*mambu* Mugrabi & Azevedo, 2016  
*mami* Mugrabi & Azevedo, 2016

*mandibulatus* Azevedo, 2003  
*mantoides* Azevedo, 2001  
*manus* Azevedo, 2003  
*matticum* (Benoît, 1957) **comb. to be proposed** from *Pseudisobrachium*  
*mausgras* Mugrabi & Azevedo, 2016  
*megadentatus* Azevedo, 2001  
*megomphalus* Evans, 1969  
*mendicus* Evans, 1969  
*mexicanus* (Westwood, 1839)  
*microculus* Azevedo, 1999  
*microdentatus* Azevedo, 2001  
*microstictus* Evans, 1969  
*microtuberculatus* Azevedo, 1999  
*minus* Terayama & Yamane, 1997  
*minutulus* Terayama, 1999  
*mirabilis* Evans, 1966  
*miriamae* Colombo & Azevedo, 2016  
*mirim* Colombo & Azevedo, 2016  
*mugrus* Mugrabi & Azevedo, 2013  
*muli* Mugrabi & Azevedo, 2016  
*multicoriaceus* Azevedo, 1999  
*mwalo* Mugrabi & Azevedo, 2016  
*nandus* Mugrabi & Azevedo, 2013  
*nanellus* Evans, 1969  
*napo* Evans, 1979  
*natnat* Mugrabi & Azevedo, 2016  
*nek* Mugrabi & Azevedo, 2016  
*neobrowni* Alencar & Azevedo, chapter 1, this volume  
*nepalensis* Terayama, 2001  
*nicaeus* Benoît, 1956  
*niuspapa* Mugrabi & Azevedo, 2016  
*nus* Mugrabi & Azevedo, 2016  
*ocellatus* Kieffer, 1911

*octavus* Azevedo, 2001  
*opis* Mugrabi & Azevedo, 2016  
*orophilus* Benoît, 1956  
*osseus* Alencar & Azevedo, 2008  
*papai* Mugrabi & Azevedo, 2016  
*parvus* Azevedo, 1999  
*pauculihirtum* (Benoît, 1957) **comb. to be proposed** from *Pseudisobrachium*\*  
*paululus* Alencar & Azevedo, 2008  
*paulus* Mugrabi & Azevedo, 2013  
*peculiares* Redighieri & Azevedo, 2006  
*pedipalpoides* Azevedo, 2001  
*pepa* Mugrabi & Azevedo, 2016  
*perparvus* Alencar & Azevedo, 2008  
*personatus* Redighieri & Azevedo, 2006  
*perturbatus* Alencar & Azevedo, 2008  
*perventriosus* Alencar & Azevedo, 2008  
*philippinensis* Terayama, 2001  
*pike* Mugrabi & Azevedo, 2016  
*pikinini* Mugrabi & Azevedo, 2016  
*pilus* Alencar & Azevedo, 2008  
*pis* Mugrabi & Azevedo, 2016  
*piscicercus* Azevedo, 2001  
*psin* Mugrabi & Azevedo, 2016  
*planus* Azevedo, 1999  
*platensis* (Bruch, 1916)  
*plaua* Mugrabi & Azevedo, 2016  
*plaumanni* Evans, 1964  
*ples* Mugrabi & Azevedo, 2016  
*polidentatus* Azevedo, 1999  
*politus* Ashmead, 1894  
*popo* Mugrabi & Azevedo, 2016  
*potyra* Colombo & Azevedo, 2016  
*prilus* Mugrabi & Azevedo, 2013

*pronus* Alencar & Azevedo, 2006  
*prophylax* Benoît, 1957  
*proximus* (Kieffer, 1904)  
*pukpuk* Mugrabi & Azevedo, 2016  
*punctatus* (Kieffer, 1910)  
*purius* Colombo & Azevedo, 2016  
*puteolus* Evans, 1969  
*pyata* Colombo & Azevedo, 2016  
*pygmaeus* (Evans, 1969)  
*ramosus* Alencar & Azevedo, 2006  
*rasissimus* Azevedo, 1999  
*rectangularis* Azevedo, 2001  
*rectilineus* Azevedo, 1999  
*refertus* Alencar & Azevedo, 2008  
*renbo* Mugrabi & Azevedo, 2016  
*retorcerens* Azevedo, 2001  
*rettenmeyeri* Evans, 1964  
*robus* Mugrabi & Azevedo, 2013  
*rokrok* Mugrabi & Azevedo, 2016  
*ros* Mugrabi & Azevedo, 2016  
*rosangelae* Colombo & Azevedo, 2016  
*rotundus* Azevedo, 1999  
*rufipalpis* Kieffer, 1910  
*rwindianus* Benoît, 1957  
*sanda* Mugrabi & Azevedo, 2016  
*sarawakensis* (Terayama & Yamane, 1997)  
*save* Mugrabi & Azevedo, 2016  
*saxatilis* Kieffer, 1912  
*scamatus* Azevedo, 1999  
*scavatus* Azevedo, 1999  
*scopatus* Redighieri & Azevedo, 2004  
*scrupeus* Evans, 1964  
*secretus* Colombo & Azevedo, 2016

*serratus* Azevedo, 1999  
*setosus* Redighieri & Azevedo, 2006  
*signatus* Alencar & Azevedo, 2008  
*simulatus* (Evans, 1969)  
*sinatus* Alencar & Azevedo, 2006  
*singularis* Evans, 1962  
*sinuatus* Azevedo, 2001  
*sirsen* Mugrabi & Azevedo, 2016  
*sis* Mugrabi & Azevedo, 2016  
*slika* Mugrabi & Azevedo, 2016  
*sno* Mugrabi & Azevedo, 2016  
*soklet* Mugrabi & Azevedo, 2016  
*solwara* Mugrabi & Azevedo, 2016  
*spiculus* Azevedo, 2001  
*spinosus* Azevedo, 2003  
*spissus* Redighieri & Azevedo, 2006  
*stellatus* Azevedo, 1999  
*strabus* Azevedo, 2003  
*strepsus* Azevedo, 2001  
*strictus* Azevedo, 1999  
*subdeformis* Azevedo, 1999  
*subpilosus* Azevedo, 1999  
*subtriangularis* Azevedo, 2001  
*suga* Mugrabi & Azevedo, 2016  
*susu* Mugrabi & Azevedo, 2016  
*switbiskit* Mugrabi & Azevedo, 2016  
*switmuli* Mugrabi & Azevedo, 2016  
*taiabocu* Colombo & Azevedo, 2016  
*tapiok* Mugrabi & Azevedo, 2016  
*taun* Mugrabi & Azevedo, 2016  
*tetracerutus* Azevedo, 2001  
*tetralobatus* Azevedo, 2001  
*thaianus* Terayama, 2001



*thysanus* Azevedo, 2003  
*ting* Mugrabi & Azevedo, 2016  
*tisa* Mugrabi & Azevedo, 2016  
*toktok* Mugrabi & Azevedo, 2016  
*tortuosus* Azevedo, 1999  
*triangularis* Azevedo, 1999  
*tridentata* (Kieffer, 1912)  
*trilobatus* Redighieri & Azevedo, 2006  
*trogon* Azevedo, 2001  
*tropoides* Azevedo, 2001  
*truncatus* Azevedo, 2003  
*tuberculatus* Ashmead, 1894  
*tubulatus* Redighieri & Azevedo, 2006  
*tudak* Mugrabi & Azevedo, 2016  
*tumbuna* Mugrabi & Azevedo, 2016  
*tupinikim* Colombo & Azevedo, 2016  
*turinus* Mugrabi & Azevedo, 2013  
*uber* Alencar & Azevedo, 2006  
*ulceratus* Evans, 1969  
*umbilicus* Azevedo, 2003  
*uncus* Alencar & Azevedo, 2008  
*undatus* Azevedo, 2003  
*unitus* Azevedo, 1999  
*vallensis* Evans, 1979  
*vampirus* Azevedo, 2003  
*verrucosus* Redighieri & Azevedo, 2004  
*verus* Mugrabi & Azevedo, 2013  
*w-aedeagus* Colombo & Azevedo, 2016  
*wailimbung* Mugrabi & Azevedo, 2016  
*wailis* Mugrabi & Azevedo, 2016  
*wara* Mugrabi & Azevedo, 2016  
*wetliva* Mugrabi & Azevedo, 2016  
*wik* Mugrabi & Azevedo, 2016

*wilwil* Mugrabi & Azevedo, 2016  
*win* Mugrabi & Azevedo, 2016  
*wusheanus* Terayama, 2001  
*xanthopus* Ashmead, 1893  
*yelo* Mugrabi & Azevedo, 2016  
*yu* (Snelling, 1996)  
*zethus* Mugrabi & Azevedo, 2013

## ***P5***

new genus to be proposed as in chapter 1, this volume  
(Figs. 33, 48.I, 50.D)

**Original description**— Alencar, chapter 1, this volume.

**Type-species**— *Apenesia juncea* Evans, 1966.

**Kind of designation**— original designation.

**Designator**— Alencar, chapter 1, this volume.

**Synonymous.** None.

**Diagnosis** ♂ (♀ unknown)

- Body size large
- Clypeus usually rectangular
- Forewing:
  - Pterostigma short and oval
  - R<sub>12v</sub>(*b*) long
  - R<sub>s2v</sub> long with distal end spectral
  - r-rs<sub>2v</sub>&R<sub>s2v</sub> junction smooth
- Hypopigium with:
  - Three stalks
  - Median stalk long with base narrow
- Genitalia with:

- o Paramere narrow and curved mesad
- o Dorsal base of paramere with a hard projection hook-like
- o Basivolsela short with an apical spine
- o Basiparamere apical margin without distinction to paramere
- o Basal ring absent

**Taxonomy.** Alencar (chapter 1, this volume) delimited P5 as a genus to include a few Neotropical species of *Apenesia* which were placed at *columbana* and *pilicornis* groups. They are similar to P4 and *Pristepyris* because of the large sized body and the clypeus rectangular. But according to Alencar (chapter 1, this volume), those features are probably due to ecological convergence since P5 is sister group of P6. P5 and P6 both share the paramere narrow and curved mesad, the dorsal base of paramere with a hard projection hook-like and the basivolsela short with an apical spine. Although, P5 are larger body sized specimens, the median stalk of hypopygium is narrow, and the basal ring is absent whereas P6 are smaller body sized specimens, the median stalk of hypopygium presents the base much larger than the apex and the basal ring is present

**Starting point.** Alencar (chapter 1, this volume), Evans (1963b).

**Distribution.** Neotropical, 10 species.

**Hosts.** *Apenesia parapolita* Evans was found in ant nest of *Ponera* (Evans 1978b).

**Check list.**

*cusco* (Evans, 1966)

*flammicornis* (Evans, 1963)

*funebri* (Evans, 1963)

*juncea* (Evans, 1966)

*pallidicornis* (Evans, 1963)

*pallidula* (Evans, 1963)

*parapolita* (Evans, 1963)

*photophila* (Ogloblin, 1930)

*pima* (Evans, 1963)

*polita* (Fouts, 1930)

## ***P7***

new genus to be proposed as in chapter 1, this volume

(Figs. 34, 48.J, 50.E-F)

**Original description**— Alencar, chapter 1, this volume.

**Type-species**— *Apenesia elegans* Terayama, 1999.

**Kind of designation**— original designation.

**Designator**— Alencar, chapter 1, this volume.

**Synonymous.** None.

**Diagnosis** ♂ (♀ unknown)

- Antenna long
- Clypeus usually short with apical margin convex
- Forewing:
  - Pterostigma lanceolate
  - R<sub>1</sub><sub>2</sub>v(*b*) long
  - r-rs<sub>2</sub>v&Rs<sub>2</sub>v junction distinct and angled
- Hypopigium with:
  - Inner surface with distinct setae
  - Median stalk long
  - Inner membrane very developed overlapping median stalk, with delimited borders
  - Apical margin thick, shape variable
- Genitalia with:
  - Paramere very narrow, curved mesad and with ventral margin setose
  - Basivolsela long and narrow
  - Basal ring large and placed laterally on genital ring

**Taxonomy.** Alencar (chapter 1, this volume) proposed this genus to include some Oriental *Apenesia* species diagnosed by having the hypopygium with inner membrane very developed, forming a thick apical margin; and the paramere very narrow and curved c-shaped. P7 is related to (P5+P4) in morphological cladistics analyses specially because of the paramere narrow. Although, in molecular analyses P7 seems to be a lineage sister to all other Pristocerinae genera, except *Pseudisobrachium* Alencar (chapter 1, this volume).

**Starting point.** Alencar (chapter 1, this volume), Lim *et. al* (2011).

**Distribution.** Oriental and Sino-Japanese, 21 species.

**Hosts.** Unknown.

**Check list.**

*chitouensis* (Terayama, 1996)  
*clara* (Xu, Terayama & He, 2002)  
*consobrina* (Kieffer, 1922)  
*daikoku* (Terayama, 1999)  
*electriphila* (Cockerell, 1917)  
*elegans* (Terayama, 1999)  
*intricata* (Kieffer, 1922)  
*kaguyahime* (Terayama, 2006)  
*kakaniensis* (Terayama, 2004)  
*ktmdana* (Terayama, 2004)  
*lathrobioides* (Westwood, 1874)  
*levicollis* (Kieffer, 1905)  
*liukueiensis* (Terayama, 1996)  
*meifuiae* (Terayama, 1996)  
*minima* (Kieffer, 1913)  
*nepalensis* (Terayama, 2004)  
*otohime* (Terayama, 1999)  
*philippinensis* (Kieffer, 1913)

*takasago* (Terayama, 1996)

*tianmuensis* (Xu, Terayama & He, 2002)

*xanthoptera* (Kieffer, 1922)

## ***P9***

new genus to be proposed as in chapter 1, this volume  
(Figs. 35, 48.K, 50.G-H)

**Original description**— Alencar, chapter 1, this volume.

**Type-species**— *Apenesia bishamon* Terayama, 1999.

**Kind of designation**— original designation.

**Designator**— Alencar, chapter 1, this volume.

**Synonymous.** None.

**Diagnosis** ♂ (♀ unknown)

- Clypeus very projected and triangular
- Notaulus irregularly foveolate
- Mesopleuron with opened anterior and inferior foveae
- Metanotum with three median foveae
- Metaposnotal median carina present
- Hypopigium with:
  - Three stalks
  - Median stalk long
- Genitalia with:
  - Paramere and basiparamere fused, without distinction
  - Apex of paramere with at least one thin and long projection
  - Basivolsela very long
  - Basal ring narrow and placed dorsal-laterally above genital ring

**Taxonomy.** P9 is a monotypic genus proposed by Alencar (chapter 1, this volume). Its only species, P9 bishamon (Terayama) is unique in having foveae in the mesopleuron among Pristocerinae. Other specimens of this genus were found in Afrotropical material.

**Starting point.** Alencar (chapter 1, this volume).

**Distribution.** Sino-japanese, 01 species.

**Hosts.** Unknown.

**Check list.**

*bishamon* (Terayama, 1999)

## ***Foenobethylus* Kieffer, 1913**

(Figs. 36, 48.L, 50.I-J)

**Original description**— Kieffer 1913d, 3(31): 257–258.

**Type-species**— *Foenobethylus gracilis* Kieffer, 1913d.

**Kind of designation**— original monotypy.

**Designator**— Kieffer 1913d, 3(31): 258.

**Diagnosis** ♂ (♀ unknown)

- Body flattened and slightly elongate
- Clypeus short, tridentate with median tooth longer than lateral ones
- Gena short
- Propleuron elongated and expose dorsally
- Pronotal collar large and well projected laterally
- Pronotum elongated and narrowed anteriorly
- Forewing with:

- R<sub>12v(a)</sub> long and oblique
- R<sub>12v(b)</sub> usually absent
- Hing wing with jugal lobe reduced or almost absent
- Protrochanter arched (similar to Epyrinae)
- Profemur extremely enlarged
- Metatrochanter usually with spine
- Metafemur with spine or small teeth
- Hypopygium with:
  - three anterior stalks
  - median stalk very long
  - anterior corner stalk-shaped
  - posterior margin emarginate
- Genitalia with:
  - Paramere wide, apex larger than base, with distinct thick setae
  - Volsella small, usually with digitus not clearly visible
  - Basivolsella distinct form basiparamere with basal margin straight
  - Aedeagus stout and cylindrical
  - Genital ring with large lateral reentrance upward and dorsal part usually produced basad

**Taxonomy.** *Foenobethylus* belongs to *Parascleroderma*-complex by the presence of propleuron elongated and expose, R<sub>12v(a)</sub> long, R<sub>12v(b)</sub> usually absent, propodeal declivity without median carina; aedeagus stout and cylindrical. However, the metatrochanter usually with spine, metafemur with spine or small teeth, hypopygium with anterior corner stalk-shaped with similar size of lateral stalks; genital ring with large lateral reentrance upward and dorsal part usually produced basad are features unique in Bethylidae.

**Starting point.** Várkonyi and Polaszek (2007) present a revision of *Foenobethylus*, including keys, descriptions and illustrations to male species. Azevedo & Lanes (2007) redescribed the holotype of the type species of the genus *Foenobethylus*, revising its diagnosis. Savergnini & Azevedo (2013) provided the most actual key to all species included.



**Distribution.** Oriental region, 10 species.

**Hosts.** Unknown

**Check list.**

*bidentatus* Várkonyi & Polaszek, 2007

*elongatus* Várkonyi & Polaszek, 2007

*emilacasellae* Várkonyi & Polaszek, 2007

*gracilis* Kieffer, 1913

*hainanensis* Liu, Chen & Xu, 2011

*pyramidis* Savernini & Azevedo, 2013

*sharkeyi* Savernini & Azevedo, 2013

*thaianus* (Terayama, 1998)

*thomascokeri* Várkonyi & Polaszek, 2007

*zhejiangensis* Liu, Chen & Xu, 2011

## ***Parascleroderma* Kieffer, 1904**

(Figs. 37-38, 48.M, 50.K)

**Original description**— Kieffer 1904a, 41: 376.

**Type-species**— *Paracleroderma fulviceps* Kieffer, 1904a.

**Kind of designation**— original designation.

**Designator**— Kieffer 1904a, 41: 376.

**Synonymous.**

*Ceratepyris* Kieffer, 1905. Synonymy by Argaman 1988 120: 144.

**Original description**— Kieffer 1905 in Kieffer & Marshall 1904–1906, 9: 246, 285–286.

**Type-species**— *Ceratepyris fuscipennis* Kieffer, 1905.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1905 in Kieffer & Marshall 1904–1906, 9: 246, 286–287.

### Diagnosis ♂

- Body flattened and slightly elongate
- Clypeus short, not strongly projecting anteriorly, apical margin variable
- Propleuron elongated
- Pronotum short, elongated and narrowed anteriorly
- Forewing with:
  - $R_{12V}(a)$  long and oblique
  - $R_{12V}(b)$  usually absent
- Metafemur usually enlarged
- Hypopygium with three stalks
- Genitalia with:
  - Paramere C-shaped in lateral view
  - Volsella small, usually with digitus not clearly visible
  - Basivolsella distinct from basiparamere with basal margin acute
  - Aedeagus stout and cylindrical

### Diagnosis ♀

- Body strongly depressed dorsoventrally
- Head usually oval
- Eye usually larger than other *Pristocerinae* female, with 10 to 50 facets
- Mandible thin
- Clypeus with apical margin truncate, thick in frontal view
- Palpal formula 5:2
- Last palpomere with long and distinct seta
- Antenna short, incrassate
- Pronotum longer than wide, with posterior margin shorter than anterior
- Anterior margin of pronotum usually convex
- Collar pronotal very short not produced laterally
- Mesoscutum small, usually subtriangular
- Metapectal-propodeal complex long, broadly in contact with mesoscutum, anterior margin wider than posterior one, lateral margin almost parallel in dorsal view
- Reduced constriction at spiracles
- Mesopleura convex and prominent in dorsal view

**Taxonomy.** *Parascleroderma* has small body, flattened in both sexes; propleuron elongated and expose, R<sub>12va</sub> oblique and long, propodeal declivity without median carina, aedeagus stout and cylindrical in males and head oval with large eyes and mesoscutum subtriangular in females. Such features are shared with *Parascleroderma*-complex which comprises beyond *Parascleroderma*, *Afgoiogfa* and *Foenobethylus*. Females are not known only to *Foenobethylus*. Despite these genera are quite similar, some differences are pointed, especially among *Foenobethylus* and *Parascleroderma*. Males of *Foenobethylus* has the head long, the metatibiae and or the metatrochanter with spines; the hypopygium with five stalks, whereas *Parascleroderma* has the head shorter; the metatibiae and metatrochanters without spines; and the hypopygium with three stalks. Today, the genera delimitation in *Parascleroderma*-complex is not clear and cladistic analyses are requested to better understand them.

Besides the problem pointed out above, Azevedo & Lanes (2007) highlighted their suspicion about Argaman (1988) nomenclatural act when he created a synonym of *Ceratepyris* Kieffer under *Parascleroderma* just because the former was represented only by males and the latter only by females. Some *Ceratepyris* species are completely different of *Parascleroderma*-complex although they also have R<sub>12v(a)</sub> oblique and long. We have analyzed some species originally described as *Ceratepyris* and we observed they are not so flattened than other genera among this complex, they have a well-marked pronotum (with median sulcus and a sharpened anterior carina), a very long mesoscutum with different position of tegulae and a forewing with narrow veins and the radial vein not so long as commonly in *Pristocerinae*.

**Starting point.** Argaman (1988) provided a general revision on *Parascleroderma*, including biological data, descriptions and illustrations of new species and key for male species. He also presented a discussion of its boundaries with *Afgoiogfa*.

**Distribution.** Cosmopolitan, 32 species.

**Hosts.** Coleoptera: *Parascleroderma scobiciae* Kieffer attacks the Bostrychidae *Scobicia chevrieri* Villa (Berland 1928) and *P. berlandi* Maneval attacks the Cleridae *Thanasimus formicarius* (Linnaeus) (Soika 1932).

**Check list.**

*arivaca* Evans, 1978  
*atayal* Terayama, 1998  
*azevedonis* Ward, 2013  
*berlandi* Maneval, 1930  
*carinata* Evans, 1964  
*cisnora* Argaman, 1988  
*claripennis* (Móczár, 1966)  
*fiturcata* Argaman, 1988  
*fulviceps* Kieffer, 1906  
*fuscipennis* (Kieffer, 1905)  
*hindola* Argaman, 1988  
*insolita* (Evans, 1963)  
*ishama* Terayama, 2006  
*jinmo* Terayama, 2006  
*maae* Xu, He & Terayama, 2002  
*minima* Evans, 1978  
*neounicolor* Alencar & Azevedo **nom. to be proposed** for *Cephalonomia unicolor*  
Fouts, 1939  
*nigra* Brues, 1910  
*nigriceps* Kieffer, 1904  
*norcasta* Argaman, 1988  
*okajimai* Terayama, 1998  
*oriana* Argaman, 1988  
*pucallpa* Evans, 1967 69:271  
*remota* (Kieffer, 1912)  
*renaiensis* Terayama, 1998  
*rugosulum* Kieffer, 1906  
*scobiciae* Kieffer, 1919  
*seychellensis* (Kieffer, 1912)  
*sulcatifrons* (Kieffer, 1908)  
*tetradentica* Lim & Lee, 2011  
*unicolor* (Westwood, 1839)

*varlinda* Argaman, 1988

## ***Pristepyris* Kieffer, 1905**

(Figs. 39, 47.A, 48.N, 51.A-B)

**Original description**— Kieffer 1905a, 29: 109, 118-119.

**Type-species**— *Pristepyris rugicollis* Kieffer, 1905a.

**Kind of designation**— subsequent designation.

**Designator**— Kieffer 1914d, 41: 421.

**Synonymous.**

*Acrepyris* Kieffer, 1905. Synonymy by Azevedo & Alencar 2009, 2287: 46.

**Original description**— Kieffer 1905 in Kieffer & Marshall 1904–1906, 9: 249.

**Type-species**— *Epyris reticulatus* Kieffer, 1904b.

**Kind of Designation**— original designation.

**Designator**— Kieffer 1905 in Kieffer & Marshall 1904–1906, 9: 249.

*Neopristocera* Yasumatsu, 1955 **nec** *Neopristocera* Benoît, 1957a. Synonymy by Evans 1963a, 129: 250.

**Original description**— Yasumatsu 1955, 10: 248.

**Type-species**— *Pristocera japonica* Yasumatsu, 1955.

**Kind of Designation**— original designation.

**Designator**— Yasumatsu 1955, 10: 248.

**Diagnosis** ♂

- Median clypeal lobe broad and short, usually truncate or depressed near antennal insertion
- Antenna long, with terminal segment long and thin with acute tip
- Pronotal disc with transverse impression parallel to posterior margin

- Metapectal-propodeal complex short, basal triangular area marked off by shallow depression and/or carina
- Mesopleuron with small callus above
- Tarsal claw tridentate
- Forewing with radial vein long
- Hypopygium with single plate
- Genitalia with:
  - Paramere usually short and rounded
  - Basivolsella long and wide, fused partially to basiparamere
  - Volsella very short and base usually constricted
  - Digitus small
  - Aedeagus with three valves

#### **Diagnosis** ♀

- Head usually longer than wide
- Eye with 10 to more than 50 facets (usually more than 15)
- Mandible thin
- Antenna short, incrassate
- Metapectal-propodeal complex strongly constricted behind spiracles
- Mesopleuron prominent in dorsal view
- Mesotibia spinose

**Taxonomy.** *Acropyris* and *Pristepyris* were considered synonymous by Azevedo and Alencar (2009), and they considered the former older than the later. However, *Pristepyris* and *Acropyris* were proposed by Kieffer in a key for Bethyridae, the former name in Kieffer (1905a) and the latter in Kieffer & Marshall (1904–1906). Both names are referenced in the year 1905 in all subsequent publications, including catalog Gordh & Móczár (1990), in which the former had been included in Epyrinae and the latter in Pristocerinae. Noting the synonymy between both names in genus level and ascertain that both had been described in the same year, Alencar & Azevedo (2009) preferred to keep the *Acropyris* name. During many years until that moment (2009), the name "*Pristepyris*" did not have any data or information that allow the recognition of identity either for species or genus level. *Pristepyris* had remain with only four species, while

*Acrepyris* had 35 valid species. Since both generic names were published by Kieffer in 1905, *Acrepyris* having been considered appropriate to maintain the stability of most species name. However, accessing the history of the name publications, it was found a violation of the priority imposed by the ICZN (1999). Understanding the mistake was due to the knowledge of the context in which the work which both names were proposed for Bethylidae.

The text of Kieffer & Marshall (1904–1906) is one of the greatest references for the comprehension of Bethylidae fauna. The book of 552 pages was not originally fully published but for sequential parts: from 01–64 pages on January 1st 1904; 65–144 pages on April 1st 1905; 145–288 pages on November 1st 1905; 289–368 pages on January 31st 1906 and 369–552 pages on October 1, 1906. In such paper, 14 new genera were proposed which represented a significant increase of Bethylidae biodiversity at the time.

However, concomitant publishing parts of this work, Kieffer has several other articles published between 1904 and 1906 with content overlapping the work of Kieffer & Marshall. For this reason, understanding priority names for some genera or species described by Kieffer is confused, if no rescue of the exact dates of publication of Kieffer publications.

Many Kieffer's genera do not have enough information to enable taxonomists identification of these taxa. Only recently, some of these taxa have been reinterpreted after rediscovery of the types which did not have their depositary place known. Then, many names have been synonymized in recent work (see Alencar & Azevedo 2009; Azevedo and Alencar 2010a; Azevedo and Alencar 2010b; Alencar & Azevedo 2011a).

Recently, when we started this review for “*Acrepyris*”, we found clearly in part of the publication in which *Acrepyris* genus is proposed that *Pristepyris* name was already a valid name. *Acrepyris* is cited as new genus in Kieffer & Marshall on page 249, published on November 1st 1905, while *Pristepyris* is mentioned as a genus already known on page 246 published in the same set pages, referring the designation of *Pristepyris* name to the publication of Kieffer (1905a). This indicates that *Pristepyris*, not *Acrepyris*, is the senior synonymous for the genus conception.

*Pristepyris* is recognized among other genera of Pristocerinae by the presence of three distinct valvae dividing the aedeagus in the male genitalia. This features is unique in Bethylidae.

The clypeus truncate, average size larger than other Bethylidae genera and the pronotal disc with transverse impression parallel to posterior margin of *Pristepyris* is also reported to *Pristocera* and some *Apenesia* species, including those of *columbana* and *pilicornis* species group of Evans (1963b). However, the male genitalia are completely different being useful to identify those genera.

*Pristepyris*, as *Acrepyris*, was a *Pristocera* subgenus but recent cladistic analyses have shown they are valid as distinct clades (Terayama 1996c, Zamprogno & Azevedo 2014). The hypopygium plate easily distinguishes both; it is simple in *Pristepyris* and strongly/deeply divided into two pieces in *Pristocera*.

The only remain problem to diagnose “*Pristepyris/Pristocera*” is the difficulty to separate female of both genera. Today, we try to separate them with features in petiolar body, since *Pristocera* females have the lateral margins projected dorsad while *Acrepyris* does not. However, it is necessary to get more biologic data, mating pairs and probably molecular data should light up the female boundaries between these genera.

In America, *Pristepyris* occurs only above Ecuador line. This is intriguing and should be investigated. A hypothesis to be tested is Amazon Forest as a barrier or the diversification clade may be related to *Apenesia* species *Pristepyris*-like.

**Starting point.** Evans (1963a) present a revision of American species including keys, descriptions and illustrations to male and female species; Terayama (2006) present a synopsis of the genus including key, diagnosis and illustrations of Japanese species. However a global revision and key are still missing.

**Distribution.** Worldwide except Australian region, 38 species.

**Hosts.** Coleoptera: Elateridae (Hyslop 1916; Hayes 1927; Bischoff 1927).

#### **Check list**

*agraensis* Kurian, 1952 **comb. to be reinstall** from *Acrepyris*

*antennatus* (Magretti, 1897) **comb. to be proposed** from *Acrepyris*

*armiferus* (Say, 1828) **comb. to be proposed** from *Acrepyris*

*atrus* (Klug, 1810) **comb. to be proposed** from *Acrepyris*

*bridwelli* (Evans, 1963) **comb. to be proposed** from *Acrepyris*



*californicus* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*chihuahua* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*cockerelli* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*dreisbachi* (Evans, 1977) **comb. to be proposed** from *Acrepyris*  
*erythropodus* (Cameron, 1888) **comb. to be proposed** from *Acrepyris*  
*fraternus* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*hyalinus* (Brues, 1906) **comb. to be proposed** from *Acrepyris*  
*intermedius* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*ishigakiensis* (Yasumatsu, 1955) **comb. to be proposed** from *Acrepyris*  
*japonicus* (Yatumatsu, 1955) **comb. to be proposed** from *Acrepyris*  
*masii* (Soika, 1933)  
*mieae* (Terayama, 1995) **comb. to be proposed** from *Acrepyris*  
*minutus* (Yasumatsu, 1955) **comb. to be proposed** from *Acrepyris*  
*nebulosus* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*orihime* (Terayama, 1999) **comb. to be proposed** from *Acrepyris*  
*oriplanus* (Kieffer, 1911) **comb. to be proposed** from *Acrepyris*  
*orizabae* (Cameron, 1897) **comb. to be proposed** from *Acrepyris*  
*otomi* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*palliditarsis* (Cameron, 1897) **comb. to be proposed** from *Acrepyris*  
*parkeri* (Evans, 1977) **comb. to be proposed** from *Acrepyris*  
*porteri* (Evans, 1964) **comb. to be proposed** from *Acrepyris*  
*quiroga* (Evans, 1964) **comb. to be proposed** from *Acrepyris*  
*rugicollis* Kieffer, 1905 **comb. to be reinstall** from *Acrepyris*  
*rugifrons* (Cameron, 1888) **comb. to be proposed** from *Acrepyris*  
*rugulosus* (Terayama, Xu & He, 2002) **comb. to be proposed** from *Acrepyris*  
*ryukyensis* (Terayama, 1999) **comb. to be proposed** from *Acrepyris*  
*sinaloa* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*sinensis* (Terayama, Xu & He, 2002) **comb. to be proposed** from *Acrepyris*  
*tainanensis* (Terayama, 1995) **comb. to be proposed** from *Acrepyris*  
*takasago* (Terayama, 1995) **comb. to be proposed** from *Acrepyris*  
*tenochca* (Evans, 1963) **comb. to be proposed** from *Acrepyris*  
*varidens* (Cameron, 1904) **comb. to be proposed** from *Acrepyris*  
*zhejiangensis* (Terayama, Xu & He, 2002) **comb. to be proposed** from *Acrepyris*

## *Pristocera* Klug, 1808

(Figs. 40, 48.O, 51.C-D)

**Original description**— Klug 1808, 2: 49.

**Type-species**— *Bethylus depressus* Fabricius, 1804.

**Kind of designation**— original monotypy.

**Designator**— Klug 1808, 2: 49.

**Synonymous.**

*Apristocera* Kieffer, 1914d. **Synonymy to be proposed.**

**Original description**— Kieffer 1914d, 41: 470.

**Type-species**— *Pristocera natalensis* Kieffer, 1911a.

**Kind of designation**— monotypy.

**Designator**— Kieffer 1914d, 41: 470.

*Dicrogenium* Stadelmann, 1894. Synonymy by Zamprogno & Azevedo 2014, 45: 45.

**Original description**— Stadelmann 1894, 20: 199-200.

**Type-species**— *Pristocera rosmarus* Stadelmann, 1892.

**Kind of Designation**— subsequent designation.

**Designator**— Masi 1939, 3: 44.

*Kathepyris* Kieffer, 1907b. Synonymy by Zamprogno & Azevedo 2014, 45: 45.

**Original description**— Kieffer 1907b, 51: 279-280.

**Type-species**— *Kathepyris nyassica* Kieffer, 1907b.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1907b, 51: 280-281.

*Mangesia* Kieffer, 1911b. Synonymy by Benoît 1963a, 119: 4.

**Original description**— Kieffer 1911b, 35: 209.

**Type-species**— *Mangesia fuscipennis* Kieffer, 1911b.

**Kind of Designation**— original designation.

**Designator**— Kieffer 1911b, 35: 209.

*Neurepyris* Kieffer, 1905a. Synonymy by Alencar & Azevedo 2011a, 4: 1.

**Original description**— Kieffer 1905a, 29: 108

**Type-species**— *Neurepyris rufiventer* Kieffer, 1913c.

**Kind of Designation**— subsequent monotypy.

**Designator**— Kieffer 1913c, 7: 107 (see Alencar & Azevedo 2011a).

*Nomineia* Kieffer, 1911a. Synonymy by Zamprogno & Azevedo 2014, 45: 45.

**Original description**— Kieffer 1911a, 80: 452.

**Type-species**— *Nomineia africana* Kieffer, 1911a.

**Kind of Designation**— original designation.

**Designator**— Kieffer 1911a, 80: 452.

*Parapristocera* Brues, 1933a. **Synonymy to be proposed.**

**Original description**— Brues 1933a, 3: 122-123.

**Type-species**— *Parapristocera skwarrae* Brues, 1933a.

**Kind of Designation**— original monotypy.

**Designator**— Brues 1933a, 3: 123.

*Trichelobrachium* Kieffer, 1914d. Synonymy Benoît 1957a, 88: 54.

**Original description**— Kieffer 1914d, 41: 425.

**Type-species**— *Pristocera obliterata* Kieffer, 1913f.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1914d, 41: 425.

**Remark**— Benoît (1957a) included *Pristocera obliterata* in *Pristocera* without any mention about nomenclatural act. Benoît (1963b) presented a synonymic list, when he included *Trichelobrachium* as *Pristocera* synonym but it is not clear if this was a new nomenclatural act. So, we concluded Benoît already considered this type species as *Pristocera* in 1957a.

*Neodicrogenium* Benoît, 1957a. Synonymy by Zamprogno & Azevedo 2014, 45: 45.

**Original description**— Benoît 1957a, 88: 34.

**Type-species**— *Neodicrogenium spina* Benoît, 1957a.

**Kind of Designation**— original designation.

**Designator**— Benoît 1957a, 88: 34.

*Diepyris* Benoît, 1957a. Synonymy by Zamprogno & Azevedo 2014, 45: 45.

**Original description**— Benoît 1957a, 88: 42.

**Type-species**— *Diepyris brunneus* Benoît, 1957a.

**Kind of Designation**— original designation.

**Designator**— Benoît 1957a, 88: 42.

### Diagnosis ♂

- Body robust, large (5 to 30 mm long)
- Antenna short
- Clypeus rectangular; apical margin slightly concave; median carina of clypeus complete
- Gena with spine present or absent
- Pronotum with anterior margin of disc usually carinate; pronotal declivity accentuated
- Propleuron junction region elevated triangularly and extending to prosternum
- Notaulus present; internal region usually foveolate
- Metanotum with medium region narrow; metanotal groove with several foveae
- Hypopygium
  - Divided into two plates
  - Hypopygial chamber present
- Genitalia quadrate with:
  - Paramere apically wide and truncated, narrow and emarginate or bilobate, with fingerlike appendages
  - Basivolsella with callus present or absent
  - Digitus generally trigger-like with crenulated apical region
  - Aedeagus simple or divided into two valves

### Diagnosis ♀

- Head usually as long as large
- Eye large, usually with more than 15 facets
- Mandible large, with two to four teeth
- Antenna short
- Metapectal-propodeal complex strongly constricted anteriorly; sides divergent posteriorly; lateral margin sulcate
- Propodeal spiracle opening usually very large
- Mesopleuron prominent in dorsal view; outer margin almost straight, inner margin convex
- Petiole with body expanded laterally and dorsad
- Probasitarsus not deflected

**Taxonomy.** The taxonomy of this genus was confused since Yasumatsu (1955) and Evans (1963a) included subgeneric classification, including *Pristepyris* (*Acrepyris* that time) as Neotropical lineage. The subgenus classification was rejected by Terayama (1996c).

The close relationship and overlapping traits with other *Pristocerinae* genera, such as *Dicrogenium*, *Neodicrogenium*, *Diepyris* and *Kathepyris* contributed to doubts in the allocation of its species until they were synonymized by Zamprogno & Azevedo (2014). All males share the divided hypopygium which was pointed as the structure that validate the monophyly of *Pristocera* sensu Zamprogno & Azevedo (2014).

*Pristocera* is the largest Bethyridae in size, some species can exceed 20 mm, mainly characterized by the hypopygium divided into two plates and with inner surface presenting a chamber where the muscles are attached.

Some species of *Pristocera* (old genera called *Dicrogenium* and *Neodicrogenium*) have a spine in the gena. This is an exclusive feature that supported to grouping some species in the *Dicrogeniini* proposed by Benoît (1963b). Although the spine is uncommon, there are any hypopygium or genitalia pattern within both that justify their genera status currently.

Krombein (1989) described species formally named as *Apenesia forchhammeri* with male and female. The sex association was done only by the locality and same trap. Here, we realized the holotype female is an *Apenesia* specimen while the male is a

*Pristocera*. Reviewing studies will be able to point if this male whether belongs to any male of *Pristocera* already known or even if it is a new species.

Here we propose two new generic junior synonyms under *Pristocera*, both monotypic, one of them fossil. We briefly discuss these acts below.

*Apristocera*: this monotypic genus was proposed by Kieffer (1914d) based on one single species previously identified as *Pristocera*. The genus definition and species description were not clearly enough to allow the recognition of new specimens to *Apristocera*. The characters listed above as diagnostic to *Apristocera* are presented in the literature (Kieffer 1914d; Kieffer 1911a) and many of them can be found in other *Pristocerinae* genera. The descriptions do not mention metasomal characters and genitalia. Although we could not check the specimen, we propose it as a synonymous of *Pristocera* sense Zamprogno & Azevedo (2014) because *Apristocera natalensis* is a large African species with antenna filiform with different antennomere sizes. *Pristocera* is a genus with one of the largest body size in Bethyridae. According to Kieffer (1911a, 1914d), *Apristocera natalensis* is 15 mm. Besides, Kieffer (1911a) mentioned the species has “*pronotum marginé en avant et en arrière*” (page 454) as diagnostic feature found in *Pristocera*.

*Parapristocera*: according to Brues (1933a), *Parapristocera* is very similar to *Pristocera*. He justified that *Parapristocera* was a different genus because the male has the nervulus interstitial, the head and thorax are smooth, not roughly sculptured, and the radial cell is narrower and longer, and the radius vein lacking only at extreme tip. However, these features are interspecific variation in *Pristocera* according to Zamprogno & Azevedo (2014). Additionally, the male has a short antenna and the female has the metapectal-propodeal complex constricted in front of the middle and gradually narrowed behind, both diagnostic features for *Pristocera*.

**Starting point.** Zamprogno & Azevedo (2014) is the most recent paper that discussed *Pristocera* status, and proposed new diagnostic features to the genus. Benoît (1963b) is a great reference to descriptions and illustration and keys of some *Pristocera* species. However a global revision is still missing.

**Distribution.** Old World, 123 species.

**Hosts.** Coleoptera: Elateridae (Evans 1978b).

**Check list.**

*abdominale* (Turner, 1915)  
*aethiopica* (Benoît, 1963)  
*africana* (Kieffer, 1911)  
*alberti* (Benoît, 1957)  
*albopilosa* (Cameron, 1904)  
*areolata* Muesebeck, 1934  
*armaticeps* (Turner, 1915)  
*atopogamia* (Turner, 1915)  
*aurata* (Benoît, 1963)  
*axitiosa* Benoît, 1957  
*basilewskyi* Benoît, 1956  
*basutoense* (Benoît, 1982)  
*bequaerti* Benoît, 1963  
*bicarinata* (Benoît, 1963)  
*brunnea* (Benoît, 1957)  
*camerunensis* Benoît, 1963  
*capensis* Benoît, 1963  
*cara* Benoît, 1957  
*cariana* Magretti, 1897  
*centrale* (Benoît, 1956)  
*changmaiensis* Terayama, 1998  
*chillaloensis* Benoît, 1963  
*chirindaense* (Benoît, 1963)  
*collare* (Benoît, 1963)  
*commune* (Turner, 1915)  
*congoense* Benoît, 1963  
*conradti* (Stadelmann, 1894)  
*damascena* Marshall, 1905  
*decellei* Benoît, 1963  
*decemdentata* Enderlein, 1901

*depressa* (Fabricius, 1805)  
*distincta* Benoît, 1963  
*draconum* Turner, 1928  
*drewsenii* Westwood, 1874  
*eironeformis* Turner, 1914  
*elongata* (Benoît, 1963)  
*erythrura* Kieffer, 1904  
*fallax* Benoît, 1963  
*felimontana* Benoît, 1963  
*ferruginea* Bischoff, 1915  
*flavicornis* (Kieffer, 1910)  
*formosana* Miwa & Sonan, 1935  
*fossilata* Benoît, 1963  
*gaullei* Kieffer, 1908  
*gigantea* Arle, 1930  
*govindrani* Kurian, 1952  
*heinii* Kohl, 1907  
*hirsutula* Turner, 1928  
*hova* Saussure, 1890 **comb. to be proposed** from *Sclerodermus*\*  
*huberi* Terayama, 2004  
*humilis* Benoît, 1963  
*incerta* (Turner, 1915)  
*jacoti* Benoît, 1963  
*juncta* Turner, 1928  
*katangensis* Benoît, 1963  
*kenyaensis* Benoît, 1963  
*kiefferi* Benoît, 1963  
*kinabalensis* Terayama, 1998  
*kwangoa* Benoît, 1963  
*laticornis* Kieffer, 1913  
*lembana* (Benoît, 1982)  
*levicollis* (Kieffer, 1905)  
*liberiense* (Benoît, 1963)



*luminosa* Benoît, 1963  
*mandjaffana* Benoît, 1963  
*maxima* (Turner, 1917)  
*meridionalis* Benoît, 1963  
*moka* Benoît, 1963  
*mufungwaense* (Benoît, 1963)  
*natalense* Kieffer, 1911 **comb. to be reinstall** from *Apristocera*  
*neocongoensis* Alencar & Azevedo **nom. to be proposed** for *Diepyris congoensis*  
Benoît, 1982  
*neolongatum* Alencar & Azevedo **nom. to be proposed** for *Dicrogenium elongatum*  
Benoît, 1963  
*neonatalense* Alencar & Azevedo **nom. to be proposed** for *Pristocera natalensis*  
Benoît, 1963  
*nigerrima* Benoît, 1957  
*nigrita* Kieffer, 1905  
*numidica* Kieffer, 1911  
*nyassica* (Kieffer, 1906)  
*obliterata* Kieffer, 1913  
*orientalis* (Cameron, 1888)  
*oriphila* Turner, 1928  
*pagana* Benoît, 1957  
*poirieri* Terayama, 2004  
*pondoensis* Benoît, 1963  
*puncticeps* Fouts, 1930  
*regina* Benoît, 1957  
*rhodosiae* Turner, 1928  
*rosmara* Stadelmann, 1892  
*rufa* Kieffer, 1905  
*rufabdrominalis* Benoît, 1963  
*ruficaudata* Westwood, 1874  
*rufiventer* (Kieffer, 1913)  
*rugosa* Enderlein, 1901  
*sampwense* Benoît, 1963

*sarawakensis* Terayama & Yamane, 1998  
*schoutedeni* (Benoît, 1963)  
*silvatica* Benoît, 1963  
*sinhalensis* Turner, 1928  
*skwarrae* (Brues, 1933) **comb. to be proposed** from *Parapristocera*  
*spina* (Benoît, 1957)  
*spinata* (Benoît, 1963)  
*spineceps* (Masi, 1939)  
*spinigera* (Turner, 1915)  
*subrufescens* Turner & Waterson, 1917  
*subviolacea* Enderlein, 1901  
*sulcata* Benoît, 1963  
*sumatrensis* Terayama, 1998  
*superba* Benoît, 1963  
*syriaca* Kohl, 1907  
*tangana* (Benoît, 1982)  
*termitophila* Benoît, 1963  
*thermophila* (Benoît, 1957)  
*tuberculata* (Turner, 1915)  
*turneri* Benoît, 1963  
*uelensis* Benoît, 1963  
*uniforme* (Benoît, 1982)  
*urundiense* (Benoît, 1956)  
*vandenbrandei* Benoît, 1963  
*vumbua* Benoît, 1963  
*zata* Zamprogno & Azevedo, 2014  
*zela* Zamprogno & Azevedo, 2014  
*zintica* Zamprogno & Azevedo, 2014  
*zonta* Zamprogno & Azevedo, 2014  
*zuncra* Zamprogno & Azevedo, 2014

# ***P10***

new genus to be proposed as in chapter 1, this volume

(Figs. 41, 48.P)

**Original description**— Alencar, chapter 1, this volume.

**Type-species**— *Apenesia nyamuragira* Benoît, 1957.

**Kind of designation**— original designation.

**Designator**— Alencar, chapter 1, this volume.

**Synonymous.** None.

**Diagnosis** ♂ (♀ unknown)

- Antenna long and setose
- Clypeus long and triangular
- Metapectal-propodeal complex elongate
- Metaposnotal median carina present
- Hypopigium with:
  - Three short stalks
  - Basal margin strongly concave between stalks
  - Apical margin strongly concave, u-shaped
  - Median surface very short
- Genitalia with:
  - Paramere long and very narrow
  - Apex of paramere with at least one thin and long projection
  - Basivolsela very short
  - Aedeagus with apical long setae
  - Basal ring narrow and placed dorsal-laterally above genital ring

**Taxonomy.** P10 is similar to *Propristocera* because of the clypeus well projected and triangular, hypopygium with three stalks short and the basal ring narrow and placed dorsal-laterally above genital ring. Although, P10 has the hypopygium with apical

margin strongly concave, u-shaped while *Propristocera* presents the hypopygium with apical margin seem to be concave (not compressed by cover slip) because the ventral surface is less sclerotized and strongly surface.

**Starting point.** Alencar (chapter 1, this volume).

**Distribution.** Afrotropical, 01 species.

**Hosts.** Unknown.

**Check list.**

*nyamuragira* (Benoît, 1957)

## ***Propristocera* Kieffer, 1905**

*Stat. rev.* to be proposed as in chapter 1, this volume

(Figs. 42, 51.E-F)

**Original description**— Kieffer 1905, 9: 247 (in Kieffer & Marshall 1904–1906).

**Type-species**— *Propristocera interrupta* Kieffer, 1905d.

**Kind of Designation**— subsequent designation.

**Designator**— Kieffer 1914d, 41: 484.

**Synonymous.**

*Afroccera* Benoît, 1983. Synonym to be proposed as in Alencar, chapter 1, this volume.

**Original description**— Benoît 1983, 97: 674-675.

**Type-species**— *Afroccera bamboutoana* Benoît, 1983.

**Kind of designation**— original designation.

**Designator**— Benoît 1983, 97: 674.

*Neopristocera* Benoît, 1957a **nec** *Neopristocera* Yasumatsu, 1955. Synonym to be proposed as in Alencar, chapter 1, this volume.

**Original description**— Benoît 1957a, 88: 44.

**Type-species**— *Neopristocera triloba* Benoît, 1957a.

**Kind of Designation**— original designation.

**Designator**— Benoît 1957a, 88: 44.

### **Diagnosis** ♂

- Median clypeal lobe projected and triangular
- Hypopygium short with:
  - Three short stalks
  - Median ventral surface less sclerotized and strongly concave
  - Apical margin trilobate when compressed in cover slip
- Genitalia with:
  - Paramere large and very developed dorsally
  - Paramere with strong concavity to fit volsella
  - Basivolsella short, distinct to basiparamere
  - Volsella large
  - Aedeagus usually with two distinct laminae
  - Basal ring narrow and present latero-dorsally

### **Diagnosis** ♀

- Head elongate
- Antennae long
- Eye usually absent
- Pronotum elongate
- Mesonotum elongate and triangular
- Mesopleuron does not cover lateral of metapectal-propodeal complex in dorsal view
- Metapectal-propodeal complex strongly constricted at its extreme anterior end

**Taxonomy.** *Propristocera* and *Neopristocera* were synonymized together under *Apenesia* by Evans (1963b, 130: 257). Both names represent some of their original species plus many *Apenesia* not placed in any group before. Alencar (chapter 1, this volume) indicated by phylogenetics analyses they form a monophyletic clade with

*Afrocer*. Alencar (chapter 1, this volume) revalidated *Propristocera* and proposed *Afrocer* and *Neopristocera* as junior synonym. *Propristocera* is diagnosed specially by the strong median concavity in outer hypopygeal surface. In some specimens this concavity is very little sclerotized and may have folds like an “accordion”. Usually the median clypeal lobe is triangular and very projected forward; mandible is one to four teeth; the paramere has a small concavity inside to accommodate the volsella which is short and detached to basiparamere; cuspis is never divided; basal ring reduced and placed latero-dorsally. This group is found in Afrotropical, Palaearctic and Oriental regions. Due to hypopygium features, some species could be related to *Prosapenesia*. However, *Prosapenesia* has median clypeal lobe very reduced, mandible large and forewing with stigma usually very large and radial vein weakly marked, differing completely from *Propristocera* which has median clypeal lobe projected forward, mandible narrow and forewing with stigma median-sized and radial vein well-marked. One couple were recorded in phoretic copulation. Females of *Propristocera* have head oval, metapectal-propodeal complex strongly constricted at its extreme anterior end; mesonotum elongate and triangular in dorsal view; mesopleuron does not cover the lateral of metapectal-propodeal complex in dorsal view; eyes usually absent.

**Starting point.** Alencar (chapter 1, this volume), Benoît (1957a) and Benoît (1983).

**Distribution.** Afrotropical, Palaearctic and Oriental regions, 24 species.

**Hosts.** Unknown.

**Check list.**

*acuta* (Benoît, 1957)*yptia* Kieffer, 1921

*bamboutoana* (Benoît, 1983)

*carinicollis* (Terayama, 2004)

*emarginata* (Santhosh & Ranjith, 2016)

*formosimonticola* (Terayama, 1996)

*flavipes* (Fouts, 1930)

*interrupta* Kieffer, 1905

*kusigematii* (Terayama, 1999)

*luzonica* (Fouts, 1930)  
*mindanaensis* (Fouts, 1930)  
*neavei* (Turner & Waterson, 1917)  
*nyama* Benoît, 1957  
*okinawensis* (Terayama, 1999)  
*orientalia* (Ranjith & Santhosh, 2016)  
*percurrens* Kieffer, 1905  
*pingtungensis* (Terayama, 1996)  
*polita* (Fouts, 1930)  
*pseudosuzannae* Benoît, 1957  
*pulchella* (Terayama, 2004)  
*sinensis* (Xu, Terayama & He, 2002)  
*suzannae* Benoît, 1957  
*tagala* (Ashmead, 1905)  
*tengu* (Terayama, 2006)  
*triloba* (Benoît, 1957)

## ***Prosapenesia* Kieffer, 1910**

(Figs. 43)

**Original description**— Kieffer 1910b, 79: 42-43.

**Type-species**— *Prosapenesia lacteipennis* Kieffer, 1910b.

**Kind of designation**— original monotypy.

**Designator**— Kieffer 1910b, 79: 43.

### **Synonymous.**

*Neusakosia* Benoît, 1981. Synonymy by Terayama 1995c, 63: 889-890.

**Original description**— Benoît 1981, 95: 839-840.

**Type-species**— *Neusakosia schoutedeni* Benoît, 1981.

**Kind of Designation**— original designation.

**Designator**— Benoît 1981, 95: 840.

*Usakosia* Kieffer, 1914f. **Synonymy to be proposed.**

**Original description**— Kieffer 1914f, 1: 203–204.

**Type-species**— *Usakosia albipennis* Kieffer, 1914f.

**Kind of Designation**— monotypy.

**Designator**— Kieffer 1914f, 1: 204.

**Diagnosis** ♂ (♀ unknown)

- Head with frons truncated
- Mandible usually very large
- Clypeus very short
- Forewing with:
  - Pterostigma remarkably large and broad
  - r-rs2v&Rs2v junction distinct and angled
  - r-rs2v&Rs2v weakly marked and very thin
- Mesotibia with strong spines at outer margin
- Hypopygium with lamellar process on outer median surface
- Paramere with concavity in inner surface to accommodate volsella

**Taxonomy.** Benoît (1981) proposed “Usakosiini” to group *Prosapenesia*, *Neusakosia* and *Usakosia* based on the presence of very large mandibles, the median clypeal lobe excavated, the frons truncated, the eyes glabrous; the forewing hyaline with pterostigma extremely large and r-rs2v&Rs2v depigmented and weakly marked, and the hypopygium with a small concavity on outer surface. Kieffer (1914f) and Benoît (1981) did not point any exclusive characteristic to delimit *Usakosia*. This genus remains with only one species which type does not have the depositary know to check taxonomic information. All information in literature are not enough to support *Usakosia* as a separate genus from *Prosapenesia* sense Terayama (1995c). Considering *Usakosia* fits perfectly well in male diagnosed characteristics we justify the proposal of this genus as a junior synonymous of *Prosapenesia*.

In this new concept, *Prosapenesia* is an Afrotropical genus endemic to desert areas of Southern Namibia and Southwestern South Africa. Its species are usually large in size and some of them have a typical orange colour what make them easy to recognize. Zamprogno & Azevedo (2014) found *Prosapenesia* as a clade close to some



*Apenesia* species. The *Apenesia* species studied in the phylogeny Zamprogno & Azevedo (2014) obtained belong to *Apenesia* P3 which have many similarities with *Prosapenesia*. Both, *Apenesia* P3 and *Prosapenesia* share the hypopygium with a concavity or lamellar process on external median surface; present median stalk short and equally sized to lateral corners of hypopygium and the paramere with concavity in inner surface to accommodate volsella. Although these features are similar, the main characteristics presented in head can easily be used to distinguish both genera. While *Prosapenesia* has the frons truncated; median clypeal lobe reduced and large mandible, *Apenesia* P3 has the head as long as large with frons not truncated; median clypeal lobe prominent, usually triangular, and narrow mandible.

**Starting point.** Benoît (1981) presented a global view of most *Prosapenesia* species. Terayama (2004a) is a complementary literature that added two species for the genus.

**Distribution.** Afrotropical region, 7 species.

**Hosts.** Unknown.

**Check list.**

*albipennis* (Kieffer, 1914) **comb. to be proposed** to be proposed from *Usakosia*

*bilobata* Benoît, 1981

*lacteipennis* Kieffer, 1910

*longimandibulata* Terayama, 2004

*princeps* (Benoît, 1981)

*schoutedeni* (Benoît, 1981)

*sesriemensis* Terayama, 2004

## ***Protisobrachium* Benoît, 1957**

(Figs. 44, 48.Q, 51.G-H)

**Original description**— Benoît 1957a, 88: 31-32.

**Type-species**— *Protisobrachium gracile* Benoît, 1957a.

**Kind of designation**— original designation.

**Designator**— Benoît 1957a, 88: 32.

**Synonymous.** None.

**Diagnosis.** ♂ (♀ unknown)

- Body elongated and short
- Eyes with long erect hairs
- Clypeus broadly produced anteriorly with a small median tooth
- Notauli absent or poorly impressed
- Forewing:
  - R<sub>12v(a)</sub> long
  - R<sub>12v(b)</sub> long
- Hypopygium with:
  - Posterior margin strongly concave medially
  - Median and lateral stalks very short and with similar length
- Genitalia with:
  - Paramere large
  - Basivolsella fused to basiparamere
  - Cuspis short
  - Aedeagus divided into two parts, dorsal part long and ventral one short and tubular

**Taxonomy.** *Protisobrachium* has the R<sub>12v(a)</sub> long similar to *Parascleroderma* complex (= *Parascleroderma*, *Foenobethylus* and *Afgoiogfa*). Despite that, the presence of clypeus broadly produced anteriorly with small median tooth and the aedeagus divided into two distinct parts resembles *Dissomphalus*. However, cladistic analysis by Terayama (1996c) included *Protisobrachium* as sister group of *Pseudisobrachium*. Species of *Protisobrachium* and many *Pseudisobrachium* have the mesosoma elongate, eyes with long and erect hairs but as mentioned by Terayama (1996c), they were treated as convergence that kept both genera as sister group. The relationship of *Protisobrachium*, *Dissomphalus*, *Parascleroderma* complex and *Pseudisobrachium* are required to better understand the taxonomic limit of each genus.

**Starting point.** Benoît (1957a) described *Protisobrachium* and two species to the genus. Both species are very well illustrated. Terayama (1995e) described and illustrated one more species of *Protisobrachium* and provided new illustrations of the type species of the genus.

**Distribution.** Afrotropical region, Oriental region, 05 species.

**Hosts.** Unknown.

**Check list.**

*asianum* Terayama, 1995

*gracile* Benoît, 1957

*pallidimanus* (Kieffer, 1912)

*rwindicum* Benoît, 1957

*transkeiense* (Turner, 1928) **comb. to be proposed** from *Pseudisobrachium*

## ***Pseudisobrachium* Kieffer, 1904**

(Figs. 45, 48.R, 51.I)

**Original description**— Kieffer 1904a, 41: 368.

**Type-species**— *Pseudisobrachium laticeps* Kieffer, 1904a.

**Kind of designation**— subsequent designation.

**Designator**— Kieffer 1906 in Kieffer & Marshall 1904–1906, 9: 297.

**Synonymous.**

*Isobrachium* Ashmead, 1893, 45: 35-40. [**nec** Förster 1856; misidentification.]

*Monepyris* Kieffer, 1905a. Synonymy by Kieffer 1906 in Kieffer & Marshall 1904–1906, 9: 297.

**Original description**— Kieffer 1905a, 29: 108.

**Type-species**— *Epyris halidai* Westwood, 1874 (junior synonymous of *Epyris subcyaneum* Haliday).

**Kind of Designation**— original designation.

**Designator**— Kieffer 1905a, 29: 108.

*Xestobethylus* Cameron, 1909b. Synonymy by Evans 1973a, 75: 194.

**Original description**— Cameron 1909b, 35: 450.

**Type-species**— *Xestobethylus pallidipes* Cameron, 1909b.

**Kind of Designation**— original monotypy.

**Designator**— Cameron 1909b, 35: 450.

*Plutobethylus* Kieffer, 1910b. Synonymy by Evans 1961, 126: 222.

**Original description**— Kieffer 1910b, 79: 51.

**Type-species**— *Plutobethylus distans* Kieffer, 1910b.

**Kind of Designation**— original designation.

**Designator**— Kieffer 1910b, 79: 51.

*Lyssepyris* Kieffer, 1913a. Synonymy by Evans 1961, 126: 222.

**Original description**— Kieffer 1913a, 7: 108.

**Type-species**— *Holepyris flavicornis* Kieffer, 1906b.

**Kind of Designation**— original designation.

**Designator**— Kieffer 1913a, 7: 108.

*Lissepyris* Kieffer, 1914d, 41: 236. [*lapsus* for *Lyssepyris*.]

*Xantepyris* Kieffer, 1913a. Synonymy by Evans 1961, 126: 222.

**Original description**— Kieffer 1913a, 7: 108.

**Type-species**— *Epyris flaviventris* Fouts, 1928.

**Kind of Designation**— original designation.

**Designator**— Kieffer 1913a, 7: 108.

*Xanthepyrus* Kieffer, 1914d, 41: 424 [unjustified emendation].

*Parisobrachium* Kieffer, 1914d. Synonymy by Evans 1961, 126: 222.

**Original description**— Kieffer 1914d, 41: 237, 424.

**Type-species**— *Rhabdepyris albipes* Kieffer, 1914d.

**Kind of Designation**— original monotypy.

**Designator**— Kieffer 1914d, 41: 424.

*Afrisobrachium* Benoît, 1957a. Synonymy by Argaman 1989, 1: 11.

**Original description**— Benoît 1957a, 88: 29.

**Type-species**— *Afrisobrachium mavortinus* Benoît, 1957a.

**Kind of Designation**— original designation.

**Designator**— Benoît 1957a, 88: 29.

*Pseudoisobrachium* Kieffer in Ogloblin 1925a, 20: 24 [unjustified emendation].

*Edapholigon* Ogloblin, 1963. Synonymy by Evans 1978b, 27: 49.

**Original description**— Ogloblin 1963, 26: 133.

**Type-species**— *Pseudisobrachium (Edapholigon) hypogeum* Ogloblin, 1963.

**Kind of Designation**— original designation.

**Designator**— Ogloblin 1963, 26: 133.

#### **Diagnosis** ♂

- Clypeus with median lobe strongly produced usually trapezoidal
- Flagellomeres equally cylindrical
- Eye usually densely covered with long hairs
- Hypopygium with:
  - Three short stalks
  - Usually with median process projection in inner surface
- Genitalia with:
  - Paramere deeply divided into separate arms, dorsal one curved and basally articulated to basiparamere
  - Inner margin of basivolsella with vannus

- Aedeagus mesoconvex with basal region narrow
- Genital ring ventrally placed
- Basal ring complete, large, triangular and ventrad

#### **Diagnosis** ♀

- Eye with single facet or absent
- Mesoscutum elongate, lateral margin slightly convergent posterad
- Mesopleuron large, bulging laterally, never reaching metapectal-propodeal complex
- Metapectal-propodeal complex strongly constricted anteriorly, forming neck between posterior main portion and anterior small position which can be bilobed
- Mesotibia with spines above

**Taxonomy.** Kieffer (1904a) defined *Pseudisobrachium* as females wingless identified by Ashmead (1893) under the name *Isobrachium*. In 1906, Kieffer synonymized *Monepyris* under *Pseudisobrachium* convinced by Baker that *Monepyris* males should be associated to *Pseudisobrachium* females despite the strong sexual dimorphism. This sexual association has been confirmed recently by finding one mating couple attached (data not published yet).

Taxonomy is almost restricted to males *Pseudisobrachium* since females are rarely collect and poorly representative in collection. According to Evans (1978b), sometimes females are taken in Berlese samples of soil or leaf litter, presumably because the sample includes a portion of an ant nest, which *Pseudisobrachium* is frequently associated.

*Pseudisobrachium* is one of the most common genera in Bethyridae field collections, especially in tropical areas and there are many new species to be described. Males of *Pseudisobrachium* with the eyes not densely covered with long hairs can run to *Apenesia*. Nevertheless, both genera can be easily separated by the shape of genitalia parameres. *Pseudisobrachium* has two distinct parameres, whereas *Apenesia* has a unique lobe. There are more genital features we can list to distinguish both genera but coincidentally, almost always it is possible to identify both parameres at the top of metasoma in *Pseudisobrachium* during the sort process without dissecting the genitalia. There is nothing recorded in Bethyridae literature that can explain that but it seems when males of *Pseudisobrachium* their parameres are projected out of the body.

*Pseudisobrachium* is very similar to *Caloapenesia* by having the body usually strongly punctuate, the eyes usually prominent, with long erect hairs, the genitalia with paramere deeply divided into separate arms and basal ring complete and ventrad. Those genitalia conditions are present only in the *Pseudisobrachium* complex among Pristocerinae (*Pseudisobrachium*, *Caloapenesia* and *Calobrachium*).

**Starting point.** Evans (1961) presented a revision of the genus in North and Central America, with key, distribution and classification in species group level. Terayama (2006) revised *Pseudisobrachium* species. Azevedo (2008) revised the Neotropical species and Gobbi & Azevedo (2010) added many species and information about the genus.

**Distribution.** Cosmopolitan, 190 species.

**Hosts.** The females are often found in ant nests, so it is suggested that they are parasitoids of myrmecophilous beetle larvae (Evans 1961; 1964; 1978b).

**Check list.**

*abdominalis* (Westwood, 1839) **comb. to be proposed** from *Sclerodermus*

*acrum* Gobbi & Azevedo, 2010

*alayo* Evans, 1969

*albipes* (Ashmead, 1894)

*albitinctum* Evans, 1966

*amplum* Waichert & Azevedo, 2004

*angulatum* Evans, 1964

*anomalum* Evans, 1961

*apache* Evans, 1961

*apenesoides* Waichert & Azevedo, 2004

*arenarium* Evans, 1961

*ashmeadi* Evans, 1961

*atriceps* (Kieffer, 1910) **comb. nov** *Dissomphalus*

*aztecum* Evans, 1961

*babaeculuscum* (Benoît, 1957)

*beckeri* Evans, 1969  
*beggsae* (Ward, 2013)  
*belokobylskyi* Gorbatovsky, 1995  
*belum* Gobbi & Azevedo, 2010  
*bifum* Gobbi & Azevedo, 2010  
*bisulcatum* Evans, 1969  
*blomi* Evans, 1961  
*boliviense* Kieffer, 1910  
*brasiliense* Kieffer, 1910  
*breviceps* Evans, 1969  
*bruesi* Evans, 1969  
*brunneum* Evans, 1961  
*burchellanium* (Westwood, 1874)  
*calidum* Evans, 1966  
*capixabum* Waichert & Azevedo, 2004  
*carbonarium* (Ashmead, 1893)  
*carolinianum* Evans, 1961  
*castaneiceps* Evans, 1966  
*castaneum* Evans, 1961  
*celum* Gobbi & Azevedo, 2010  
*chacoense* Evans, 1973  
*chilense* Evans, 1969  
*clypeatum* Evans, 1961  
*collinum* (Ashmead, 1894)  
*colombium* Vargas & Terayama, 2002  
*colombiensis* Terayama, 2004  
*comanche* Evans, 1961  
*complanatum* Evans, 1969  
*concinnum* Evans, 1969  
*cooperi* Evans, 1961  
*corvinum* Evans, 1969  
*costaricanum* Evans, 1961  
*coxalis* (Cameron, 1888)



*crassicornis* (Westwood, 1874)  
*crassum* Evans, 1961  
*cruciferum* (Kieffer, 1912)  
*cuspidatum* Waichert & Azevedo, 2004  
*dalmati* Evans, 1961  
*danum* Gobbi & Azevedo, 2010  
*demissum* Evans, 1967  
*deplanatum* Evans, 1969  
*digum* Gobbi & Azevedo, 2010  
*distans* (Kieffer, 1910)  
*distinguedum* Kieffer, 1904  
*elegantulum* Ogloblin, 1925  
*elium* Gobbi & Azevedo, 2010  
*erythrocephalum* Evans, 1973  
*ferum* Gobbi & Azevedo, 2010  
*fialai* Hoffer, 1936  
*filum* Waichert & Azevedo, 2004  
*flavicornis* (Kieffer, 1906)  
*flavinervis* Fouts, 1928  
*flaviventre* (Kieffer, 1904)  
*formosum* Waichert & Azevedo, 2004  
*fulleri* Terayama, 2004  
*fuschanensis* Terayama, 2004  
*fuscicornis* Evans, 1969  
*gabrum* Gobbi & Azevedo, 2010  
*genum* Gobbi & Azevedo, 2010  
*gibbosum* Evans, 1961  
*gigas* Evans, 1961  
*gobum* Gobbi & Azevedo, 2010  
*graciliventre* Ogloblin, 1925  
*haemorrhoidalis* (Westwood, 1874)  
*haywardi* Ogloblin, 1950  
*holum* Gobbi & Azevedo, 2010

*hongkongense* Terayama, 1996  
*howdeni* Evans, 1969  
*hurdi* Evans, 1961  
*hypogeum* Ogloblin, 1963  
*illipum* Evans, 1969  
*inchoatum* Kieffer, 1910  
*intentum* Waichert & Azevedo, 2004  
*intermedium* Kieffer, 1904  
*itamum* Gobbi & Azevedo, 2010  
*ivaum* Gobbi & Azevedo, 2010  
*jamaicense* Evans, 1969  
*jethum* Gobbi & Azevedo, 2010  
*koreana* Lim & Lee, 2011  
*krombeinbi* Evans, 1961  
*laisum* Gobbi & Azevedo, 2010  
*laticeps* Kieffer, 1904  
*latum* Waichert & Azevedo, 2004  
*lepidum* Terayama, 2004  
*leptanillae* Duchaussoy, 1916  
*lidum* Gobbi & Azevedo, 2010  
*lini* Terayama, 2004  
*luisae* Vargas & Terayama, 2002  
*lurdum* Gobbi & Azevedo, 2010  
*macrops* Evans, 1961  
*magnum* Waichert & Azevedo, 2004  
*manni* Evans, 1961  
*marum* Gobbi & Azevedo, 2010  
*masoni* Evans, 1967  
*mattheusi* Evans, 1961  
*merklei* Bruch, 1917  
*micheneri* Evans, 1961  
*nichoacanum* Evans, 1961  
*minimum* Evans, 1961

*minutissimum* Evans, 1961  
*monticola* Kieffer, 1913  
*montivagum* Evans, 1964  
*mrazi* Ogloblin, 1925  
*nambui* Terayama, 2006  
*nepalensis* Terayama, 2004  
*nibum* Gobbi & Azevedo, 2010  
*nigriculum* Evans, 1961  
*obscurum* Evans, 1961  
*occidentale* Evans, 1961  
*ogloblini* Evans, 1964  
*oligocenicum* Theobaldi, 1937  
*onoyamai* Terayama, 1999  
*opimum* Waichert & Azevedo, 2004  
*optimum* Evans, 1964  
*otiosum* Evans, 1961  
*otum* Gobbi & Azevedo, 2010  
*pallidicorne* Kieffer, 1910  
*pallidinervis* Duchaussoy, 1916  
*pallidipes* (Cameron, 1909)  
*pallidum* Evans, 1961  
*paotaoanum* Terayama, 2004  
*parcum* Evans, 1969  
*paucipunctatum* Fouts, 1928  
*pauxillum* Evans, 1969  
*perpunctatum* Evans, 1961  
*persimile* Evans, 1961  
*petiolatum* Evans, 1961  
*philippinarum* Kieffer, 1922  
*plaumanni* Evans, 1964  
*porteri* Evans, 1969  
*praecipuum* Evans, 1969  
*pretum* Gobbi & Azevedo, 2010

*prolongatum* (Provancher, 1881)  
*pseudoobscurum* Evans, 1969  
*pubescens* Kieffer, 1906  
*pulcherrimum* Evans, 1964  
*pusillum* Evans, 1961  
*quirum* Gobbi & Azevedo, 2010  
*rafum* Gobbi & Azevedo, 2010  
*rapotorti* Ogloblin, 1963  
*rettenmeyeri* Evans, 1961  
*ricum* Gobbi & Azevedo, 2010  
*rotundum* Waichert & Azevedo, 2004  
*roubali* Menozzi, 1925  
*rufiventre* (Ashmead, 1893)  
*rufopictum* Evans, 1961  
*ryukyuanum* Terayama, 1999  
*silvicolum* Terayama, 2004  
*solenopsidicola* Bruch, 1917  
*solenopsiphilum* Ogloblin, 1963  
*stangei* Evans, 1969  
*steinbachi* Evans, 1966  
*subcyaneum* (Haliday, 1838)  
*superbum* Evans, 1961  
*suprum* Gobbi & Azevedo, 2010  
*ternarium* Evans, 1969  
*terresi* Mann, 1915  
*testaceipes* Kieffer, 1906  
*texanum* Evans, 1961  
*tidum* Gobbi & Azevedo, 2010  
*timberlakei* Evans, 1978  
*transversum* Evans, 1969  
*triacutum* Waichert & Azevedo, 2004  
*tridens* Evans, 1969  
*tucumanum* Evans, 1969

*turbinatum* Evans, 1969  
*unidens* Kieffer, 1922  
*uruguayense* Ogloblin, 1938  
*urum* Gobbi & Azevedo, 2010  
*ventriosum* Waichert & Azevedo, 2004  
*visum* Gobbi & Azevedo, 2010  
*weneri* Evans, 1967  
*xicum* Gobbi & Azevedo, 2010  
*zandum* Gobbi & Azevedo, 2010  
*zeteki* Evans, 1961

## *Scaphepyris* Kieffer, 1904

(Figs. 47. B-H)

**Original description**— Kieffer 1904a, 41: 370.

**Type-species**— *Scaphepyris rufus* Kieffer, 1904.

**Kind of designation**— monotypy.

**Designator**— Kieffer 1904a, 41: 370.

**Synonymous.** None.

**Diagnosis** ♀ (♂ unknown)

- Body weakly flattened
- Head as long as wide
- Antennae short
- Eye reduced
- Clypeus with median lobe well developed, apical margin subangulate
- Lateral of pronotum moderately arched
- Mesonotum triangulate and short; not divided into mesoscutum and scutellum
- Metapectal-propodeal complex weakly constricted anteriorly
- Mesopleuron expanded laterally; subtegular groove long

- Mesotibia very spinose

**Taxonomy.** The genus has been reported from Kieffer (1905a, 29: 102) authorship, according to Gordh & Móczár (1990) and Lanes & Azevedo (2007). Although Kieffer (1905a) cited *Scaphepyris* as new genus and *S. rufus* as new species in a key, the genus was first mentioned in Kieffer (1904a) when *S. rufus* was first described and mentioned as type species of the genus. Thus the correct date of this genus is 1904 in Kieffer (1904a p. 370) rather than 1905 in Kieffer (1905a, p.102). Kieffer (1908c, 1914d) cited *Scaphepyris* as a genus in 1904. Many nomenclatural acts in Bethylinidae are doubtful as pointed to *Scaphepyris* because of publications dates of many Kieffer 1905's papers are confused.

*Scaphepyris* was first included in Scleroderminae. Lanes & Azevedo (2007) were able to find the type for analysis and transferred it to Pristocerinae because of the presence of the diagnostic characters shared with females of other genera of this subfamily, such as the eyes being extremely reduced, the absence of ocelli and wings, the constriction between the metapectal-propodeal complex and the mesonotum, and the mesopleuron clearly visible in dorsal view.

*Scaphepyris* is similar to some *Apenesia* female by having the metapectal-propodeal complex weakly constricted, the mesotibiae very spinose, and the mesopleuron large in dorsal view. But *Scaphepyris* has the mesopleuron with an elongate upper groove, the clypeus with median lobe very projected and its apical margin subangulate, whereas *Apenesia* has the mesopleuron smooth, the clypeus with median lobe short or somewhat projected and its apical margin emarginate or straight. According to Lanes & Azevedo (2007), it might be possible that the female of *Scaphepyris* represents one of genera known only from males since the sexual dimorphism is strong in Pristocerinae, particularly *Protisobrachium* Benoît and *Neoapenesia* Terayama because they are the only two genera from Oriental region with female unknown. In other words, *Scaphepyris rufus* could be placed as one different species of *Apenesia*.

**Starting point.** Lanes & Azevedo (2007) redescribed both genus and the type species, providing good illustrations for recognition of new specimens.

**Distribution.** Oriental region, 01 species.

**Hosts.** Unknown.

**Check list.**

*rufus* Kieffer, 1904

## ***Trichiscus* Benoît, 1956**

(Figs. 46, 48.S, 51.J-K)

**Original description**— Benoît 1956, 51: 562 (as subgenus of *Dissomphalus* Ashmead).

**Type-species**— *Dissomphalus (Trichiscus) wittei* Benoît, 1956.

**Kind of designation**— original monotypy.

**Designator**— Benoît 1956, 51: 562.

**Synonymous.** None.

**Diagnosis.**

- Body robust and short
- Clypeus prominent, its median lobe not well-defined, median area elevated with anterior margin slightly concave, forming two saliences
- Pronotum with anterior margin rounded
- Forewing with R<sub>12v(a)</sub> long
- Metasoma short with cross-section subcircular
- Metasomal tergite I longer than II
- Metasomal tergite II reduced, shorter than III, its posterior margin strongly excavated
- Metasomal tergite III with tergal process consisting of some paralleled rows of setae placed on anterior third of lateral surface
- Hypopygium with:
  - Median stalk very wide, apex usually rounded

- Lateral stalk conspicuous
- Posterior margin usually emarginate
- Genitalia with:
  - Paramere with apical surface folded into outer and inner laminae
  - Basiparamere distinctly separated from basivolsella on ventral side; apical surface horizontal, angled inward
  - Digitus with hypertrophied membranous ramous giving rise from out surface of basal area.
  - Basivolsella with inner border thickened
  - Aedeagus divided into dorsal body and ventral ramus
  - Aedeagal apodeme short, never surpassing the genital ring
  - Base of aedeagus covered by dorsal diamond-shaped lamina
  - Genital ring very wide laterally

**Taxonomy.** *Trichiscus* was first proposed as a subgenus of *Dissomphalus* (see Benoît 1956) due to the body robust, the clypeus prominent, its median lobe not well-defined, the metasoma broad and short with tergal process, the aedeagus divided into dorsal body and ventral ramus. In 1986, Benoît discussed some differences between *Trichiscus* and *Dissomphalus*, stating that the former has the second tergite very reduced, the tergal process on third tergite, and the genitalia with large rami of aedeagus and cuspis with appendix, whereas *Dissomphalus* have the second tergite very wide; the tergal process, when present, on the second tergite, and genitalia with rami of aedeagus very developed. Because of those differences, Benoît (1986) elevated *Trichiscus* to the genus rank. It is clear *Dissomphalus* and *Trichiscus* are closed related (Terayama 1996c) but their position should be better investigated under cladistic approach.

**Starting point.** Azevedo (2014b) presented an extensive revision about *Trichiscus*, a key and illustrations to all species of the genus. Benoît (1957a) present very good illustration of *Trichiscus wittei* (Benoît 1956) dorsal body.

**Distribution.** Afrotropical, 14 species.

**Hosts.** Unknown.



### **Check list.**

*briani* Azevedo, 2014  
*camargoi* Azevedo, 2014  
*copel&* Azevedo, 2014  
*denisi* Azevedo, 2014  
*jimi* Azevedo, 2014  
*lubo*i Azevedo, 2014  
*lynn*ae Azevedo, 2014  
*moure*i Azevedo, 2014  
*noort*i Azevedo, 2014  
*norm*ani Azevedo, 2014  
*oh*li Azevedo, 2014  
*suzanna*e Benoît, 1986  
*witte*i (Benoît, 1956)  
*zupark*oi Azevedo, 2014

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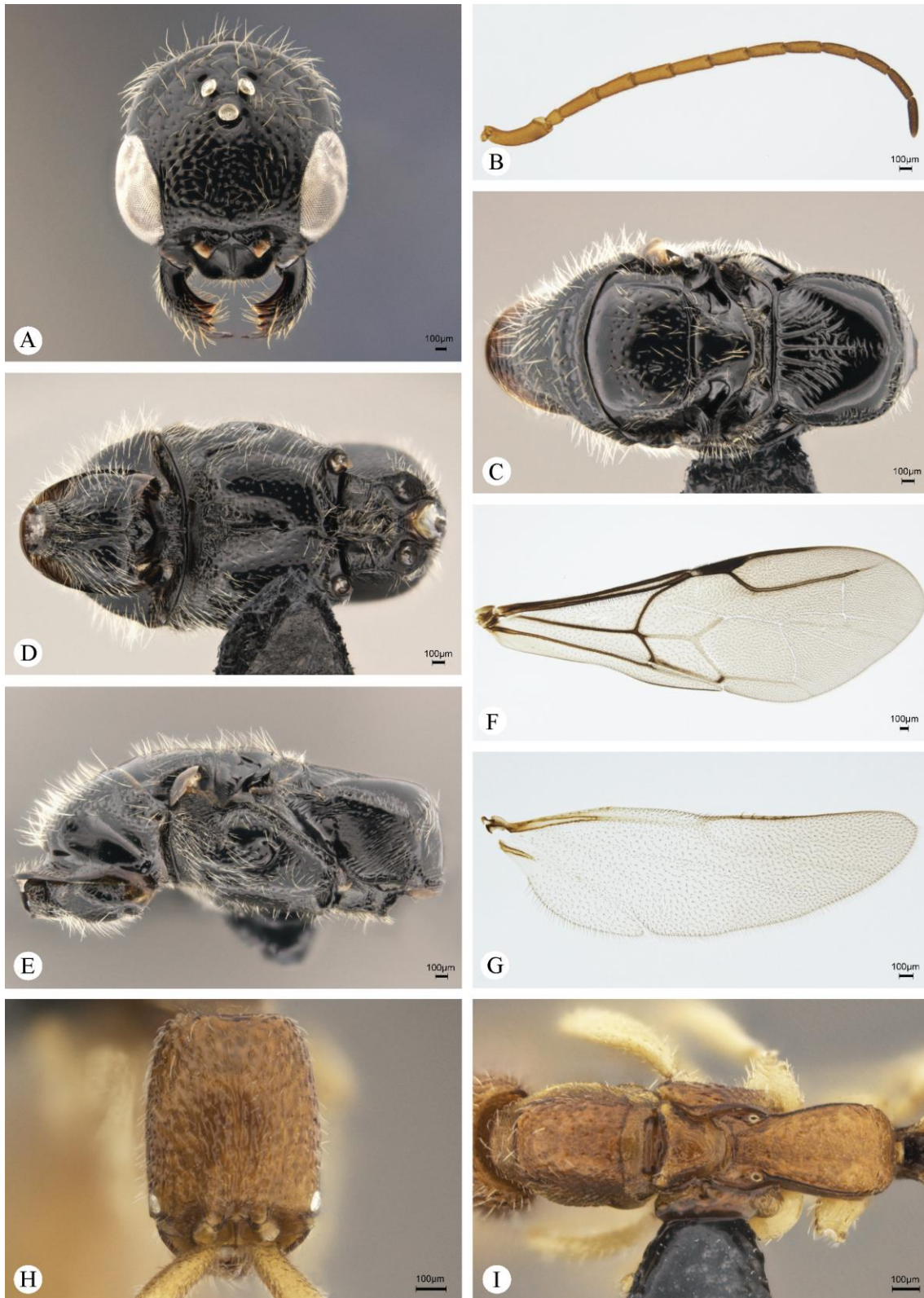
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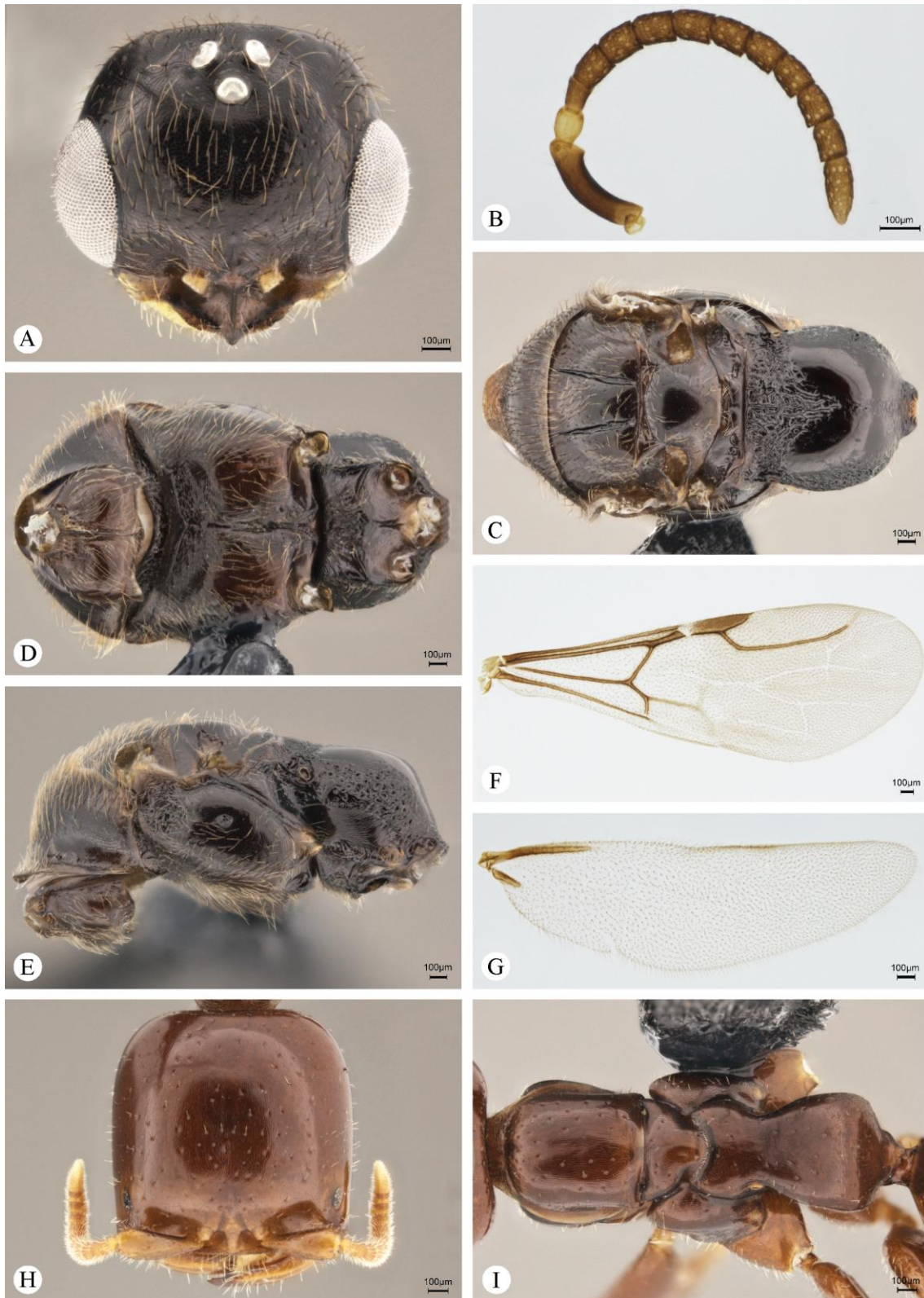
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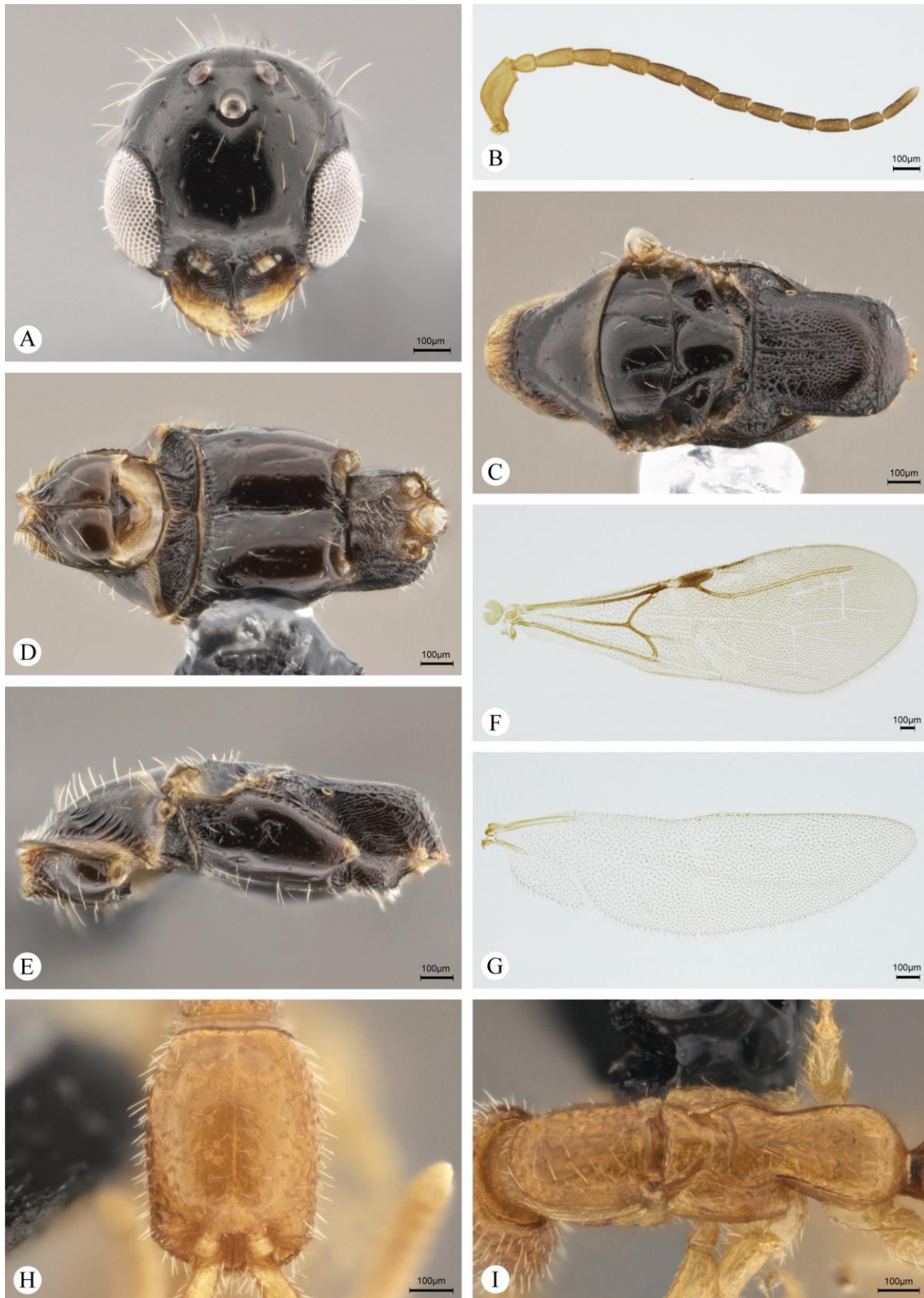


**FIGURE 26.** *P4*, A-G male, H-I Female. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Head, dorsal view; I Mesosoma, dorsal view.





**FIGURE 27.** *Apenesia*, A-G male, H-I Female. A. Head, dorsal view; B. Antenna, anterior view; C. C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Head, dorsal view; I Mesosoma, dorsal view.

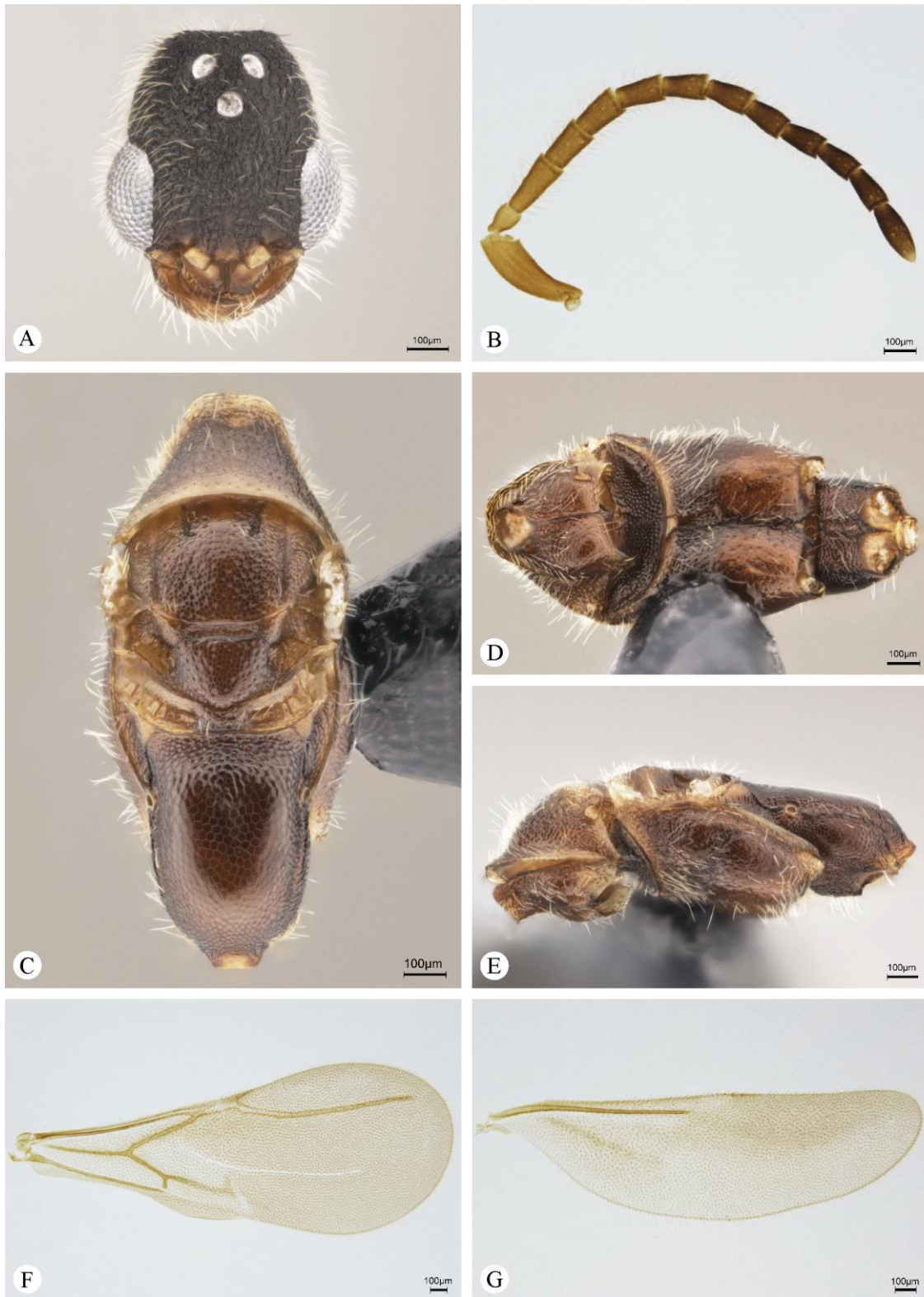


**FIGURE 28.** *P6*, A-G male, H-I Female. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Head, dorsal view; I Mesosoma, dorsal view.



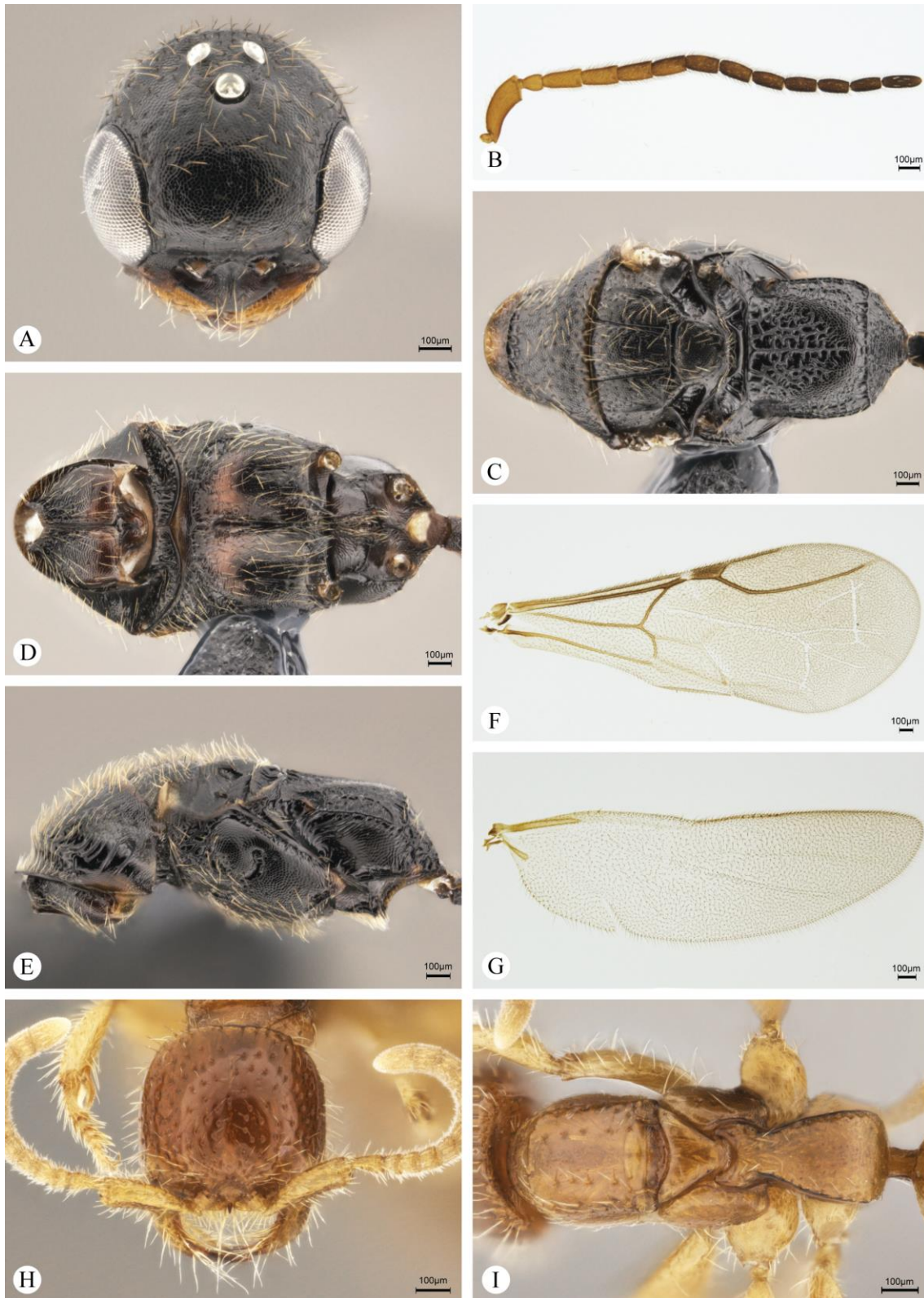


**FIGURE 29.** *Caloapenesia*, male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view.

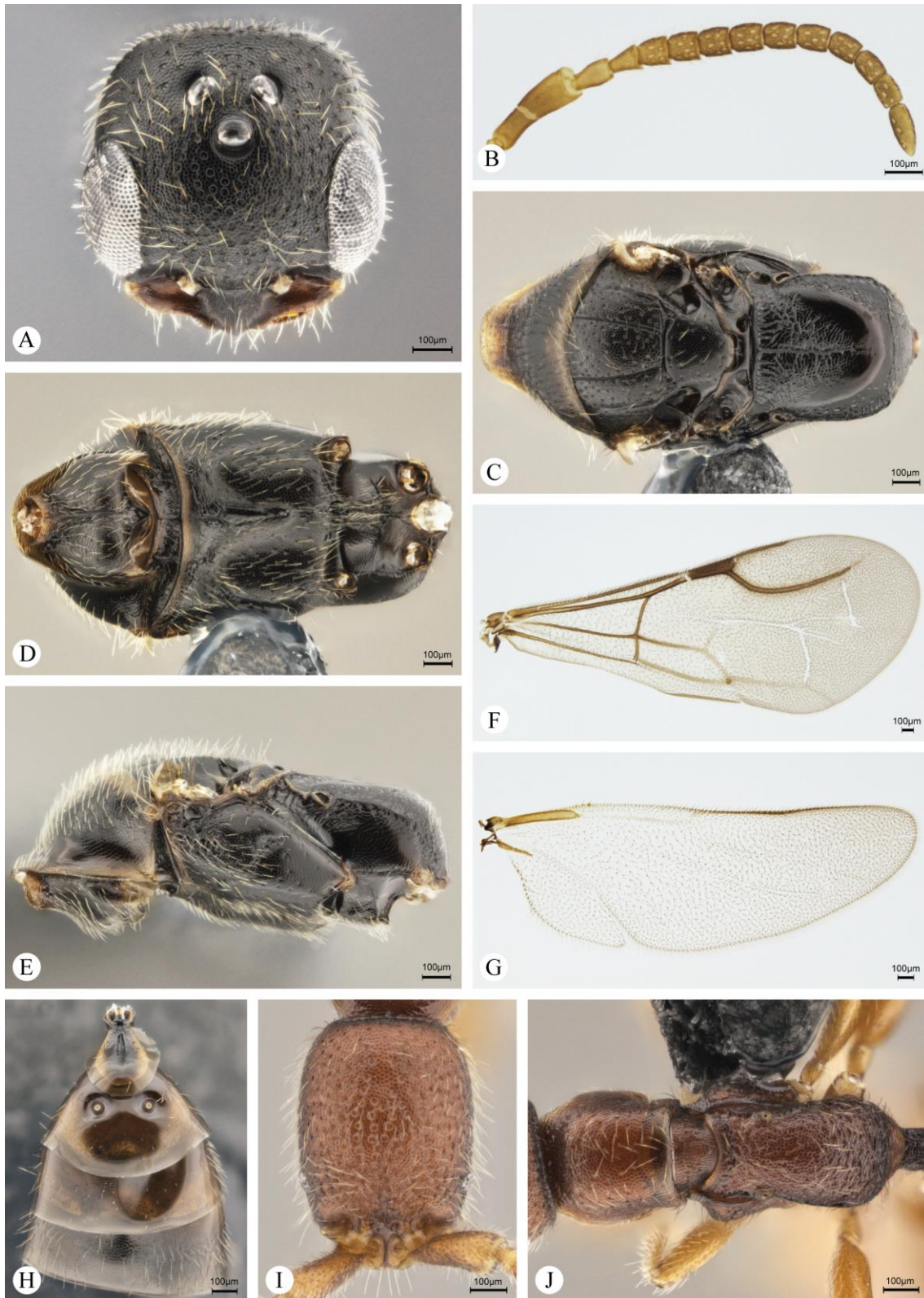


**FIGURE 28.** *Calobrachium*, male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view.



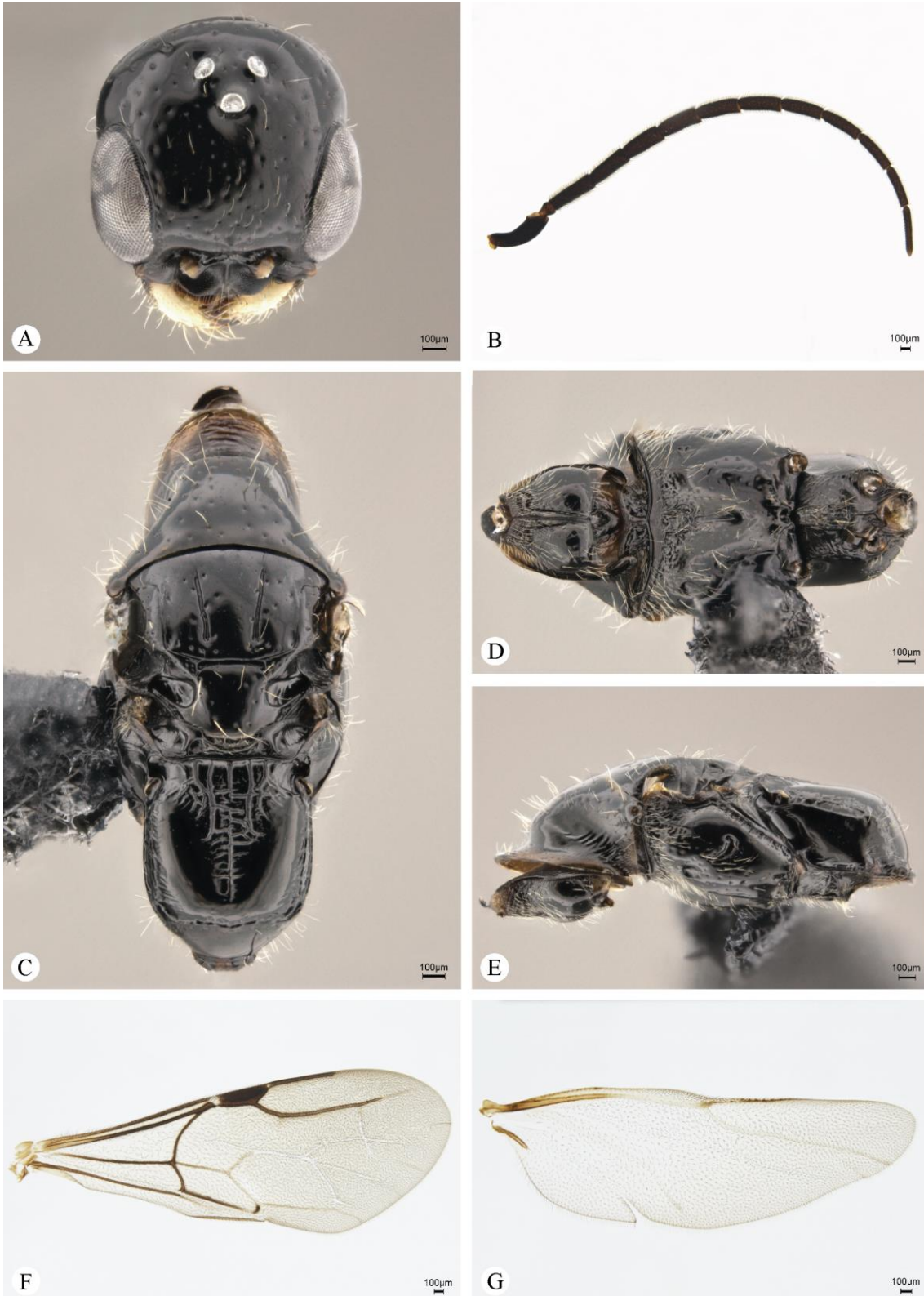


**FIGURE 29.** *Cleistopyris*, A-G male, H-I Female. A. Head, dorsal view; B. Antenna, anterior view; C. C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Head, dorsal view; I. Mesosoma, dorsal view.

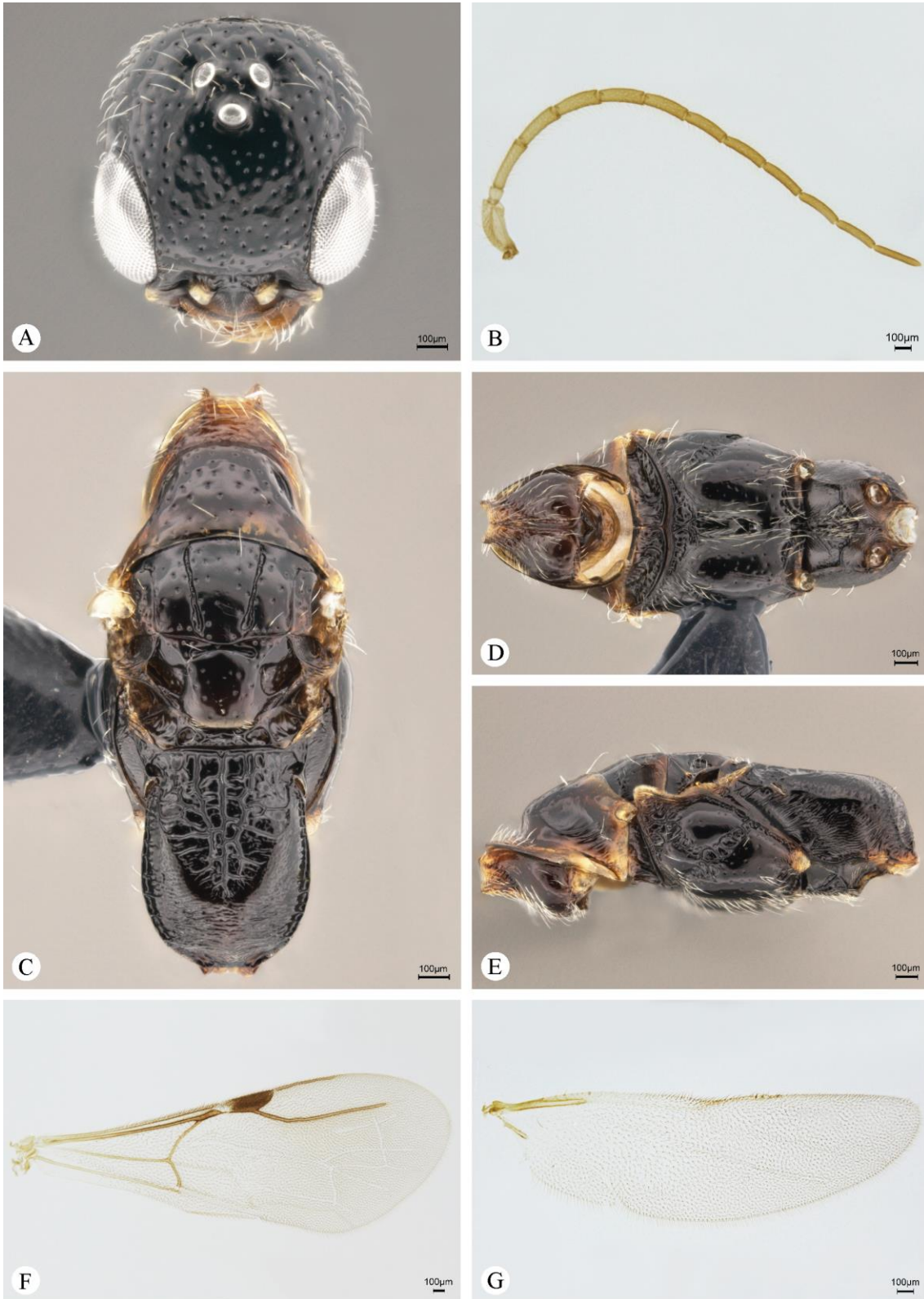


**FIGURE 30.** *Dissomphalus*, A-H male, I-J Female. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Metasoma, tergal process. I. Head, dorsal view; J. Mesosoma, dorsal view.



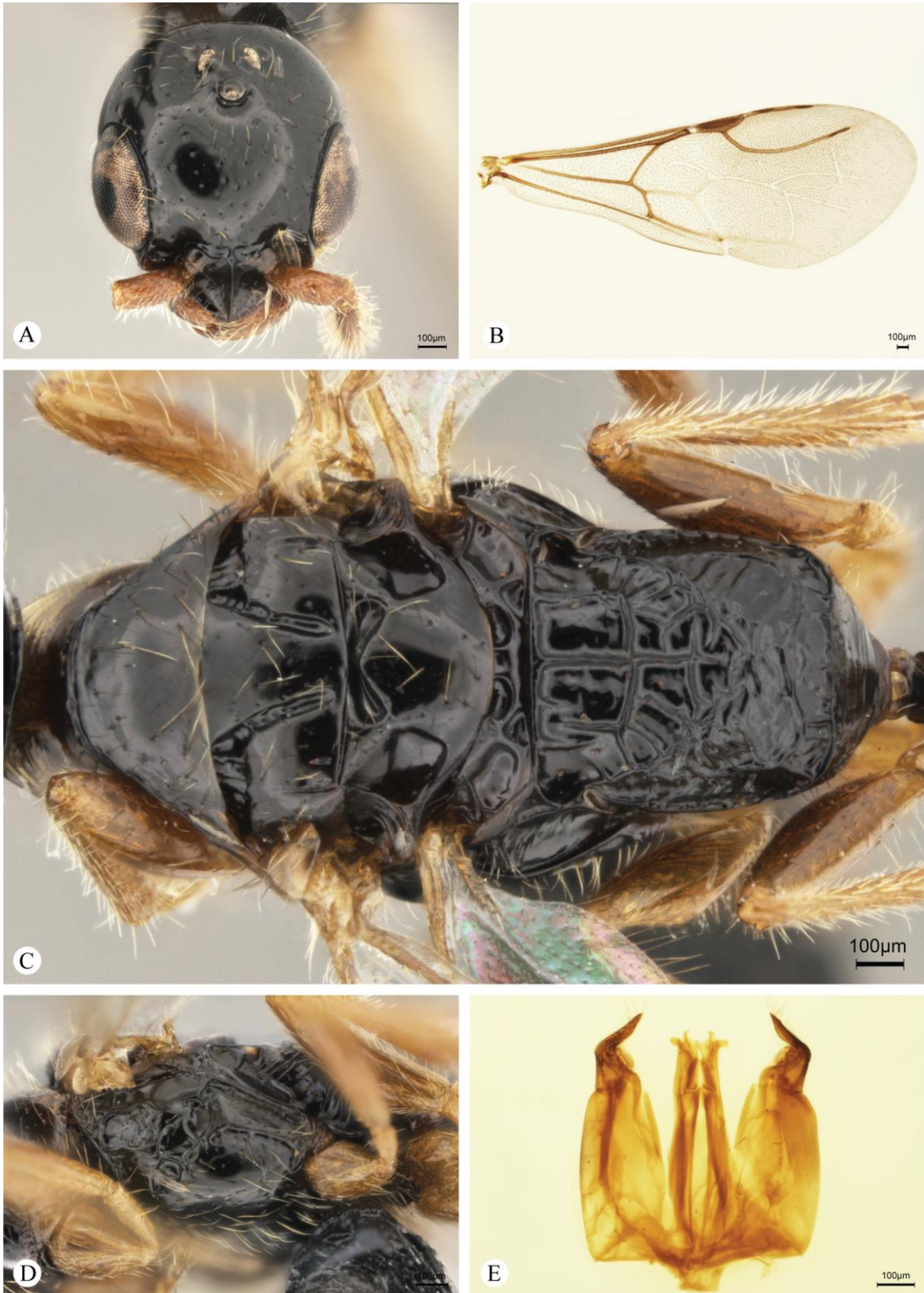


**FIGURE 31.** *P5*, male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view.

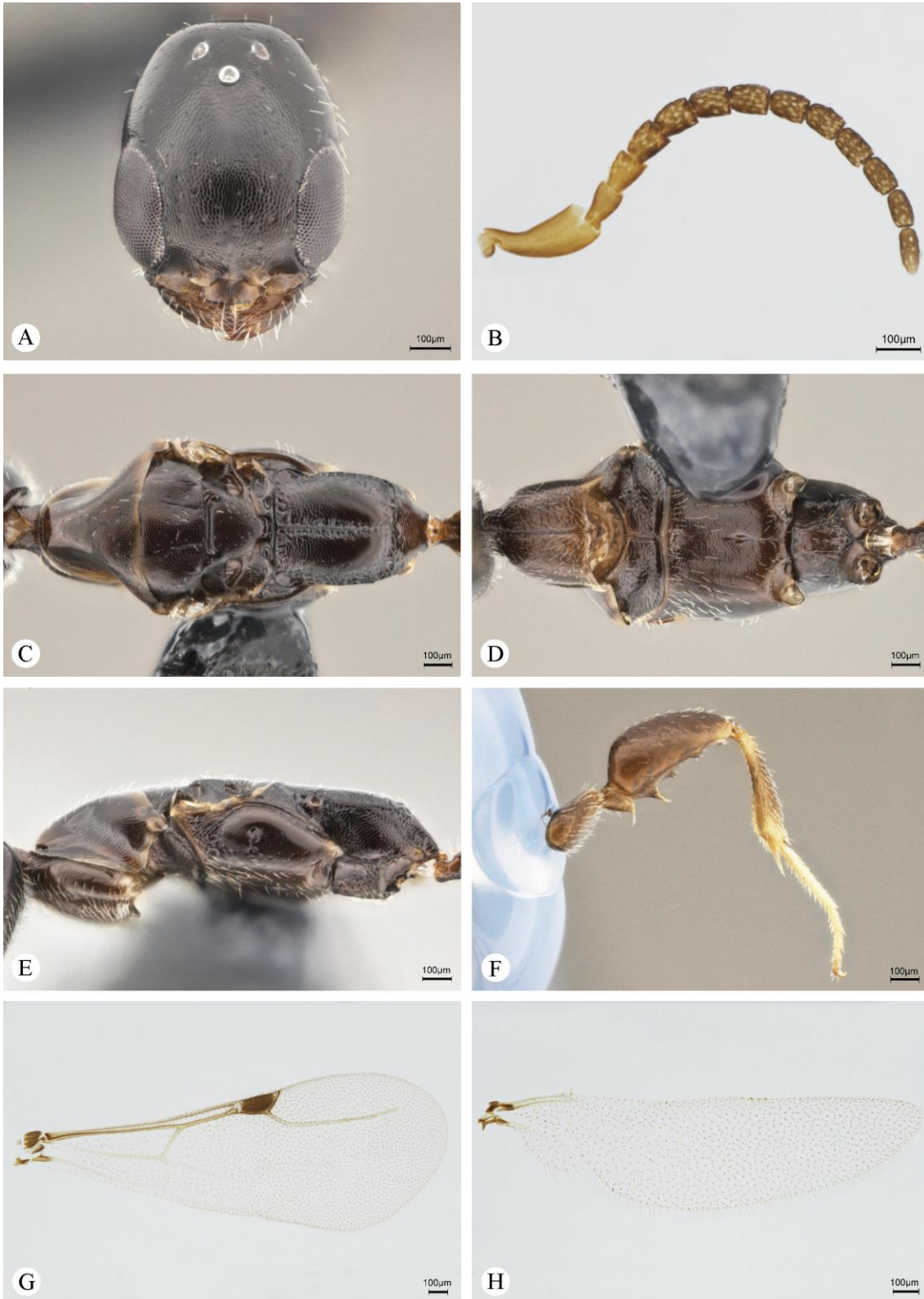


**FIGURE 32.** *P7*, male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view.



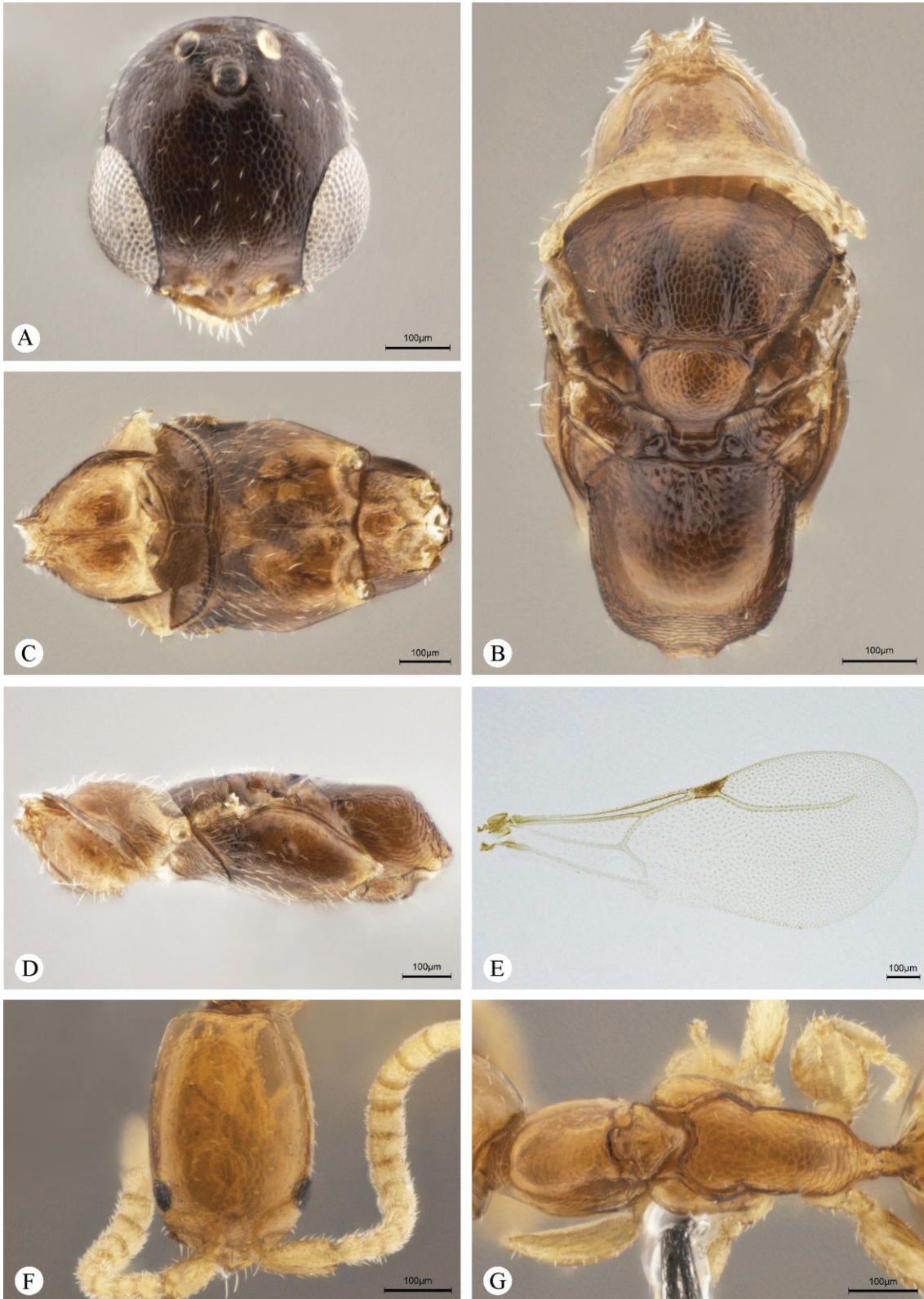


**FIGURE 33.** *P9*, male. A. head, dorsal view; B. Forewing, dorsal view; C. Mesosoma, dorsal view; D. Mesopleura. E. Genitalia, ventral view.

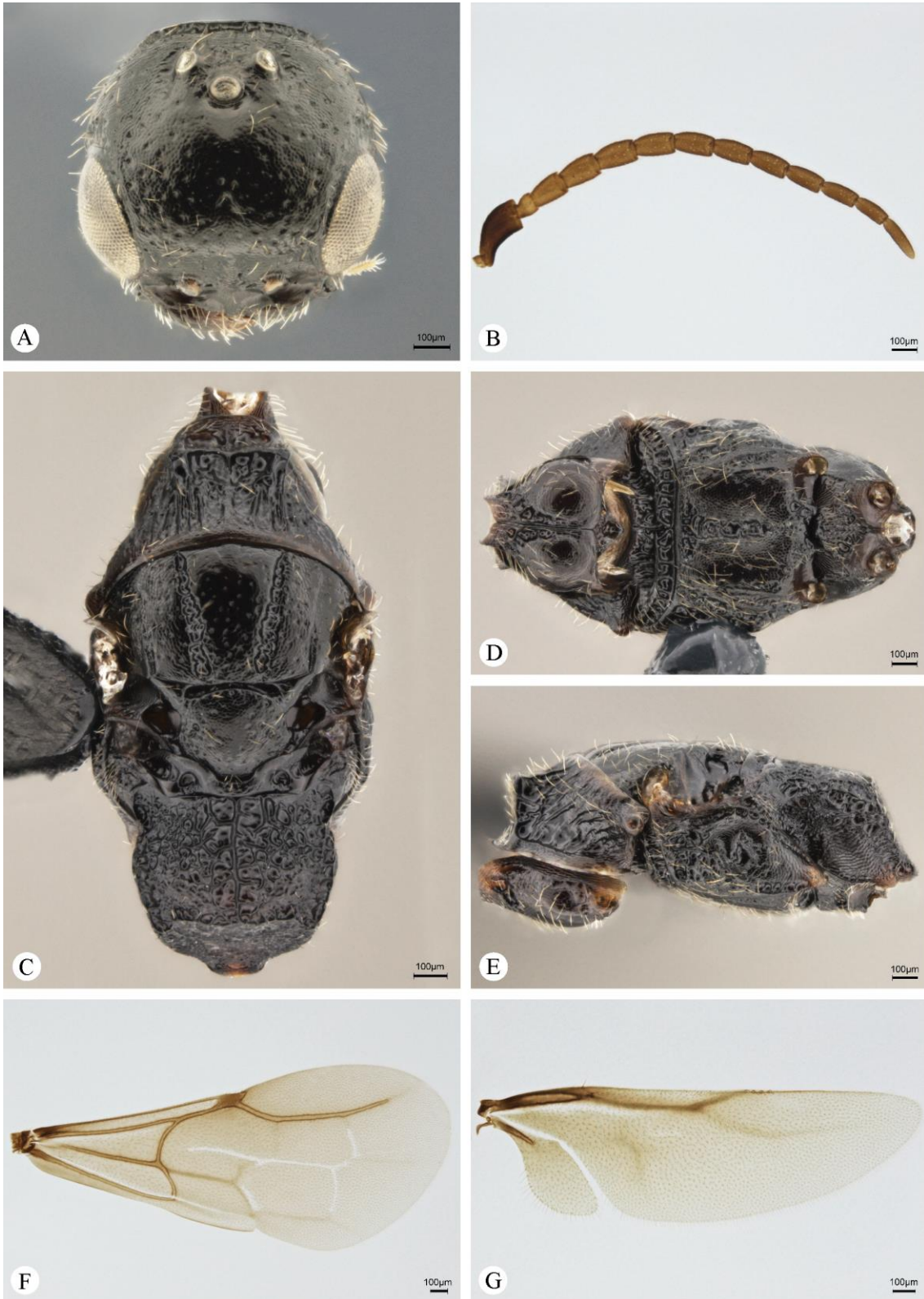


**FIGURE 34.** *Foenobethylus*, male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Metaleg, anterior view; G. Forewing, dorsal view; H. Hind wing, dorsal view.



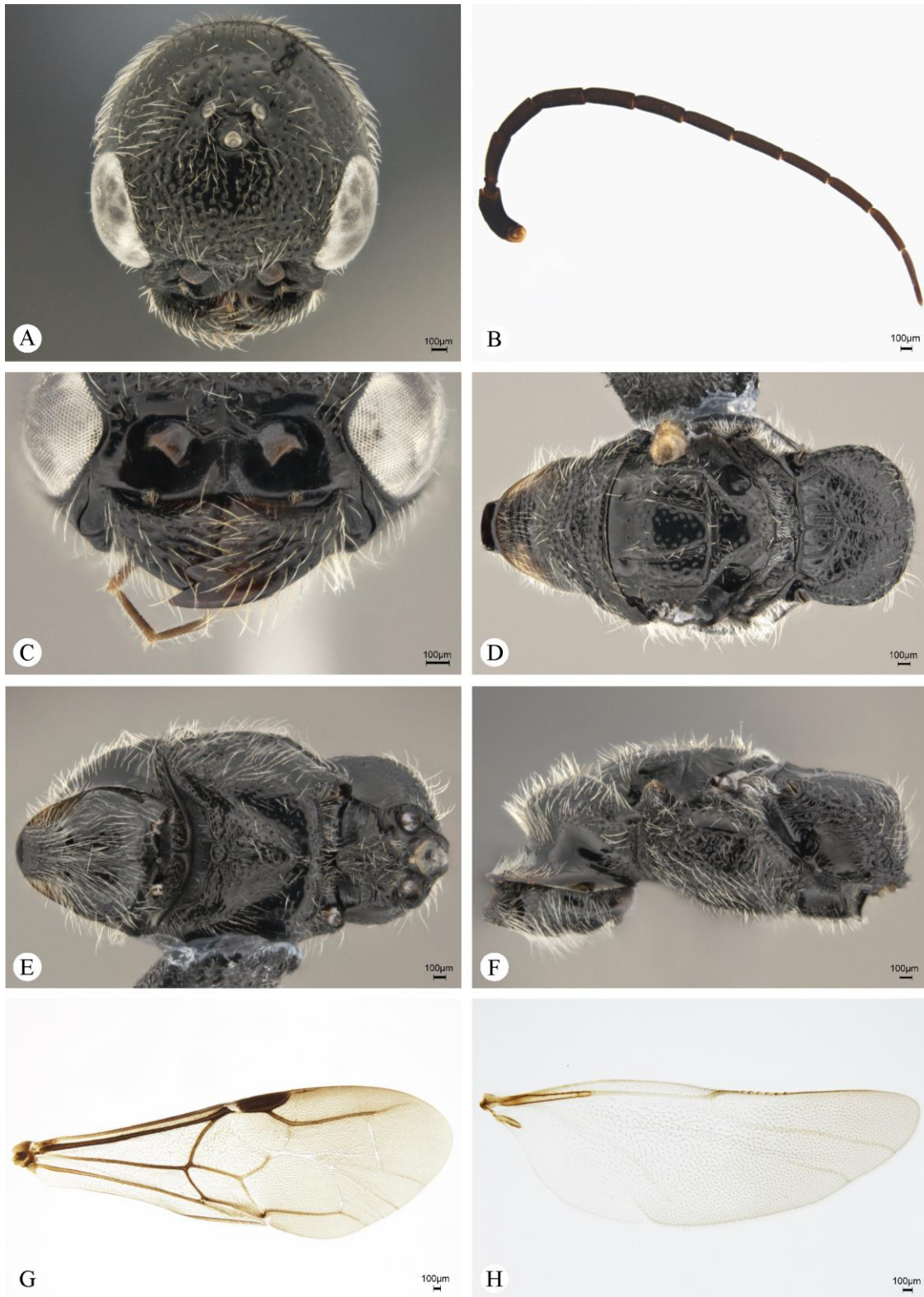


**FIGURE 35.** *Parascleroderma* (pronotum-ecarinate style), A-E male, F-G Female. A. Head, dorsal view; B-D. Mesosoma (B dorsal view, C ventral view, D lateral view); E. Forewing, dorsal view; H. Head, dorsal view; I. Mesosoma, dorsal view.

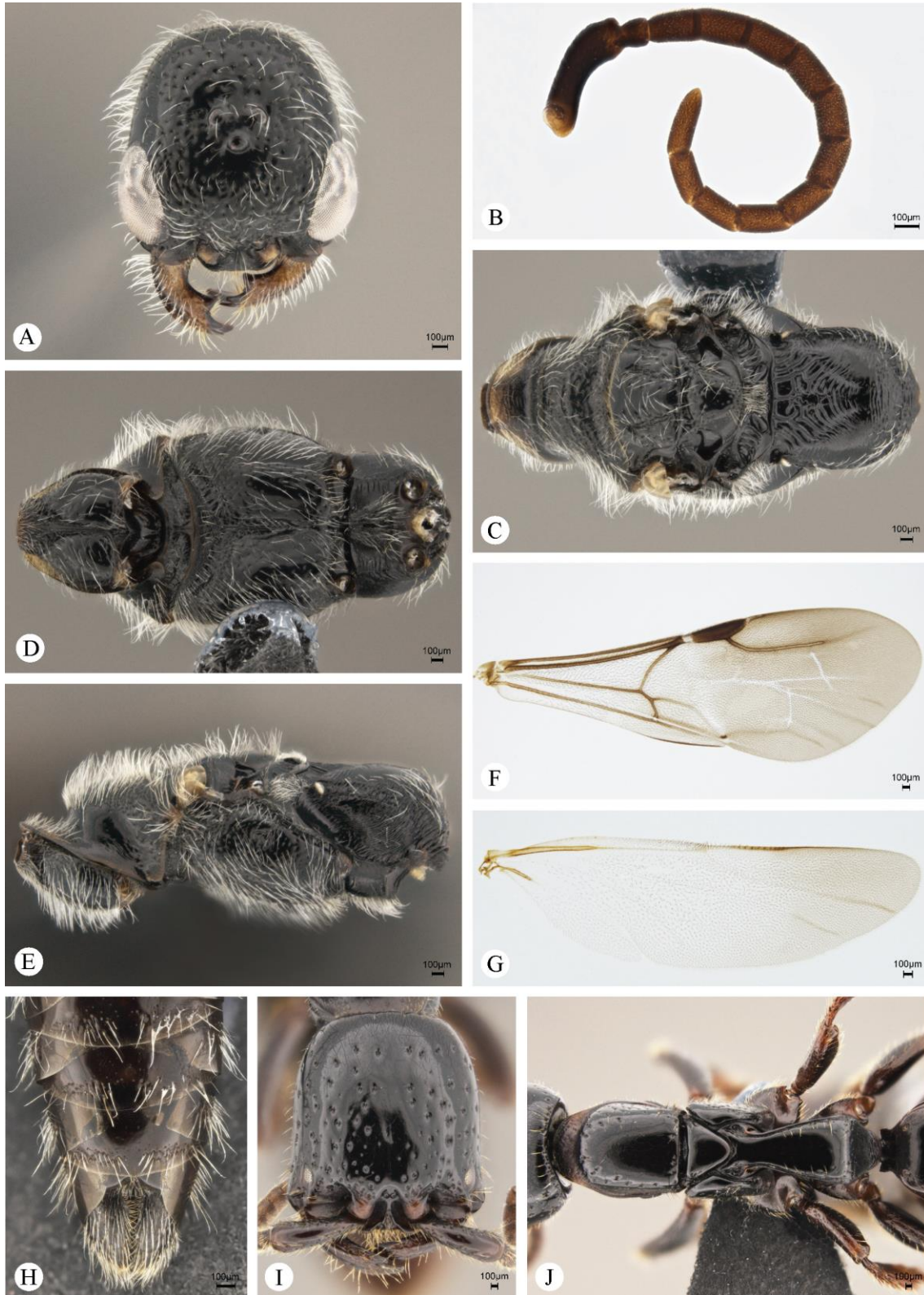


**FIGURE 36.** *Parascleroderma* (*Ceratepyris* style, pronotum-carinate style), male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view.



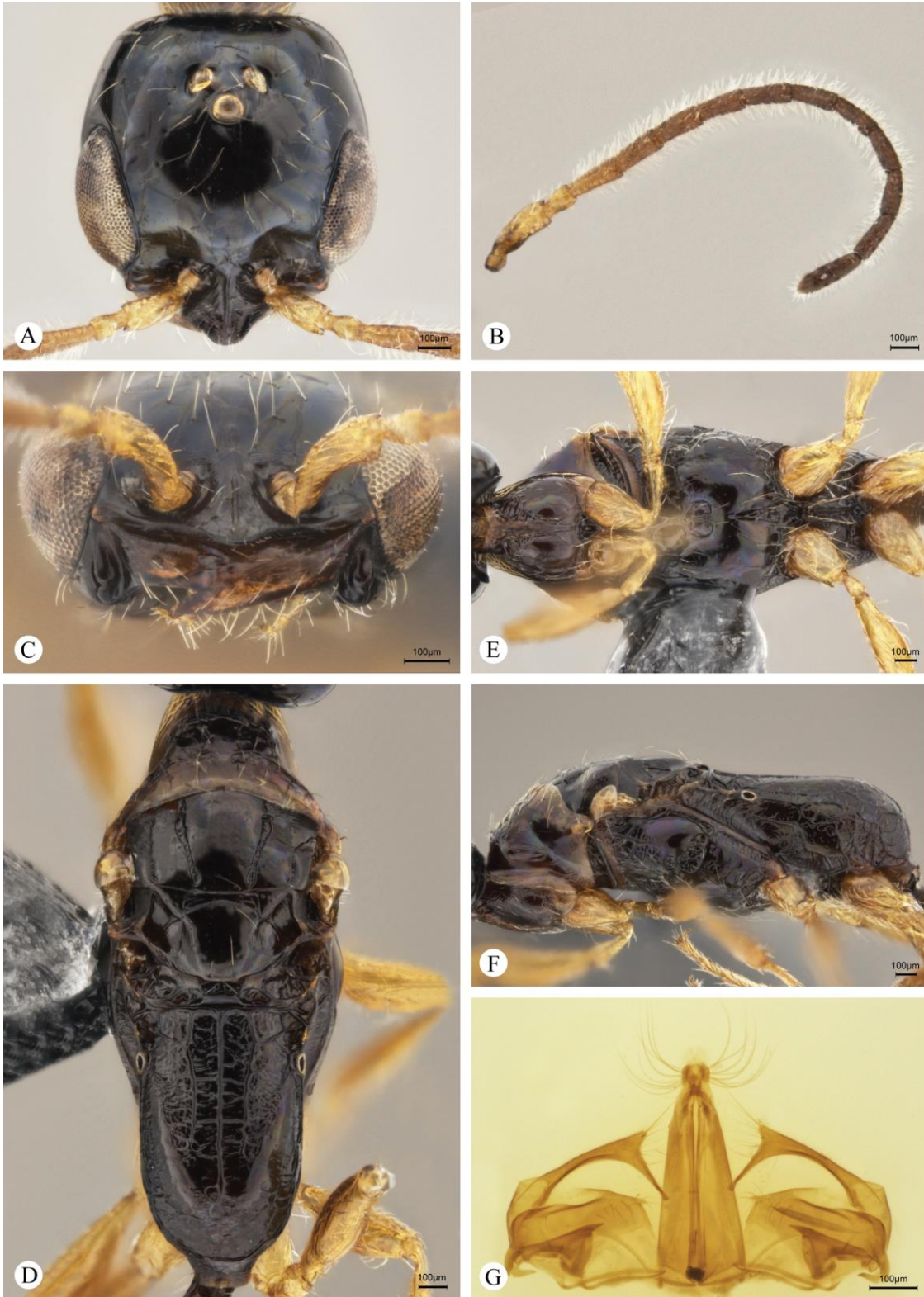


**FIGURE 37.** *Pristepyris*, male. A. Head, dorsal view; B. Antenna, anterior view; C. Mandible, frontal view; D-F. Mesosoma (D dorsal view, E ventral view, F lateral view); G. Forewing, dorsal view; H. Hind wing, dorsal view.

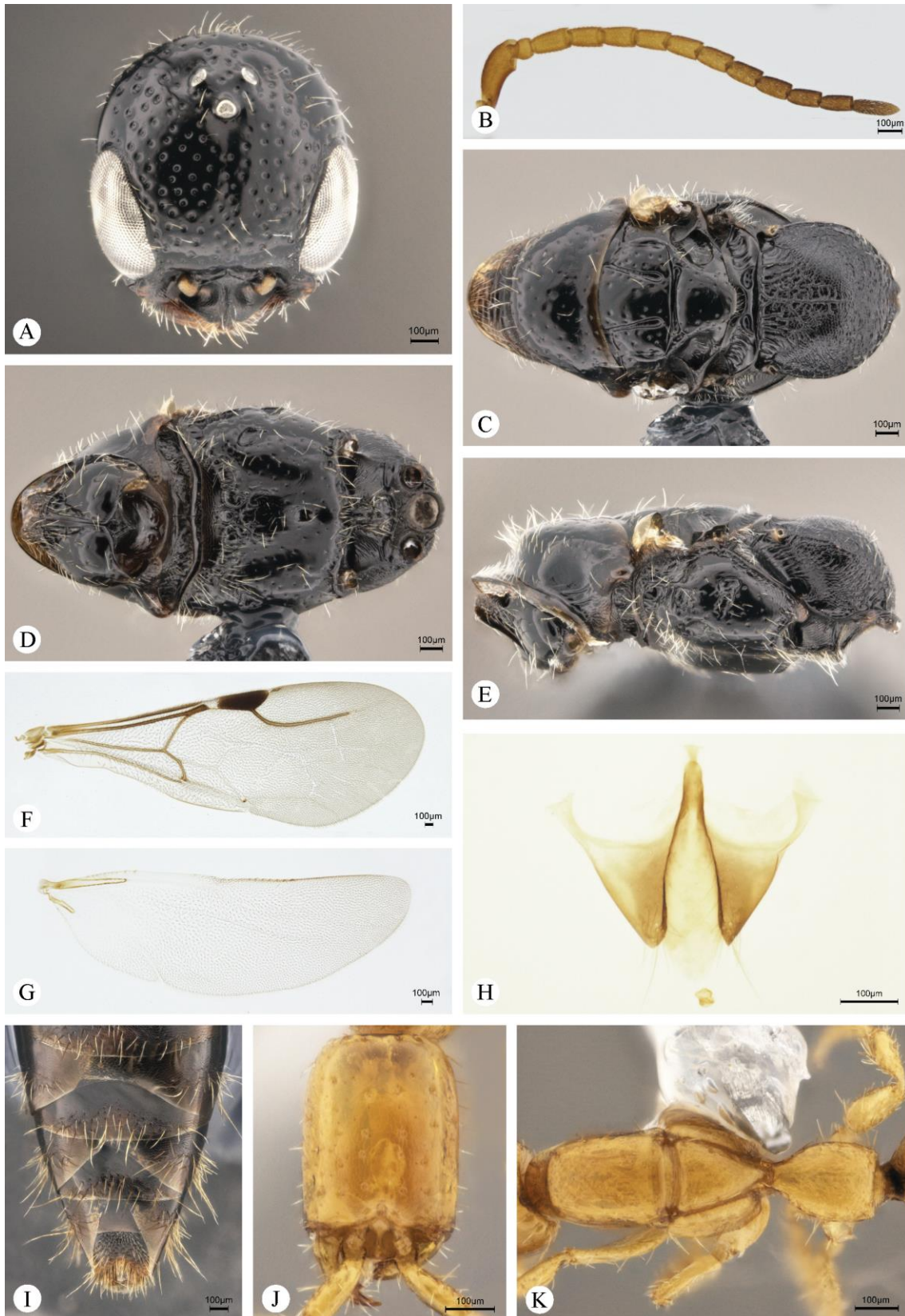


**FIGURE 38.** *Pristocera*, A-H male, I-J Female. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Metasoma, hypopygium. I. Head, dorsal view; J. Mesosoma, dorsal view.



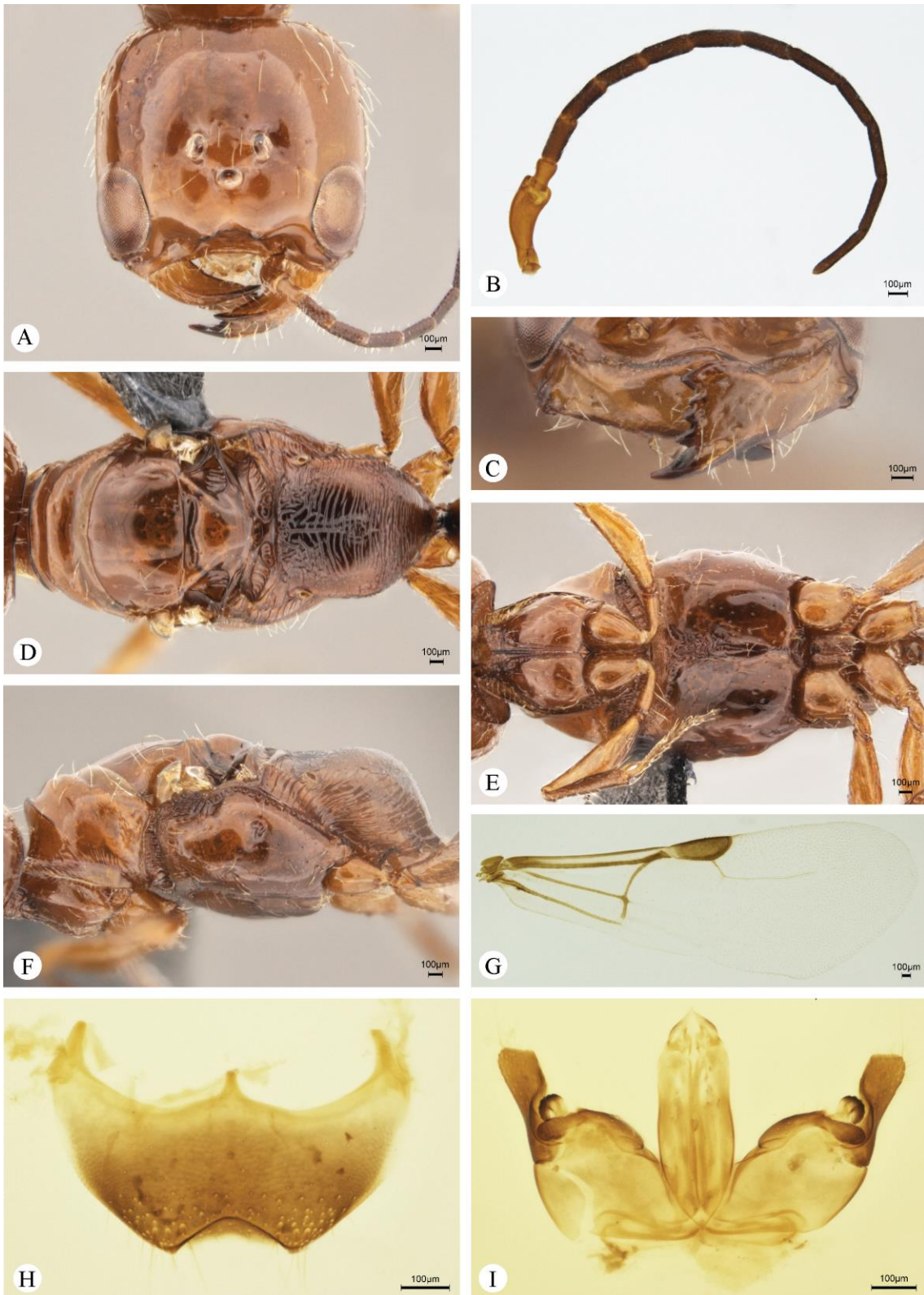


**FIGURE 39.** *P10*, male. A. Head, dorsal view; B. Antenna, anterior view; C. Mandible, frontal view; D-F. Mesosoma (D dorsal view, E ventral view, F lateral view); G. Genitalia, dorsal view.

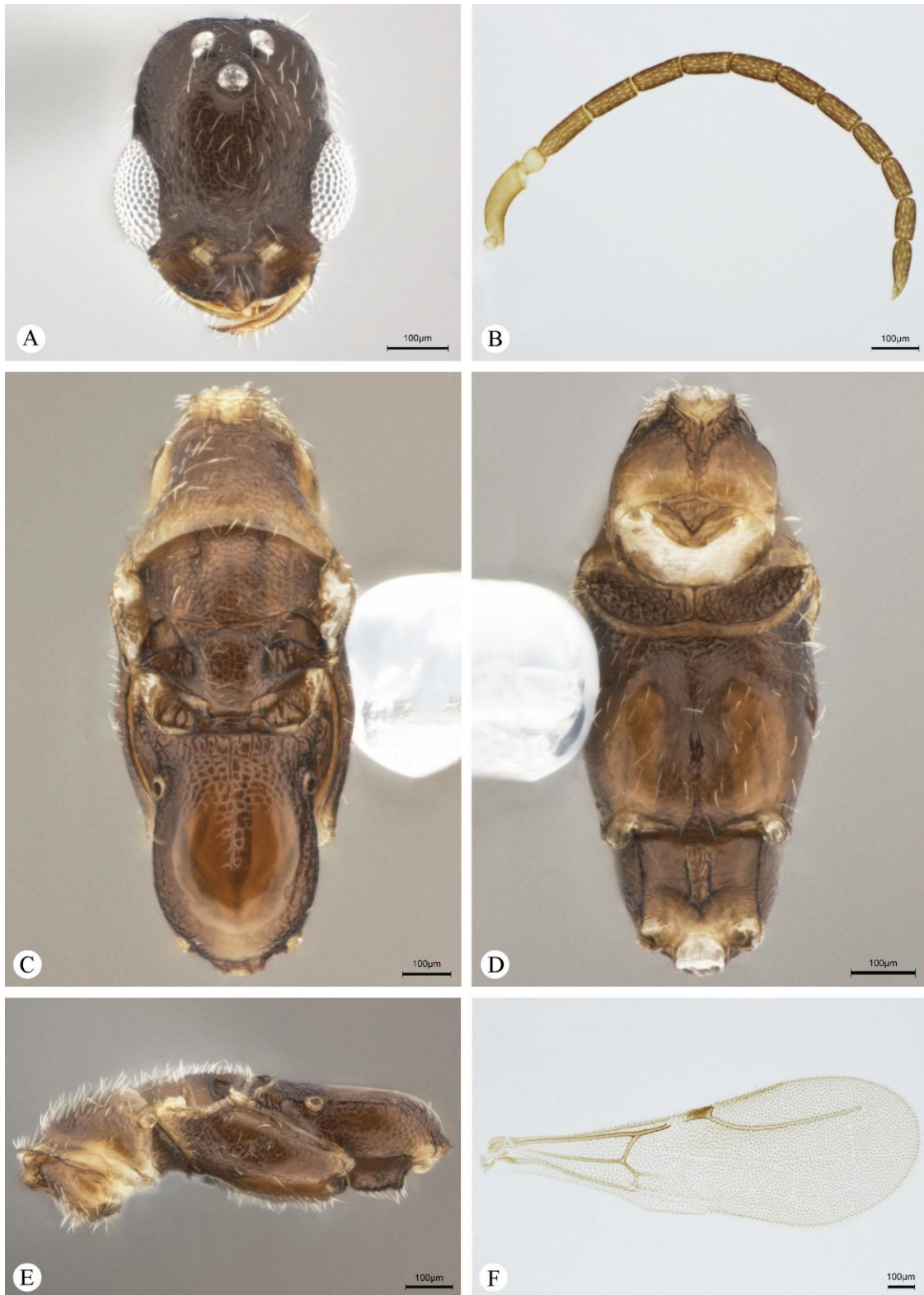


**FIGURE 40.** *Propristocera*, A-I male, J-K Female. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Hypopygium. I. Metasoma, hypopygium. I. Head, dorsal view; J. Mesosoma, dorsal view.



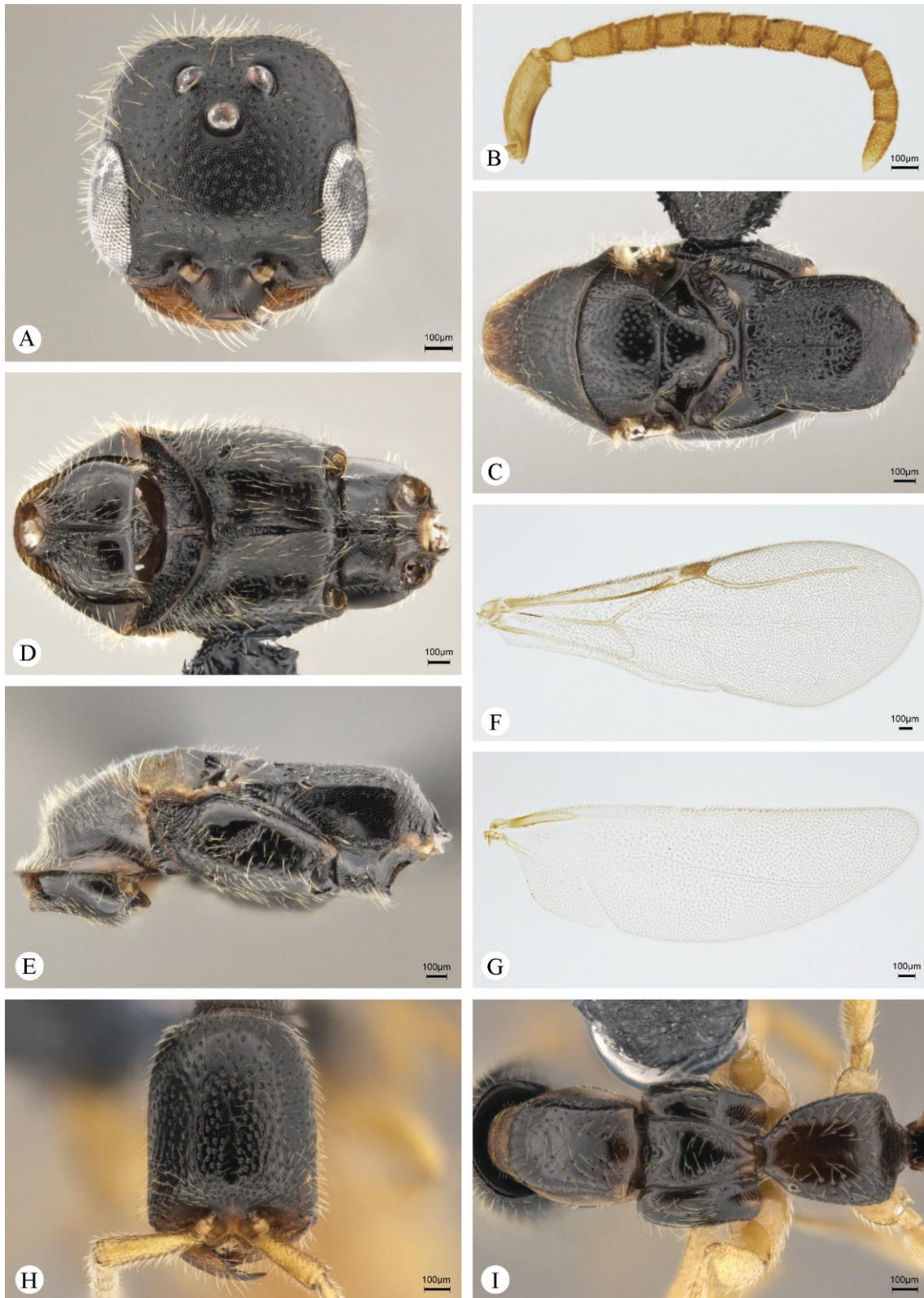


**FIGURE 41.** *Prosapenesia*, male. A. Head, dorsal view; B. Antenna, anterior view; C. Mandible, frontal view; D-F. Mesosoma (D dorsal view, E ventral view, F lateral view); G. Forewing, dorsal view; H. Hypopygium; I. Genitalia, ventral view.

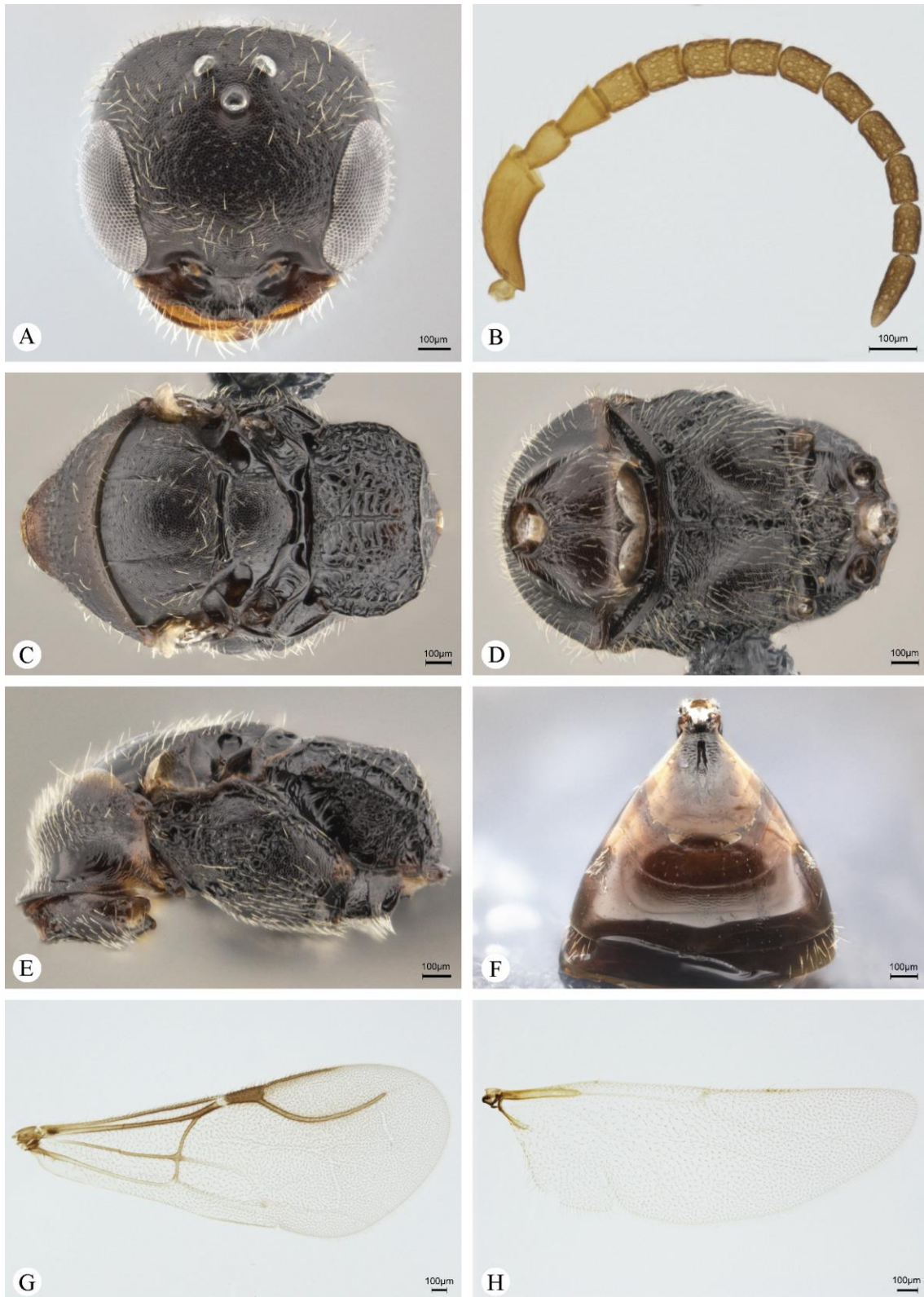


**FIGURE 42.** *Protisobrachium*, male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view.



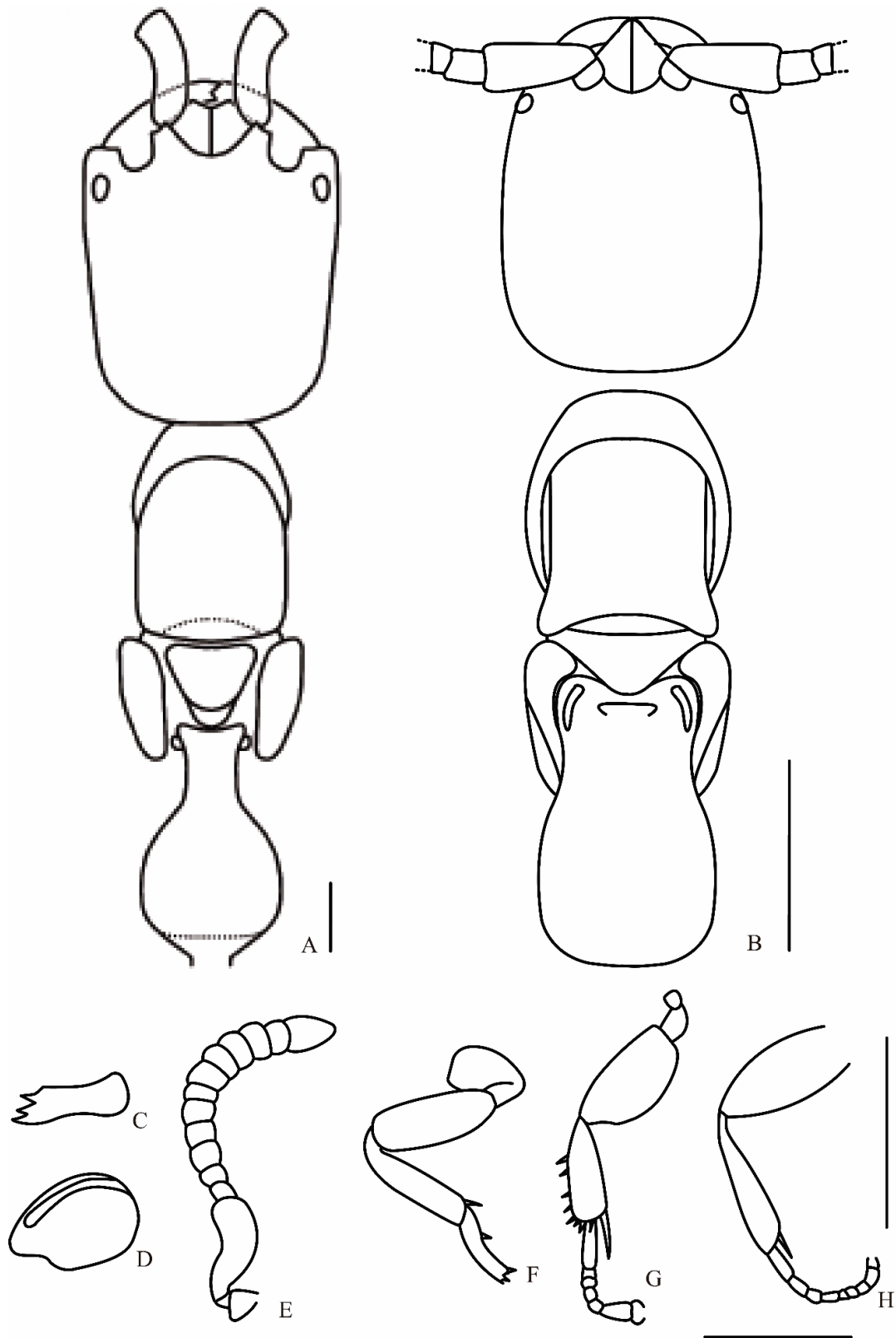


**FIGURE 43.** *Pseudisobrachium*, A-G male, H-I Female. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Forewing, dorsal view; G. Hind wing, dorsal view; H. Head, dorsal view; I. Mesosoma, dorsal view.

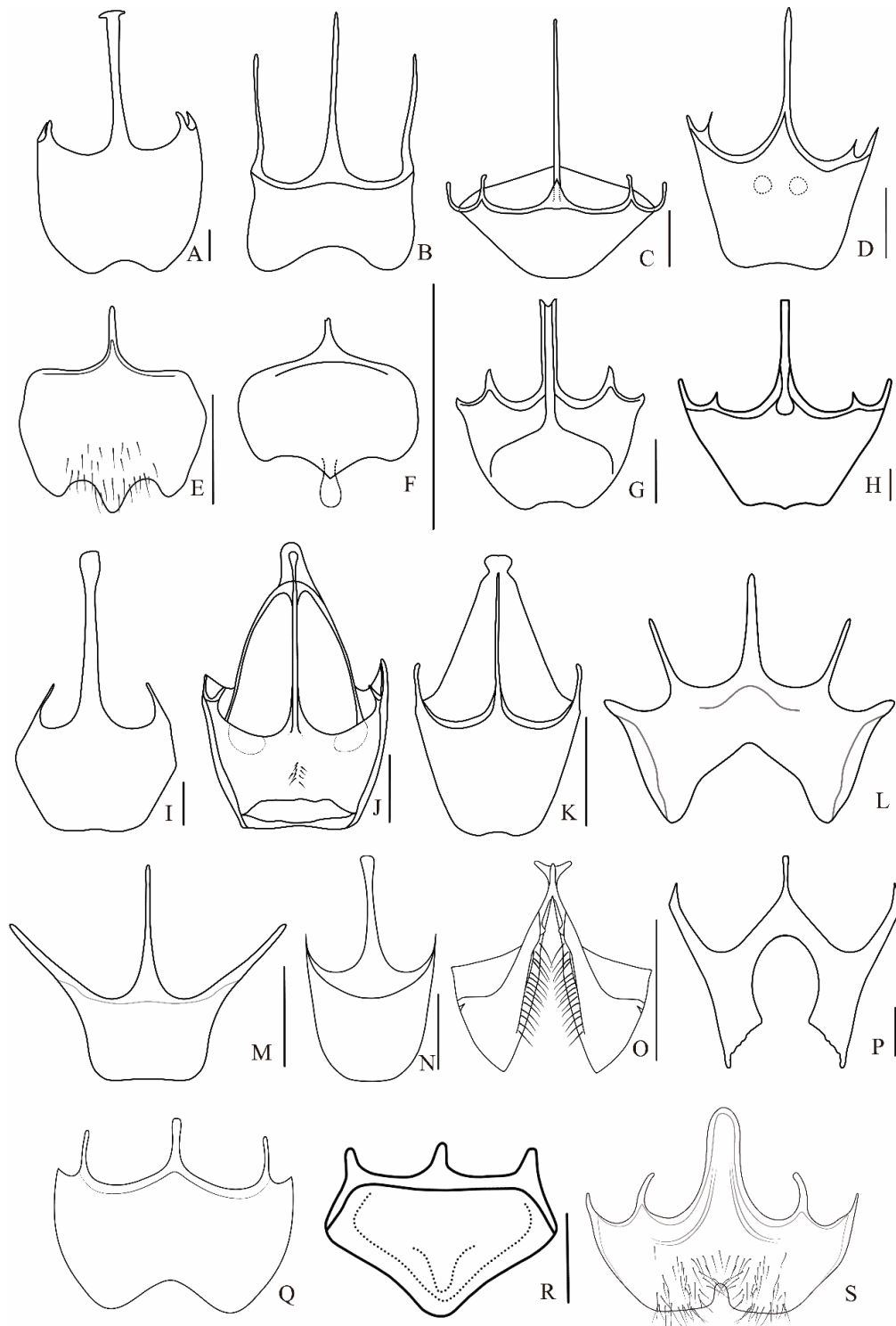


**FIGURE 44.** *Trichiscus*, male. A. Head, dorsal view; B. Antenna, anterior view; C-E. Mesosoma (C dorsal view, D ventral view, E lateral view); F. Metasoma, tergal process. G. Forewing, dorsal view; H. Hind wing, dorsal view.

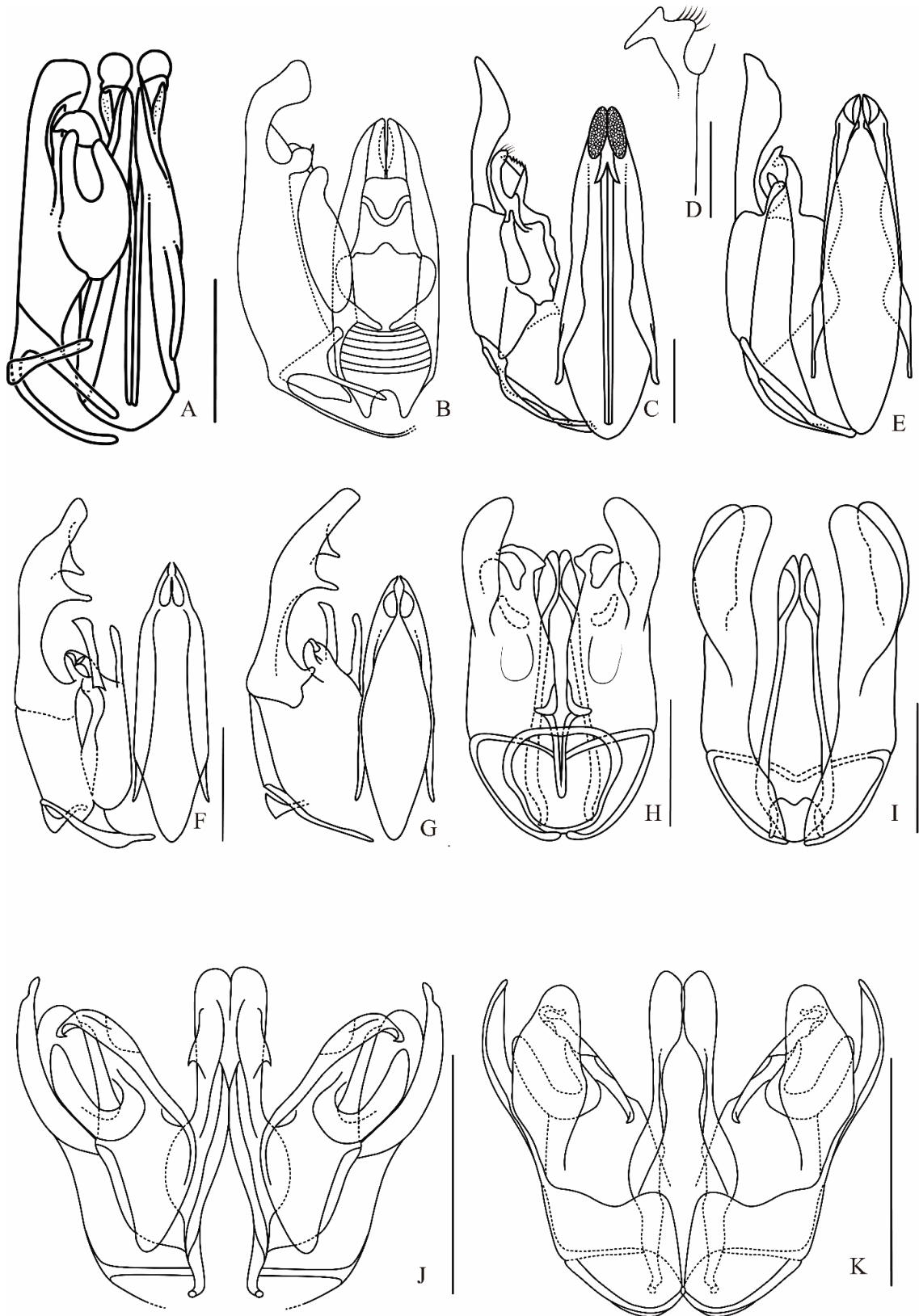




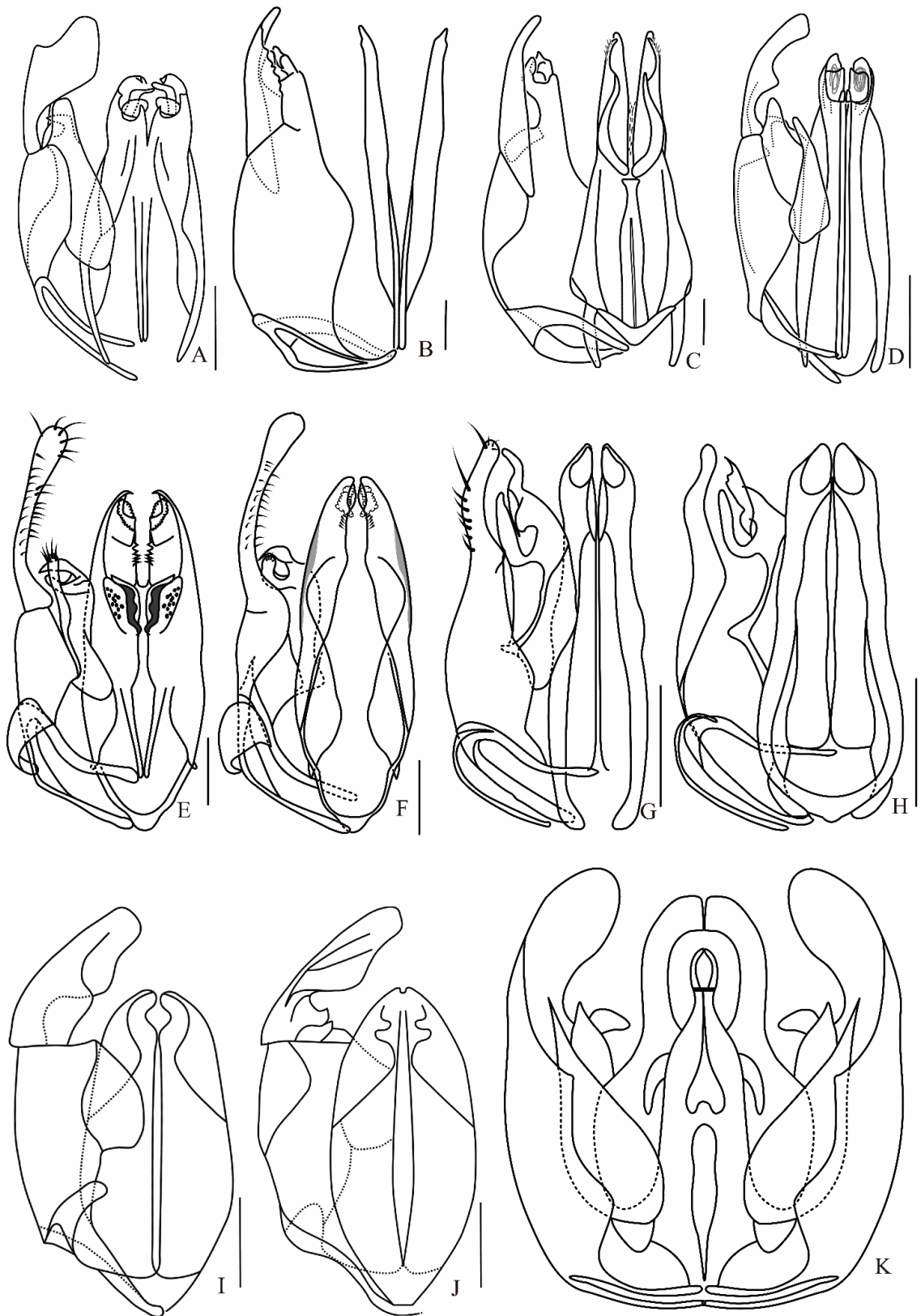
**FIGURE 47.** Females. A. *Pristepyris*, body, dorsal view; B-H. *Scaphepyris* [redraw digitally from Lanes & Azevedo 2007], B. Body, dorsal view; C. Mandible, frontal view; D. Mesopleuron, lateral view; E. Antenna, anterior view; F. Proleg, dorsal view; G. Hind wing, dorsal view; H. Metasoma, hypopygium. I. Head, dorsal view; J. Mesosoma, dorsal view.



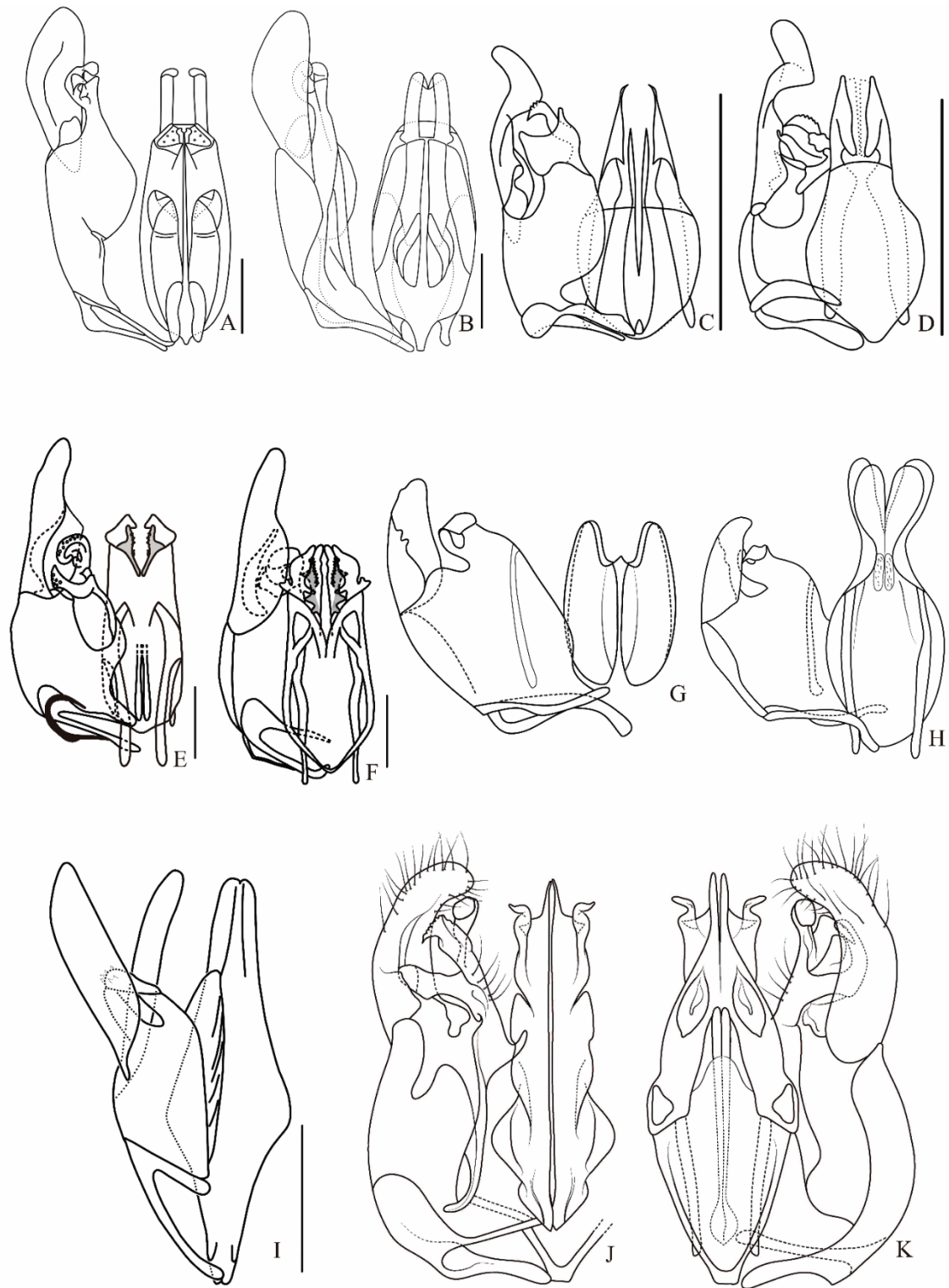
**FIGURE 48.** Hypopygium, external view. A. *P4*; B. *Afgoiogfa* [redraw digitally from Argaman 1988]; C. *Apenesia*; D. *P6*; E. *Caloapenesia* [redraw digitally from Gobbi & Azevedo 2014]; F. *Calobrachium* [redraw digitally from Gobbi & Azevedo 2016]; G. *Cleistepyris*; H. *Dissomphalus*; I. *Dracunesia*; J. *Eleganesia*; K. *P10*; L. *Foenobethylus* [redraw digitally from Savergnini & Azevedo 2013]; M. *Parascleroderma*; N. *Pristepyris* [redraw digitally from Azevedo & Alencar 2009]; O. *Pristocera* [redraw digitally from Alencar & Azevedo 2011]; P. *P10*; Q. *Protisobrachium*; R. *Pseudisobrachium*; S. *Trichiscus* [redraw digitally from Azevedo 2014].



**FIGURE 49.** Genitalia. A. P4; B. *Afoiogfa* [redraw digitally from Argaman 1988]; C-E. *Apenesia*; F-G. P6; H-I. *Caloapenesia* [redraw digitally from Gobbi & Azevedo 2014]; J-K. *Calobrachium* [redraw digitally from Gobbi & Azevedo 2016]. (A, B, C, F, H, J ventral view; E, G, I, K dorsal view; D lateral view of cuspis).



**FIGURE 50.** Genitalia. A. *Cleistopyris*; B-C. *Dissomphalus*; D. P5; E-F. P7; G-H. P9; I-J. *Foenobethylus* [redraw digitally from Savergnini & Azevedo 2013]; K. *Parascleroderma* [redraw digitally from Argaman 1988]. (A, B, D, E, G, I, K ventral view; C, F, H, J dorsal view)



**FIGURE 51.** Genitalia. A-B. *Pristepyis* [redraw digitally from Azevedo & Alencar 2009]; C-D. *Pristocera* [redraw digitally from Alencar & Azevedo 2011]; E-F. *Propristocera* [redraw digitally from Savergnini & Azevedo 2013]; G-H. *Protisobrachium*; I. *Pseudisobrachium*; J-K. *Trichiscus*. (A, C, E, G, I, J ventral view; B, D, F, H, K dorsal view).