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

Sistemática filogenética de Epyrinae (Hymenoptera, Bethylidae)

WESLEY DONDONI COLOMBO

Vitória, ES
Maio de 2021

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WESLEY DONDONI COLOMBO

Orientador: Celso Oliveira Azevedo
Coorientadora: 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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Wesley Dondoni Colombo

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“Science is a willingness to accept facts even when they are opposed to wishes.”

Burrhus Frederic Skinner.

Science and Human Behavior, 2012, p. 12

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RESUMO

Epyrinae são a segunda subfamília mais diversa de Bethylidae, com aproximadamente 950 espécies conhecidas e possuem 13 gêneros válidos, dos quais 12 são viventes: *Anisepyris* Kieffer; *Aspidepyris* Evans; *Bakeriella* Kieffer; *Calyozina* Enderlein; *Chlorepyris* Kieffer; *Disepyris* Kieffer; *Epyris* Westwood; *Formosiepyris* Terayama; *Holepyris* Kieffer; *Laelius* Ashmead; *Trachepyris* Kieffer e *Xenepyris* Kieffer; e um é extinto: †*Elektroepyris*. Os Epyrinae tiveram uma história taxonômica complexa e apenas na última década foram recuperados como monofiléticos. Devido à dificuldade em delimitar os Epyrinae, muitos táxons genéricos foram consequentemente classificados inadequadamente. Estudos que revisem o conceito dos gêneros de Epyrinae são necessários e urgentes, mas têm sido negligenciados devido à dificuldade de interpretação da diversidade morfoestrutural do grupo. Neste sentido, surgem os dados moleculares que tem auxiliado a elucidar os impasses morfoestruturais. Nesta tese, a diversidade dos Epyrinae foi explorada tanto alfataxonomicamente, quanto filogeneticamente, por meio de dados moleculares e morfológicos, através da reconstrução de árvores filogenéticas, sob os diferentes critérios de otimização (Máxima Parcimônia, Inferência Bayesiana e Máxima Verossimilhança). Adicionalmente, a paleodiversidade da subfamília foi revisada e ao final desta proposta, os Epyrinae foram organizados e redefinidos e a evolução de suas linhagens discutida. Esta tese é composta por quatro capítulos, sendo que os três primeiros objetivaram explorar e listar os padrões morfológicos e moleculares dos Epyrinae, fornecendo dados e informações para o último capítulo, que objetivou testar o monofiletismo dos gêneros de Epyrinae. No Capítulo 1, é apresentada uma revisão alfataxonômica dos Epyrinae da Papua Nova Guiné, visando explorar e listar os padrões morfológicos e preencher lacunas do conhecimento taxonômico do Velho Mundo. Foram reconhecidas, tanto morfologicamente quanto molecularmente 39 espécies, das quais 36 são novas e descritas. No Capítulo 2, o gênero extinto †*Elektroepyris* foi revisado e cladisticamente posicionado. Foram codificados 69 caracteres morfológicos, por meio da Máxima Parcimônia e representantes de todas as subfamílias de Bethylidae, viventes ou extintos, foram inseridos na análise. †*Elektroepyris* foi recuperado como uma linhagem independente de todas as outras subfamílias de Bethylidae e por isto, uma nova subfamília, †Elektroepyrinae, foi descrita, baseada em uma autapomorfia nomeada asa anterior com a terceira abscissa da nervura Cu. No Capítulo 3, a paleodiversidade dos Epyrinae foi revisada alfataxonomicamente. Trinta espécies extintas de Epyrinae foram reconhecidas, distribuídas em seis gêneros

(*Anisepyris*, *Chlorepyris*, *Epyris*, †*Gloxinius*, *Holepyris* e *Laelius*). Um novo gênero, †*Gloxinius*, foi proposto para a subfamília, para alocar †*G. bifossatus* e duas espécies foram transferidas de *Epyris* para *Chlorepyris*. Três espécies foram transferidas de *Epyris* para Pristocerinae: †*Merascylla* é proposto para alocar a espécie †*M. atavellus*, e outras duas espécies são transferidos para *Pseudisobrachium*. Uma espécie é transferida de *Epyris* para Scleroderminae: †*Mael* é proposto para alocar a espécie †*M. longiceps*. A espécie †*Laelius nudipennis* não é um betilídeo e foi transferida para Platygastroidea *incertae sedis*. No Capítulo 4, foi realizada uma análise de Inferência Bayesiana para reconstruir uma topologia de Evidência Total a partir de uma matriz com 195 táxons terminais e 3599 caracteres, sendo 232 caracteres morfológicos e os genes 16S, 18S, 28S, COI e Cytb. Este é o primeiro estudo filogenético que examinou todos os 42 nomes genéricos de Epyrinae, incluindo sinônimos juniores e táxons extintos. Os resultados recuperaram *Anisepyris*, *Bakeriella*, *Calyozina*, *Chlorepyris*, *Disepyris*, *Laelius*, e *Trachepyris* como monofiléticos e *Formosiepyris*, *Epyris*, e *Holepyris* como polifiléticos. Dois novos gêneros são propostos, *GenusA* será proposto como **gen. nov.** e *GenusB* será proposto como **gen. nov.**, e seis gêneros foram revalidados, sendo cinco sinônimos juniores de *Epyris* e um de *Holepyris*: *Calyoza* será proposto como **stat. rev.**, *Dolus* será proposto como **stat. rev.**, *Muellerella* será proposto como **stat. rev.**, *Psilepyris* será proposto como **stat. rev.**, *Rysepyris* será proposto como **stat. rev.** e *Trissepyris* será proposto como **stat. rev.** Além disto, todas as 962 espécies de Epyrinae foram revisadas via observação direta do holótipo, ilustrações ou literatura e foram distribuídas ao longo de 17 gêneros: *Anisepyris*, *Aspidepyris*, *Bakeriella*, *Calyoza* será proposto como **stat. rev.**, *Calyozina*, *Chlorepyris*, *Dolus* será proposto como **stat. rev.**, *Epyris*, *GenusA* será proposto como **gen. nov.**, *GenusB* será proposto como **gen. nov.**, †*Gloxinius*, *Holepyris*, *Laelius*, *Muellerella* será proposto como **stat. rev.**, *Psilepyris* será proposto como **stat. rev.**, *Rysepyris* será proposto como **stat. rev.** e *Trissepyris* será proposto como **stat. rev.**

ABSTRACT

Epyrinae are the second most diverse subfamily of Bethylidae, with approximately 950 described species and 13 valid genera, of which 12 are extant: *Anisepyris* Kieffer; *Aspidepyris* Evans; *Bakeriella* Kieffer; *Calyozina* Enderlein; *Chlorepyris* Kieffer; *Disepyris* Kieffer; *Epyris* Westwood; *Formosiepyris* Terayama; *Holepyris* Kieffer; *Laelius* Ashmead; *Trachepyris* Kieffer and *Xenepyris* Kieffer; and one is extinct: †*Elektroepyris*. Epyrinae have a complex taxonomic history and only in the last decade their monophyly has recovered. Due to the difficulty in delimiting Epyrinae, many generic taxa were consequently classified inappropriately. Studies revising the concept of the epyrine genera are necessary and crucial, but they have been neglected due to the difficulty in interpreting morphostructural diversity. As a solution, molecular data has been used to help elucidate the morphostructural impasses. In this dissertation, the diversity of Epyrinae is explored, both alphaxonomically and phylogenetically, through molecular and morphological data, and by reconstructing phylogenetic trees, under different optimization criteria (Maximum Parsimony, Bayesian Inference and Maximum Likelihood). Additionally, the subfamily's paleodiversity was revised and, at the end, the Epyrinae were organized and redefined and the evolution of their lineages discussed. This thesis consists of four chapters, the first three of which aimed to explore and list the morphological and molecular patterns of the Epyrinae, providing data and information for the last chapter, which aimed to test the monophyly of the Epyrinae genera. In Chapter 1, an alpha-taxonomic review of Epyrinae from Papua New Guinea is present, exploring and listing morphological patterns and filling in gaps in Old World taxonomic knowledge. Finally, 39 species were recognized, both morphologically and molecularly, of which 36 are new and described. In Chapter 2, the extinct genus †*Elektroepyris* was revised and cladistically positioned. Morphological characters were coded, summing up to 69. The caracteres were used to perform Maximum Parsimony reconstruction, including representatives of all subfamilies of Bethylidae, extant or extinct. †*Elektroepyris* was recovered as a lineage distinct from other subfamilies of Bethylidae and for this reason, a new subfamily, †Elektroepyrinae, was described, based on an autapomorphy of the anterior wing with the third abscissa of the Cu vein. In Chapter 3, the paleodiversity of Epyrinae was reviewed alpha-taxonomically. Thirty extinct species of Epyrinae were recognized, distributed in six genera (*Anisepyris*, *Chlorepyris*, *Epyris*, †*Gloxinius*, *Holepyris* and *Laelius*). A new genus, †*Gloxinius*, has been proposed for the subfamily to allocate †*G. bifossatus* and two species were transferred from *Epyris* to

Chlorepyris. Three species were transferred from *Epyris* to Pristocerinae: †*Merascylla* is proposed to allocate the species †*M. atavellus*, and two other species are transferred to *Pseudisobrachium*. One species is transferred from *Epyris* to Scleroderminae: †*Mael* is proposed to allocate the species †*M. longiceps*. The species †*Laelius nudipennis* is not a bethylid and has been transferred to Platygastroidea *incertae sedis*. In Chapter 4, a Bayesian inference analysis was performed to reconstruct a total evidence topology from a matrix with 195 terminal taxa and 3599 characters, containing 232 morphological characters and the genes 16S, 18S, 28S, COI and Cytb. This is the first phylogenetic study that examined all 42 generic names of Epyrinae, including junior synonyms and extinct taxa. The results recovered *Anisepyris*, *Bakeriella*, *Calyozina*, *Chlorepyris*, *Disepyris*, *Laelius*, and *Trachepyris* as monophyletic and *Formosiepyris*, *Epyris*, and *Holepyris* as polyphyletic. Two new genera are proposed, *GenusA* to be proposed as **gen. nov.** and *GenusB* to be proposed as **gen. nov.**, and six genera were revalidated, five junior synonyms of *Epyris* and one of *Holepyris*: *Calyoza* to be proposed as **stat. rev.**, *Dolus* to be proposed as **stat. rev.**, *Muellerella* to be proposed as **stat. rev.**, *Psilepyris* to be proposed as **stat. rev.**, *Rysepyris* to be proposed as **stat. rev.** and *Trissepyris* to be proposed as **stat. rev.** In addition, all 962 species of Epyrinae were reviewed via direct observation of the holotype, illustrations, or literature and were distributed over 17 genera: *Anisepyris*, *Aspidepyris*, *Bakeriella*, *Calyoza* to be proposed as **stat. rev.**, *Calyozina*, *Chlorepyris*, *Dolus* to be proposed as **stat. rev.**, *Epyris*, *GenusA* to be proposed as **gen. nov.**, *GenusB* to be proposed as **gen. nov.**, †*Gloxinius*, *Holepyris*, *Laelius*, *Muellerella* to be proposed as **stat. rev.**, *Psilepyris* to be proposed as **stat. rev.**, *Rysepyris* to be proposed as **stat. rev.** and *Trissepyris* to be proposed as **stat. rev.**.

APRESENTAÇÃO

Biografia: de Barracão ao doutorado

Nasci no dia 22 de novembro de 1992, em Santa Teresa – Espírito Santo. Desde o primeiro ano de vida até a conclusão da minha graduação, eu morei e vivi em um distrito de Santa Teresa, chamado São João de Petrópolis e carinhosamente apelidado de "Barracão".

Sou o mais novo dos três filhos dos meus pais, Frederico e Rosangela. Minha família é simples, assim como as demais que vivem na roça. A Biologia surgiu muito cedo na minha vida, pois sempre fui apaixonado por dinossauros e meu quarto era repleto de brinquedos pré-históricos, que até hoje eles ainda existem, mas foram passados para a próxima geração, meus amados sobrinhos.

Esta minha paixão só foi aumentando, na medida que ingressei na Escola Estadual de Ensino Fundamental e Médio "Frederico Pretti". Escola esta que estudei todos os meus 13 anos do Ensino Básico e tive contato com profissionais maravilhosos, principalmente o Prof. Selso Luís Izabel. Selso ministrou aulas de Ciências e Biologia para mim, durante sete anos, e provavelmente foi o professor que manteve aquela semente que começava a germinar para o fantástico mundo da Biologia e claro, para que hoje eu estivesse aqui.

Com os recém 17 anos e concluindo o Ensino Médio, chegou o momento de escolher a tão almejada graduação, realidade um pouco distante para muitos oriundos de regiões rurais. Muitas pessoas falavam para tentar Medicina, Engenharias, entre outras, mas eu queria ser, Paleontólogo. Sim, eu queria trabalhar com dinossauros. Porém, Paleontologia é uma Pós-graduação, logo, eu deveria escolher alguma graduação relacionada, e eis que a Biologia venceu.

Curso escolhido e uma pitada de sorte, o Instituto Federal do Espírito Santo – *Campus* Santa Teresa (IFES-ST) ofertou sua primeira seleção para cursos superiores, com vagas para o curso de Licenciatura em Ciências Biológicas. Este Instituto se localiza há pouco menos de 20 minutos de caminhada da minha residência. Nesta época, eu não podia tentar outras instituições ou sair de casa, pois minha mãe, infelizmente estava na fase terminal do câncer e meu avô acamado, logo, eu tinha responsabilidades.

Com o sonho de ser Paleontólogo ali, me guiando, ingressei no Curso de Licenciatura em Ciências Biológicas do IFES-ST, em 2010 e até hoje, lembro de sentar-se no auditório, durante a aula inaugural, com um misto de sensações perpassando cada célula

do meu corpo. Aproveito para ressaltar que foi neste momento que descobri que existia Mestrado e Doutorado, através da apresentação dos meus professores. Logo no início da minha graduação, conheci a professora Isabel Alencar, ministrando a disciplina de Introdução a Biologia. Imediatamente conversei com ela sobre minhas perspectivas de trabalho. Pois, ela era a única Zoóloga que se encontrava, até o momento, no IFES-ST. Para minha surpresa, ela trabalhava com insetos e me convidou a conhecer este grupo.

Comecei a trabalhar com a Isabel e juntos, no primeiro ano de graduação, organizamos uma Coleção Entomológica didática para o IFES-ST. No segundo ano, ela me encorajou a submeter um projeto de Iniciação Científica. O tema proposto foi "*Os Impactos da Produção Bibliográfica de Benoit para Bethylidae*". Apesar de não conhecer oficialmente um Bethylidae, neste momento eu comecei a me familiarizar com alguns termos, nomes e estudos científicos. O projeto foi aprovado, porém na mesma época fui chamado para estagiar no Laboratório de Biologia e ele foi repassado para outro bolsista. Logo, meu contato com os Bethylidae foi adiado.

Trabalhando no Laboratório de Biologia eu tive o primeiro contato com um escorpião vivo e neste exato momento, eu "abandonei" os insetos e comecei a focar exclusivamente nos escorpiões. A minha ligação com os escorpiões é tão significativa, que até hoje, eventualmente, desenvolvo atividades relacionadas. Eles foram os objetos de estudo do meu primeiro artigo, da minha monografia de conclusão de curso, além da minha monografia da especialização em Ensino de Biologia.

Concluindo a minha graduação, eu sonhava seguir para o mestrado e depois o doutorado. Eis que Isabel me apresenta para o seu orientador, Celso Azevedo. Entretanto, no primeiro ano que tentei a seleção do PPGBAN-UFES, não fui aprovado e fui obrigado a trabalhar em outros locais para me sustentar e confesso que achava que ser mestre e doutor não passava de um sonho bobo. Afinal, como um mero aluno do interior de Santa Teresa iria competir com alunos formados na UFES, que em relação ao IFES estava muito mais estruturada e preparada. Neste período, eu cheguei inclusive a ser caixa de supermercado e não querer mais seguir o ramo da Biologia.

O ano de 2014 foi muito turbulento. Eu comecei trabalhando como caixa de supermercado e em março assumindo a posição de professor de Biologia na mesma escola que eu havia estudado todo o meu ensino básico. Logo em maio outra oportunidade surgiu e eu assumi outra escola, agora como professor de Ciências. Nesta segunda escola, no final do ano, eu fui convidado para ser o diretor no ano de 2015, o que, além de me surpreender,

me trouxe alegria, afinal, eu com meus 22 anos, havia sido convidado para ser gestor de uma escola.

Nesta mesma época, o PPGBAN-UFES abriu novamente a seleção de mestrado e mesmo desanimado, eu fui novamente conversar com o Celso, sobre minha perspectiva de tentar o mestrado sob a orientação dele. Porém, eu não sabia nada de Bethylidae, nada de Taxonomia, nada de Sistemática, e tinha poucas chances de ser aprovado pela minha ignorância com o tal inglês. Lembro como se fosse ontem, na nossa reunião, Celso me perguntou com o que eu gostaria de trabalhar e acreditem, eu disse: "*...com a mesma vespa que foi publicada no Facebook do laboratório*". Mas qual vespa? Não sabia... não conhecia nada daquele mundo. Então, Isabel disse: "*Dissomphalus*". Sim! Foi assim que escolhi meu objeto de estudo. Acho que posso dizer, foi amor à primeira foto.

Para minha surpresa, eu fui aprovado no mestrado e ingressei nele em 2015 e com o desenrolar da minha dissertação percebi que não fui enganado pela foto e nem pela Isabel. *Dissomphalus* e Celso foram as melhores escolhas que eu poderia ter feito, e estou realmente agradecido por isto. Me descobri no mundo da Sistemática e não me vejo em outro caminho a não ser este. Porém, ainda não estava totalmente realizado, faltava adicionar a Paleontologia nesta mistura.

No final do mestrado, em 2016, eu tentei a duas seleções de doutorado, uma no próprio PPGBAN-UFES e outra no PGZOO-UFMG e para minha surpresa, fui aprovado em ambas. Eu escolhi o PPGBAN-UFES porque queria continuar estudando e me aprofundando em Bethylidae. Eu tinha duas opções de projetos para a tese, a primeira com Sistemática Filogenética de *Dissomphalus* e a segunda, Sistemática Filogenética de *Epyris*. Visando me desafiar e explorar o máximo possível da diversidade dos betilídeos, eu me aventurei com os *Epyris*.

Epyris é um gênero desafiador e atualmente considerado o maior problema taxonômico de Bethylidae. No decorrer do estudo ficou evidente que era impossível estudar *Epyris* isoladamente, pois este gênero está sobreposto com praticamente todos os outros Epyrinae e neste momento outras hipóteses foram lançadas para a subfamília e a pergunta da minha tese foi redesenhada para "quem são os Epyrinae?". Sendo assim, meu projeto de tese ficou intitulado "Sistemática filogenética de Epyrinae (Hymenoptera, Bethylidae).

Paralelamente, eu desenvolvi trabalhos com outras subfamílias de Bethylidae, que me forneceram uma visão amplificada da família e das metodologias relacionadas à

Sistemática Biológica, porém vale destacar que eu tive a oportunidade de trabalhar com os tão sonhados fósseis e adicionar a Paleontologia na minha vida. Desenvolvi e publiquei quatro trabalhos relacionados à paleodiversidade de Bethylidae, dos quais dois estão inseridos aqui, como capítulos. Hoje, ao final desta tese, me considero um profissional realizado e feliz com minhas escolhas e espero continuar trabalhando com Sistemática de Bethylidae, linha de pesquisa na qual me sinto realizado e realmente feliz.

Trabalhos paralelos ao doutorado

Ao longo dos quatro anos do meu doutorado (03/2017–05/2021), eu desenvolvi e publiquei, em parceria com pesquisadores nacionais e internacionais, 13 artigos científicos e três capítulos de livro. Destes, três estão incluídos nesta tese como capítulos e os demais são relacionados a outros táxons. No total, foram descritas 94 espécies, 11 gêneros e uma subfamília.

Foram publicados trabalhos envolvendo outros betilídeos (Azevedo *et al.* 2018a; 2018b; 2020; Colombo & Azevedo 2019; 2020; Colombo *et al.* 2018; 2020a; 2020b; 2020c; 2021; Vargas *et al.* 2020), escorpiões (Colombo & Alencar 2017), Pompilidae (Waichert *et al.* 2018), Odonata (Furieri & Colombo 2020; Furieri *et al.* 2020) e sobre a fauna ameaçada do Espírito Santo (Fraga *et al.* 2019).

REFERÊNCIAS BIBLIOGRÁFICAS

Azevedo, C.O., Alencar, I.D.C.C., Colombo, W.D. (2018a) Pairs in copulation of the highly dimorphic genus *Pristocera* Klug (Hymenoptera, Bethylidae) from Madagascar solve taxonomic problems of male-female associations. *Zootaxa*, 4433(1), p.1–49.

Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas, J.M.R., Lim, J. (2018b) Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, 4489(1), p.1–294.

Azevedo, C.O., Vargas, J.M.R., Colombo, W.D. (2020) Synopsis of world *Discleroderma* Kieffer (Hymenoptera, Bethylidae). *Zootaxa*, 4742(3), p.467–480.

Colombo, W.D., Alencar, I.D.C.C. (2017) Escorpiões: um estudo de caso com alunos do Ensino Fundamental em escolas dos municípios de Santa Teresa e São Roque do Canaã, Espírito Santo, Brasil. *Boletim do Museu de Biologia Mello Leitão (Nova Série)*, 39(1), p.39–67.

Colombo, W.D., Alencar, I.D.C.C., Limeira-de-Oliveira, F., Azevedo, C.O. (2018) New species and records of *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) from Cerrado, Caatinga and relicts of the Atlantic Forest from northeastern Brazil. *Zootaxa*, 4462(1), p.1–40.

Colombo, W.D., Azevedo, C.O. (2019) Synopsis of the fossil Scleroderminae (Hymenoptera, Bethylidae) with description of a new genus and four new species from Baltic amber. *Historical Biology* [published online], p.1–9.

Colombo, W.D., Azevedo, C.O. (2020) Revalidation of the polymorphic genus *Acephalonomia* (Hymenoptera: Bethylidae) and description of a new species from Micronesia. *European Journal of Entomology*, 117, p.235–242

Colombo, W.D., Gobbi, F.T., Perkovsky, E.E., Azevedo, C.O. (2020a) Synopsis of the fossil Pristocerinae (Hymenoptera, Bethylidae), with description of two new genera and six species from Burmese, Taimyr, Baltic and Rovno ambers. *Historical Biology* [published online], p.1–17.

Colombo, W.D., Perkovsky, E.E., Azevedo, C.O. (2020b) Phylogenetic overview of flat wasps (Hymenoptera, Bethylidae) reveals Elektroepyrinae, a new fossil subfamily. *Palaeoentomology*, 3(3), p.269–283

Colombo, W.D., Perkovsky, E.E., Waichert, C., Azevedo, C.O. (2021) Synopsis of the fossil flat wasps Epyrinae (Hymenoptera, Bethylidae), with description of three new genera and 10 new species. *Journal of Systematic Palaeontology*, 19, p.1–51.

Colombo, W.D., Waichert, C., Azevedo, C.O. (2020c) Molecular and morphological species delimitation of Epyrinae (Hymenoptera: Bethylidae) from Papua New Guinea. In: Robillard, T., Legendre, F., Villemant, C., Leponce, M. (Eds), *Insects of Mount Wilhelm, Papua New Guinea*. Muséum national d'Histoire naturelle, vol. 2., Paris, 599p.

Fraga, C.N., Peixoto, A.L., Leite, Y.L.R., Santos, N.D., Oliveira, J.R.P.M., Sylvestre, L.S., Schwartsburd, P.B., Tuler, A.C., Freitas, J., Lírio, E.J., Couto, D.R., Dutra, V.F., Waichert, C., Sobrinho, T.G., Hostim-Silva, M., Ferreira, R.B., Bérnils, R.S., Costa, L.P., Chaves, F.G., Formigoni, M.H., Silva, J.P., Ribeiro, R.S., Reis, J.C.L., Capellão, R.T., Lima, R.O., Saiter, F.Z., *et al.* (2019) Lista da fauna e flora ameaçadas de extinção no estado do Espírito Santo. In: Fraga, C.N, Formigoni, M.H. & Chaves, F.G. (Eds.), *Fauna e flora ameaçadas de extinção no estado do Espírito Santo. Instituto Nacional da Mata Atlântica*, vol. 1., Espírito Santo, 432p.

Furieri, K.S., Colombo, W.D. (2020) A contribuição da coleção entomológica da Reserva Natural Vale para Odonata (Insecta). In: Oliveira-Júnior, J.M.B., Calvão, L.B. (Eds), *Tópicos Integrados de Zoologia 2*. Atene Editora, Paraná, 115p.

Furieri, K.S., Fraga, F.B., Tribull, C.M., Colombo, W.D. (2020) Description of two females of *Leptagrion* Selys (Odonata: Coenagrionidae). *Zootaxa*, 4821(2), p.343–352.

Vargas, J.M.R., Colombo, W.D., Azevedo, C.O. (2020) Revisited phylogeny of Scleroderminae (Hymenoptera: Bethylidae) reveals a plastic evolutionary history. *Arthropod Systematics and Phylogeny*, 78(2), p.217–243

Waichert, C., Colombo, W.D., von Dohlen, C., Pitts, J.P. (2018) Taxonomic contributions to *Ageniella* Banks, 1912 (Hymenoptera: Pompilidae) from Brazil. *Zootaxa*, 4403(1), p.133–153.

CAPÍTULO I

Molecular and morphological species delimitation of Epyrinae (Hymenoptera, Bethylidae) from Papua New Guinea[1]

ABSTRACT

The fauna of Epyrinae from Papua New Guinea is revised by using molecular, the Cytochrome C Oxidase Subunit I (COI) mitochondrial gene and morphological data. This study is based on the observation of 115 specimens of Epyrinae from Mount Wilhelm and Wanang Conservation Area. Twenty-one species of *Chlorepyris*, six species of *Epyris* and nine species of *Holepyris* were recognized, all of them described and illustrated as new to Science: *Chlorepyris abelam* Colombo & Azevedo n. sp., *C. angu* Colombo & Azevedo n. sp., *C. baining* Colombo & Azevedo n. sp., *C. baruya* Colombo & Azevedo n. sp., *C. biangai* Colombo & Azevedo n. sp., *C. bilibil* Colombo & Azevedo n. sp., *C. chambri* Colombo & Azevedo n. sp., *C. duna* Colombo & Azevedo n. sp., *C. enga* Colombo & Azevedo n. sp., *C. etoro* Colombo & Azevedo n. sp., *C. fore* Colombo & Azevedo n. sp., *C. gadsup* Colombo & Azevedo n. sp., *C. gogodala* Colombo & Azevedo n sp., *C. haroli* Colombo & Azevedo n. sp., *C. hewa* Colombo & Azevedo n. sp., *C. huli* Colombo & Azevedo n. sp., *C. iatmul* Colombo & Azevedo n. sp., *C. kaluli* Colombo & Azevedo n. sp., *C. koteka* Colombo & Azevedo n. sp., *C. kwoma* Colombo & Azevedo n. sp., *C. maisin* Colombo & Azevedo n. sp., *Epyris melpa* Colombo & Azevedo n. sp., *E. mian* Colombo & Azevedo n. sp., *E. min* Colombo & Azevedo n. sp., *E. motu* Colombo & Azevedo n. sp., *E. mundugumor* Colombo & Azevedo n. sp., *E. ogea* Colombo & Azevedo n. sp., *Holepyris orokaiva* Colombo & Azevedo n. sp., *H. sambia* Colombo & Azevedo n. sp., *H. swagap* Colombo & Azevedo n. sp., *H. tairora* Colombo & Azevedo n. sp., *H. telefol* Colombo & Azevedo n. sp., *H. tsembaga* Colombo & Azevedo n. sp., *H. wiru* Colombo & Azevedo n. sp., *H. yaifo* Colombo & Azevedo n. sp., and *H. zia* Colombo & Azevedo n. sp. Three species already reported from Papua New Guinea are investigated: *Epyris erraticus* Smith, *E. interruptus* Kieffer and *Chlorepyris armatus* (Kieffer). *Holepyris* is recorded for the first time from Papua New Guinea, making Epyrinae now known from three genera. A key for all genera and species of Epyrinae in Papua New Guinea is provided.

[1] Capítulo publicado e formatado seguindo as instruções para os autores do Jornal *Mémoires du Muséum national d'histoire naturelle*.

RÉSUMÉ

La faune des Epyrinae de Papouasie-Nouvelle-Guinée est révisée à l'aide de données moléculaires, avec le marqueur mitochondrial Cytochrome C Oxydase sous-unité 1 (COI), et morphologiques. Cette étude s'appuie sur l'observation de 115 spécimens d'Epyrinae provenant du Mont Wilhelm et de Wanang Conservation Area. Vingt et une espèces de *Chlorepyris*, six espèces d'*Epyris* et neuf espèces de *Holepyris* ont été reconnues, toutes décrites et illustrées comme nouvelles pour la science: *Chlorepyris abelam* Colombo & Azevedo n. sp., *C. angu* Colombo & Azevedo n. sp., *C. baining* Colombo & Azevedo n. sp., *C. baruya* Colombo & Azevedo n. sp, *C. biangai* Colombo & Azevedo n. sp., *C. bilibil* Colombo & Azevedo n. sp., *C. chambri* Colombo & Azevedo n. sp., *C. duna* Colombo & Azevedo n. sp., *C. enga* Colombo & Azevedo n. sp, *C. etoro* Colombo & Azevedo n. sp., *C. fore* Colombo & Azevedo n. sp., *C. gadsup* Colombo & Azevedo n. sp., *C. gogodala* Colombo & Azevedo n. sp., *C. haroli* Colombo & Azevedo n. sp, *C. hewa* Colombo & Azevedo n. sp., *C. huli* Colombo & Azevedo n. sp., *C. iatmul* Colombo & Azevedo n. sp., *C. kaluli* Colombo & Azevedo n. sp., *C. koteka* Colombo & Azevedo n. sp, *C. kwoma* Colombo & Azevedo n. sp., *C. maisin* Colombo & Azevedo n. sp., *Epyris melpa* Colombo & Azevedo n. sp., *E. mian* Colombo & Azevedo n. sp., *E. min* Colombo & Azevedo n. sp, *E. motu* Colombo & Azevedo n. sp., *E. mundugumor* Colombo & Azevedo n. sp., *E. ogea* Colombo & Azevedo n. sp., *Holepyris orokaiva* Colombo & Azevedo n. sp, *H. sambia* Colombo & Azevedo n. sp., *H. swagap* Colombo & Azevedo n. sp., *H. tairora* Colombo & Azevedo n. sp., *H. telefol* Colombo & Azevedo n. sp., *H. tsembaga* Colombo & Azevedo n. sp, *H. wiru* Colombo & Azevedo n. sp., *H. yaifo* Colombo & Azevedo n. sp. et *H. zia* Colombo & Azevedo n. sp. Trois espèces déjà signalées en Papouasie-Nouvelle-Guinée sont examinées: *Epyris erraticus* Smith, *E. interruptus* Kieffer et *Chlorepyris armatus* (Kieffer). *Holepyris* est signalé pour la première fois en Papouasie-Nouvelle-Guinée, amenant à trois le nombre de genres d'Epyrinae connus pour ce pays. Une clé pour tous les genres et espèces d'Epyrinae en Papouasie-Nouvelle-Guinée est fournie.

INTRODUCTION

Epyrinae are currently the second most speciose subfamily of Bethylidae and the most diverse group of Bethylidae in morphological terms (Alencar & Azevedo 2013). Epyrinae have approximately 930 species described and 13 genera (Azevedo *et al.* 2018).

Although cosmopolitan, few species occur in the Oceanian region (sense Holt *et al.* 2013). Currently, there are 46 species of Epyrinae recorded for this region, being 39 from Philippines, two from Hawaii, two from Indonesia and three from Papua New Guinea (PNG).

Papua New Guinea (PNG) is the second largest island on Earth, harboring an impressive diversity of climates zones and landforms (Leponce *et al.* 2016). Three species of Epyrinae have been reported to PNG. Among the genera of Epyrinae, *Epyris* Westwood and *Chlorepyris* Kieffer are cosmopolitan and have three species recorded from New Guinea: *Epyris erraticus* Smith, *Epyris interruptus* Kieffer and *Chlorepyris armatus* (Kieffer). Herein, we record one more genus from this island, *Holepyris* Kieffer, summing the fauna of Epyrinae up to three genera and 39 species.

Once again, the material analyzed in this study and the uncovering of several species of Epyrinae reveals that the knowledge on this subfamily, and the three above-mentioned genera, is underestimated. Finally, we propose for the first time in Bethylidae genetic distance analyses based on the mitochondrial Cytochrome C Oxidase Subunit I (COI), aiming to improve delimitation of the species.

MATERIAL AND METHODS

Collection and taxonomic methods

This study was based on 115 specimens of Epyrinae collected in PNG (Figure 1), in a rainforest transect (Mount Wilhelm and Wanang Conservation Area, Madang province) during the "Our Planet Reviewed – Papua New Guinea 2012-2013" expedition, which was launched by the Muséum national d'Histoire naturelle (MNHN, Paris, Philippe Bouchet) and Pro-Natura International (PNI, Paris, Olivier Pascal) in association with the Royal Belgian Institute of Natural Sciences (RBINS, Brussels, Maurice Leponce) and the New Guinea Binatang Research Center (NGBRC, Madang, Vojtech Novotny).

The samples were collected with Malaise traps and flight interception traps in 2012, for more details, see Leponce *et al.* 2016. The material belongs to and it is deposited at Muséum national d'Histoire naturelle (MNHN, Paris, curator: Claire Villemant), with retentions in the Universidade Federal do Espírito Santo (UFES, Brazil, curator: Marcelo T. Tavares) as specified.

The holotypes of *Epyris interruptus* and *Chlorepyris armatus* are deposited in the Museo Civico di Storia Naturale (MCSN, Genova, curator: Maria Tavano) and were

examined, photographed, illustrated and redescribed. The holotype of *Epyris erraticus* is supposed to be at the Natural History Museum in London (Gordh & Móczár 1990) but was not found, so that we have analyzed it through its original description.

The nomenclature of the integument generally follows Harris (1979) and the Hymenoptera Anatomy Ontology project (HAO) (Yoder *et al.* 2010). Terminology of external morphology follows Evans (1964), Azevedo (1999) and Kawada *et al.* (2015), and those of male genitalia follow Snodgrass (1941). Taxonomic characters related to genitalia and hypopygium were examined; such structures were previously dissected according to the Proteinase K protocol described by Martinelli *et al.* (2017).

We illustrated and highlighted the following morphological characters used for delimitation of species: clypeus (Figure 2A), mandibles (Figures 2B, 3A, 3J), eyes (Figures 2C, 3B, 3K), frontal line (Figure 2D), occipital carina (Figure 3C), pronotum (Figure 3L), anterior mesofurcal pit (Figure 3D), posterior mesofurcal pit (Figure 3E), metafurcal pit (Figure 3F), metasternum (Figure 3G), anterior mesopleural fovea (Figure 3M), mesopleural pit (Figure 3N), lower mesopleural fovea (Figure 3O), mesopleural suture (Figure 3P), notaulus (Figures 2E, 3Q), parapsidal signum (Figure 2F), forewing flexion lines (Figure 2G), forewing 2r-rs&Rs veins (Figure 2H), mesoscutellar foveae (Figures 2I, 3R), metascutellum (Figure 2J), metapostnotal anterior margin (Figure 2K), metapostnotal median carina (Figure 2L), first metapostnotal carina (Figures 2M, 3S), metapostnotal-propodeal suture (Figures 2N, 3T), metatibia (Figure 2O), petiole (Figures 2P, 3H, 3W), and metasoma (Figures 2Q, 3I, 3Y).

The specimens analyzed were compared with types, vouchers and original descriptions of the species reported from PNG, Indonesia, Philippines, Hawaii, and Australia.

The specific epithets of all new species refer to ethnic groups or languages from PNG.

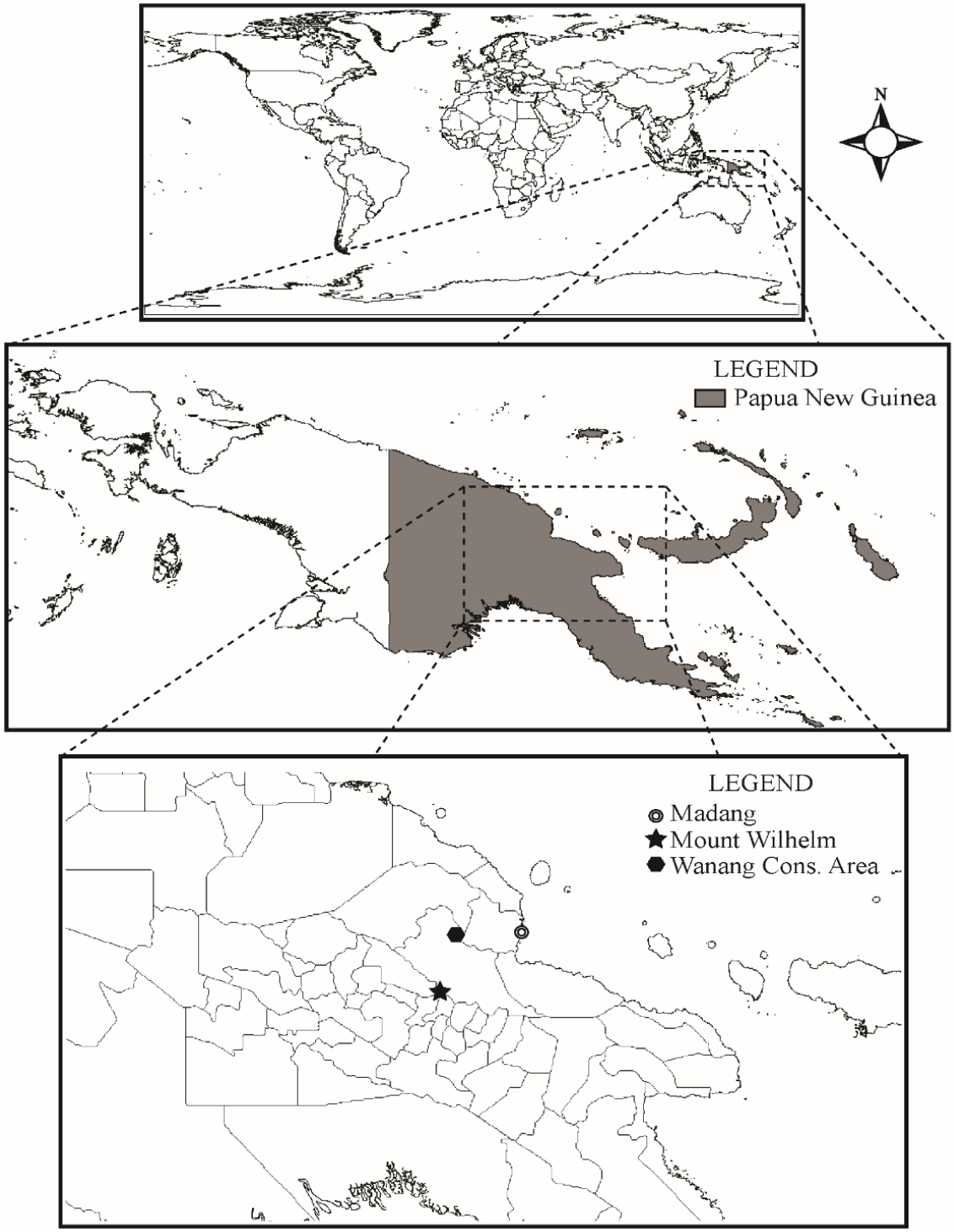

FIGURE 1. Location of the two collecting areas in Papua New Guinea Madang province (◎: Mount Wilhelm (★) and Wanang Conservation Area (□).

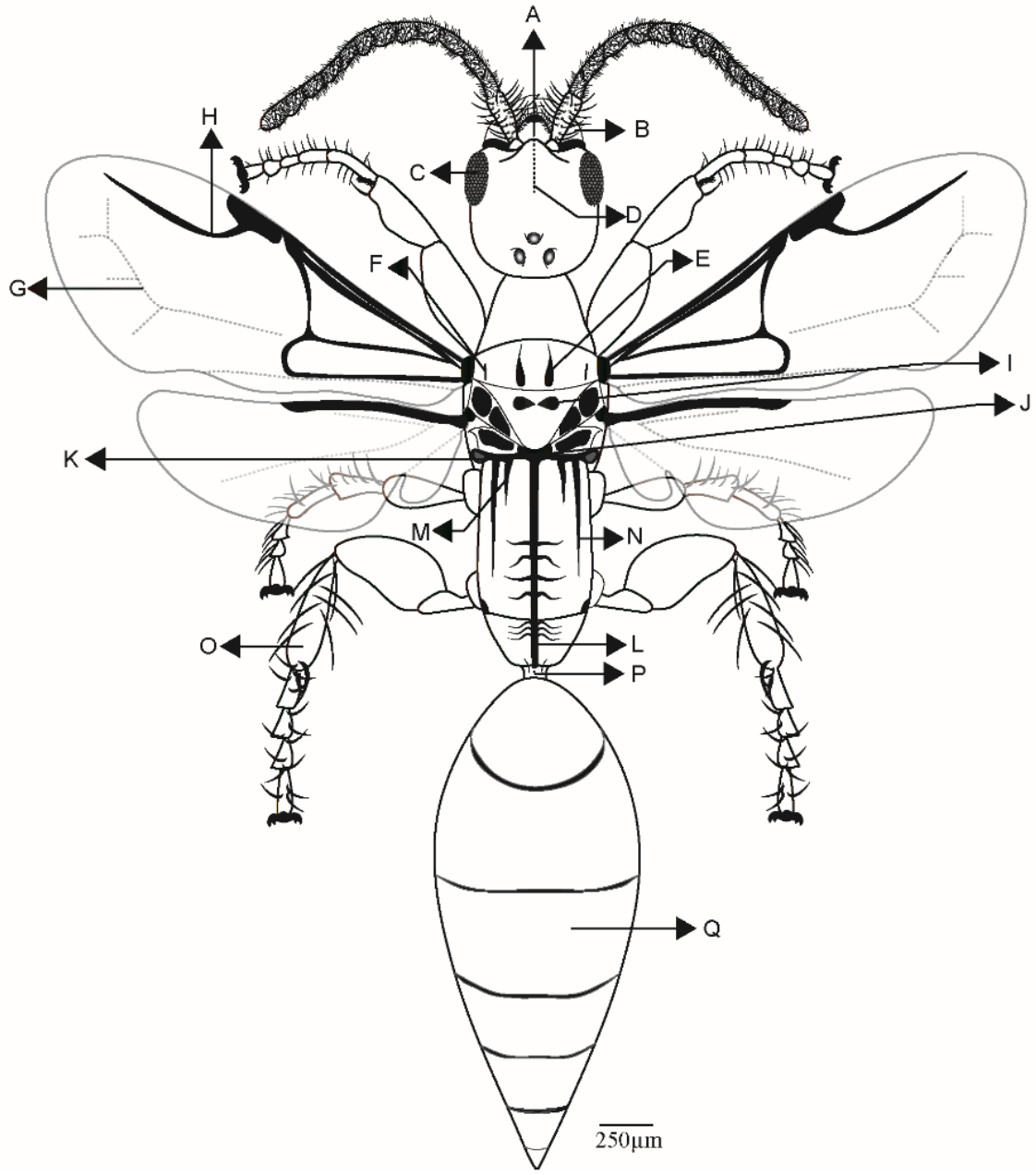

FIGURE 2. Bethylidae. Morphological characters in dorsal view. **A**, clypeus; **B**, mandible; **C**, eye; **D**, frontal line; **E**, notaulus; **F**, parapsidal signum; **G**, flexion lines of the forewing; **H**, forewing 2r-rs&Rs vein; **I**, mesoscutellar fovea; **J**, metascutellum; **K**, metapostnotal anterior margin; **L**, metapostnotal median carina; **M**, first metapostnotal carina; **N**, metapostnotal-propodeal suture; **O**, metatibia; **P**, petiole; **Q**, metasoma. Scale bar: 250 µm.

The images were taken under a Leica Z16 APO stereomicroscope coupled to a Leica DFC 2 video camera by Leica Microsystems (Switzerland) under Modular Dome Illumination System by Kawada & Buffington (2016). To combine images, we used the Helicon Focus (HeliconSoft) and saved them in 300 DPI. The characters of the male genital structures were drawn in camera lucida adapted to a Leica DM 2500 microscope, then scanned into Photoshop and saved in 600 DPI.

For each specimen, illustrations were made as follows: head in dorsal view; mandible frontal view; mesosoma dorsal, ventral and lateral views; forewing in dorsal view and male genitalia in dorsal, ventral and lateral views. All photographs and drawings were based on holotypes or paratypes.

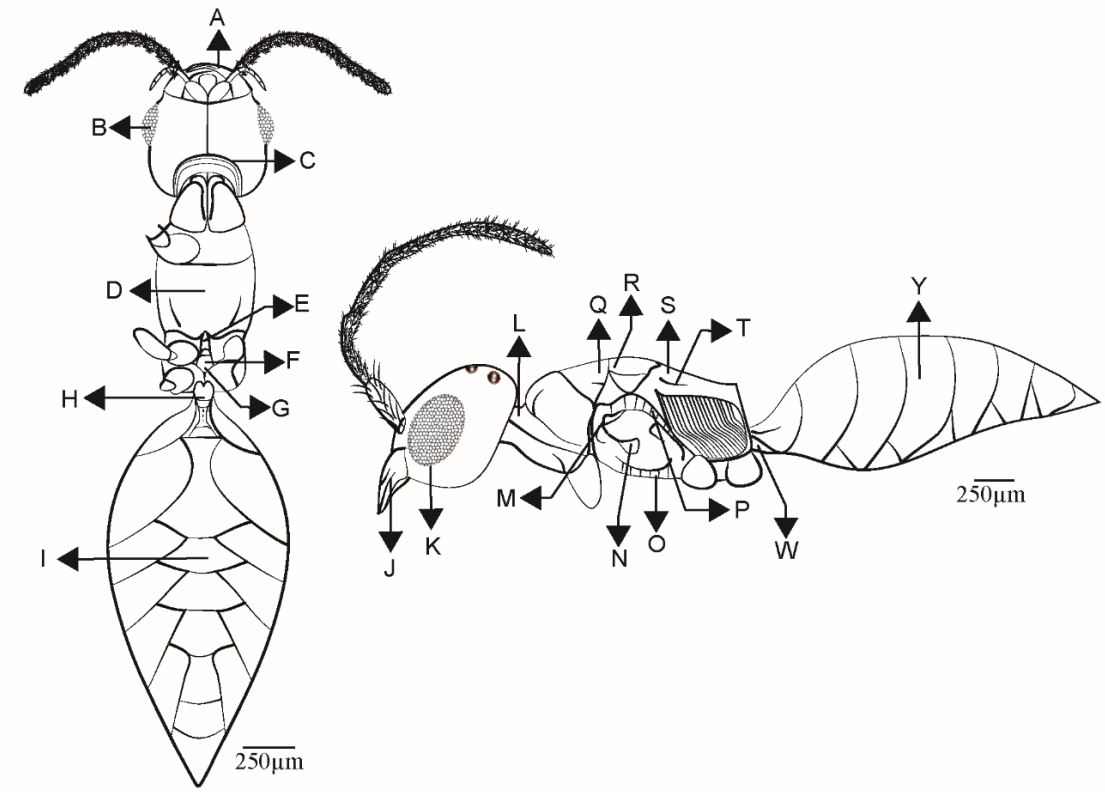

FIGURE 3. Bethylidae. Morphological characters in ventral view. **A**, mandible; **B**, eye; **C**, occipital carina; **D**, anterior mesofurcal pit; **E**, posterior mesofurcal pit; **F**, metafurcal pit; **G**, metasternum; **H**, petiole; **I**, metasoma; Bethylidae. Morphological characters in lateral view; **J**, mandible; **K**, eye; **L**, pronotum; **M**, anterior mesopleural fovea; **N**, mesopleural pit; **O**, lower mesopleural fovea; **P**, mesopleural suture; **Q**, notaulus; **R**, mesoscutellar fovea; **S**, first metapostnotal carina; **T**, metapostnotal-propodeal suture; **W**, petiole; **Y**, metasoma. Scale bar: 250 µm.

Molecular methods

For molecular protocols, we selected 37 specimens (11♀ and 26♂) of Epyrinae representing the morphospecies and the morphological variation previously recognized during morphospecies identification. All female representatives were included for potential conspecific male-female association. The DNA was extracted from the metasoma and mesosoma of the 37 adult specimens by using the NucleoSpin® Tissue Kit according to the manufacturer's protocol. The metasoma and head were disassembled to provide orifice to the reagents.

Standard PCR procedures and primers proposed by Folmer *et al.* (1994) were used to amplify the mitochondrial gene COI. Thermal setup of primers LCO1490/HCO2198 (Folmer *et al.* 1994) was: a 1-minute initial denaturation at 95°C followed by 43 cycles of 45-second denaturation at 95°C, 45 seconds of annealing at 47°C, 45 seconds extension at 47°C, and a 3-minute final extension at 72°C.

The amplification products were detected in 1.5% agarose gel electrophoresis (AGE), and then successful products were purified using an enzymatic procedure with the ExoSAP-IT® kit (USB Corporation) incubated at 37°C for 15 minutes to degrade remaining primers and nucleotides and finally, incubated at 80°C for 15 minutes to inactivate ExoSAP-IT reagent. The eligible products were then sequenced in a T3500 Genetic Analyzer.

The returned forward and reverse chromatograms were examined and trimmed with MEGA 6 (Molecular Evolutionary Genetics Analysis version 6.0, Tamura *et al.* 2013). The alignments were made, adjusted, and edited manually in MEGA6.

Species delimitation methods

The nucleotide alignment was used to reconstruct a maximum likelihood phylogeny and to access genetic variability within the genera and species. The phylogenetic analysis was performed in RAxML (Stamatakis 2014) through CIPRES portal Science Gateway V. 3.0 (Miller *et al.* 2010) with GTRGAMMA model of nucleotide evolution; clades support were accessed by 1,000 bootstrap replications. We included three males of the genus *Apenesia* Westwood (Bethylidae, Pristocerinae) also collected in PNG, to root the tree (Figure 4).

The Kimura-2-parameter K2P model of base substitution was selected for pairwise distances calculation, which was made in MEGA6. The model was chosen to provide more accurate comparison between results as previous studies with Hymenoptera use K2P as model (Jiang *et al.* 2015; Waichert *et al.* 2015).

DNA barcoding based on a short fragment of mitochondrial DNA can provide an effective tool for species diagnosis (Zhu *et al.* 2017). Its effectiveness as a tool for rapid identification of species, and sex association, has been reported in some groups of insects, such as Hemiptera (Lee *et al.* 2011; Zhu *et al.* 2017), Hymenoptera (Smith *et al.* 2008), Coleoptera (Löbl & Leschen 2005), and Lepidoptera (Hajibabaei *et al.* 2006) for instance.

RESULTS

Molecular protocol and distance analyses

A COI sequence was amplified from 34 specimens out of 37 sampled (Table 1). The length of the nucleotide sequences varied from 633-709 bp. As expected for Hymenoptera (Crozier *et al.* 1989; Simon *et al.* 1994; Li *et al.* 2010), adenine (A) and thymine (T) had the highest frequency (A=37.0%, C=11.8%, G=11.5%, T=39.4%).

We recognized 21 species of *Chlorepyris*, nine species of *Holepyris* and six species of *Epyris*. Considering that the sampling effort was low, these results indicate that *Chlorepyris* is the most diverse genus of Epyrinae in this region, and the potential for more species in future expeditions is high.

TABLE 1. Terminal taxa of PNG Epyrinae molecular analysis with GenBank codes.

Genbank code	Specimen voucher	Species	Sex
MK051186	W10	*Chlorepyris abelam* Colombo & Azevedo **n. sp.**	♂
MK051187	W20	*Chlorepyris gogodala* Colombo & Azevedo **n. sp.**	♂
MK051188	W21	*Chlorepyris haroli* Colombo & Azevedo **n. sp.**	♂
MK051189	W22	*Chlorepyris hewa* Colombo & Azevedo **n. sp.**	♂
MK051190	W23	*Chlorepyris huli* Colombo & Azevedo **n. sp.**	♂
MK051191	W24	*Chlorepyris iatmul* Colombo & Azevedo **n. sp.**	♀
MK051192	W25	*Chlorepyris kaluli* Colombo & Azevedo **n. sp.**	♀
MK051193	W27	*Chlorepyris koteka* Colombo & Azevedo **n. sp.**	♀
MK051194	W28	*Chlorepyris bilibil* Colombo & Azevedo **n. sp.**	♀
MK051195	W12	*Chlorepyris baining* Colombo & Azevedo **n. sp.**	♂
MK051196	W31	*Chlorepyris maisin* Colombo & Azevedo **n. sp.**	♀
MK051197	W11	*Chlorepyris angu* Colombo & Azevedo **n. sp.**	♂
MK051198	W26	*Epyris ogea* Colombo & Azevedo **n. sp.**	♀
MK051199	W32	*Epyris melpa* Colombo & Azevedo **n. sp.**	♂
MK051200	W33	*Epyris mian* Colombo & Azevedo **n. sp.**	♂
MK051201	W34	*Epyris min* Colombo & Azevedo **n. sp.**	♂
MK051202	W35	*Epyris motu* Colombo & Azevedo **n. sp.**	♀
MK051203	W29	*Epyris mundugumor* Colombo & Azevedo **n. sp.**	♀
MK051204	W1	*Holepyris orokaiva* Colombo & Azevedo **n. sp.**	♂
MK051205	W6	*Holepyris telefol* Colombo & Azevedo **n. sp.**	♂
MK051206	W7	*Holepyris tsembaga* Colombo & Azevedo **n. sp.**	♂
MK051207	W2	*Holepyris sambia* Colombo & Azevedo **n. sp.**	♂
MK051208	W13	*Chlorepyris baruya* Colombo & Azevedo **n. sp.**	♂
MK051209	W3	*Holepyris swagap* Colombo & Azevedo **n. sp.**	♂
MK051210	W8	*Holepyris wiru* Colombo & Azevedo **n. sp.**	♀
MK051211	W9	*Holepyris zia* Colombo & Azevedo **n. sp.**	♀

MK051212	W5	*Holepyris tairora* Colombo & Azevedo **n. sp.**	♂
MK051213	W30	*Chlorepyris kwoma* Colombo & Azevedo **n. sp.**	♀
MK051214	W14	*Chlorepyris bilibil* Colombo & Azevedo **n. sp.**	♂
MK051215	W15	*Chlorepyris chambri* Colombo & Azevedo **n. sp.**	♂
MK051216	W16	*Chlorepyris enga* Colombo & Azevedo **n. sp.**	♂
MK051217	W17	*Chlorepyris etoro* Colombo & Azevedo **n. sp.**	♂
MK051218	W18	*Chlorepyris fore* Colombo & Azevedo **n. sp.**	♂
MK051219	W19	*Chlorepyris gadsup* Colombo & Azevedo **n. sp.**	♂

Our results pointed to sex association. Conspecifics male and female specimens of *Chlorepyris* were associated based on identical nucleotide sequences. In the genus *Holepyris*, the lowest genetic distance observed between the species was 3%, but these taxa are morphologically distinct, especially in the male genitalia features. In *Chlorepyris*, besides the conspecific specimens that presented 0% of genetic distance, the minimum interspecific variation was 3%. *Epyris* presented lineages genetically distant, the shortest nucleotide distance among species was 10%. Overall, the mean genetic distance found among the lineages of Epyrinae in PNG was 24% variation (Figure 4).

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1	*C. abelam*																																					
2	*C. angu*	0,13																																				
3	*C. baining*	0,15	0,18																																			
4	*C. barsya*	0,13	0,18	0,06																																		
5	*C. bilibil* (male)	0,14	0,17	0,08	0,06																																	
6	*C. bilibil* (female)	0,14	0,17	0,08	0,06	0,00																																
7	*C. chambri*	0,07	0,15	0,15	0,13	0,14	0,14																															
8	*C. enga*	0,12	0,15	0,15	0,15	0,13	0,13	0,13																														
9	*C. etoro*	0,13	0,16	0,16	0,16	0,14	0,14	0,12	0,14																													
10	*C. fore*	0,12	0,17	0,15	0,17	0,16	0,16	0,14	0,15	0,12																												
11	*C. gadsup*	0,08	0,13	0,15	0,13	0,12	0,12	0,10	0,12	0,14	0,14																											
12	*C. gogodala*	0,17	0,22	0,15	0,16	0,15	0,14	0,15	0,18	0,17	0,21	0,18																										
13	*C. haroli*	0,17	0,20	0,15	0,16	0,15	0,15	0,16	0,17	0,20	0,21	0,18	0,17																									
14	*C. hewa*	0,14	0,17	0,07	0,03	0,06	0,06	0,13	0,14	0,14	0,17	0,12	0,16	0,15																								
15	*C. huli*	0,06	0,13	0,15	0,13	0,13	0,12	0,05	0,12	0,12	0,13	0,08	0,14	0,17	0,13																							
16	*C. latmul*	0,13	0,19	0,14	0,13	0,14	0,13	0,13	0,15	0,17	0,19	0,15	0,13	0,18	0,12	0,12																						
17	*C. kaluli*	0,15	0,20	0,14	0,15	0,14	0,14	0,14	0,16	0,16	0,18	0,17	0,09	0,16	0,14	0,14	0,11																					
18	*C. koteka*	0,13	0,16	0,12	0,11	0,11	0,11	0,11	0,16	0,16	0,18	0,14	0,13	0,14	0,10	0,12	0,13	0,14																				
19	*C. kwoma*	0,08	0,14	0,15	0,14	0,14	0,14	0,07	0,12	0,13	0,14	0,11	0,17	0,18	0,14	0,06	0,14	0,16	0,13																			
20	*C. massin*	0,12	0,19	0,12	0,12	0,12	0,12	0,12	0,13	0,14	0,17	0,14	0,16	0,17	0,11	0,13	0,12	0,13	0,13	0,15																		
21	*E. melpa*	0,26	0,26	0,26	0,24	0,22	0,22	0,27	0,22	0,26	0,29	0,24	0,25	0,25	0,24	0,25	0,25	0,24	0,26	0,25	0,24																	
22	*E. mian*	0,18	0,23	0,19	0,18	0,19	0,19	0,19	0,19	0,21	0,24	0,18	0,21	0,20	0,18	0,20	0,19	0,20	0,19	0,22	0,18	0,25																
23	*E. min*	0,20	0,23	0,19	0,20	0,19	0,18	0,21	0,21	0,24	0,25	0,20	0,20	0,24	0,19	0,20	0,20	0,19	0,19	0,22	0,18	0,21	0,18															
24	*E. motu*	0,16	0,21	0,16	0,16	0,17	0,17	0,18	0,17	0,18	0,22	0,18	0,19	0,18	0,17	0,17	0,20	0,17	0,17	0,18	0,18	0,22	0,09	0,17														
25	*E. wundugumor*	0,22	0,28	0,20	0,19	0,20	0,20	0,22	0,22	0,23	0,26	0,20	0,22	0,25	0,19	0,22	0,23	0,18	0,21	0,24	0,19	0,23	0,18	0,13	0,16													
26	*E. ogea*	0,20	0,23	0,18	0,20	0,19	0,19	0,20	0,21	0,22	0,25	0,21	0,20	0,19	0,19	0,21	0,19	0,21	0,20	0,22	0,20	0,24	0,23	0,19	0,21	0,22												
27	*H. orokaiva*	0,14	0,20	0,17	0,15	0,14	0,14	0,14	0,13	0,16	0,18	0,15	0,19	0,18	0,15	0,14	0,17	0,16	0,15	0,16	0,14	0,22	0,19	0,19	0,18	0,20	0,18											
28	*H. telefol*	0,17	0,21	0,18	0,17	0,18	0,18	0,19	0,16	0,21	0,22	0,19	0,19	0,22	0,17	0,18	0,19	0,17	0,21	0,19	0,18	0,27	0,19	0,20	0,19	0,22	0,23	0,13										
29	*H. trembaga*	0,17	0,21	0,17	0,16	0,17	0,16	0,16	0,16	0,19	0,19	0,17	0,20	0,23	0,15	0,15	0,17	0,17	0,16	0,18	0,17	0,25	0,19	0,18	0,18	0,21	0,24	0,08	0,14									
30	*H. zambia*	0,19	0,23	0,21	0,21	0,20	0,20	0,17	0,18	0,22	0,22	0,20	0,20	0,27	0,20	0,18	0,19	0,20	0,20	0,20	0,18	0,26	0,24	0,22	0,22	0,24	0,22	0,11	0,16	0,12								
31	*H. zwagap*	0,18	0,22	0,19	0,18	0,17	0,17	0,18	0,20	0,21	0,23	0,18	0,20	0,24	0,18	0,16	0,17	0,18	0,18	0,19	0,20	0,28	0,21	0,22	0,18	0,23	0,23	0,15	0,15	0,16	0,16							
32	*H. tairora*	0,18	0,20	0,17	0,16	0,17	0,16	0,17	0,18	0,21	0,21	0,16	0,20	0,24	0,16	0,16	0,19	0,19	0,17	0,18	0,18	0,24	0,22	0,21	0,20	0,21	0,23	0,12	0,16	0,13	0,14	0,16						
33	*H. wiru*	0,15	0,19	0,17	0,16	0,15	0,15	0,15	0,14	0,16	0,19	0,16	0,19	0,20	0,16	0,15	0,18	0,18	0,17	0,17	0,15	0,23	0,20	0,20	0,19	0,21	0,18	0,03	0,13	0,09	0,11	0,15	0,13					
34	*H. zia*	0,17	0,20	0,17	0,17	0,17	0,17	0,15	0,17	0,18	0,19	0,17	0,21	0,21	0,15	0,15	0,17	0,19	0,19	0,18	0,16	0,25	0,18	0,21	0,18	0,22	0,21	0,08	0,14	0,08	0,14	0,17	0,15	0,09				
35	*A. sp.* 227	0,30	0,29	0,33	0,30	0,31	0,31	0,30	0,30	0,30	0,33	0,30	0,29	0,34	0,29	0,28	0,30	0,29	0,31	0,29	0,32	0,33	0,30	0,32	0,30	0,32	0,35	0,30	0,30	0,29	0,33	0,32	0,33	0,29	0,31			
36	*A. sp.* 228	0,29	0,35	0,31	0,29	0,29	0,29	0,32	0,33	0,32	0,38	0,29	0,32	0,34	0,29	0,32	0,33	0,32	0,30	0,32	0,31	0,34	0,31	0,30	0,30	0,31	0,36	0,30	0,33	0,33	0,36	0,37	0,34	0,32	0,35	0,22		
37	*A. sp.* 229	0,31	0,31	0,34	0,31	0,32	0,32	0,32	0,31	0,30	0,35	0,31	0,31	0,34	0,31	0,29	0,31	0,30	0,32	0,30	0,33	0,34	0,31	0,33	0,31	0,33	0,37	0,31	0,31	0,30	0,34	0,33	0,34	0,30	0,32	0,01	0,23	

FIGURE 4. Genetic distances between the species of tree of PNG Epyrinae from PNG.

When the nucleotide divergence was low, but the morphology presented differences, the morphological analysis prevailed. Different morphological data has been crucial to delimit and diagnose species (Waichert & Azevedo 2009; Alencar & Azevedo 2013).

Phylogenetics analysis

The resulting analysis of PNG Epyrinae likelihood tree supported Epyrinae (Bootstrap=100), but the genera sampled here were not reconstructed with support (Figure 5). *Holepyris* was the only lineage of Epyrinae recovered with statistical support (Bootstrap=100); whereas *Epyris* had at least four lineages, considering Bootstrap values >70. Species of *Chlorepyris* nested together but the cluster is statically unsupported (Bootstrap=39), splitting into two clusters with bootstrap values=37 and 80. The supported clade of *Chlorepyris* included nine species.

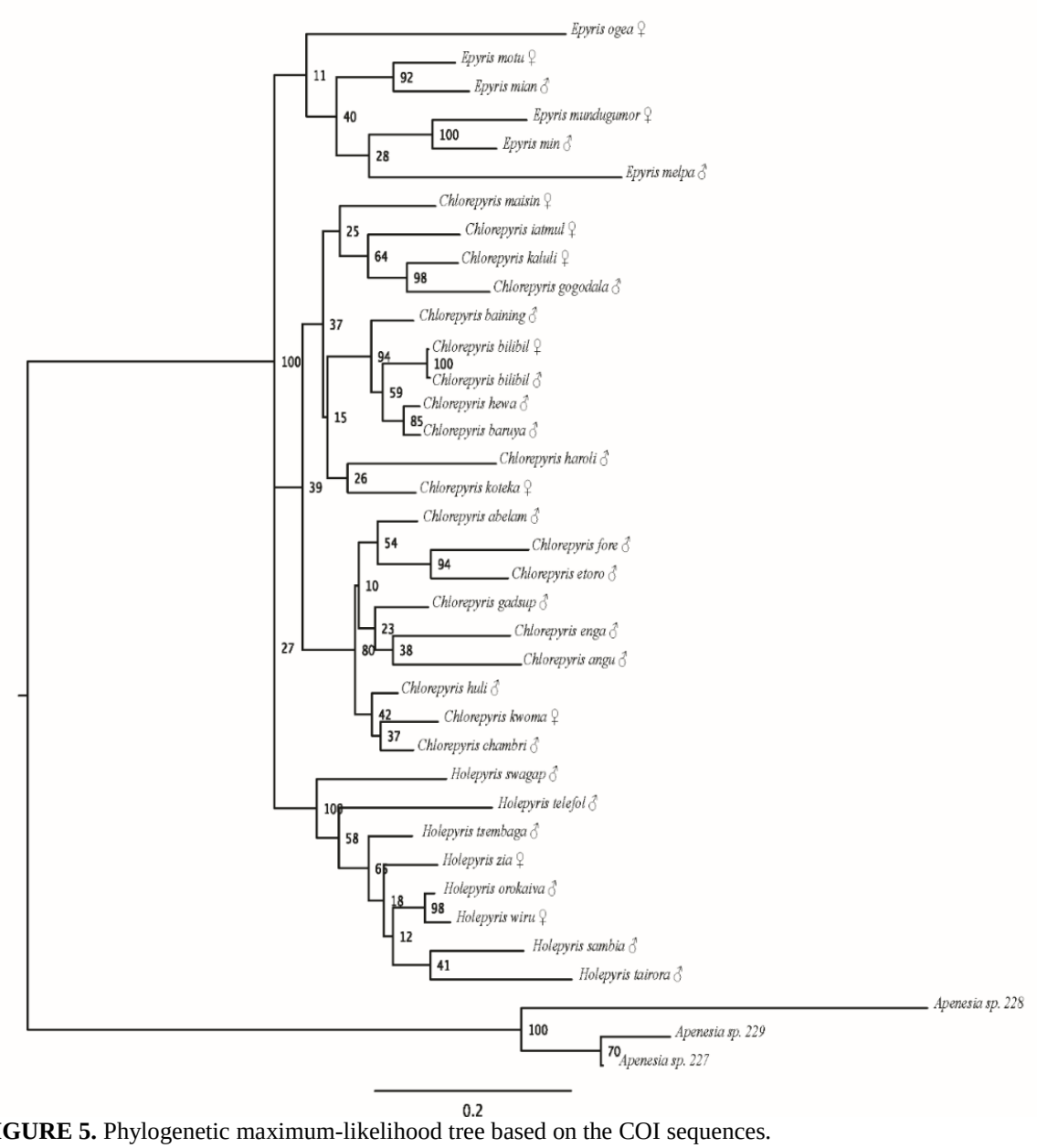

FIGURE 5. Phylogenetic maximum-likelihood tree based on the COI sequences.

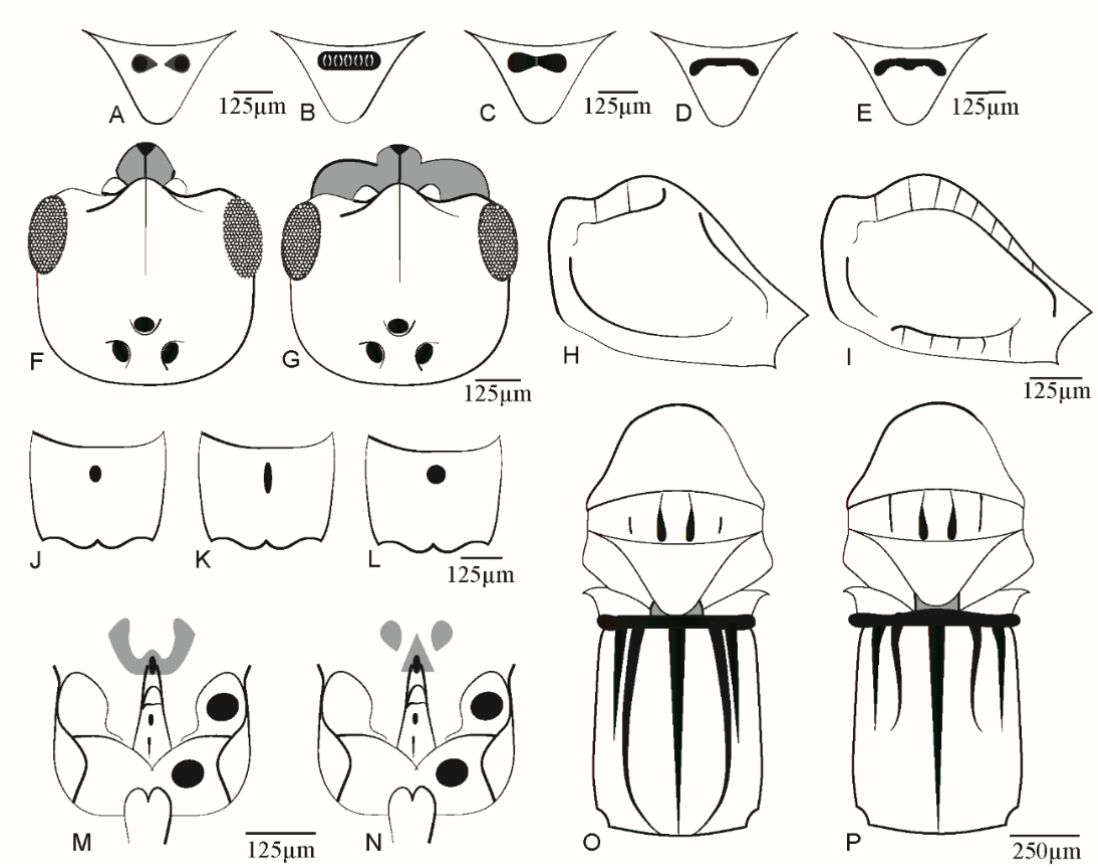

FIGURE 6. Figures of the key to Epyrinae from PNG. **A**, mesoscutellar fovea never connected by evident sulcus, large (*E. niger* pattern); **B**, mesoscutellar fovea connected by evident sulcus, non-projected sides, trabeculate; **C**, mesoscutellar fovea connected by evident sulcus, non-projected sides, not trabeculate, small elevation present; **D**, mesoscutellar foveae connected by evident sulcus, projected sides, ocuppying almost all mesoscutellum; **E**, mesoscutellar fovea connected by evident sulcus, M-shaped; **F**, clypeal lateral lobe never developed; **G**, clypeal lateral lobe well developed; **H**, mesopleuron with anterior mesopleural fovea connected with lower mesopleural fovea, lower mesopleural fovea not trabeculate, subalar impression not connected with mesopleural suture, and mesopleural suture not trabeculate; **I**, mesopleuron with anterior mesopleural fovea not connected with lower mesopleural fovea, lower mesopleural fovea trabeculate, subalar impression connected with mesopleural suture, and mesopleural suture trabeculate; **J**, posterior mesofurcal pit oval; **K**, posterior mesofurcal pit elongated; **L**, posterior mesofurcal pit circular; **M**, metafurcal pit inserted into crown-shaped depression; **N**, metafurcal pit inserted into triangle-shaped depression; **O**, parapsidal signum smaller than notaulus, mesoscutellum with posterior margin touching from metapostnotal anterior margin, first metapostnotal carina as long as metapostnotal median carina, convergent posteriorly, and metapostnotal-propodeal suture smaller than first metapostnotal carina; **P**, parapsidal signum as long as notaulus, mesoscutellum with posterior margin not touching from metapostnotal anterior margin, first metapostnotal carina smaller than metapostnotal median carina, divergent posteriorly, and metapostnotal-propodeal suture as long as first metapostnotal carina.

Key to genera of Epyrinae from Papua New Guinea

1. Mesoscutellar foveae never connected by evident sulcus ... *Epyris* Westwood, 1832 (Figure 6A) ... 3
- Mesoscutellar foveae connected by evident sulcus (Figure 6B-6E) ... 2

2. Lateral clypeal lobe well projected forward ... *Holepyris* Kieffer, 1904 (Figure 6G) ... 10
- Lateral clypeal lobe very short ... *Chlorepyris* Kieffer, 1913 (Figure 6F) ... 18

3. Female ... 4
- Male ... 7

4. Metapostnotal median carina not visible posteriorly ... *Epyris erraticus* Smith, 1860
- Metapostnotal median carina visible posteriorly ... 5

5. Median clypeal lobe tridentate; mandible with four distal teeth; body strongly punctate ... *Epyris ogea* Colombo & Azevedo **n. sp.**
- Median clypeal lobe rounded; mandible with five distal teeth; body weakly punctate ... 6

6. Pedicel shorter than flagellomere I; eye setose; parapsidal signum as long as notaulus (Figure 6P) ... *Epyris motu* Colombo & Azevedo **n. sp.**
- Pedicel as long as flagellomere I; eye glabrous; parapsidal signum shorter than notaulus (Figure 6O) ... *Epyris mundugumor* Colombo & Azevedo **n. sp.**

7. Lower mesopleural fovea connected to upper mesopleural fovea ... *Epyris interruptus* Kieffer, 1904
- Lower mesopleural fovea not connected to upper mesopleural fovea ... 8

8. Median clypeal lobe straight; mesopleural suture not trabeculate (Figure 6H); parapsidal signum shorter than notaulus (Figure 6O) ... *Epyris melpa* Colombo & Azevedo **n. sp.**
- Median clypeal lobe rounded; mesopleural suture trabeculate (Figure 6I); parapsidal signum as long as notaulus (Figure 6P) ... 9

9. Anterior and lower mesopleural foveae not connected (Figure 6I); lower mesopleural fovea trabeculate (Figure 6I); first metapostnotal carina as long as metapostnotal median carina (Figure 6O) ... *Epyris mian* Colombo & Azevedo **n. sp.**
- Anterior mesopleural fovea ill defined; lower mesopleural fovea not trabeculate (Figure 6H); first metapostnotal carina shorter than metapostnotal median carina (Figure 6P) ... *Epyris min* Colombo & Azevedo **n. sp.**

10. Female ... 11
- Male ... 13

11. Mesoscutellar sulcus not trabeculate, small elevation present (Figure 6C) ... *Holepyris wiru* Colombo & Azevedo **n. sp.**
- Mesoscutellar sulcus trabeculate, small elevation absent (Figure 6B) ... 12

12. Mandible with one distal teeth; median clypeal lobe angulate ... *Holepyris yaifo* Colombo & Azevedo **n. sp.**
- Mandible with two distal teeth; median clypeal lobe rounded ... *Holepyris zia* Colombo & Azevedo **n. sp.**

13. Median clypeal lobe sharpened; posterior margin of mesoscutellum touching metapostnotal anterior margin (Figure 6O) ... *Holepyris telefol* Colombo & Azevedo **n. sp.**
- Median clypeal lobe rounded; posterior margin of mesoscutellum not touching metapostnotal anterior margin (Figure 6P) ... 14

14. Posterior margin of mesoscutellum foveolate; first metapostnotal carina straight (Figure 6O) ... *Holepyris tsembaga* Colombo & Azevedo **n. sp.**
- Posterior margin of mesoscutellum not foveolate; first metapostnotal carina outcurved or incurved (Figure 6P) ... 15

15. Parapsidal signum shorter than notaulus (Figure 6O); lower mesopleural fovea ill defined ... 16
- Parapsidal signum longer than notaulus (Figure 6P); lower mesopleural fovea without trabeculae (Figure 6H) ... 17

16. Pedicel as long as flagellomere I; forewing with three distal flexion lines; mesoscutellar sulcus trabeculate (Figure 6B) ... *Holepyris sambia* Colombo & Azevedo **n. sp.**
- Pedicel shorter flagellomere I; forewing with four distal flexion lines; mesoscutellar sulcus not trabeculate (Figure 6C) ... *Holepyris orokaiva* Colombo & Azevedo **n. sp.**

17. Anterior and lower mesopleural foveae not connected (Figure 6I); notaulus present ... *Holepyris swagap* Colombo & Azevedo **n. sp.**
- Anterior and lower mesopleural foveae connected (Figure 6H); notaulus absent ... *Holepyris tairora* Colombo & Azevedo **n. sp.**

18. Female ... 19
– Male ... 25

19. Ventral margin of mandible with two teeth ... *Chlorepyris armatus* (Kieffer, 1904)
– Ventral margin of mandible without teeth ... 20

20. Anterior and lower mesopleural foveae not connected (Figure 6I) ... 21
– Anterior and lower mesopleural foveae connected (Figure 6H) ... *Chlorepyris bilibil* Colombo & Azevedo **n. sp.**

21. Lower mesopleural fovea not trabeculate (Figure 6H) ... 22
– Lower mesopleural fovea trabeculate (Figure 6I) ... 23

22. Pedicel as long as flagellomere I; posterior mesofurcal pit oval (Figure 6J); metapostnotal anterior carina outcurved (Figure 6P) ... *Chlorepyris iatmul* Colombo & Azevedo **n. sp.**
- Pedicel longer than flagellomere I; posterior mesofurcal pit elongated (Figure 6K); metapostnotal anterior carina straight (Figure 6O) ... *Chlorepyris koteka* Colombo & Azevedo **n. sp.**

23. Pronotum coriaceous; posterior margin of mesoscutellum not touching metapostnotal anterior margin (Figure 6P) ... 24
- Pronotum shiny; posterior margin of mesoscutellum touching metapostnotal anterior margin (Figure 6O) ... *Chlorepyris maisin* Colombo & Azevedo **n. sp.**

24. Posterior mesofurcal pit circular (Figure 6L); first metapostnotal carina as long as metapostnotal median carina (Figure 6O) ... *Chlorepyris kaluli* Colombo & Azevedo **n. sp.**

- Posterior mesofurcal pit elongated (Figure 6K); first metapostnotal carina shorter than metapostnotal median carina (Figure 6P) ... *Chlorepyris kwoma* Colombo & Azevedo **n. sp.**

25. Posterior margin of mesoscutellar sulcus notched medially (Figure 6E) ... 26
- Posterior margin of mesoscutellar sulcus straight medially (Figure 6D) ... 30

26. Anterior and lower mesopleural foveae not connected (Figure 6I) ... 27
- Anterior and lower mesopleural foveae connected (Figure 6H) ... 28

27. Mandible with four distal teeth ... *Chlorepyris fore* Colombo & Azevedo **n. sp.**
- Mandible with five distal teeth ... *Chlorepyris abelam* Colombo & Azevedo **n. sp.**

28. Pedicel shorter than flagellomere I; frontal line absent; pronotum polished; metafurcal pit inserted into crown-shaped depression (Figure 6M) ... *Chlorepyris etoro* Colombo & Azevedo **n. sp.**
- Pedicel as long as flagellomere I; frontal line present; pronotum punctate; metafurcal pit inserted into triangle-shaped depression (Figure 6N) ... 29

29. Frons polished; posterior margin of mesoscutellum touching anterior margin of metapectal-propodeal complex (Figure 6O); first metapostnotal carina diverging posteriorly to metapostnotal median carina (Figure 6P) ... *Chlorepyris chambri* Colombo & Azevedo **n. sp.**
- Frons coriaceous; posterior margin of mesoscutellum not touching anterior margin of metapectal-propodeal complex (Figure 6P); first metapostnotal carina converging posteriorly to metapostnotal median carina (Figure 6O) ... *Chlorepyris enga* Colombo & Azevedo **n. sp.**

30. Pedicel shorter than flagellomere I ... 31
- Pedicel as long as or longer than flagellomere I ... 34

31. Anterior and lower mesopleural foveae not connected (Figure 6I) ... 32
- Anterior and lower mesopleural foveae connected (Figure 6H) ... 33

32. Anterior margin of mesoscutellar sulcus straight medially ... *Chlorepyris angu* Colombo & Azevedo **n. sp.**
- Anterior margin of mesoscutellar sulcus notched medially ... *Chlorepyris biangai* Colombo & Azevedo **n. sp.**

33. Mesopleuron with subalar impression not connected with mesopleural suture (Figure 6H); parapsidal signum shorter than notaulus (Figure 6O) ... *Chlorepyris baruya* Colombo & Azevedo **n. sp.**
- Mesopleuron with subalar impression connected with mesopleural suture (Figure 6I); parapsidal signum as long as notaulus (Figure 6P) ... *Chlorepyris huli* Colombo & Azevedo **n. sp.**

34. Pedicel longer than flagellomere I ... 35
- Pedicel as long as flagellomere I ... 36

35. Mesopleuron with anterior and lower mesopleural foveae connected; mesopleural suture ill-defined ... *Chlorepyris gadsup* Colombo & Azevedo **n. sp.**
- Mesopleuron with anterior and lower mesopleural foveae not connected; mesopleural suture defined ... *Chlorepyris duna* Colombo & Azevedo **n. sp.**

36. First metapostnotal carina as long as metapostnotal median carina (Figure 6O) ... 37
- First metapostnotal carina shorter than metapostnotal median carina (Figure 6P) ... 38

37. First metapostnotal carina straight ... *Chlorepyris bilibil* Colombo & Azevedo **n. sp.**
- First metapostnotal carina converging posteriorly to metapostnotal median carina (Figure 6O) ... *Chlorepyris baining* Colombo & Azevedo **n. sp.**

38. Metatibia spinose; metapostnotal-propodeal suture as long as first metapostnotal carina (Figure 6P) ... *Chlorepyris hewa* Colombo & Azevedo **n. sp.**
- Metatibia not spinose; metapostnotal-propodeal suture shorter than first metapostnotal carina (Figure 6O) ... 39

39. Lower mesopleural fovea not trabeculate; mesopleuron suture not trabeculate ... *Chlorepyris gogodala* Colombo & Azevedo **n. sp.**
- Lower mesopleural fovea ill defined; mesopleuron suture trabeculate ... *Chlorepyris haroli* Colombo & Azevedo **n. sp.**

SYSTEMATIC PART

Genus *CHLOREPYRIS* Kieffer, 1913

Chlorepyris Kieffer, 1913. Type-species: *Chlorepyris semiviridis* Kieffer, 1913.

Chlorepyris armatus (Kieffer, 1904)

Figure 7

Rhabdepyris armatus Kieffer, 1904: 410-411.

Chlorepyris armatus – Azevedo *et al.* 2018: 148.

TYPE MATERIAL — Holotype, ♀, N. Guinea S. E. [probably **Papua New Guinea**]. Hughibagu, Loria, V-IX/1991 (MCSN). [examined].

REDESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with three distal teeth, ventral margin with two twisted teeth. Clypeus with rounded median lobe, not visible dorsally, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel smaller than flagellomere I. Eye weakly setose.

Frons weakly coriaceous and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum as long as notaulus. Forewing with ill defined distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, narrower medially, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, straight posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia with spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — Waichert & Azevedo (2009) redesigned *Rhabdepyris* Kieffer, 1904 under phylogenetic approach, making several new combinations. *Rhabdepyris armatus* was kept in *Rhabdepyris* because the authors were not able to locate its holotype, so that the species was not analyzed. Azevedo *et al.* (2018) transferred *R. armatus* to the genus *Chlorepyris* but did not provide details on this nomenclatural act. Here, analyzing the holotype, we concluded that this species belongs to *Chlorepyris* by having the pronotum punctate, coriaceous, and the mesoscutellar fovea connected by evident sulcus, not trabeculate. We did not find new specimens of *C. armatus* hindering molecular and phylogenetics analyses. This species is morphologically different from the other *Chlorepyris* species because it has the mandibles with five distal teeth, two are located in the ventral margin; the median clypeal lobe not visible dorsally; the posterior portion of the metapectal-propodeal complex polished. The teeth in the ventral margin of the mandibles have already been diagnosed for other Epyrinae, mainly in *Epyris afer* (Magretti, 1884) and related lineages (Stein *et al.* 2011).

DISTRIBUTION — Papua New Guinea.

***Chlorepyris abelam* Colombo & Azevedo n. sp.**

Figures 8-9

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 26-27/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 4, understorey, Malaise - MAL-MW1700D-02/16-d02, P2217-11357 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 29-30/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1700D-05/16-d05, P2220-8756 (MNHN); ♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 26-27/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-02/16-d02, P2169-11358 (MNHN); ♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 29-30/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-05/16-d05, P2172-8760 (MNHN); , Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 30-31/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-06/16-d06, P2173-8766 (MNHN); ♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 29-30/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1700D-05/16-d05, P2220-8756 (MNHN); ♂, Province Madang, Mount Wilhelm (-5.759910, 145.2347), 1700m, 26-27/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW1700B-02/16-d02, P2185-11356 (MNHN); 2♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 25-26/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1700D-01/16-d01, P2216-11361 (MNHN); ♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 09-10/11/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1700D-16/16-d16, P2231-8804 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings amber; metasoma reddish. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye glabrous. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into

triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin notched medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia with few spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere as long as basiparamere in lateral view, apex straight, not arched inward, dorsal margin straight; basiparamere wide, covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex aligned to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex aligned to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

VARIATIONS — Paramere with apex weakly rounded and arched inward.

REMARKS — This species is morphologically similar to *Chlorepyris etoro* **n. sp.** and *C. fore* **n. sp.** by having the median clypeal lobe rounded, the eye glabrous, the notauli complete, the mesoscutellar sulcus with the posterior margin notched medially and the mesopleuron with the lower fovea trabeculate. However, *Chlorepyris abelam* **n. sp.** has the paramere with the apex straight, not arched inward, the apex of the digitus is aligned to the apex of cuspis and the apex of aedeagus aligned to the apex of digitus; whereas *C. etoro* **n. sp.** has the paramere with the apex sharpened, not arched inward, the digitus with apex anterior to the apex of cuspis and the apex of aedeagus anterior to the apex of digitus, and *C. fore* **n. sp.** has the paramere with rounded apex, weakly arched inward, the digitus with apex anterior to the apex of cuspis and the apex of aedeagus aligned to the apex of digitus. These species are phylogenetic and genetically distant to each other, with nucleotide sequences differing 14% in their content (Figure 4).

ETYMOLOGY — The epithet *abelam* refers to Abelam people who live in the East Sepik province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Chlorepyris angu* Colombo & Azevedo n. sp.**

Figures 10-11

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.741031, 145.3294), 200m, 30-31/10/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-06/16-d06, P1019-11963 (MNHN). Paratypes. **Papua New Guinea**. ♂, Province Madang, Mount Wilhelm, (-5.739897, 145.3297), 200m, 27-28/10/2012, leg Dilu, Ray, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW0200A-03/16-d03, P1000-11953 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna light brown; wings hyaline; metasoma reddish. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, narrower medially, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, divergent. Metatibia with few spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere longer than basiparamere in lateral view, apex sharpened, not arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex aligned to apex of cuspis, its posterior margin crenulate;

aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with opaque projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris enga* **n. sp.** by having the mandibles with five distal teeth, the clypeus with the median lobe rounded, the occipital carina absent, the paramere longer than the basiparamere in lateral view, and the apex of cuspis anterior to the apex of paramere. However, *C. angu* **n. sp.** has the mesoscutellar sulcus with the posterior margin straight medially, the metapostnotal-propodeal suture is divergent to the metapostnotal median carina and the apex of the aedeagus is anterior to the apex of digitus; whereas *C. enga* **n. sp.** has the mesoscutellar sulcus with the posterior margin notched medially, the metapostnotal-propodeal suture converging posteriorly to the metapostnotal median carina and the apex of aedeagus is aligned to the apex of digitus. These species are phylogenetic and genetically distant to each other, with nucleotide sequences differing 17% in their content (Figure 4).

ETYMOLOGY — The epithet *angu* refers to Angu ethinic who live in the mountainous region of south-western Morobe, a province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris baining* Colombo & Azevedo n. sp.**

Figures 12-13

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200 m, 28-29/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1200A-04/16-d04, P1781-11307 (MNHN). Paratypes. **Papua New Guinea**. ♂, Province Madang, Mount Wilhelm (-5.720903, 145.2715), 1200 m, 25-26/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW1200C-01/16-d01, P1810-11292 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.732698, 145.2556), 700 m, 08-09/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0700B-15/16-d15, P1418-11285 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.721022, 145.2703), 1200 m, 26-27/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW1200B-02/16-d02, P1795-11299 (MNHN); 1♂, Province Madang, Mount Wilhelm (-

5.741031, 145.3294), 200 m, 07-08/11/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-14/16-d14, P1027-11973 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings hyaline; metasoma yellowish. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye weakly setose. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into crown-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, incomplete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, narrower medially, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly. Metatibia with few spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere shorter than basiparamere in lateral view, apex rounded, not arched inward, dorsal margin incurved; basiparamere wide, covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin smooth; aedeagus bottle-shaped, its apex posterior to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris baruya* **n. sp.** by having the mandibles with five distal teeth, the median clypeal lobe rounded, the flagellar pubescence appressed, the eyes weakly setose, the mesoscutellar sulcus with the posterior margin straight medially, the lower fovea trabeculate and the paramere shorter than the basiparamere in lateral view. However, *C. baining* **n. sp.** has the pedicel as long as flagellomere I and the anterior and lower mesopleural foveae are not connected; whereas *C. baruya* **n. sp.** has the pedicel shorter than the flagellomere I and the anterior and lower

mesopleural foveae connected. The genetic distance between *C. baining* **n. sp.** and *C. baruya* **n. sp.** was of 6% (Figure 4) and reconstructed as sister taxa in the phylogenetic analyses.

ETYMOLOGY — The epithet *baining* refers to the Baining ethnic, the first inhabitants of the Gazelle Peninsula of East New Britain, Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris baruya* Colombo & Azevedo n. sp.**

Figures 14-15

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720903, 145.2715), 1200 m, 25-26/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW1200C-01/16-d01, P1810-11292 (MNHN). Paratypes. **Papua New Guinea**. ♂, Province Madang, Mount Wilhelm (-5.732698, 145.2556), 700 m, 08-09/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0700B-15/16-d15, P1418-11285 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole dark brown; antenna brown; wings hyaline; metasoma light brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye weakly setose. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into crown-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first

metapostnotal carina, converging posteriorly. Metatibia with many spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere shorter than basiparamere in lateral view, apex rounded, weakly arched inward, dorsal margin incurved; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin crenulate; aedeagus bottle-shaped, its apex posterior to apex of digitus, ventral margin with opaque projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris hewa* **n. sp.** by having the median clypeal lobe rounded, the flagellar pubescence appressed, the notauli complete, the mesoscutellar sulcus with the posterior margin straight medially, the paramere shorter than the basiparamere in lateral view, and the apex of aedeagus posterior to the apex of digitus. However, *Chlorepyris baruya* **n. sp.** has the pedicel shorter than the flagellomere I, the frons is polished, the frontal line is present and the lower mesopleural fovea is trabeculate; whereas *C. hewa* **n. sp.** has the pedicel as long as flagellomere I, the frons coriaceous, the frontal line is absent, and the lower mesopleural fovea is ill defined. The genetic distance between these species is low, 3% (Figure 4), the lowest nucleotide distance among all species of *Chlorepyris*.

ETYMOLOGY — The epithet *baruya* refers to Baruya ethinic, a tribe in the highlands of Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris biangai* Colombo & Azevedo n. sp.**

Figures 16-17

TYPE MATERIAL — Holotype, ♂, **Papua-New-Guinea**, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 09-10/11/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1700D-16/16-d16, P2231-8804 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings amber; metasoma reddish. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short,

not visible dorsally. Antenna with flagellar pubescence appressed; pedicel longer than flagellomere I. Eye glabrous. Frons polished and punctate. Frontal line absent. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, anterior margin of mesoscutellar sulcus notched medially, weakly inclined, narrower medially, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina incomplete, visible posteriorly; first metapostnotal carina longer than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture longer than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere longer than basiparamere in lateral view, apex rounded, weakly arched inward, dorsal margin incurved, strongly setose; basiparamere wide, covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin smooth; aedeagus bottle-shaped, its apex posterior to apex of digitus, ventral margin with opaque projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically and genetically similar to *Chlorepyris angu* **n. sp.** by having the mandible with five distal teeth, median clypeal lobe rounded, the flagellar pubescence appressed, the metafurcal pit inserted into triangle-shaped depression, the mesoscutellar sulcus with the posterior margin straight medially, and the paramere longer than the basiparamere in lateral view. However, *Chlorepyris biangai* **n. sp.** has the pedicel longer than the flagellomere I, frontal line absent, and aedeagus bottle-shaped with apex posterior to apex of digitus; whereas *C. angu* **n. sp.** has the pedicel shorter than the flagellomere I, frontal line present, and aedeagus bottle-shaped with apex anterior to apex of digitus.

ETYMOLOGY — The epithet *biangai* refers to Biangai ethinic, an ethnic group living on the slopes of the upper Bulolo vally, in Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris bilibil* Colombo & Azevedo n. sp.**

Figures 18-20

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 20-21/11/2012, leg Basset, Plot 1, understorey; Malaise - MAL-WAN01-D03, P4902-9231 (MNHN). Allotype, ♀, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.741031, 145.3294), 200m, 07-08/11/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-14/16-d14, P1027-11973 (MNHN). Paratypes. **Papua New Guinea**. ♀, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700 m, 29-30/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-05/16-d05, P1440-11993 (MNHN).

DESCRIPTION — *Male* (Figures 18-19). Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole dark brown; antenna brown; wings hyaline; metasoma dark brown to light brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye weakly setose. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, straight; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia with many spines. Petiolar root with apex strongly incurved.

Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere shorter than basiparamere in lateral view, apex rounded, arched inward, dorsal margin incurved; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin serrated, the aedeagus bottle-shaped, its apex posterior to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female (Figure 20). Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with two distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye weakly setose. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, straight; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia with few spines. Petiolar root with apex strongly incurved. Metasoma polished.

REMARKS — The male of this species is morphologically similar to *Chlorepyris hewa* **n. sp.** by having the median clypeal lobe rounded, the flagellar pubescence appressed, the notauli complete, the mesoscutellar sulcus with the posterior margin straight medially, the paramere shorter than the basiparamere in lateral view, the apex of cuspis anterior to the apex of paramere, the apex of aedeagus posterior to the apex of digitus. However, *Chlorepyris bilibil* **n. sp.** has the frontal line present, the anterior and lower mesopleural foveae not connected and the lower mesopleural fovea trabeculate; whereas *C. hewa* **n. sp.** has the frontal line absent, the anterior and lower mesopleural foveae connected, and the lower mesopleural fovea ill defined.

The female is morphologically similar to *C. koteka* **n. sp.** by having the mandibles with two distal teeth, the mesoscutellar sulcus with the posterior margin straight medially and the metapostnotal-propodeal suture shorter than the first metapostnotal carina. However, *Chlorepyris bilibil* **n. sp.** has the pedicel as long as flagellomere I, the frons is polished, the pronotum is shiny and the anterior and lower mesopleural fovea are connected; whereas *C. koteka* **n. sp.** has the pedicel longer than the flagellomere I, the frons is coriaceous, the pronotum is coriaceous and the anterior and lower mesopleural foveae are not connected.

The genetic distance between male and female of *Chlorepyris bilibil* **n. sp.** was of 0% (Figure 4) and they were associated based on molecular evidence.

ETYMOLOGY — The epithet *bilibil* refers to Bilibil ethnic who lived on the island offshore from Madang.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris chambri* Colombo & Azevedo n. sp.**

Figures 21-22

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720903, 145.2715), 1200 m, 28-29/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW1200C-04/16-d04, P1813-11304 (MNHN). Paratypes. **Papua New Guinea**. ♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 25-26/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-01/16-d01, P1436-11978 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna brown; wings hyaline; metasoma dark brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye glabrous. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs

vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, narrower medially, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, divergent; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere as long as basiparamere in lateral view, apex sharpened, not arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris huli* **n. sp.** by having the mandibles with five distal teeth, the median clypeal lobe rounded, the frontal line present, the mesoscutellar sulcus with the posterior margin straight medially and the apex of cuspis anterior to the apex of paramere. However, *Chlorepyris chambri* **n. sp.** has the paramere shorter than the basiparamere in lateral view, the paramere has the apex rounded, arched inward and the apex of aedeagus is posterior to the apex of digitus; whereas *C. huli* **n. sp.** has the paramere with apex sharpened, weakly arched inward and apex of aedeagus is anterior to the apex of digitus. These species are phylogenetic and genetically distant to each other, with nucleotide sequences differing 5% in their content (Figure 4).

ETYMOLOGY — The epithet *chambri* refers to the Chambri ethnic, previously spelled Tchambuli, an ethnic group in the Chambri Lakes region in the East Sepik province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris duna* Colombo & Azevedo n. sp.**

Figures 23-24

TYPE MATERIAL — Holotype, ♂, **Papua-New-Guinea**, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700 m, 29-30/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-05/16-d05, P1440-11993 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings hyaline; metasoma reddish. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel longer than flagellomere I. Eye glabrous. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein weakly angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere as long as basiparamere in lateral view, apex rounded, weakly arched inward, dorsal margin incurved; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin crenulate; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with opaque projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically and genetically similar to *Chlorepyris gadsup* **n. sp.** by having the mandible with five distal teeth, median clypeal lobe rounded, the flagellar pubescence appressed, the pedicel longer than the flagellomere I, the metafurcal pit inserted into triangle-shaped depression, and the mesoscutellar sulcus with the posterior margin straight medially. However, *Chlorepyris duna* **n. sp.** has the eye

glabrous, mesopleuron with anterior and lower mesopleural foveae not connected, and first metapostnotal carina shorter than metapostnotal median carina, whereas *C. gadsup* **n. sp.** has the eye weakly setose, mesopleuron with anterior and lower mesopleural foveae connected, and first metapostnotal carina longer than metapostnotal median carina.

ETYMOLOGY — The epithet *duna* refers to Duna ethinic, an indigenous people of Papua New Guinea (also known as Yuna) who live in the north-western area of the Southern Highlands Province.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris enga* Colombo & Azevedo n. sp.**

Figures 25-26

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200 m, 27-28/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-03/16-d03, P1828-11300 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna brown; wings hyaline; metasoma dark brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye weakly setose. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin notched medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with

apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere longer than basiparamere in lateral view, apex rounded, very arched and expanded inward, dorsal margin outcurved; basiparamere wide, covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex aligned to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris angu* **n. sp.** by having the mandibles with five distal teeth, the clypeus with a rounded median lobe, the occipital carina absent, the paramere longer than the basiparamere in lateral view, and the volsella with the apex of cuspis anterior to the apex of paramere. However, *C. enga* **n. sp.** has the mesoscutellar sulcus with the posterior margin notched medially, the metapostnotal-propodeal suture converges posteriorly to metapostnotal median carina and the apex of the aedeagus is aligned to the apex of digitus; whereas *C. angu* **n. sp.** has the mesoscutellar sulcus with the posterior margin straight medially, the metapostnotal-propodeal suture diverges from the metapostnotal median carina and the aedeagus has its apex anterior to apex of digitus. The genetic distance between *Chlorepyris enga* **n. sp.** and *Chlorepyris angu* **n. sp.** was of 17% (Figure 4).

ETYMOLOGY — The epithet *enga* refers to Enga language of the East New Guinea Highlands spoken by a quarter-million people in Enga Province, Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris etoro* Colombo & Azevedo n. sp.**

Figures 27-28

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm, (-5.758978, 145.1861), 2200 m, 27-28/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW2200A-12/16-d12, P2569-11884 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings amber. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere

I. Eye glabrous. Frons polished and punctate. Frontal line present. Pronotum polished and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into crown-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea not trabeculate; subalar impression connected with mesopleural suture; mesopleural suture not trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin notched medially, weakly inclined, evenly wide, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere shorter than basiparamere in lateral view, apex sharpened, not arched inward, dorsal margin incurved; basiparamere wide, covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris fore* **n. sp.** by having the median clypeal lobe rounded, the eyes glabrous, the posterior mesofurcal pit elongated, the notauli complete and the mesoscutellar sulcus with the posterior margin notched medially. *Chlorepyris etoro* **n. sp.**, however, has the mandibles with five distal teeth, the frons is polished, the frontal line is absent, the anterior and lower mesopleural foveae are connected, the male paramere is shorter than the basiparamere in lateral view and the apex of the aedeagus is anterior to the apex of digitus; whereas *C. fore* **n. sp.** has the mandibles with four distal teeth, the frons is coriaceous, the frontal line is present, the anterior and lower mesopleural foveae are not connected, the male paramere is as long as the basiparamere in lateral view and the apex of the aedeagus is aligned to the apex of digitus. The genetic distance between *C. fore* **n. sp.** and *C. etoro* **n. sp.** was of 14% (Figure 4).

ETYMOLOGY — The epithet *etoro* refers to the Etoro, or Edolo, a tribe and ethnic group of Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris fore* Colombo & Azevedo n. sp.**

Figures 29-30

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200 m, 04-05/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-11/16-d11, P1836-11337 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole dark brown; antenna brown; wings hyaline; metasoma light brown. Mandible with four distal teeth. Clypeus with median lobe rounded, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin notched medially, weakly inclined, evenly wide, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, divergent; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere as long as basiparamere in lateral view, apex rounded, weakly arched inward, dorsal margin incurved; basiparamere wide, covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin crenulate; aedeagus bottle-

shaped, its apex aligned to apex of digitus, ventral margin with opaque projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris etoro* **n. sp.** by having the median clypeal lobe rounded, the eyes glabrous, the posterior mesofurcal pit elongated, the notauli complete and the mesoscutellar sulcus with the posterior margin notched medially. However, *Chlorepyris fore* **n. sp.** has the mandibles with four distal teeth, the frons is coriaceous, the frontal line is present, the anterior and lower mesopleural foveae are not connected; whereas *Chlorepyris etoro* **n. sp.** has the mandibles with five distal teeth, the frons is polished, the frontal line is absent, the anterior and lower mesopleural foveae are connected. The genetic distance between these species was of 14% (Figure 4).

ETYMOLOGY — The epithet fore refers to the *Fore* ethnic that lives in the Okapa District of the Eastern Highlands Province, Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris gadsup* Colombo & Azevedo n. sp.**

Figures 31-32

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200 m, 26-27/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-02/16-d02, P1827-11296 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna brown; wings hyaline; metasoma dark brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel longer than flagellomere I. Eye weakly setose. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture ill defined. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs

vein angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, divergent; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia with few spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere as long as basiparamere in lateral view, apex rounded, not arched inward, dorsal margin outcurved; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin smooth; aedeagus bottle-shaped, its apex aligned to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris chambri* **n. sp.** by having the mandibles with five distal teeth, the median clypeal lobe rounded, the first metapostnotal carina divergent posteriorly to the metapostnotal median carina and the paramere as long as the basiparamere in lateral view. However, *C. gadsup* **n. sp.** has the pedicel longer than the flagellomere I and the mesoscutellar sulcus with the posterior margin straight medially; whereas *C. chambri* **n. sp.** has the pedicel as long as the flagellomere I and the mesoscutellar sulcus with the posterior margin notched medially. The genetic distance between *C. gadsup* **n. sp.** and *C. chambri* **n. sp.** was of 11% and between the male of *C. gadsup* **n. sp.** and *C. abelam* **n. sp.** was 8% (Figure 4). Thus, the lack of morphological and molecular evidences suggest that *C. chambri* **n. sp.** and *C. gadsup* **n. sp.** are two distinguished species.

ETYMOLOGY — The epithet *gadsup* refers to the Gadsup ethnic that lives in the Eastern Highlands of Papua New Guinea in or near the Aiyura Valley.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris gogodala* Colombo & Azevedo n. sp.**

Figures 33-34

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 26-27/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-02/16-d02, P1827-11296 (MNHN). Paratypes. **Papua New Guinea**. 2♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700 m, 26-27/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-02/16-d02, P1437-11982 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700 m, 27-28/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-03/16-d03, P1438-11983 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700 m, 09-10/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-16/16-d16, P1451-11290 (MNHN); 1♂, Province Madang, Mount Wilhelm, (-5.720874,145.2695), 1200 m, 31-01/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-07/16-d07, P1832-11316 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.732698, 145.2556), 700 m, 28-29/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0700B-04/16-d04, P1407-11997 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole dark brown; antenna brown; wings hyaline; metasoma light brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea ill defined; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly

incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere shorter than basiparamere in lateral view, apex rounded, weakly arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin smooth; aedeagus bottle-shaped, its apex aligned to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

VARIATIONS — Digitus with posterior margin crenulate.

REMARKS — This species is morphologically similar to *Chlorepyris angu* **n. sp.** by having the mandibles with five distal teeth, the median clypeal lobe is rounded, the eyes are glabrous and the mesoscutellar sulcus has the posterior margin straight medially. However, *C. gogodala* **n. sp.** has the pedicel as long as the flagellomere I, the lower mesopleural fovea is ill defined, the mesopleural subalar impression is disconnected with the mesopleural suture; whereas *C. angu* **n. sp.** has the pedicel shorter than the flagellomere I, the lower mesopleural fovea is trabeculate, and the mesopleural subalar impression is connected with the mesopleural suture. Although these species resemble morphologically, they are genetically distant with 25% of nucleotide sequence divergence (Figure 4).

ETYMOLOGY — The epithet *gogodala* refers to the Gogodala ethnic who lives in the Middle Fly District of the Western Province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Chlorepyris haroli* Colombo & Azevedo n. sp.**

Figures 35-36

TYPE MATERIAL — Holotype, ♂, **Papua-New-Guinea**, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200 m, 29-30/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1200A-05/16-d05, P1782-11308 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole dark brown; antenna brown; wings hyaline; metasoma light brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as

flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea not trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture not trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere as long as basiparamere in lateral view, apex rounded, weakly arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex posterior to apex of digitus, ventral margin without translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris abelam* **n. sp.** by having the mandibles with five distal teeth, the mesoscutellum with posterior margin not touching the metapostnotal anterior margin, the first metapostnotal carina converging posteriorly to the metapostnotal median carina, the apex of cuspis anterior to the apex of paramere and the digitus with the posterior margin serrated. *Chlorepyris haroli* **n. sp.**, however, has the pedicel as long as flagellomere I, the frons is coriaceous, the mesopleural subalar impression is disconnected with the mesopleural suture and the mesoscutellar sulcus has the posterior margin straight medially; whereas *C. abelam* **n. sp.** has the pedicel shorter than the flagellomere I, the frons is polished, the mesopleural subalar impression is connected with the mesopleural suture and the mesoscutellar sulcus has the posterior margin notched medially. The genetic distance between *C. abelam* **n. sp.** and *C. haroli* **n. sp.** was of 19% (Figure 4).

ETYMOLOGY — The epithet *haroli* refers to the Haroli indigenous people who live in the Hela Province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris hewa* Colombo & Azevedo n. sp.**

Figures 37-38

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.739897, 145.3297), 200m, 25-26/10/2012, leg Dilu, Ray, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0200D-01/16-d01, P1045-11941 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Mount Wilhelm (-5.741031, 145.3294), 200 m, 25-26/10/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-01/16-d01, P1014-11947 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700 m, 30-31/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-06/16-d06, P2173-8766 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.732698, 145.2556), 700 m, 09-10/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0700B-16/16-d16, P1810-11292 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna light brown; wings hyaline; metasoma dark brown to light brown; metasoma light brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye weakly setose. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea ill defined; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal

carina shorter than metapostnotal median carina, straight; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly. Metatibia with many spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere shorter than basiparamere in lateral view, apex rounded, not arched inward, dorsal margin incurved; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex aligned to apex of cuspis, its posterior margin crenulate; aedeagus bottle-shaped, its apex posterior to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically and phylogenetically close related to *Chlorepyris baruya* **n. sp.** by having the median clypeal lobe rounded, the flagellar pubescence appressed, the notauli complete, the mesoscutellar sulcus with the posterior margin straight medially, the paramere shorter than the basiparamere in lateral view, and the apex of aedeagus posterior to the apex of digitus. However, *C. hewa* **n. sp.** has the pedicel as long as flagellomere I, the frons is coriaceous, the frontal line is absent and the lower mesopleural fovea is ill defined; whereas *C. baruya* **n. sp.** has the pedicel shorter than the flagellomere I, the frons is polished, the frontal line is present and the lower mesopleural fovea is trabeculate. The nucleotide sequences of *C. hewa* **n. sp.** and *C. baruya* **n. sp.** diverge 3% (Figure 4). This value was the lowest genetic distance found among the studied species of *Chlorepyris*.

ETYMOLOGY — The epithet *hewa* refers to the Hewa indigenous people who live in the Koroba Lake Kopiago Electorate of Hela Province of Papua New Guinea, near the junction of the Strickland River.

DISTRIBUTION — Papua New Guinea (Madang).

***Chlorepyris huli* Colombo & Azevedo n. sp.**

Figures 39-40

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200 m, 04-05/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-11/16-d11, P2225-11337 (MNHN). Paratypes. **Papua New Guinea**. 2♂, Province Madang, Mount Wilhelm (-5.759910, 145.2347), 1700 m, 26-27/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot

2, understorey; Malaise - MAL-MW1700B-02/16-d02, P2185-11356 (MNHN); ♂, Province Madang, Mount Wilhelm (-5.732514, 145.2568), 700 m, 28-29/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW0700C-04/16-d04, P1423-11996 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings hyaline; metasoma dark brown to light brown. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye glabrous. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum as long as notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, straight; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin straight. Genitalia: paramere longer than basiparamere in lateral view, apex sharpened, weakly arched inward, dorsal margin incurved; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex anterior to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris chambri* **n. sp.** by having the mandibles with five distal teeth, the median clypeal lobe rounded, the frontal line present, the mesoscutellar sulcus with the posterior margin straight medially and the apex of cuspis anterior to the apex of paramere. However, *Chlorepyris huli* **n. sp.** has the paramere longer than the basiparamere in lateral view, the paramere has the apex

sharpened, weakly arched inward, and the apex of the aedeagus is anterior to the apex of digitus; whereas *C. chambri* **n. sp.** has the paramere shorter than the basiparamere in lateral view, the paramere has the apex rounded, arched inward and the apex of aedeagus is posterior to the apex of digitus; whereas. The genetic distance between *C. huli* **n. sp.** and *C. chambri* **n. sp.** was of 5% (Figure 4).

ETYMOLOGY — The epithet *huli* refers to the Huli indigenous ethnic who live in the Hela Province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Chlorepyris iatmul* Colombo & Azevedo n. sp.**

Figure 41

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175 m, 03-04/12/2012, leg Basset, Plot 1, understorey; Malaise - MAL-WAN01-D16, P4915-11066 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with three distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye weakly setose. Frons weakly coriaceous and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit oval. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea not trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal

complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, straight. Metatibia with few spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris kaluli* **n. sp.** by having the median clypeal lobe rounded, the eyes weakly setose and the mesoscutellar sulcus with the posterior margin straight medially. *Chlorepyris iatmul* **n. sp.,** however, has the mandibles with three distal teeth, the pedicel is as long as flagellomere I, the posterior mesofurcal pit is oval and the lower mesopleural fovea is not trabeculate; whereas *C. kaluli* **n. sp.** has the mandibles with two distal teeth, the pedicel is shorter than the flagellomere I, the posterior mesofurcal pit is circular and the lower mesopleural fovea is trabeculate. The genetic distance between *Chlorepyris iatmul* **n. sp.** and *Chlorepyris kaluli* **n. sp.** was of 12% (Figure 4).

ETYMOLOGY — The epithet *iatmul* refers to the Iatmul large ethnic group who inhabits around two-dozen politically autonomous villages along the middle Sepik River in Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Chlorepyris kaluli* Colombo & Azevedo n. sp.**

Figure 42

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175 m, 03-04/12/2012, leg Basset, Plot 1, understorey; Malaise - MAL-WAN01-D16, P4915-11066 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna light brown; wings hyaline; metasoma dark brown. Mandible with two distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye weakly setose. Frons weakly coriaceous and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit circular. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and

lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is similar to *Chlorepyris iatmul* **n. sp.** by having the median clypeal lobe rounded, the eyes weakly setose and the mesoscutellar sulcus with the posterior margin straight medially. *Chlorepyris kaluli* **n. sp.,** however, has the mandibles with two distal teeth, the pedicel is shorter than the flagellomere I, the posterior mesofurcal pit is circular and the lower mesopleural fovea is trabeculate; whereas *C. iatmul* **n. sp.** has the mandibles with three distal teeth, the pedicel is as long as the flagellomere I, the posterior mesofurcal pit is oval and the lower mesopleural fovea is not trabeculate. The genetic distance between *C. kaluli* **n. sp.** and *C. iatmul* **n. sp.** was of 12% (Figure 4).

ETYMOLOGY — The epithet *kaluli* refers to Kaluli, a large clan of non-literate indigenous people who live in the rain forests of Great Papuan Plateau in Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Chlorepyris koteka* Colombo & Azevedo n. sp.**

Figure 43

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175 m, 26-27/11/2012, leg Gewa, Damag, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-WAN-D-11/16-d11, P542-867 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings hyaline; metasoma light brown.

Mandible with two distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel longer than flagellomere I. Eye weakly setose. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea not trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin, very thin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — Females of this species are morphologically similar to females of *Chlorepyris bilibil* **n. sp.** by having the mandibles with two distal teeth, the mesoscutellar sulcus with the posterior margin straight medially and the metapostnotal-propodeal suture shorter than the first metapostnotal carina. *Chlorepyris koteka* **n. sp.**, however, has the pedicel longer than the flagellomere I, the frons is coriaceous, the pronotum is coriaceous and the anterior and lower mesopleural foveae are not connected; whereas *C. bilibil* **n. sp.** has the pedicel as long as the flagellomere I, the frons is polished, the pronotum is shiny, and the anterior and the lower mesopleural foveae are connected. The genetic divergence between *C. koteka* **n. sp.** and *C. bilibil* **n. sp.** was of 12%, lacking morphological and molecular evidences to associate them. Finally, our results showed a male of *C. hewa* **n. sp.** as the molecularly closest species to *C. koteka* **n. sp.** (11% divergence). This high nucleotide divergence, compared to the observed in this study (Figure 4), prevents us from sex associating them.

ETYMOLOGY — The epithet *koteka* refers to the Koteka ethnic who lives in West Papua.

DISTRIBUTION — Papua New Guinea.

***Chlorepyris kwoma* Colombo & Azevedo n. sp.**

Figure 44

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Mount Wilhelm, (-5.741031, 145.3294), 200m, 09-10/11/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-16/16-d16, P1029-11974 (MNHN).

DESCRIPTION — *Female.* Pronotum, mesoscutum, metapectal-propodeal complex and petiole black; metasoma light brown; wings hyaline. Head lost. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris kaluli* **n. sp.** by having the pronotum punctate and coriaceous, the anterior and lower mesopleural foveae not connected; the lower mesopleural fovea trabeculate, the notauli complete and the mesoscutellar sulcus with the posterior margin straight medially. *Chlorepyris kwoma* **n. sp.**, however, has the posterior mesofurcal pit elongated and the first metapostnotal carina shorter than the metapostnotal median carina; whereas *C. kaluli* **n. sp.** has the posterior mesofurcal pit circular and the metapostnotal carina as long as the metapostnotal median carina. The nucleotide sequences of *C. kwoma* **n. sp.** and *C. kaluli* **n. sp.** diverged 18%. The lowest genetic distance observed between the female of *C. kwoma* **n. sp.** and the male of *C. huli* **n. sp.** or the male of *C. chambri* **n. sp.** was 7% (Figure 4).

ETYMOLOGY — The epithet *kwoma* refers to the Kwoma ethnic who lives in the northeastern New Guinea, in the Peilungupo mountains north of the Sepik River.

DISTRIBUTION — Papua New Guinea.

***Chlorepyris maisin* Colombo & Azevedo n. sp.**

Figure 45

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175 m, 24-25/11/2012, leg Basset, Plot 1, understorey; Malaise - MAL-WAN01-D07, P4906-935 (MNHN). Paratypes. **Papua New Guinea**. 1♀, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700 m, 29-30/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-05/16-d05, P1440-11993 (MNHN); 1♀, Province Madang, Mount Wilhelm (-5.732514, 145.2568), 700 m, 27-28/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW0700C-03/16-d03, P1421-11988 (MNHN); 1♀, Province Madang, Mount Wilhelm (-5.741031, 145.3294), 200 m, 01-02/11/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-08/16-d08, P1021-11967 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma light brown; wings hyaline. Mandible with five distal teeth. Clypeus with rounded median lobe, high in lateral view, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel longer than flagellomere I. Eye weakly setose. Frons polished and punctate. Frontal line present. Pronotum punctate and shiny. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar sulcus with posterior margin straight medially, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median

carina, converging posteriorly; metapostnotal-propodeal suture shorter than first metapostnotal carina, converging posteriorly. Metatibia with few spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is morphologically similar to *Chlorepyris kaluli* **n. sp.** by having the clypeus with the median lobe rounded, the eyes weakly setose, the frontal line present, the anterior and lower mesopleural foveae not connected, the suture mesopleural trabeculate, the notauli complete and the mesoscutellar sulcus with the posterior margin straight medially. *Chlorepyris maisin* **n. sp.**, however, has the mandibles with five distal teeth, the pedicel is longer than flagellomere I, the frons is polished and the posterior mesofurcal pit is elongated; whereas *C. kaluli* **n. sp.** has the mandibles with two distal teeth, the pedicel is shorter than flagellomere I, the frons is weakly coriaceous and the posterior mesofurcal pit is circular. The genetic divergence between *C. maisin* **n. sp.** and *C. kaluli* **n. sp.** was of 14%., lacking morphological and molecular evidences to associate them. Finally, our results showed a male of *C. hewa* **n. sp.** as the molecularly closest species to *C. maisin* **n. sp.** (12% divergence). This high nucleotide divergence, compared to the observed in this study (Figure 4), prevents us from sex associating them.

ETYMOLOGY — The epithet *maisin* refers to the Maisin indigenous people who live in Oro Province in Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

Genus *EPYRIS* Westwood, 1832

Epyris Westwood, 1832. Type-species *Epyris niger* Westwood, 1832.

***Epyris erraticus* Smith, 1860**

Epyris erraticus Smith, 1860: 136

TYPE MATERIAL — Holotype, ♀, [probably **Papua New Guinea**], Dory, [lost], [not examined].

DIAGNOSIS — *Female.* Head black; wings fuscuous; tibiae and tarsi obscure ferruginous; ovipositor rufo-testaceous. Head oblong, transverse behind, lateral angles rounded, scattered strong punctures. Eye large, oval, placed forwards. Antenna fulvous beneath, 13-jointed. Pronotum and mesonotum shining, strong punctate. Metapectal-

propodeal complex quadrate, truncate, with three carinae not extending posteriorly, between carinae roughly striated transversely, beyond which striation is much finer. Metasoma polished and shining.

Male. Unknown.

REMARKS — We were not able to find the holotype of *E. erraticus*. According to Gordh & Móczar (1990), it is supposed to be deposited at the entomological collection of The Natural History Museum in London. However, the curator confirmed that this type is not there. We redescribe the original description of Smith (1860) to update nomenclatural terms currently used. The description lacks diagnostic characters for the valid genera of Epyrinae, such as the mesoscutellar fovea connected or not connected by evident sulcus, and mesopleuron. Based on the original description, this species can be distinguished from the other species of Epyrinae studied here, because the three carinae of the metapectal-propodeal complex (probably median carina, first metapostnotal carina, and metapostnotal-propodeal suture) are not visible posteriorly and in all the other species of Epyrinae, the median carina is visible posteriorly.

DISTRIBUTION — Papua New Guinea.

***Epyris interruptus* Kieffer, 1904**

Figures 46-47

TYPE MATERIAL — Holotype, ♂, N. Guinea S. E. [probably **Papua New Guinea**], Hatam, VI/1875, leg. Beccari (MCSN).

REDESCRIPTION — *Male*. Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with four distal teeth. Clypeus with straight median lobe, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye weakly setose. Frons coriaceous and punctate. Frontal line absent. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior mesopleural fovea not connected with lower mesopleural fovea; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum as long as notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea not connected by evident sulcus, not trabeculate, large, separated each other by thin septum, weakly inclined, bean-shaped,

touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere smaller than basiparamere in lateral view, apex rounded, not arched inward, dorsal margin straight, strongly divided; basiparamere short; cuspis with apex anterior to apex of paramere, without small basal projection; digitus with apex not aligned to apex of cuspis, its posterior margin crenulate; aedeagus bottle-shaped, its apex posterior to apex of digitus, ventral margin ill defined, base of apodeme dilated.

Female. Unknown.

REMARKS — Kieffer (1904) described *Epyris interruptus*, and subsequently described *Parepyris* Kieffer, transferring *E. interruptus* to *Parepyris* (Kieffer 1914), and designated it as its type-species. Evans (1964) synonimized *Parepyris* with *Epyris*, returning the species to *E. interruptus*. Here, we describe for the first time the characters of the male genitalia of this species, and we conclude that male genitalia do not follow the reported patterns for *Epyris*. We did not find in the new analyzed specimens, representatives of this species to delimit molecular and phylogenetically this species in relation to the other *Epyris*. We have raised the question whether *Parepyris* can be considered a valid genus and have its reinstalled, but we do not have, at the moment, sufficient information to perform the nomenclatural act, keeping the species *E. interruptus* as valid for *Epyris*. Future molecular analyses with more genes and samples are required to better address such hypothesis. This species is different from the others of *Epyris* because it has the genitalia with very short paramere, much smaller than aedeagus and the well developed aedeagus.

DISTRIBUTION — Papua New Guinea.

***Epyris melpa* Colombo & Azevedo n. sp.**

Figures 48-49

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.7599114%5.2347), 1700m, 26-27/10/2012, leg Valeba, Tulei, Novotny,

Leponce, Plot 2, understorey; Malaise - MAL-MW1700B-02/16-d02, P21851-11356 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings amber; metasoma dark brown to yellowish. Mandible with five distal teeth. Clypeus with straight median lobe, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line absent. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior mesopleural fovea ill defined; lower mesopleural fovea not trabeculate; subalar impression connected with mesopleural suture; mesopleural suture not trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein angled. Mesoscutellar fovea not connected by evident sulcus, not trabeculate, large, separated each other by thin septum, weakly inclined, bean-shaped, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina sinuous; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture as long as first metapostnotal carina, ill defined. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere longer than basiparamere in lateral view, apex sharpened, not arched inward, dorsal margin straight; basiparamere short; cuspis with apex anterior to apex of paramere, without small basal projection; digitus with apex aligned to apex of cuspis, its posterior margin crenulate; aedeagus bottle-shaped, its apex aligned to apex of digitus, ventral margin ill defined, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically unique among the Epyrinae from PNG because it has the paramere longer than the basiparamere in lateral view, the apex is sharpened, not arched inward, very thin and the digitus has the apex bifurcated. *Epyris melpa* **n. sp.** is distinguished molecularly as well, the lowest genetic distance observed between *Epyris melpa* **n. sp.** and the remaining species was between *E. min* **n. sp.** (25%) (Figure 4).

This species is unmistakably addressed to the old genus *Artiepyris* Kieffer, mainly by having the paramere very slender. This genus was synonymized with *Epyris* by Evans (1964), which was considered as subgenus of *Epyris*. The females of both groups are very similar to each other, but the males are distinguished by the characters discussed above. The high molecular divergence of 25% from the other species of *Epryis* lead us to question whether such synonymy is correct, and perhaps *Artiepyris* should be reinstalled. Future molecular analyses with more genes and samples are required to better address such hypotheses.

ETYMOLOGY — The epithet *melpa* refers to the Melpa language spoken by about 130,000 people predominantly in Mount Hagen and the surrounding district of Western Highlands Province, Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Epyris mian* Colombo & Azevedo n. sp.**

Figures 50-51

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 28-29/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-04/16-d04, P1829-11306 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Mount Wilhelm (-5.721022, 145.2703), 1200m, 26-27/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW1200B-02/16-d02, P1795-11299 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings hyaline; metasoma light brown. Mandible with five distal teeth. Clypeus with rounded median lobe, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye glabrous. Frons polished and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum as long as than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea not connected by evident sulcus, not

trabeculate, large, separated each other by thin septum, weakly inclined, bean-shaped, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, ill defined; metapostnotal-propodeal suture as long as first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere absent; basiparamere wide, not covering aedeagal base; volsella without small basal projection; digitus with apex posterior to apex of cuspis, its posterior margin denticulate; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin ill defined, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is unique among the *Epyris* because it presents the frontal line, the anterior and lower mesopleural foveae are not connected, the lower mesopleural fovea is trabeculate, the mesopleural subalar impression is not connected with the mesopleural suture and the metapectal-propodeal complex has the first metapostnotal carina as long as the metapostnotal median carina. The molecularly closest species observed in this study was *E. motu* **n. sp.**, known from females only, with 10% divergence (Figure 4).

ETYMOLOGY — The epithet *mian* refers to the Mian ethnic who lives in the Telefomin district of the Sandaun province in Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Epyris min* Colombo & Azevedo n. sp.**

Figures 52-53

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 25-26/11/2012, leg Basset, Plot 2, understorey; Malaise - MAL-WAN02-D08, P4923-9045 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with five distal teeth. Clypeus with rounded median lobe, lateral lobe short, not visible dorsally.

Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line absent. Pronotum polished and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior mesopleural fovea ill defined; lower mesopleural fovea not trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum as long as notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea not connected by evident sulcus, not trabeculate, large, separated each other by thin septum, weakly inclined, bean-shaped, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture longer than first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere as long as basiparamere in lateral view, apex rounded, not arched inward, dorsal margin straight; basiparamere short; cuspis with apex anterior to apex of paramere, without small basal projection; digitus with apex aligned to apex of cuspis, its posterior margin smooth; aedeagus bottle-shaped, its apex aligned to apex of digitus, ventral margin ill defined, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is distinguished from the other Papua New Guinean species of *Epyris* by having the metapostnotal anterior carina straight and the metapostnotal-propodeal suture longer than the first metapostnotal carina, converging posteriorly to the metapostnotal median carina. The lowest genetic distance observed was with a female representative of *E. mundugumor* **n. sp.**, with 15% divergence (Figure 4).

ETYMOLOGY — The epithet *min* refers to the Min cultural group who lives in the West Sepik Province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Epyris motu* Colombo & Azevedo n. sp.**

Figure 54

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 19-20/11/2012, leg Basset, Plot 2, understorey; Malaise - MAL-WAN02-D02, P4917-9225 (MNHN).

DESCRIPTION — *Female.* Head weakly metallic, the pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings hyaline; metasoma dark brown to reddish. Mandible with five distal teeth. Clypeus with rounded median lobe, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel shorter than flagellomere I. Eye setose. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea not trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum as long as notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea not connected by evident sulcus, not trabeculate, large, separated each other by large septum, weakly inclined, bean-shaped, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, straight; metapostnotal-propodeal suture longer than first metapostnotal carina, straight. Metatibia with many spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is distinguished from the other Papua New Guinean species of *Epyris* by having the parapsidal signum as long as the notauli and the mesoscutellum with the posterior margin touching metapostnotal anterior margin. The molecularly closest species observed is *Epyris mian* **n. sp.**, with COI sequences differing 10% of their nucleotides (Figure 4).

ETYMOLOGY — The epithet *motu* refers to Motu native inhabitants who live in the along the southern coastal area of the Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Epyris mundugumor* Colombo & Azevedo n. sp.**

Figure 55

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 26-27/11/2012, leg Basset, Plot 2, understorey; Malaise - MAL-WAN02-D09, P4924-8658 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with five distal teeth. Clypeus with rounded median lobe, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye glabrous. Frons weakly coriaceous and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit elongated, shallow. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea not trabeculate; subalar impression not connected with mesopleural suture; mesopleural suture trabeculate. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea not connected by evident sulcus, not trabeculate, large, separated each other by thin septum, weakly inclined, bean-shaped, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, straight; metapostnotal-propodeal suture longer than first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is distinguished from the other Papua New Guinean species of *Epyris* by having the pedicel as long as the flagellomere I and the eyes glabrous. The molecularly closest species observed is *Epyris mian* **n. sp.**, known from males, with COI sequences differing 15% of their nucleotides (Figure 4).

ETYMOLOGY — The epithet *mundugumor* refers to Mundugumor tribe who lives in the Sepik River region in Papua New Guinea's North West.

DISTRIBUTION — Papua New Guinea.

***Epyris ogea* Colombo & Azevedo n. sp.**

Figure 56

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 28-29/11/2012, leg Gewa, Damag, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-WAN-D-13/16-d13, P0544-15389 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with four distal teeth. Clypeus with tridentate median lobe, lateral lobe short, not visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye setose. Frons coriaceous and punctate. Frontal line absent. Pronotum punctate and coriaceous. Posterior mesofurcal pit oval. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea ill defined; subalar impression not connected with mesopleural suture; mesopleural suture ill defined. Notaulus drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea not connected by evident sulcus, not trabeculate, large, separated each other by thin septum, weakly inclined, bean-shaped, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture longer than first metapostnotal carina, converging posteriorly to metapostnotal median carina. Metatibia without spines. Petiolar root with apex strongly incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is distinguished from the other Papua New Guinean species of *Epyris* by having the median clypeal lobe tridentate and the body strongly punctate. The molecularly closest species observed is *Epyris min* **n. sp.**, with COI sequences differing 21% of their nucleotides (Figure 4).

ETYMOLOGY — The epithet *ogea* refers to Ogea ethnic who lives in the Madang Province of Papua New Guinea speaking the Ogea language.

DISTRIBUTION — Papua New Guinea.

Genus *HOLEPYRIS* Kieffer, 1904

Holepyris Kieffer 1904. Type-species: *Holepyris africanus* Kieffer, 1904

***Holepyris orokaiva* Colombo & Azevedo n. sp.**

Figures 57-58

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.721022, 145.2703). 1200m, 25-26/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW1200B-01/16-d01, P1794-11295 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 04-05/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-11/16-d11, P1446-11270 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720903, 145.2715), 1200m, 05-06/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW1200C-12/16-d12, P1821-11343 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 25-26/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1200A-01/16-d01, P1778-11294 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720903, 145.2715), 1200m, 26-27/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW1200C-02/16-d02, P1811-11303 (MNHN); 1♂, Papua-New-Guinea, Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 24-25/11/2012, leg Basset, Plot 3, understorey; Malaise - MAL-WAN03-D07, P4938-18131 (MNHN); 1♂, Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 23-24/11/2012, leg Basset, Plot 3, understorey; Malaise - MAL-WAN03-D06, P4937-9083 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with one distal tooth. Clypeus with rounded median lobe, lateral lobe well developed, straight, visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line absent. Pronotum punctate and coriaceous. Pronotal disc with anterior margin carinate, posterior margin with small foveae. Posterior mesofurcal pit thin. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior mesopleural fovea ill defined; lower mesopleural fovea ill defined; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Mesoscutellum without posterior margin foveolate. Notaulus not drop-

shaped, incomplete. Parapsidal signum shorter than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, not trabeculate, small elevation present, transversally, narrower medially, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture longer than first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere shorter than basiparamere in lateral view, apex rounded, not arched inward, dorsal margin straight; basiparamere wide, covering aedeagal base, translucent, ill defined; cuspis with apex anterior to apex of paramere, without small basal projection; digitus with apex aligned to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with apex with translucent projection, base of apodeme dilated.

Female. Unknown.

VARIATIONS — Clypeus with lateral lobe rounded.

REMARKS — This species is similar to *Holepyris swagap* **n. sp.** by having the median clypeal lobe rounded, the eyes glabrous, the forewing with four distal flexion lines and the mesoscutellar fovea connected by an evident sulcus, which is not trabeculate and has a small elevation. However, *Holepyris orokaiva* **n. sp.** has the posterior mesofurcal pit thin, inserted into a triangle-shaped depression, the lower mesopleural fovea is ill defined, the paramere is shorter than the basiparamere in lateral view and the digitus is as long as the cuspis; whereas *H. swagap* **n. sp.** has the posterior mesofurcal pit foveolate, inserted into an ill defined depression, the lower mesopleural fovea is not trabeculate, the paramere is longer than the basiparamere in lateral view and the digitus has the apex anterior to apex of cuspis. The genetic distance between *H. orokaiva* **n. sp.** and *H. swagap* **n. sp.** was of 17%, but the molecularly closest species is *H. wiru* **n. sp.** with DNA sequences diverging 3% (Figure 4). *Holepyris orokaiva* **n. sp.** is known from males only; whereas *H. wiru* **n. sp.** is known from females; the genetic distance, however, is superior than expected from coespecifics. Besides sexual dimorphism, this species has the pedicel shorter than flagellomere I; eye glabrous; metafurcal pit inserted into triangle-shaped depression; notauli present and forewing with four distal flexion lines; whereas *H. wiru* **n. sp.** has the

pedicel as long as flagellomere I; eye setose; metafurcal pit inserted into crown-shaped depression; notauli absent, and forewing with two distal flexion lines.

ETYMOLOGY — The epithet *orokaiva* refers to Orokaiva people indigenous to Papua New Guinea, who occupied what is now Oro Province and the periphery of the area they inhabited was marked by the Owen Stanley Range in the south, German New Guinea in the west and the Hydrographers Range in the south.

DISTRIBUTION — Papua New Guinea.

***Holepyris sambia* Colombo & Azevedo n. sp.**

Figures 59-60

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 19-20/11/2012, leg Gewa, Damag, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-WAN-D-04/16-d04, P0535-9036 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 23-24/11/2012, leg Gewa, Damag, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-WAN-D-08/16-d08, P0539-9071 (MNHN); 1♂, Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 20-21/11/2012, leg Basset, Plot 2, understorey; Malaise - MAL-WAN02-D03, P4918-9228 (MNHN); 1♂, Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 19-20/11/2012, leg Basset, Plot 3, understorey; Malaise - MAL-WAN03-D02, P4933-9222 (MNHN); 2♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 26-27/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW0700A-02/16-d02, P1389-11985 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.732698, 145.2556), 700m, 29-30/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0700B-05/16-d05, P1408-11994 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 02-03/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-09/16-d09, P1444-11262 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.741031, 145.3294), 200m, 25-26/10/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-01/16-d01, P1014-11947 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 04-05/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1200A-11/16-d11, P1788-11331 (MNHN); 1♂, Province Madang, Mount Wilhelm (-

5.761029,145.1860), 2200m, 29-30/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW2200C-14/16-d14, P1603-11900 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 25-26/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-01/16-d01, P1826-11293 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 26-27/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-02/16-d02, P1437-11982 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 30-31/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-06/16-d06, P1441-11252 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 01-02/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-08/16-d08, P1833-11320 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 02-03/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-09/16-d09, P1834-11327 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with one distal tooth. Clypeus with rounded median lobe, lateral lobe well developed, straight, visible dorsally. Antenna with flagellar pubescence erect; pedicel as long as flagellomere I. Eye glabrous. Frons coriaceous. Frontal line present. Pronotum punctate and coriaceous. Pronotal disc with anterior margin carinate, posterior margin with small foveae. Posterior mesofurcal pit thin. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior mesopleural fovea ill defined; lower mesopleural fovea ill defined; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Mesoscutellum without posterior margin foveolate. Notaulus not drop-shaped, incomplete. Parapsidal signum shorter than notaulus. Forewing with three distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, trabeculate, small elevation absent, transversally, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture longer than first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere as long

as basiparamere in lateral view, apex sharpened, not arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base, translucent, ill defined; apex of cuspis aligned with apex of paramere, without small basal projection; digitus with apex anterior to apex of cuspis, its posterior margin crenulate; aedeagus bottle-shaped, its apex aligned to apex of digitus, ventral margin with apex ill defined, base of apodeme dilated.

Female. Unknown.

VARIATIONS — Aedeagus with apex sickle-shaped in ventral view.

REMARKS — This species is morphologically similar to *Holepyris tairora* **n. sp.** by having the median clypeal lobe rounded, the eyes glabrous, the posterior mesofurcal pit thin, the mesoscutellum with the posterior margin polished, the forewing with three distal flexion lines, the mesoscutellar fovea connected by an evident sulcus, trabeculate, without a small elevation and the apex of cuspis aligned to the apex of paramere. *Holepyris sambia* **n. sp.**, however, has the pedicel as long as the flagellomere I; the metafurcal pit is inserted into a triangle-shaped depression, the notauli is present and the paramere is as long as the basiparamere in lateral view; whereas *H. tairora* **n. sp.** has the pedicel shorter than the flagellomere I; the metafurcal pit is inserted into an ill defined depression, the notauli is absent and the paramere is longer than the basiparamere in lateral view. The genetic distance between *H. sambia* **n. sp.** and *H. tairora* **n. sp.** was of 15% (Figure 4), thus, we do not have either morphological or molecular evidences to associate them into one single species.

ETYMOLOGY — The epithet *sambia* refers to the Sambia ethnic who lives the fringes of the Eastern Highlands Province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Holepyris swagap* Colombo & Azevedo n. sp.**

Figures 61-62

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.758978, 145.1861), 2200m, 17-18/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW2200A-02/16-d02, P2559-11906 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma dark brown; wings hyaline. Mandible with one

distal tooth. Clypeus with rounded median lobe, lateral lobe well developed, rounded, visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye glabrous. Frons polished and punctate. Frontal line present. Pronotum punctate and coriaceous. Pronotal disc with anterior margin carinate, posterior margin with small foveae. Posterior mesofurcal pit foveolate. Metafurcal pit inserted into ill defined depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea not trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Mesoscutellum without posterior margin foveolate. Notaulus not drop-shaped, incomplete. Parapsidal signum longer than notaulus. Forewing with four distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, not trabeculate, small elevation present, transversally, evenly wide, not touching mesoscutellar lateral margin, rectangular. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture longer than first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere longer than basiparamere in lateral view, apex rounded, not arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base, translucent, ill defined; apex of cuspis anterior to apex of paramere; with small basal projection; digitus with apex anterior to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with apex with translucent projection, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Holepyris orokaiva* **n. sp.** by having the median clypeal lobe rounded, the eyes glabrous, the forewing with four distal flexion lines and the mesoscutellar fovea connected by an evident sulcus, not trabeculate, with a small elevation present. *Holepyris swagap* **n. sp.**, however, has the posterior mesofurcal pit foveolate, inserted into an ill defined depression, the lower mesopleural fovea is not trabeculate, the paramere is longer than the basiparamere in lateral view and the digitus has the apex anterior to the apex of cuspis; whereas *H. orokaiva* **n. sp.** has the posterior mesofurcal pit thin, inserted into a triangle-shaped depression, the lower mesopleural fovea is ill defined, the paramere is shorter than the basiparamere in lateral

view and the digitus is as long as the cuspis. The genetic distance between *H. swagap* **n. sp.** and *H. orokaiva* **n. sp.** was of 17% (Figure 4).

ETYMOLOGY — The epithet *swagap* refers to the Swagap indigenous tribes who live in a village that sits above the waters of the Sepik River, named Sawagap in Papua New Guinea. They are also known as the Insect Tribe.

DISTRIBUTION — Papua New Guinea.

***Holepyris tairora* Colombo & Azevedo n. sp.**

Figures 63-64

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.759910, 145.2347), 1700m, 26-27/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW1700B-02/16-d02, P2185-11356 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Mount Wilhelm (-5.720903, 145.2715), 1200m, 05-06/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW1200C-12/16-d12, P1821-11343 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.758978, 145.1861), 2200m, 27-28/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW2200D-12/16-d12, P2617-11887 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.760178, 145.1863), 2200m, 25-26/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW2200B-10/16-d10, P2583-11940 (MNHN); 2♂, Province Madang, Mount Wilhelm (-5.758978, 145.1861), 2200m, 30-31/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW2200D-15/16-d15, P2620-11879 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.761029, 145.1860), 2200m, 25-26/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW2200C-10/16-d10, P2599-11939 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.758978, 145.1861), 2200m, 27-28/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW2200A-12/16-d12, P2569-11884 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole dark brown; antenna and metasoma light brown; wings hyaline. Mandible with one distal tooth. Clypeus with rounded median lobe, lateral lobe well developed, straight, visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line present. Pronotum punctate

and coriaceous. Pronotal disc with anterior margin carinate, posterior margin with small foveae. Posterior mesofurcal pit thin. Metafurcal pit inserted into ill defined depression. Mesopleuron with anterior and lower mesopleural foveae connected; lower mesopleural fovea not trabeculate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Mesoscutellum without posterior margin foveolate. Notaulus absent. Parapsidal signum longer than notaulus. Forewing with three distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, trabeculate, small elevation absent, transversally, corners as wide as, not touching mesoscutellar lateral margin, rectangular. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, ill defined; metapostnotal-propodeal suture longer than first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere longer than basiparamere in lateral view, apex rounded, not arched inward, dorsal margin incurved; basiparamere wide, not covering aedeagal base, translucent, ill defined; apex of cuspis aligned with apex of paramere, without small basal projection; digitus with apex aligned to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with apex ill defined, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is morphologically similar to *Holepyris sambia* **n. sp.** by having the median clypeal lobe rounded, the eyes glabrous, the posterior mesofurcal pit thin, the posterior margin of mesoscutellum not foveolate, the forewing with three distal flexion lines, the mesoscutellar fovea connected by an evident sulcus, trabeculate and without a small elevation and the apex of cuspis aligned to the apex of paramere. *Holepyris tairora* **n. sp.**, however, has the pedicel shorter than the flagellomere I, the metafurcal pit is inserted into an ill defined depression, the notauli is absent and the paramere is longer than the basiparamere in lateral view; whereas *H. sambia* **n. sp.** has the pedicel as long as the flagellomere I, the metafurcal pit is inserted into a triangle-shaped depression, the notauli is present and the paramere is as long as the basiparamere in lateral view. The genetic sequences diverged 15% between *H. tairora* **n. sp.** and *H. sambia* **n. sp.** (Figure 4), supporting our decision to consider them two separate lineages.

ETYMOLOGY — The epithet *tairora* refers to the Tairora tribal group who live in Eastern Highlands of Papua New Guinea in or near the Aiyura Valley.

DISTRIBUTION — Papua New Guinea.

***Holepyris telefol* Colombo & Azevedo n. sp.**

Figures 65-66

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 26-27/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-02/16-d02, P1437-11982 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 28-29/10/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-04/16-d04, P1439-11998 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 01-02/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-08/16-d08, P1833-11320 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 05-06/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-12/16-d12, P1447-11275 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720903, 145.2715), 1200m, 25-26/10/2012, leg Philip, Alois, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW1200C-01/16-d01, P1810-11292 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.731961, 145.2522), 700m, 04-05/11/2012, leg Keltim, Uma, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW0700D-11/16-d11, P1446-11270 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 31-01/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1200D-07/16-d07, P1832-11316 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.758978, 145.1861), 2200m, 18-19/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW2200A-03/16-d03, P2560-11913 (MNHN); 1♂, Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 24-25/11/2012, leg Basset, Plot 1, understorey; Malaise - MAL-WAN01-D07, P4906-0935 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.720874, 145.2695), 1200m, 31-01/11/2012, leg Philip, Alois, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1200A-07/16-d07, P1784-11318 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna light brown; wings hyaline; metasoma dark brown. Mandible with one distal tooth. Clypeus with angulate median lobe, lateral lobe well developed, rounded, visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous and punctate. Frontal line absent. Pronotum punctate and coriaceous. Pronotal disc with anterior margin carinate, posterior margin with small foveae. Posterior mesofurcal pit foveolate. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea foveolate; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Mesoscutellum with posterior margin foveolate. Notaulus not drop-shaped, incomplete. Parapsidal signum as long as notaulus. Forewing with three distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, trabeculate, small elevation absent, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina outcurved; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, converging posteriorly; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly to metapostnotal median carina. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere longer than basiparamere in lateral view, apex rounded, not arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base, translucent, ill defined; apex of cuspis aligned with apex of paramere, without small basal projection; digitus with apex aligned to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with apex ill defined, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is very different of all other Papuan species by having the median clypeal lobe with sharpened. The lowest genetic distance observed between the male of *Holepyris orokaiva* **n. sp.** and the female of *H. wiru* **n. sp.** was 14% (Figure 4).

ETYMOLOGY — The epithet *telefol* refers to Telefol tribal group who live in Sandaun Province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Holepyris tsembaga* Colombo & Azevedo n. sp.**

Figures 67-68

TYPE MATERIAL — Holotype, ♂, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.761029, 145.1860), 2200m, 18-19/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 3, understorey; Malaise - MAL-MW2200C-03/16-d03, P2592-11915 (MNHN). Paratypes. **Papua New Guinea**. 1♂, Province Madang, Mount Wilhelm (-5.758978, 145.1861), 2200m, 20-21/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW2200A-05/16-d05, P2562-11894 (MNHN); 1♂, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 25-26/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-01/16-d01, P2168-11360 (MNHN).

DESCRIPTION — *Male.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole dark brown; antenna brown; wings hyaline; metasoma dark brown to light brown. Mandible with one distal tooth. Clypeus with rounded median lobe, lateral lobe well developed, straight, visible dorsally. Antenna with flagellar pubescence erect; pedicel shorter than flagellomere I. Eye glabrous. Frons coriaceous. Frontal line absent. Pronotum polished and coriaceous. Pronotal disc with anterior margin carinate, posterior margin with small foveae. Posterior mesofurcal pit elongated, deep. Metafurcal pit inserted into crown-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea ill defined, transversally, evenly wide, not touching mesoscutellar lateral margin; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Mesoscutellum with posterior margin foveolate. Notaulus not drop-shaped, incomplete. Parapsidal signum as long as notaulus. Forewing with three distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, not trabeculate, small elevation present. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina shorter than metapostnotal median carina, straight; metapostnotal-propodeal suture shorter than first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished. Hypopygeal posterior margin outcurved. Genitalia: paramere longer than basiparamere in lateral view,

apex rounded, not arched inward, dorsal margin straight; basiparamere wide, covering aedeagal base, opaque, rabbit ear-shaped; cuspis with apex anterior to apex of paramere, without small basal projection; digitus with apex anterior to apex of cuspis, its posterior margin serrated; aedeagus bottle-shaped, its apex anterior to apex of digitus, ventral margin with apex ill defined, base of apodeme dilated.

Female. Unknown.

REMARKS — This species is distinguished from the other Papua New Guinean species of *Holepyris* by having the basiparamere wide with rabbit ear-shaped, opaque and as long as the paramere. The molecularly closest species observed is *H. orokaiva* **n. sp.**, with COI sequences differing 8% of their nucleotides (Figure 4).

ETYMOLOGY — The epithet *tsembaga* refers to the Tsembaga group of horticulturists who live in the highlands of New Guinea.

DISTRIBUTION — Papua New Guinea.

***Holepyris wiru* Colombo & Azevedo n. sp.**

Figure 69

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Province Madang, Mount Wilhelm (-5.758978, 145.1861), 2200m, 26-27/10/2012, leg Mogia, Lilip, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW2200A-11/16-d11, P2568-11931 (MNHN). Paratypes. **Papua New Guinea**. 1♀, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 09-10/11/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-16/16-d16, P2183-8801 (MNHN); 1♀, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 07-08/11/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-14/16-d14, P2181-8797 (MNHN); 1♀ Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 25-26/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-01/16-d01, P2168-11360 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna dark brown; wings hyaline; metasoma light brown. Mandible with two distal teeth. Clypeus with rounded median lobe, lateral lobe well developed, rounded, visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye setose. Frons coriaceous and punctate. Frontal line present.

Pronotum punctate and coriaceous. Posterior mesofurcal pit circular. Metafurcal pit inserted into crown-shaped depression. Mesopleuron with anterior mesopleural fovea ill defined; lower mesopleural fovea ill defined; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus absent. Parapsidal signum longer than notaulus. Forewing with two distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, not trabeculate, small elevation present, transversally, narrower medially, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, straight; metapostnotal-propodeal suture as long as first metapostnotal carina, straight. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is morphologically similar to *Holepyris zia* **n. sp.** by having the median clypeal lobe rounded, the mandibles with two distal teeth and the forewing with two distal flexion lines. *Holepyris wiru* **n. sp.,** however, has the metapostnotal-propodeal suture straight, the notauli is absent and the mesoscutellar fovea is connected by an evident sulcus, polished with a small elevation; whereas *H. zia* **n. sp.** has the metapostnotal-propodeal suture converging posteriorly to the metapostnotal median carina, the notauli is present and the mesoscutellar fovea is connected by an evident sulcus, trabeculate without a small elevation. The genetic distance between *H. wiru* **n. sp.** and *H. zia* **n. sp.** was of 10%, supporting our decision to consider two distinguished species. *Holepyris wiru* **n. sp.** is genetically close to *H. orokaiva* **n. sp.** (3%)**,** which is known from males. Besides sexual dimorphism this species has the pedicel as long as flagellomere I; eye setose; metafurcal pit inserted into crown-shaped depression; notauli absent and forewing with two distal flexion lines; whereas *H. orokaiva* **n. sp.** has the pedicel shorter than flagellomere I; eye glabrous; metafurcal pit inserted into triangle-shaped depression; notauli present and forewing with four distal flexion lines.

ETYMOLOGY — The epithet *wiru* refers to the Wiru people who live in the Southern Highlands Province of Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

***Holepyris yaifo* Colombo & Azevedo n. sp.**

Figure 70

TYPE MATERIAL — Holotype, ♀, **Papua-New-Guinea**, Province Madang, Mount Wilhelm (-5.741031, 145.3294), 200m, 31-01/11/2012, leg Dilu, Ray, Novotny, Leponce, Plot 2, understorey; Malaise - MAL-MW0200B-07/16-d07, P1020-11968 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna light brown; wings hyaline; metasoma dark brown. Mandible with one distal teeth. Clypeus with angulate median lobe, lateral lobe well developed, rounded, visible dorsally. Antenna with flagellar pubescence erect; pedicel smaller than flagellomere I. Eye setose. Frons coriaceous and punctate. Frontal line absent. Pronotum punctate and coriaceous. Posterior mesofurcal pit circular. Metafurcal pit inserted into triangle-shaped depression. Mesopleuron with anterior mesopleural fovea ill defined; lower mesopleural fovea ill defined; subalar impression connected with mesopleural suture; mesopleural suture not trabeculate. Notaulus absent. Parapsidal signum longer than notaulus. Forewing with two distal flexion lines, 2r-rs&Rs vein not rounded. Mesoscutellar fovea connected by evident sulcus, trabeculate, small elevation absent, weakly inclined, narrower medially, touching mesoscutellar lateral margin. Mesoscutellum with posterior margin touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as metapostnotal median carina, diverging posteriorly; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is morphologically similar to *Holepyris zia* **n. sp.** by having the antenna eye setose, posterior mesofurcal pit circular, forewing with two distal flexion lines, and first metapostnotal carina as long as metapostnotal median carina. However, *Holepyris yaifo* **n. sp.,** has the notauli absent, metafurcal pit inserted into triangle-shaped depression, and mesopleural suture not trabeculate; whereas *H. zia* **n. sp.** has the notauli present, metafurcal pit inserted into crown-shaped depression, and mesopleural suture trabeculate. The genetic distance was not performed because the specimen was found after molecular analysis.

ETYMOLOGY — The epithet *yaifo* refers to the Yaifo people who live in the remote tribe in the Chimbu Province of Papua New Guinea in the highlands.

DISTRIBUTION — Papua New Guinea.

***Holepyris zia* Colombo & Azevedo n. sp.**

Figure 71

TYPE MATERIAL — Holotype, ♀, **Papua New Guinea**. Papua-New-Guinea, Province Madang, Wanang 3 station (-5.22767, 145.0797), 175m, 29-30/11/2012, leg Basset, Plot 3, understorey; Malaise - MAL-WAN03-D12, P4943-1176 (MNHN). Paratypes. **Papua New Guinea**. 1♀, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 26-27/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW1700A-02/16-d02, P2169-11358 (MNHN); 1♀, Province Madang, Mount Wilhelm (-5.739897, 145.3297), 200m, 30-31/10/2012, leg Dilu, Ray, Novotny, Leponce, Plot 1, understorey; Malaise - MAL-MW0200A-06/16-d06, P1003-11961 (MNHN); 1♀, Province Madang, Mount Wilhelm (-5.759269, 145.2356), 1700m, 25-26/10/2012, leg Valeba, Tulei, Novotny, Leponce, Plot 4, understorey; Malaise - MAL-MW1700D-01/16-d01, P2216-11361 (MNHN).

DESCRIPTION — *Female.* Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; antenna and metasoma light brown; wings hyaline. Mandible with two distal teeth. Clypeus with rounded median lobe, lateral lobe well developed, rounded, visible dorsally. Antenna with flagellar pubescence appressed; pedicel as long as flagellomere I. Eye setose. Frons coriaceous and punctate. Frontal line present. Pronotum punctate and coriaceous. Posterior mesofurcal pit circular. Metafurcal pit inserted into crown-shaped depression. Mesopleuron with anterior and lower mesopleural foveae not connected; lower mesopleural fovea ill defined; subalar impression connected with mesopleural suture; mesopleural suture trabeculate. Notaulus not drop-shaped, complete. Parapsidal signum shorter than notaulus. Forewing with two distal flexion lines, 2r-rs&Rs vein not angled. Mesoscutellar fovea connected by evident sulcus, trabeculate, small elevation absent, weakly inclined, evenly wide, not touching mesoscutellar lateral margin. Mesoscutellum with posterior margin not touching metapostnotal anterior margin. Metapectal-propodeal complex with metapostnotal anterior carina straight; metapostnotal median carina complete, visible posteriorly; first metapostnotal carina as long as

metapostnotal median carina, straight; metapostnotal-propodeal suture as long as first metapostnotal carina, converging posteriorly to metapostnotal median carina. Metatibia without spines. Petiolar root with apex incurved. Metasoma polished.

Male. Unknown.

REMARKS — This species is morphologically similar to *Holepyris wiru* **n. sp.** by having the median clypeal lobe rounded, the mandibles with two distal teeth and the forewing with two distal flexion lines. *Holepyris zia* **n. sp.**, howeve, has the metapostnotal-propodeal suture converging posteriorly to the metapostnotal median carina, the notauli is present and the mesoscutellar fovea is connected by an evident sulcus, trabeculate without small elevation; whereas *H. wiru* **n. sp.** has the metapostnotal-propodeal straight suture, the notauli is absent and the mesoscutellar fovea is connected by an evident sulcus, not trabeculate and with a small elevation. *Holepyris zia* **n. sp.** and *H. wiru* **n. sp.** diverged 10% of their COI sequences; and the lowest genetic distance observed between the female of *H. zia* **n. sp.** and the male of *H. orokaiva* **n. sp.** or the male of *H. tsembaga* **n. sp.** was 8% (Figure 4).

ETYMOLOGY — The epithet *zia* refers to the Zia tribe who lives in the lower Waria Valley in Morobe Province, Papua New Guinea.

DISTRIBUTION — Papua New Guinea.

DISCUSSION

This is the first study of Epyrinae in which the species are hypothesized based on both morphological and molecular evidences. Here we report three genera to Papua New Guinea namely *Chlorepyris*, *Epyris* and *Holepyris* summing up to 36 species of Epyrinae.

Currently, it is difficult to establish the identity of the species of Epyrinae, mainly because most of the description are outdated and some types are lost. In Bethylidae, identification at the species level is difficult because of the lack of unique diagnostic characters, and usually requires the detailed analyses of male genitalia, making them determinant in the taxonomy of the group. Some species have different morphological characteristics in male and female, in species of Pristocerinae for example, which show high sexual dimorphism (see Azevedo *et al.* 2016). We emphasize that in morphological terms, the subfamily Epyrinae is the most complex in Bethylidae (Alencar & Azevedo 2013). Moreover, taxonomic keys, representatives from both sexes and taxonomic revisions are scarce in Epyrinae.

We were able to distinguish morphological patterns among species of *Chlorepyris*, *Epyris* and *Holepyris*, showing generic and specific morphological boundaries. Some genera are easily delimited, for example *Holepyris* presented a more conserved morphology, whereas *Epyris* is a very complex genus and urges a taxonomic revision as suggested by previous works (Waichert & Azevedo 2009; Alencar & Azevedo 2013). Among the most conserved structures within the genera, we highlight the tarsal claw, the flexion lines and the posterior hypopygeal margins of the specimens. Peculiarities in the male genitalia are much generalized for each genus, for instance, the basiparameres are wide, covering the aedeagal base in *Chlorepyris*, and the volsella with cuspis is very long in *Holepyris*. We found some variations between males and females, mainly in the flexion lines of forewing, mesoscutellar foveae, and mandibles.

In Bethylidae, molecular studies are scarce (see Carr *et al.* 2010, Jiang *et al.* 2015, Alencar *et al.* 2018). The reconstructed phylogenetic tree based on the COI sequences (Figure 4) endorses those of Carr *et al.* (2010) and Alencar & Azevedo (2013), showing the subfamily Epyrinae monophyletic but with conflictic genera boundaries.

The phylogenetic tree, assisted with morphological examination, led to sex association. The identical genetic material indicates conspecificity in female and male representatives of *Chlorepyris bilibil* Colombo & Azevedo **n. sp.** In the genus *Holepyris*, the lowest genetic distance observed between species was 3% (*H. wiru* Colombo & Azevedo **n. sp.** and *H. orokaiva* Colombo & Azevedo **n. sp.**), but the species are morphologically distinct, especially for characteristics of the male genitalia. In *Chlorepyris*, besides specimens of *Chlorepyris bilibil* Colombo & Azevedo **n. sp.** that presented 0% of genetic distance, other species presented genetic distance superior to 5% divergence, but also were morphologically different. Finally, in *Epyris* the shortest distance was 10%, indicating that the diversity was probably poorly sampled and that the genus might be composed of several lineages and needs more sampling effort and taxonomic revision. Han *et al.* (2018), using COI barcodes in bumble bees (Hymenoptera: Apidae), detected distinct clades with large interspecific genetic distances (> 3%), and recent clades with low interspecific genetic distances (range: 1.2-2.7%), similar to what we found in PNG, supporting our results and taxonomic acts. Finally, all species were delimited based on morphological and genetic data.

The genera of Epyrinae vary by 3-30% of their COI genetic distances. We need to emphasize that high genetic distance, such as above 18% as in *Epyris melpa* **n. sp.**, for

example, may be considered intergeneric values. Therefore, we conclude that some lineage currently identified as *Epyris*, might be better placed as distinct genera. However, further morphological, and molecular analyzes must be achieved before nomenclatural acts are carried out. *Chlorepyris* also presented high genetic variation (~15%), but the morphology of the species is conserved and the phylogenetic analysis indicates common ancestry. Finally, *Holepyris* is less variable in both morphological characters, and molecular sequences.

The reduced number of specimens (35) and lack of duplicates used in the molecular analysis unabled us to discuss intraspecific genetic variation. However, since this is the first attempt to study Epyrinae based on molecular data, we strongly suggest new studies to support these findings.

Finally, this is our third contribution on the Bethylidae fauna of PNG. Mugrabi & Azevedo (2016) cited 91 species of *Dissomphalus* Ashmead, 1893, and Vargas & Azevedo (2016) reported one species of *Galodoxa* Nagy, 1974. Considering the present contribution, there are 131 known species of Bethylidae in PNG up to date.

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REFERENCES

ALENCAR I. D. C. C., WAICHERT C. & AZEVEDO C. O . 2018 — Opening Pandora's box of Pristocerinae: molecular and morphological phylogenies of *Apenesia* (Hymenoptera, Bethylidae) reveal several hidden genera. *Systematic Entomology* 43: 1-29. https://doi.org/10.1111/syen.12295

ALENCAR I. D. C. C. & AZEVEDO C. O . 2013 — Reclassification of Epyrini (Hymenoptera: Bethylidae): a tribal approach with commentary on their genera. *Systematic Entomology* 38: 45-80. https://doi.org/10.1111/j.1365-3113.2012.00648.x

AZEVEDO C. O . 1999 — Revision of the Neotropical *Dissomphalus* Ashmead, 1893 (Hymenoptera, Bethylidae) with median tergal process. *Arquivos de Zoologia* 35: 301-394. https://doi.org/10.11606/issn.2176-7793.v35i4p301-394

AZEVEDO C. O ., COLOMBO W. D., ALENCAR I. D. C. C., BRITO C. D. & WAICHERT C. 2016 — Pairs in phoretic copulation, a tool for male-female association in highly dimorphic insects of the wasp genus *Dissomphalus* Ashmead (Hymenoptera, Bethylidae). *Zoologia* 33(6): e20160076. https://doi.org/10.1590/s1984-4689zool-20160076

AZEVEDO C. O ., ALENCAR I. D. C. C., RAMOS M. S., BARBOSA D. N., COLOMBO W. D., VARGAS J. M. R. & LIM J. 2018 — Global Guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4489(1): 1-294. https://doi.org/10.11646/zootaxa.4489.1.1

CARR M., YOUNG J. P. W. & MAYHEW P. J. 2010 — Phylogeny of bethylid wasps (Hymenoptera: Bethylidae) inferred from 28S and 16S rRNA genes. *Insect Systematics and Evolution* 41: 55-73. https://doi.org/10.1163/187631210X486995

CROZIER R. H ., CROZIER Y. C. & MACKINLAY A. G. 1989 — The COI and COII region of honeybee mitochondrial DNA: evidence for variation in insect mitochondrial evolutionary rates. *Molecular Biology Evolution* 6: 399-411.

EVANS H. E . 1964 — *A synopsis of the American Bethylidae (Hymenoptera, Aculeata)*. Bulletin of the Museum of Comparative Zoology 132: 1-222. http://www.biodiversitylibrary.org/page/4315704

FOLMER O., BLACK M., HOEH W., LUTZ R. & VRIJENHOEK R. 1994 — DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294-299.

GORDH G. & MÓCZÁR L. 1990 — A catalog of the world Bethylidae (Hymenoptera, Aculeata). Memoirs of the American Entomological Institute 46:1-364.

HAJIBABAEI M., JANZEN D. H , BURNS J. M, HALLWACHS W. & HEBERT P. D. N. 2006 — DNA barcodes distinguish species of tropical Lepidoptera. *Proceedings of the National Academy of Sciences of the United States of America* 103(4): 968-971. https://doi.org/10.1073/pnas.0510466103

HAN T., KIM S. H., YOO N H.J., PARK I.G. & PARK H. 2018 - Genetic variations of DNA barcoding region of bumble bees (Hymenoptera: Apidae) from South Korea. *Mitochondrial DNA* Part A 30, 30-42. https://doi.org/10.1080/24701394.2018.1450396

HARRIS R. A . 1979 — A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1-31.

HOLT B. G., LESSARD J. P., BORREGAARD M. K., FRITZ S. A ., ARAÚJO M. B ., DIMITROV D., FABRE P. H ., GRAHAM C. H ., GRAVES G. R ., JØNSSON K. A ., NOGUÉS-BRAVO D., WANG Z., WHITTAKER R. J., FJELDSÅ J. & RAHBEK C. 2013 — An update of Wallace's zoogeographic regions of the world. *Science* 339(6115): 74-78. https://doi.org/10.1126/science.1228282

JIANG Y., YANG Z., WANG X. & HOU Y. 2015 — Molecular identification of sibling species of *Sclerodermus* (Hymenoptera: Bethylidae) that parasitize buprestid and cerambycid beetles by using partial sequences of mitochondrial DNA Cytochrome Oxidase Subunit 1 and 28S ribosomal RNA gene. *PLoS ONE* 10(3): e0119573. https://doi.org/10.1371/journal.pone.0119573

KAWADA R. & BUFFINGTON M. L . 2016 — A scalable and modular dome illumination system for scientific microphotography on a budget. *PLoS ONE* 11(5): e0153426. https://doi.org/10.1371/journal.pone.0153426

KAWADA R., LANES G. O . & AZEVEDO C. O . 2015 — Evolution of metapostnotum in flat wasps (Hymenoptera, Bethylidae): implications for homology assessments in Chrysidoidea. *PLoS ONE* 10 (10): e0140051. https://doi.org/10.1371/journal.pone.0140051

KIEFFER J. J. 1904 — Description de nouveaux Dryininae et Bethylinae. Du Musée Civique de Gênes. *Annali del Museo Civico di Storia Naturale di Genova* 41: 351-412.

KIEFFER J. J. 1905 — Description de noveaux Proctotrypides exotiques avec une planche et une figure dans le texte. *Société Scientifique de Bruxelles* 29(2): 95-142.

KIEFFER J. J. 1914 — Bethylinae Das Tierreich. *Akademie der Wissenschaften zu Berlin* 41: 228-595.

LEE W., KIM H., LIM J., CHOI H. R , KIM Y., KIM Y. S., JI J. Y, FOOTTIT R. G. & LEE S. 2011 — Barcoding aphids (Hemiptera: Aphididae) of the Korean Peninsula: updating the global data set. *Molecular Ecology Resources* 11(1): 32-37. https://doi.org/10.1111/j.1755-0998.2010.02877.x

LEPONCE M., NOVOTNY V., PASCAL O., ROBILLARD T., LEGENDRE F., VILLEMANT C., MUNZINGER J., MOLINO J.F., DREW R., ODEGAARD F., SCHMIDL J., TISHECHKIN A., SAM K., BICKEL D., DAHL C., DAMAS K., FAYLE T. M., GEWA B., JACQUEMIN J., KELTIM M., KLIMES P., KOANE B., KUA J., MANTILLERI A., MOGIA M., MOLEM K., MOSES J., NOWATUO H., ORIVEL J., PINTAUD J.C., ROISIN Y., SAM L., SIKI B., SOLDATI L., SOULIER-PERKINS A., TULAI S., YOMBAI J., WARDHAUGH C. & BASSET Y. 2016 — Land module of Our Planet Reviewed - Papua New Guinea: aims, methods and first taxonomical results, *in* Robillard T., Legendre F., Villemant C. & Leponce M. (eds), Insects of Mount Wilhelm, Papua New Guinea. Muséum national d'Histoire naturelle, Paris : 11-48 (Mémoires du Muséum national d'Histoire naturelle; 209). ISBN : 978-2-85653-784-8.

LI Y., ZHOU X., FENG G., HU H., NIU L., HEBERT P. D. N. & HUANG D. 2010 — COI and IT S2 sequences delimit species, reveal cryptic taxa and host specificity of fig-associated *Sycophila* (Hymenoptera, Eurytomidae). *Molecular Ecology Resources* 10: 31-40. https://doi.org/10.1111/j.1755-0998.2009.02671.x

LOBL I. & LESCHEN R. A . B . 2005 — Demography of coleopterists and their thoughts on DNA barcoding and the phylocode, with commentary. *Coleopterists Bulletin* 59(3): 284-292. https://doi.org/10.1649/850.1

MAGRETTI P. 1884 — Risultati di raccolte imenotterologiche nell' Africa orientale. *Annali de Museo Civico di Storia Naturale d'Genova* 21(1): 523-636.

MARTINELLI A. B ., WAICHERT C., BARBOSA D. N., FAGUNDES V. & AZEVEDO C. O . 2017 — The use of Proteinase K to access genitalia morphology, vouchering and DNA extraction in minute wasps. *Anais da Academia Brasileira de Ciências* 89(3): 1629-1633. https://doi.org/10.1590/0001-3765201720160825

MILLER M. A ., PFEIFFER W. & SCHWARTZ T. 2010 — Creating the CIPRES Science Gateway for Inference of Large Phylogenetic Trees; *SC10 Workshop on Gateway Computing Environments* (GCE10).

MUGRABI D. F & AZEVEDO C. O . 2016 — Description of 91 new species of *Dissomphalus* Ashmead (Hymenoptera: Bethylidae) from New Guinea Island and surrounded areas, *in* ROBILLAR D T., LEGENDRE F., VILLEMANT C. & LEPONCE M. (eds), Insects of Mount Wilhelm, Papua New Guinea. Muséum national d'Histoire naturelle, Paris : 451-564 (Mémoires du Muséum national d'Histoire naturelle; 209).

PACKER L. & RUZ L. 2017 — DNA barcoding the bees (Hymenoptera: Apoidea) of Chile: species discovery in a reasonably well known bee fauna with the description of a new species of Lonchopria (Colletidae). *Genome* 60(5): 414-430. https://doi.org/10.1139/gen-2016-0071

SIMON C., FRATI F., BECKENBACH A., CRESPI B., LIU H. & FLOOK P. 1994 — Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87, 651-701. https://doi.org/10.1093/aesa/87.6.651

SMITH F. 1860 — Descriptions of hymenopterous insects collected by Mr. A. R. Wallace in the islands of Batchian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea. *Journal of the Proceeding of the Linnean Society, Zoology* Suplement, 5: 93-143.

SMITH M. A ., RODRIGUEZ J. J., WHITFIELD J. B ., DEANS A. R ., JANZEND. H ., HALLWACHS W. & HEBERT P. D. N. 2008 — Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proceedings of the National Academy of Sciences of the United States of America* 105(34): 12359-12364. https://doi.org/10.1073/pnas.0805319105

SNODGRASS R. G. 1941 — *The male genitalia of Hymenoptera*. Smithsonian Miscellaneous Collections 99(14): 1-86.

SOLDATI L., CONDAMINE F. L ., CLAMENS A. L ., MOGIAM. & KERGOAT G. J. 2016 — The Tenebrionidae (Coleoptera) of Mount Wilhelm and Wanang, with description of a new species and a preliminary phylogeny of Stenochiinae, *in* ROBILLAR D T., LEGENDRE F., VILLEMANT C. & LEPONCE M. (eds), Insects of Mount Wilhelm, Papua New Guinea. Muséum national d'Histoire naturelle, Paris : 49-82 (Mémoires du Muséum national d'Histoire naturelle; 209).

STAMATAKIS A. 2014 — RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics* 30(9): 1312-1313. https://doi.org/10.1093/bioinformatics/btu033

STEIN P. R . W., ALENCAR I. D. C. C., BARBOSA D. N. & AZEVEDO C. O . 2014 — Revision of *Epyris afer* (Magretti, 1884), comb. rev. (Hymenoptera: Bethylidae) with new synonymy and description of two new species. *Zootaxa* 3032: 17-32. https://doi.org/10.11646/zootaxa.3032.1.2

TAMURA K., STECHER G., PETERSON D., FILIPSKI A. & KUMAR S. 2013 — MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30(12): 2725-2729. https://doi.org/10.1093/molbev/mst197

TERAYAMA M. 2003 — Phylogenetic Systematics of the family Bethylidae (Insecta: Hymenoptera) Part II. Keys to subfamilies, tribes and genera in the world. *Academic Reports of the Faculty of Engineering of Tokyo Polytechnic University* 26: 16-29.

VARGAS R. J. M. & AZEVEDO C. O . 2016 — Discovery of the male of *Galodoxa* Nagy (Hymenoptera: Bethylidae), with emended generic diagnosis, *in* ROBILLAR D T., LEGENDRE F., VILLEMANT C. & LEPONCE M. (eds), Insects of Mount Wilhelm, Papua New Guinea. Muséum national d'Histoire naturelle, Paris : 393-406 (Mémoires du Muséum national d'Histoire naturelle; 209).

WAICHERT C. & AZEVEDO C. O . 2009 — Phylogenetic analysis of *Rhabdepyris* (Hymenoptera: Bethylidae) and redefinition of generic limits based on morphological characters. *Zootaxa* 2284: 1-29. https://doi.org/10.11646/zootaxa.2284.1.1

WAICHERT C., VON DOHLEN C. D. & PITT S, J. P. 2015 — Resurrection, revision and molecular phylogenetics of *Eragenia* Banks with implications for Ageniellini systematics (Hymenoptera: Pompilidae). *Systematic Entomology* 40, 291-321. https://doi.org/10.1111/syen.12101

WESTWOOD J. O . 1832 — Descriptions of several new British forms amongst the parasitic hymenopterous insects. *London and Edinburgh Philosophical Magazine and Journal of Science* 1: 27-129. http://www.biodiversitylibrary.org/page/15699063

YODER M. J., MIKÓ I., SELT MANN K. C., BERTO NE M. A . & DEANS A. R . 2010 — A gross anatomy ontology for Hymenoptera. *PLoS ONE* 5: e15991. https://doi.org/10.1371/journal.pone.0015991

ZHU X., CHEN J., CHEN R., JIANG L. & QIAO G. 2017 — DNA barcoding and species delimitation of Chaitophorinae (Hemiptera, Aphididae). *ZooKeys* (656): 25-50. https://doi.org/10.3897/zookeys.656.11440

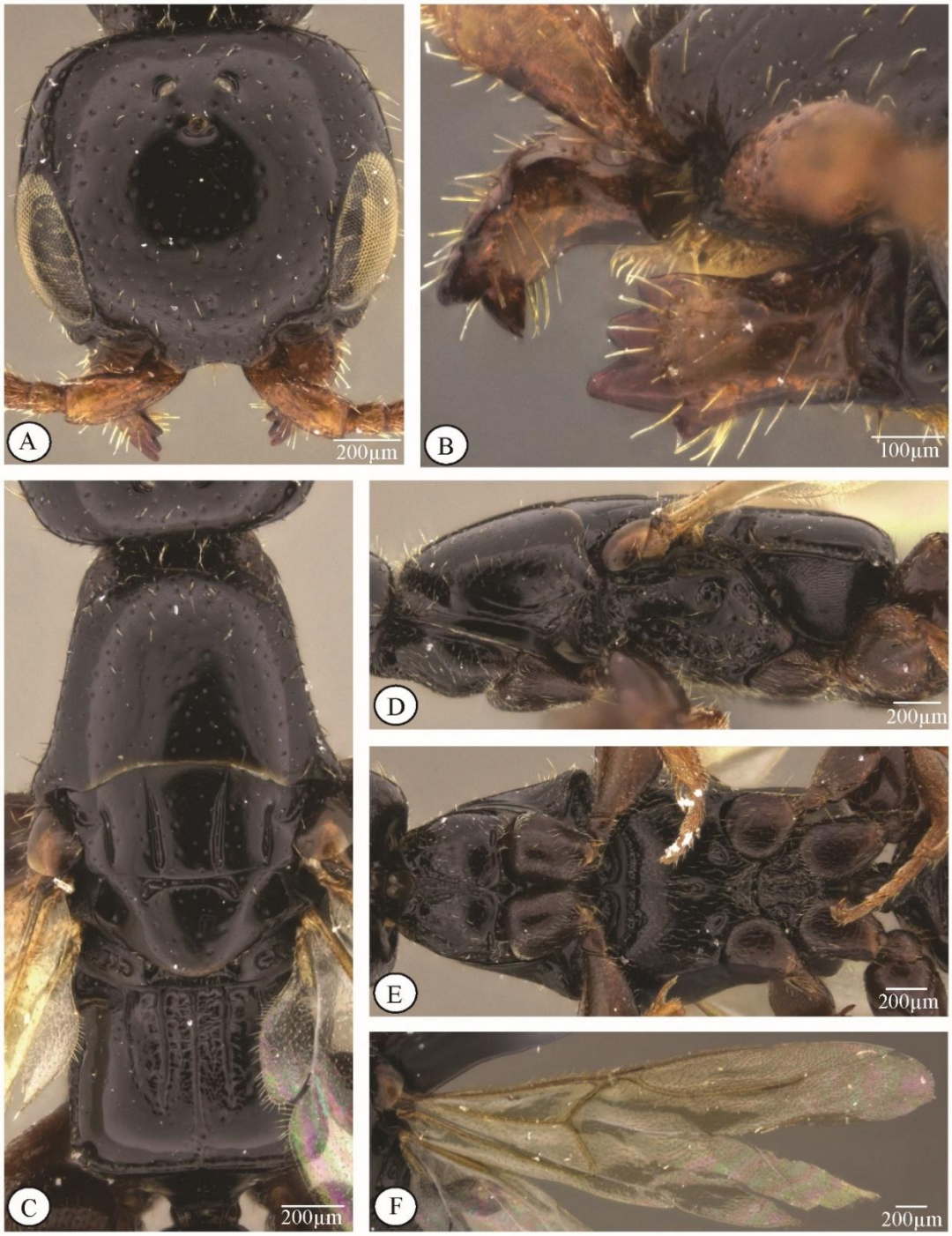

FIGURE 7. *Chlorepyris armatus* (Kieffer, 1904), holotype female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

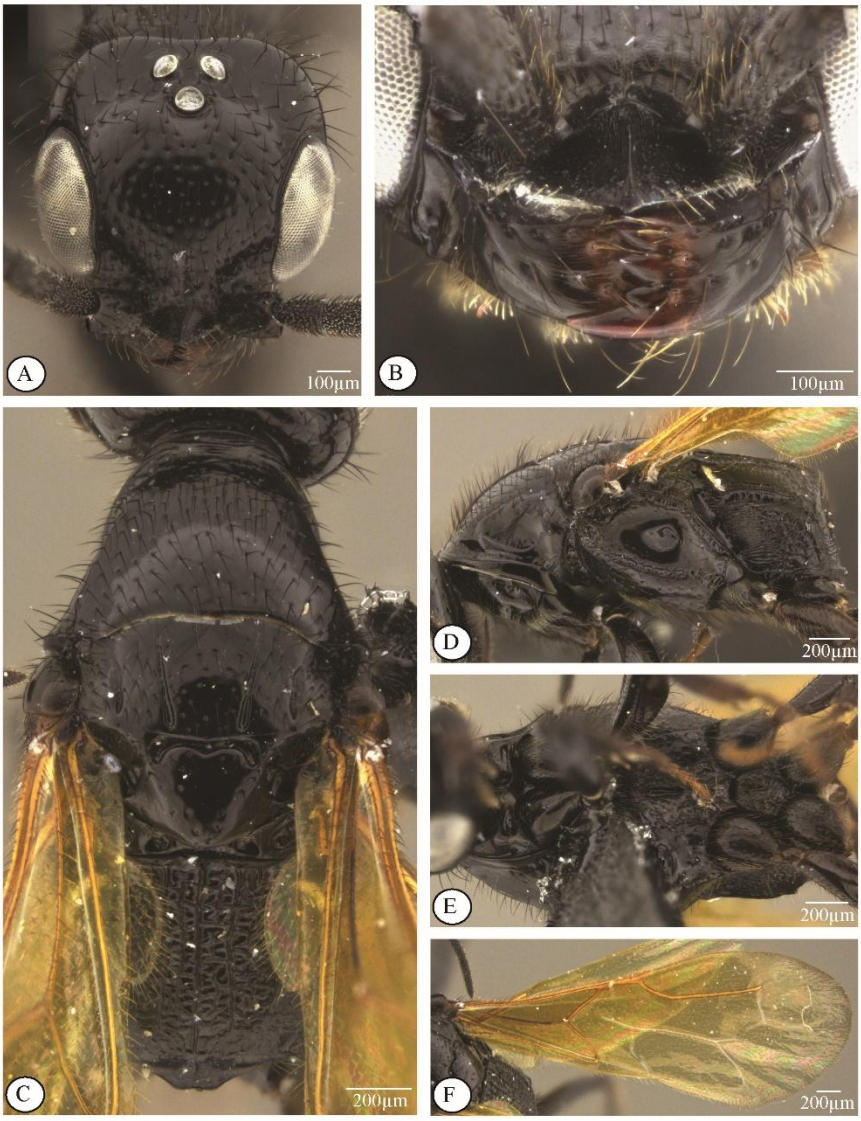

FIGURE 8. *Chlorepyris abelam* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; D, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

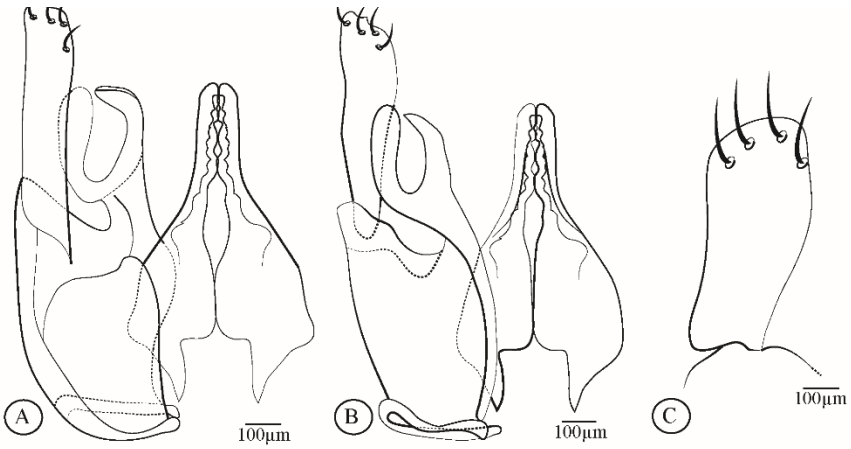

FIGURE 9. *Chlorepyris abelam* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

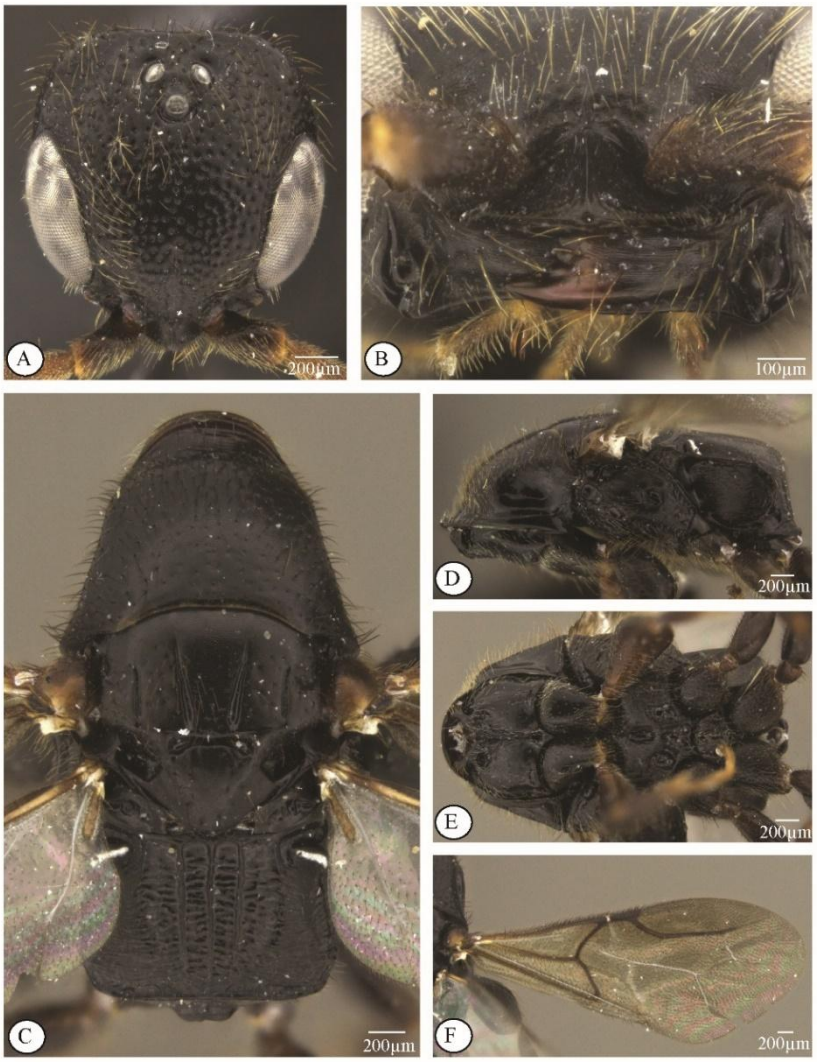

FIGURE 10. *Chlorepyris angu* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; D, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

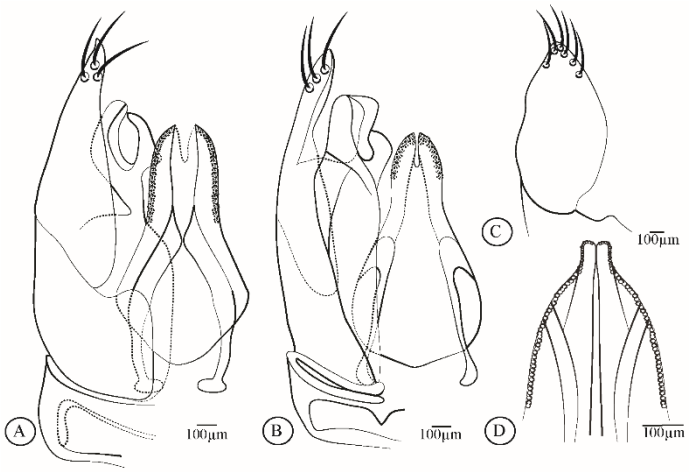

FIGURE 11. *Chlorepyris angu* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view; **D**, Apex of aedeagus in dorsal view.

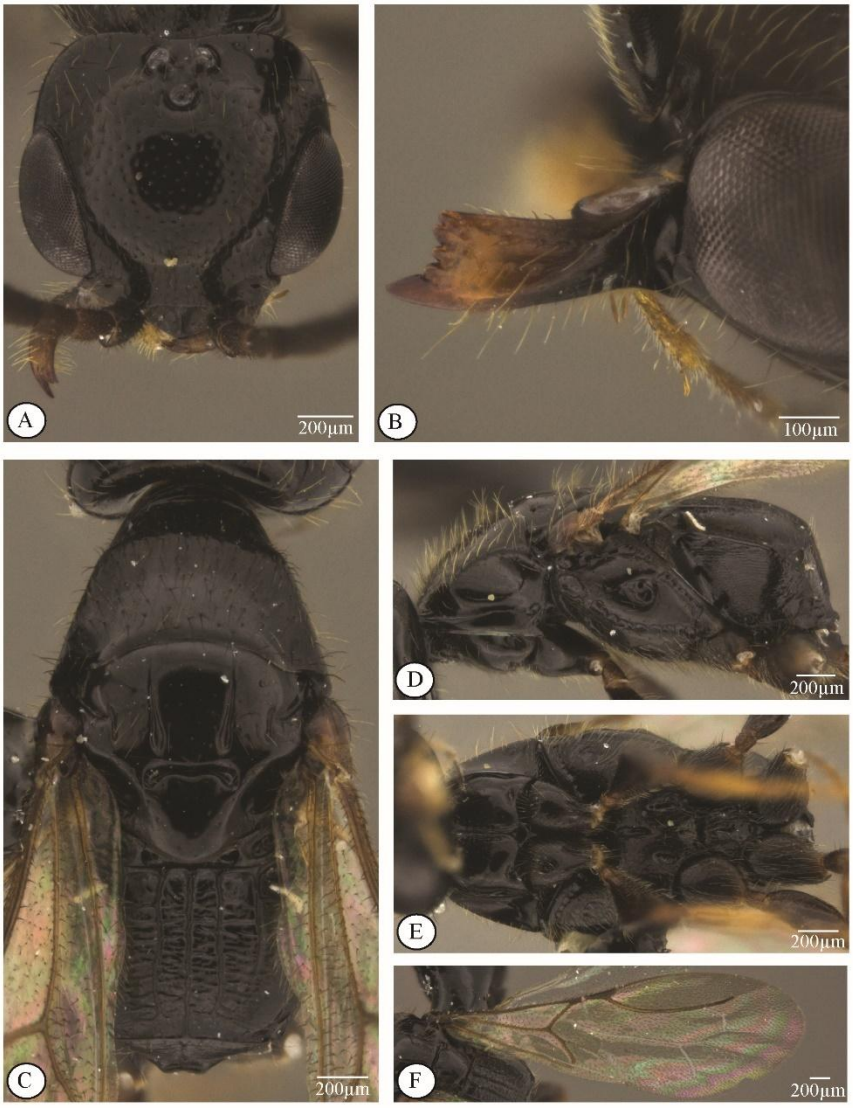

FIGURE 12. *Chlorepyris baining* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

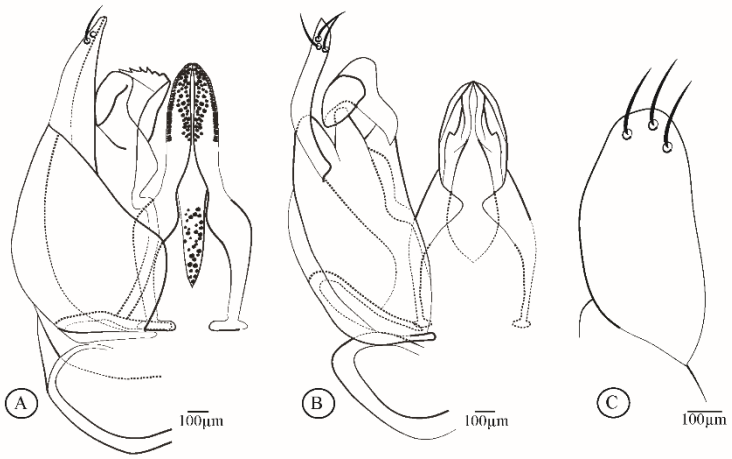

FIGURE 13. *Chlorepyris baining* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

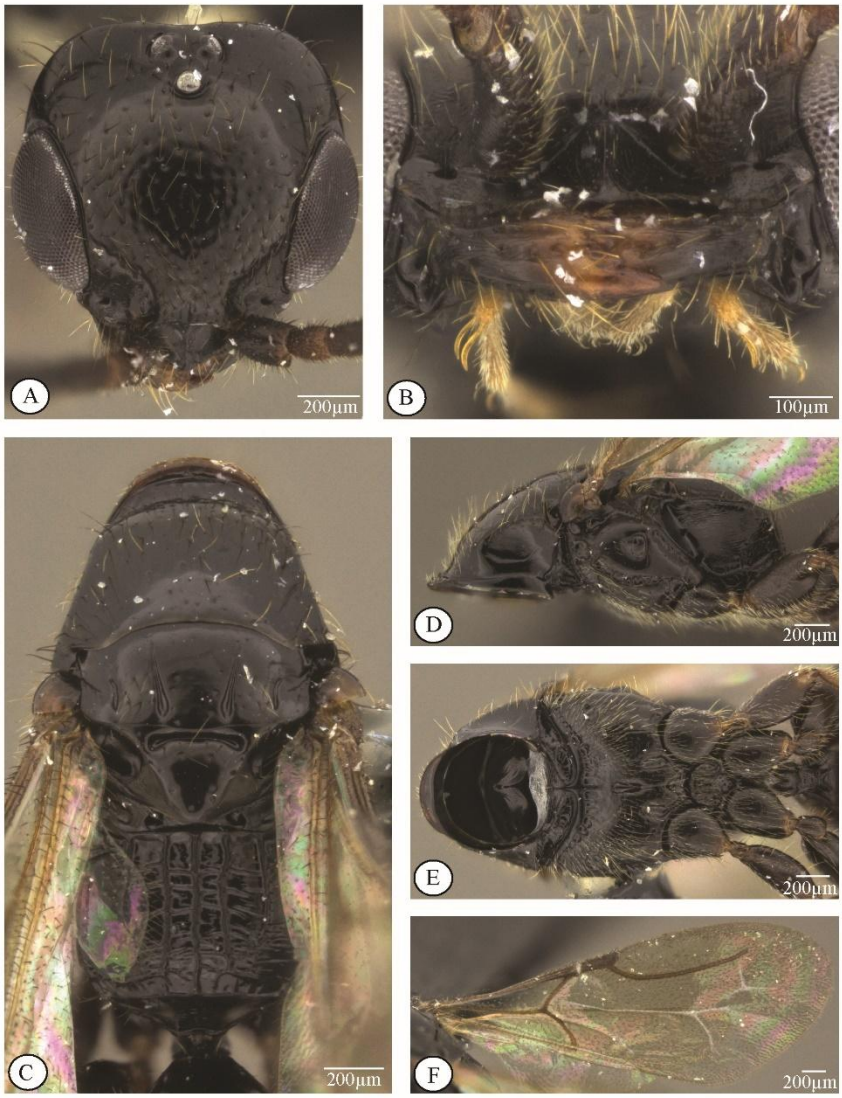

FIGURE 14. *Chlorepyris baruya* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

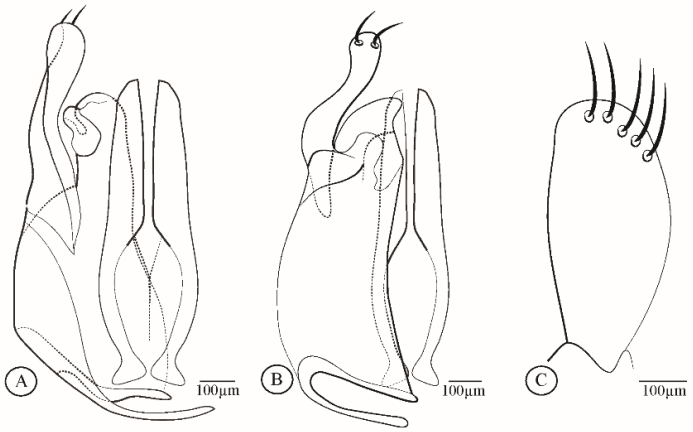

FIGURE 15. *Chlorepyris baruya* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

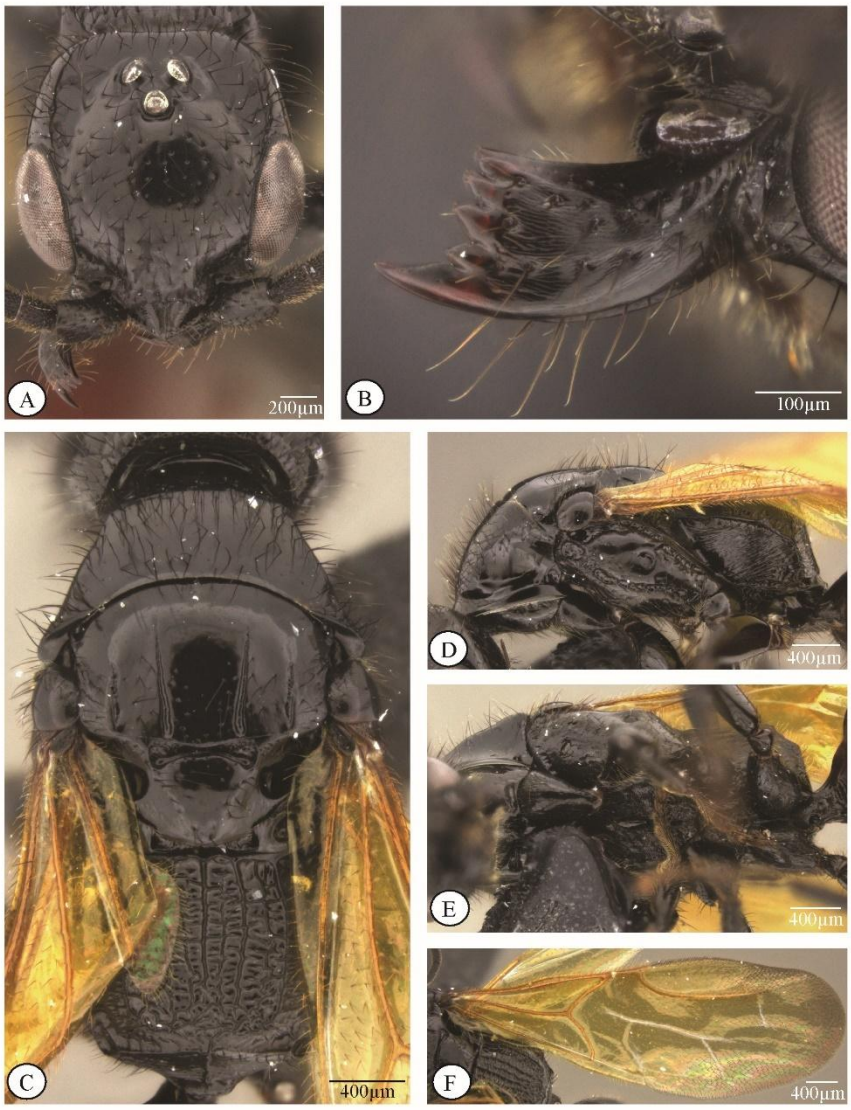

FIGURE 16. *Chlorepyris biangai* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

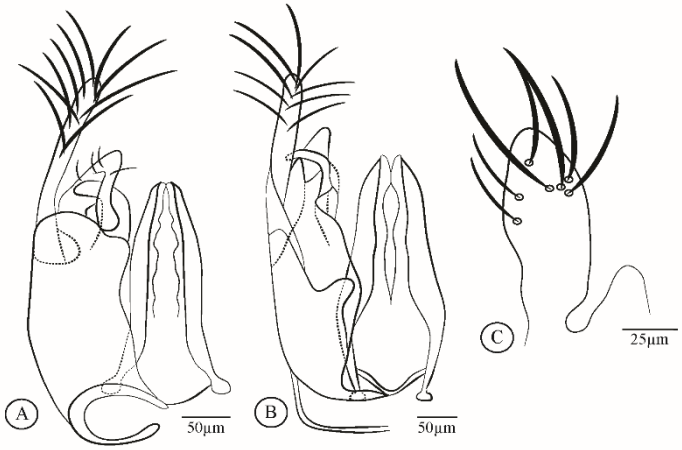

FIGURE 17. *Chlorepyris biangai* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

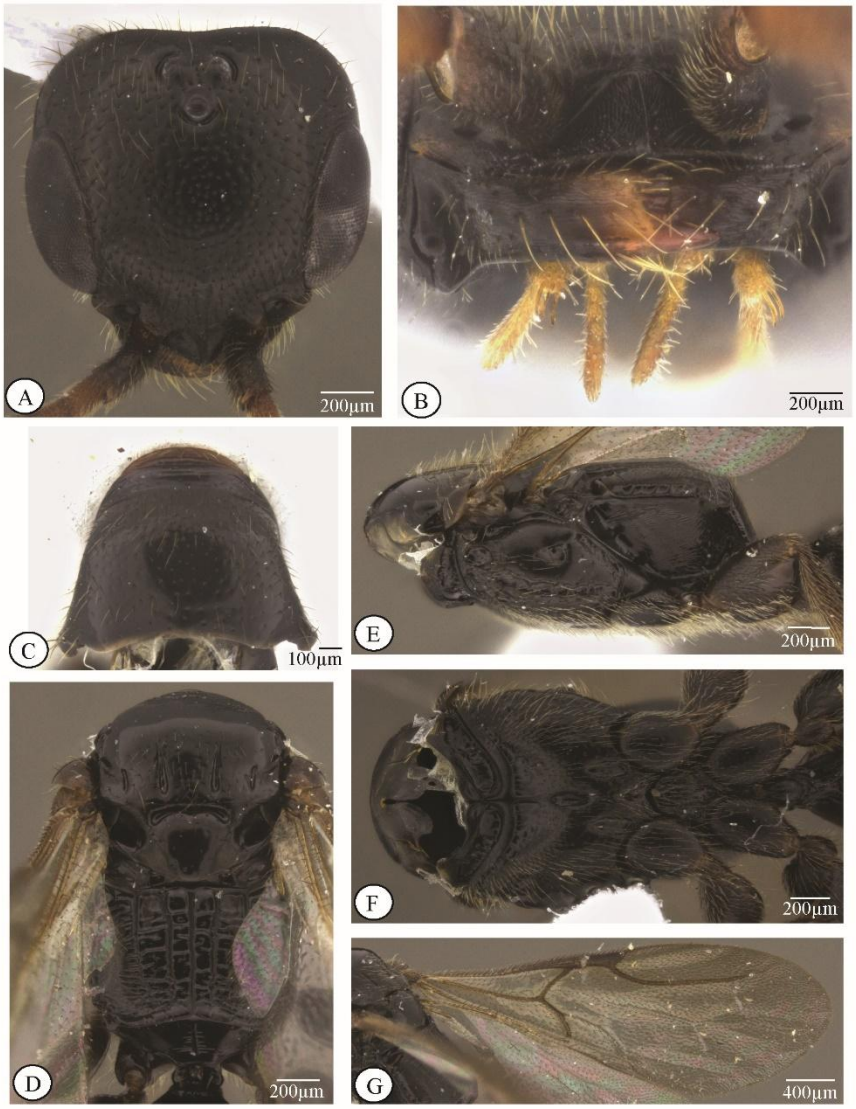

FIGURE 18. *Chlorepyris bilibil* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, pronotum in dorsal view; **D**, mesosoma in dorsal view; **E**, mesosoma in lateral view; **F**, mesosoma in ventral view; **G**, forewing in dorsal view.

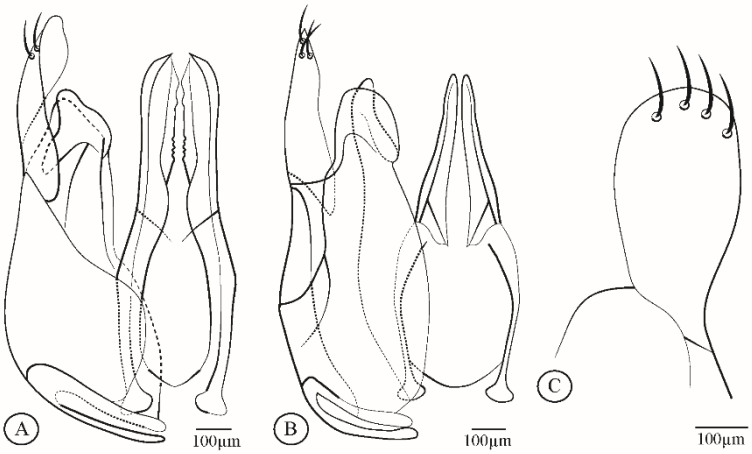

FIGURE 19. *Chlorepyris bilibil* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

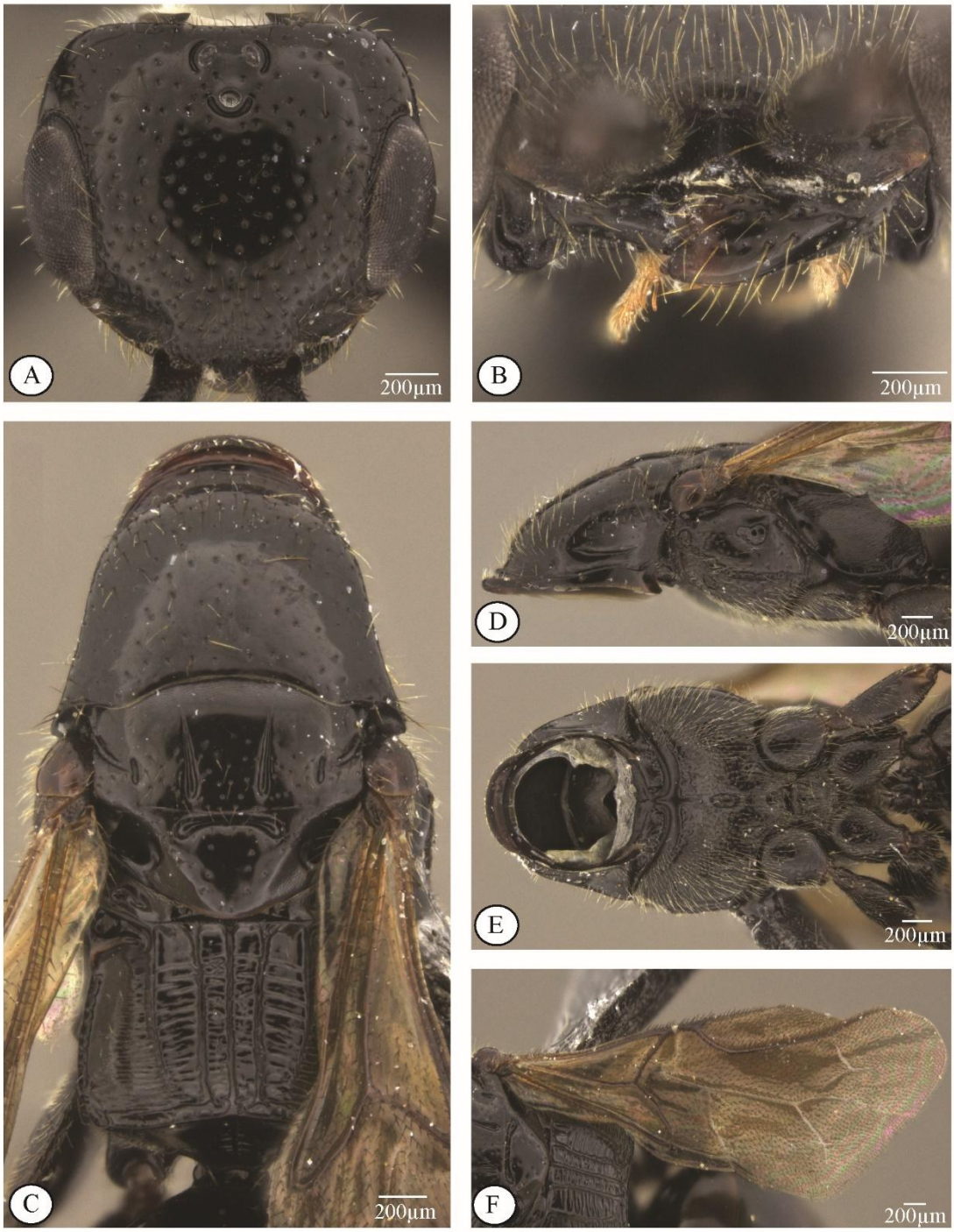

FIGURE 20. *Chlorepyris bilibil* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

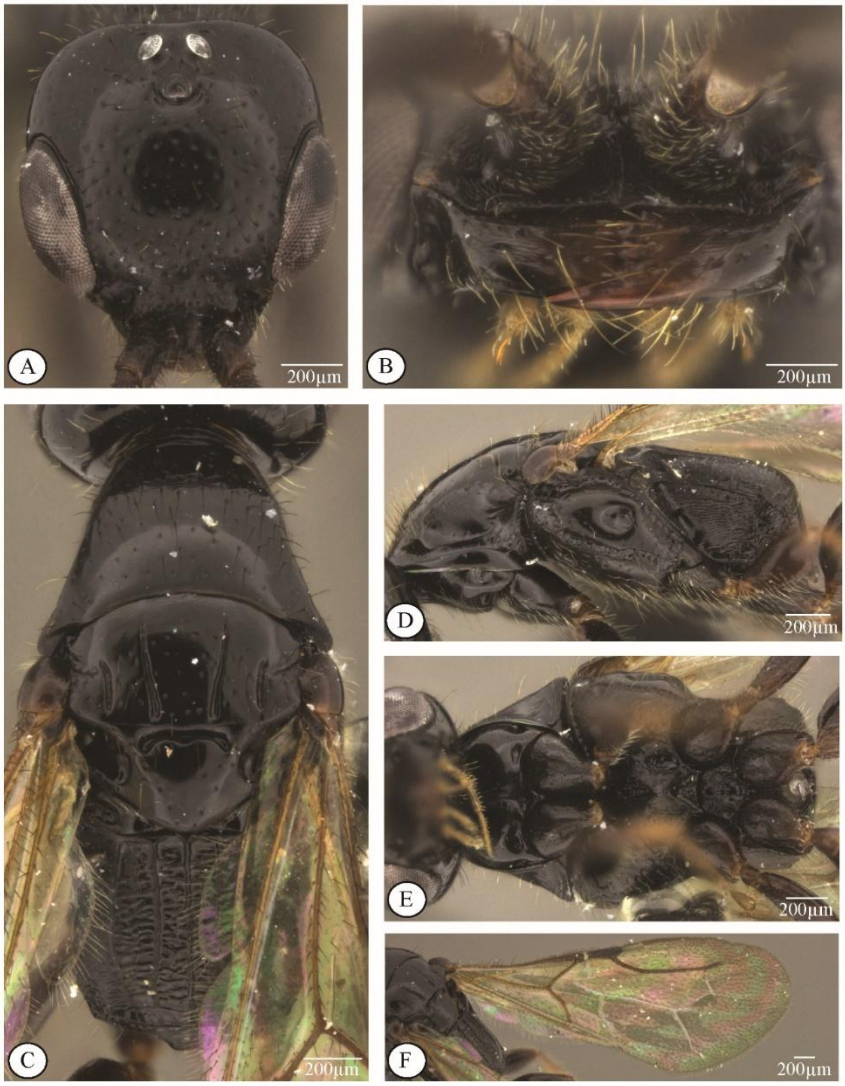

FIGURE 21. *Chlorepyris chambri* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

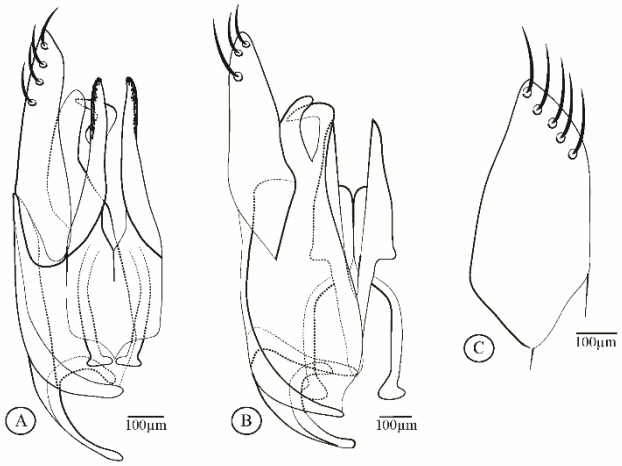

FIGURE 22. *Chlorepyris chambri* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

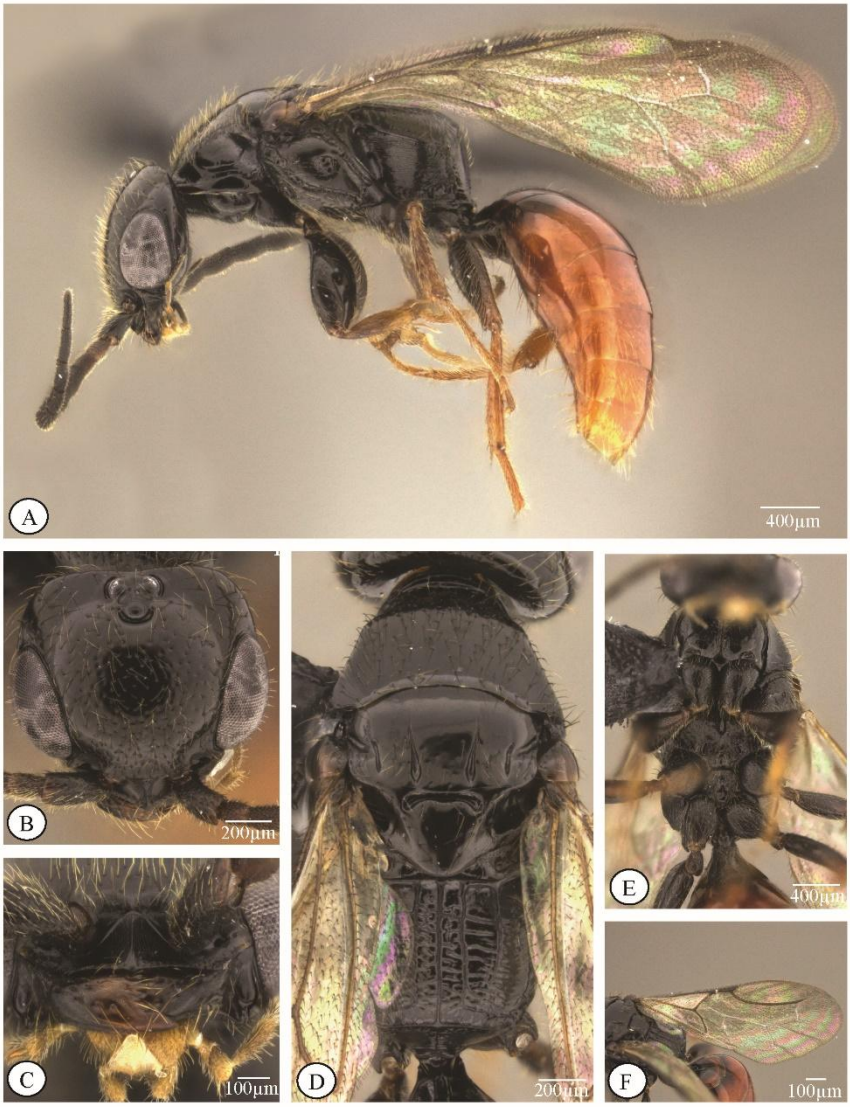

FIGURE 23. *Chlorepyris duna* Colombo & Azevedo n. sp., male. **A**, body in lateral view; **B**, head in dorsal view; **C**, mandible in frontal view; **D**, mesosoma in dorsal view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

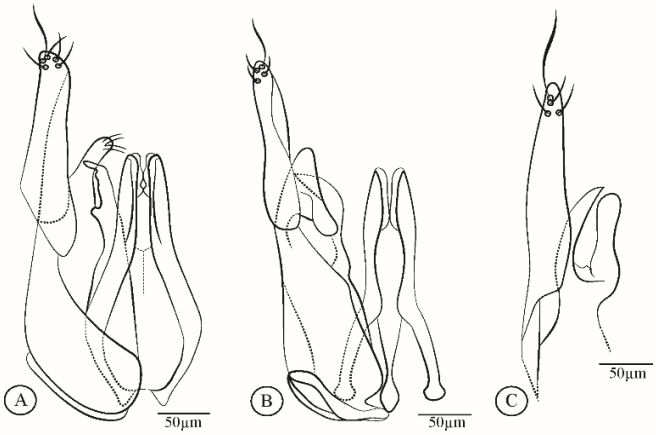

FIGURE 24. *Chlorepyris duna* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

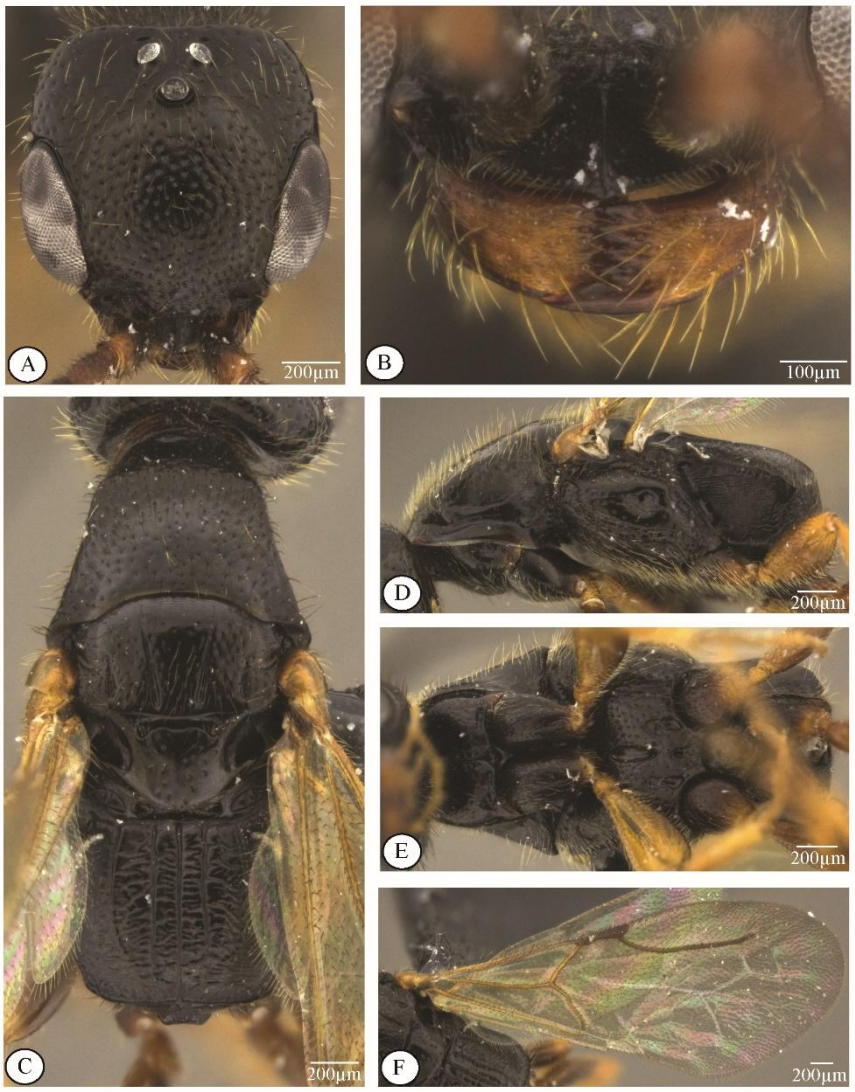

FIGURE 25. *Chlorepyris enga* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

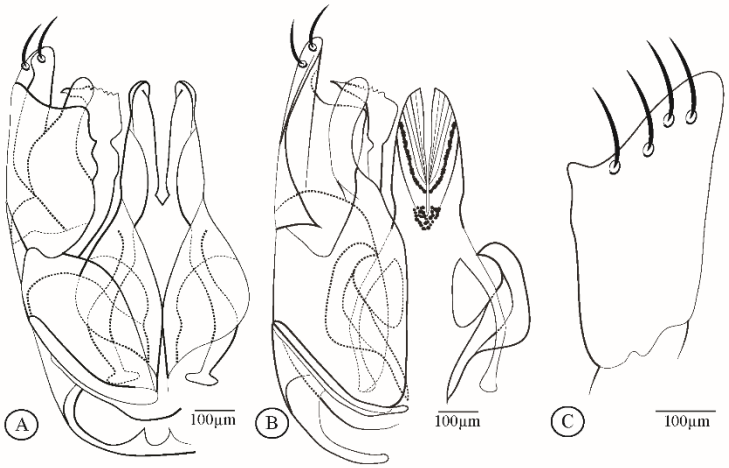

FIGURE 26. *Chlorepyris enga* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

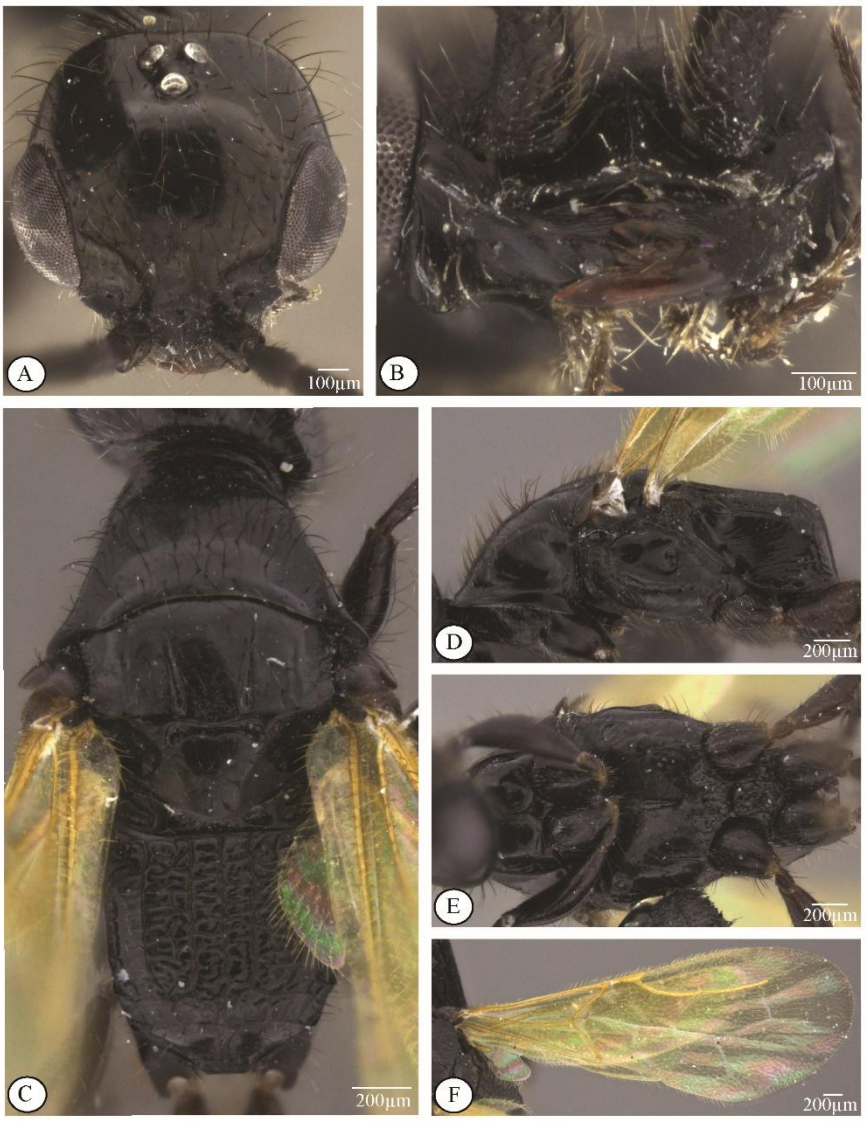

FIGURE 27. *Chlorepyris etoro* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

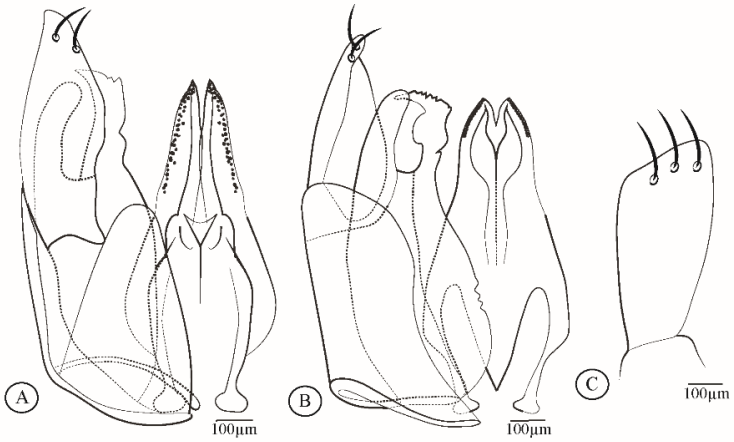

FIGURE 28. *Chlorepyris etoro* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

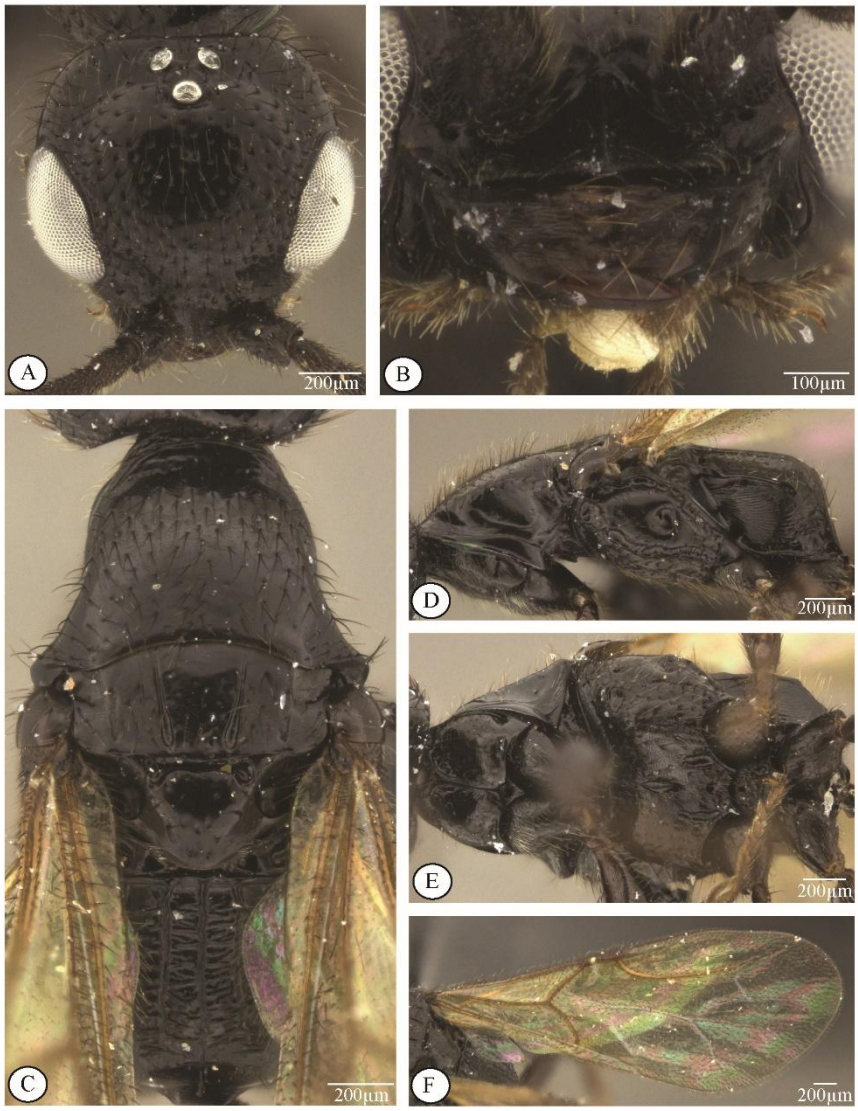

FIGURE 29. *Chlorepyris fore* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

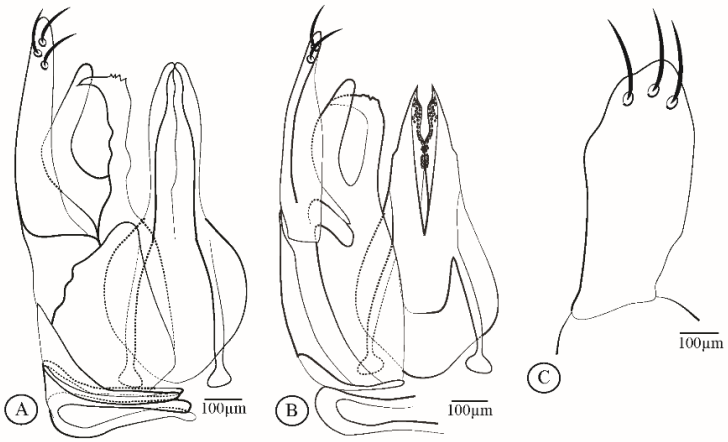

FIGURE 30. *Chlorepyris fore* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

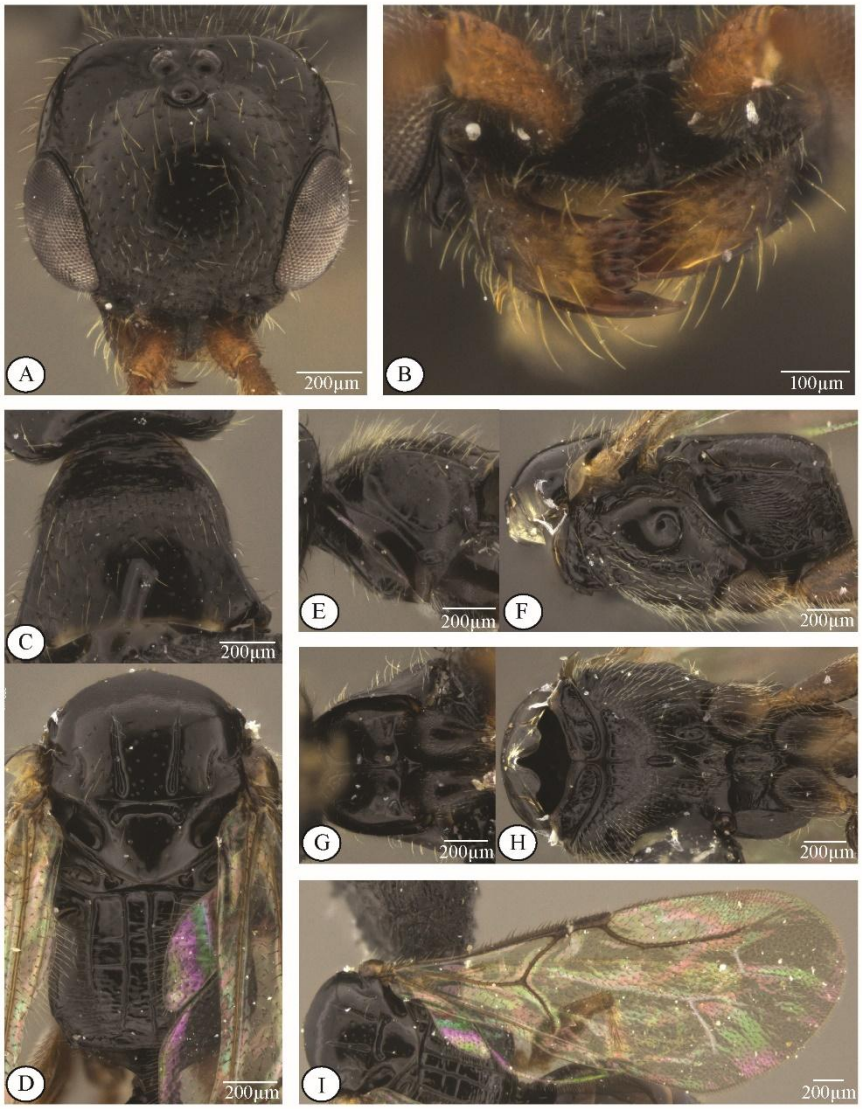

FIGURE 31. *Chlorepyris gadsup* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, pronotum in dorsal view; **D**, mesosoma in dorsal view; **E**, pronotum in lateral view; **F**, mesosoma in lateral view; **G**, pronotum in ventral view; **H**, mesosoma in ventral view; **I**, forewing in dorsal view.

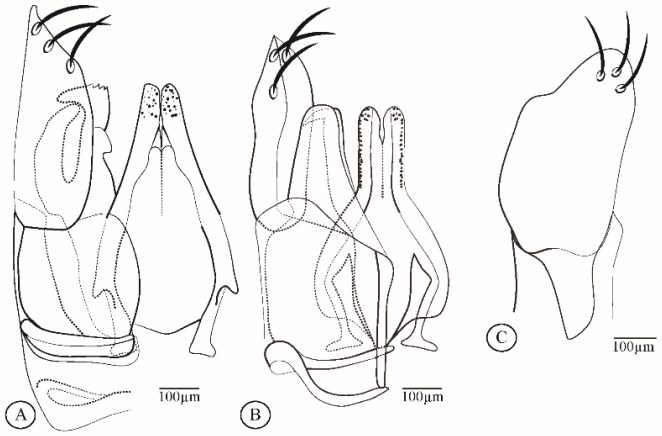

FIGURE 32. *Chlorepyris gadsup* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

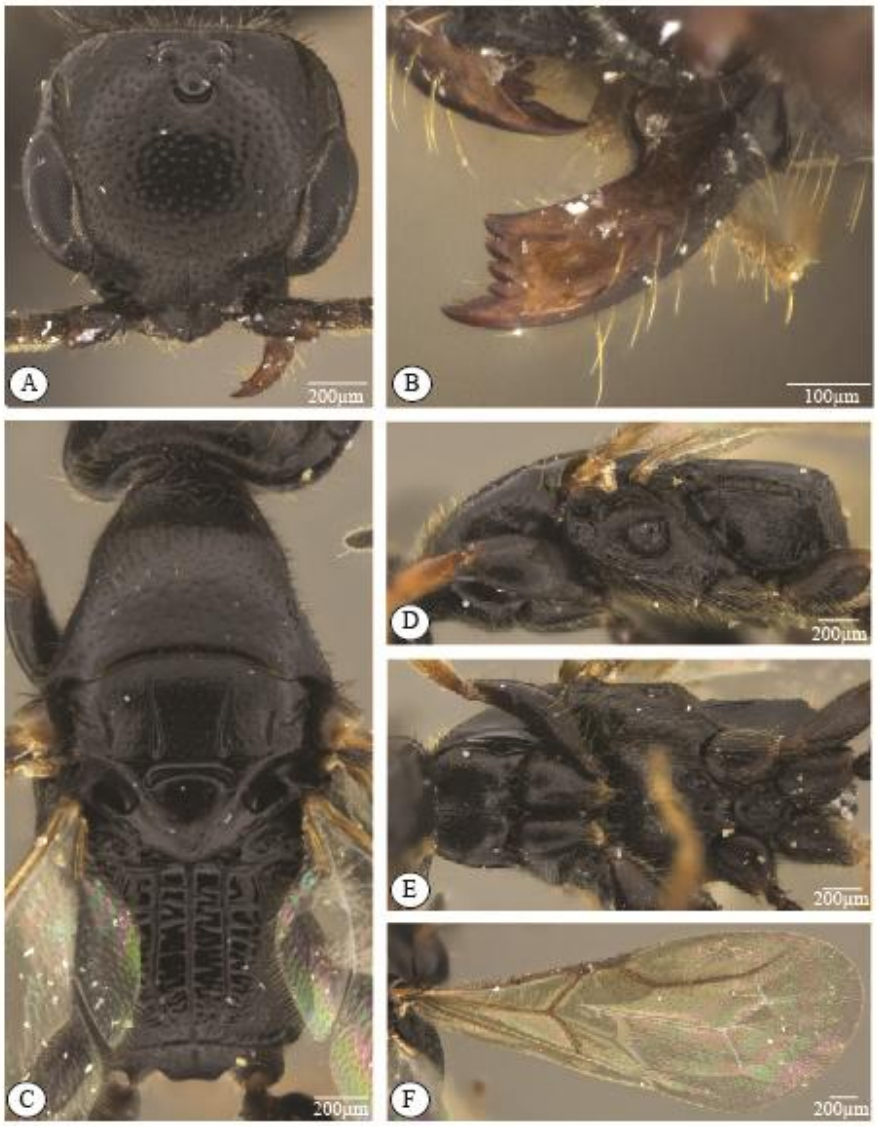

FIGURE 33. *Chlorepyris gogodala* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, pronotum in dorsal view; **D**, mesosoma in dorsal view; **E**, pronotum in lateral view; **F**, mesosoma in lateral view; **G**, pronotum in ventral view; **H**, mesosoma in ventral view; **I**, forewing in dorsal view.

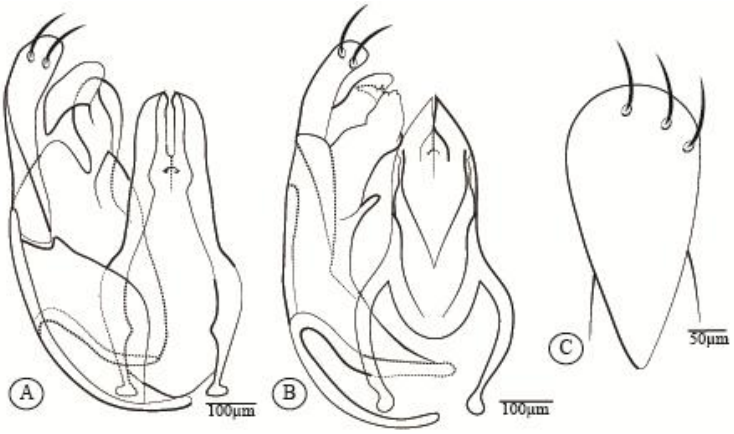

FIGURE 34. *Chlorepyris gogodala* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

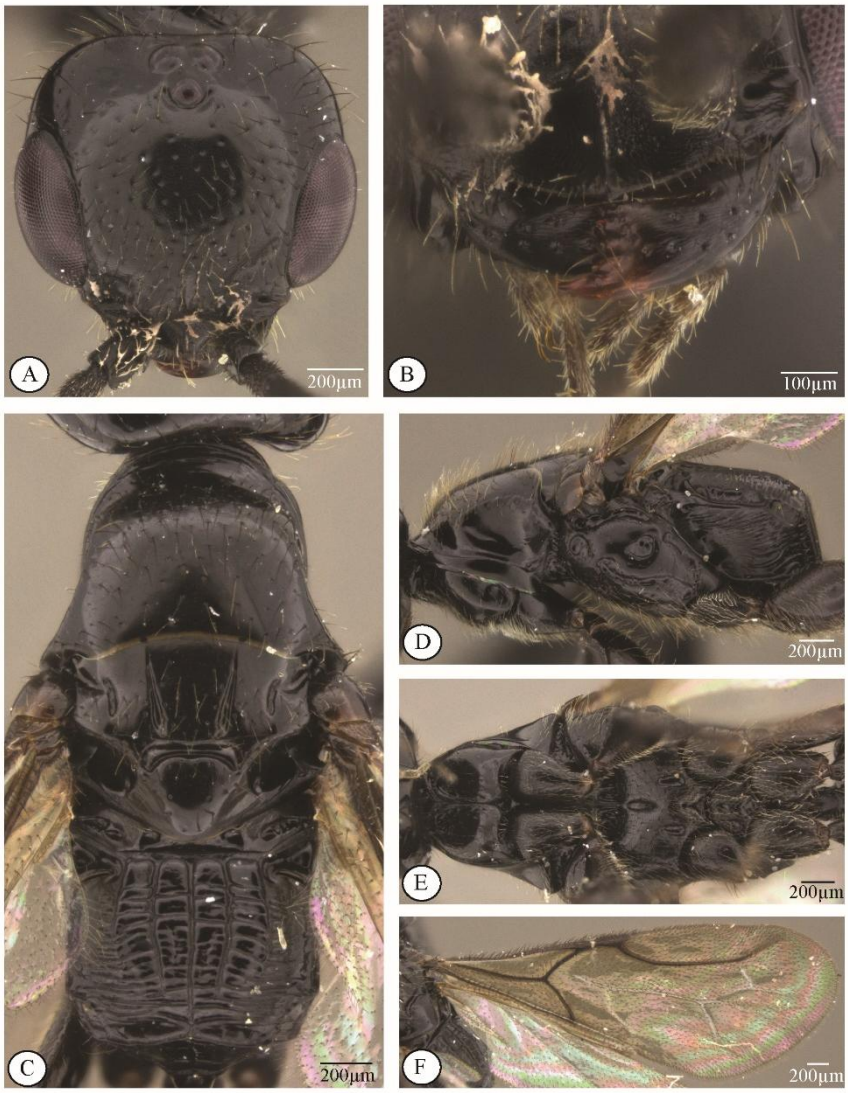

FIGURE 35. *Chlorepyris haroli* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

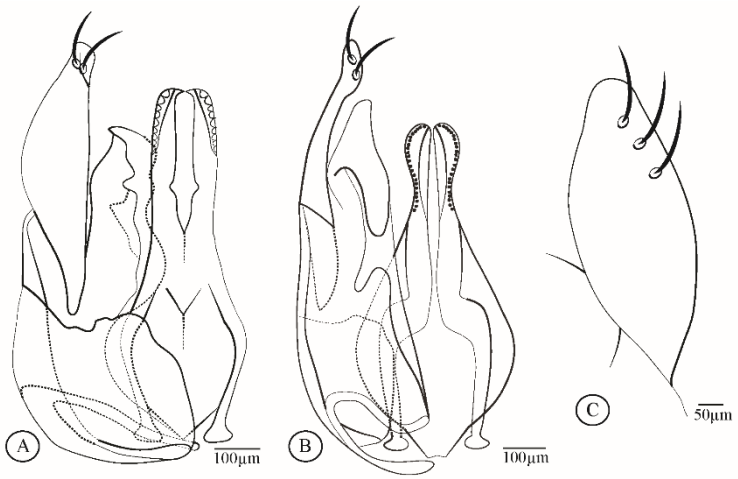

FIGURE 36. *Chlorepyris haroli* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

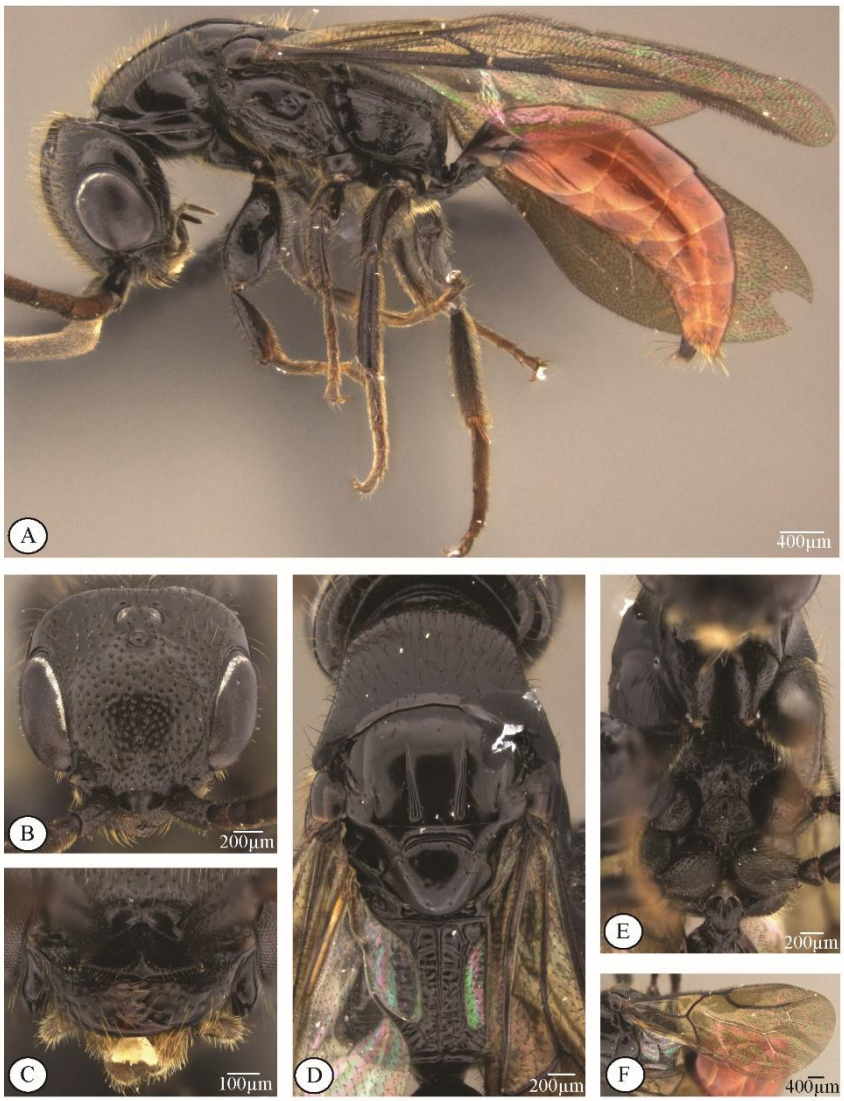

FIGURE 37. *Chlorepyris hewa* Colombo & Azevedo n. sp., male. **A**, body in lateral view; **B**, head in dorsal view; **C**, mandible in frontal view; **D**, mesosoma in dorsal view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

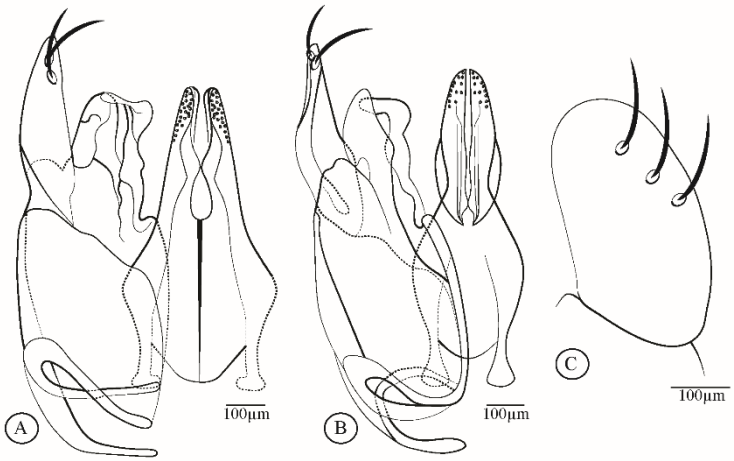

FIGURE 38. *Chlorepyris hewa* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

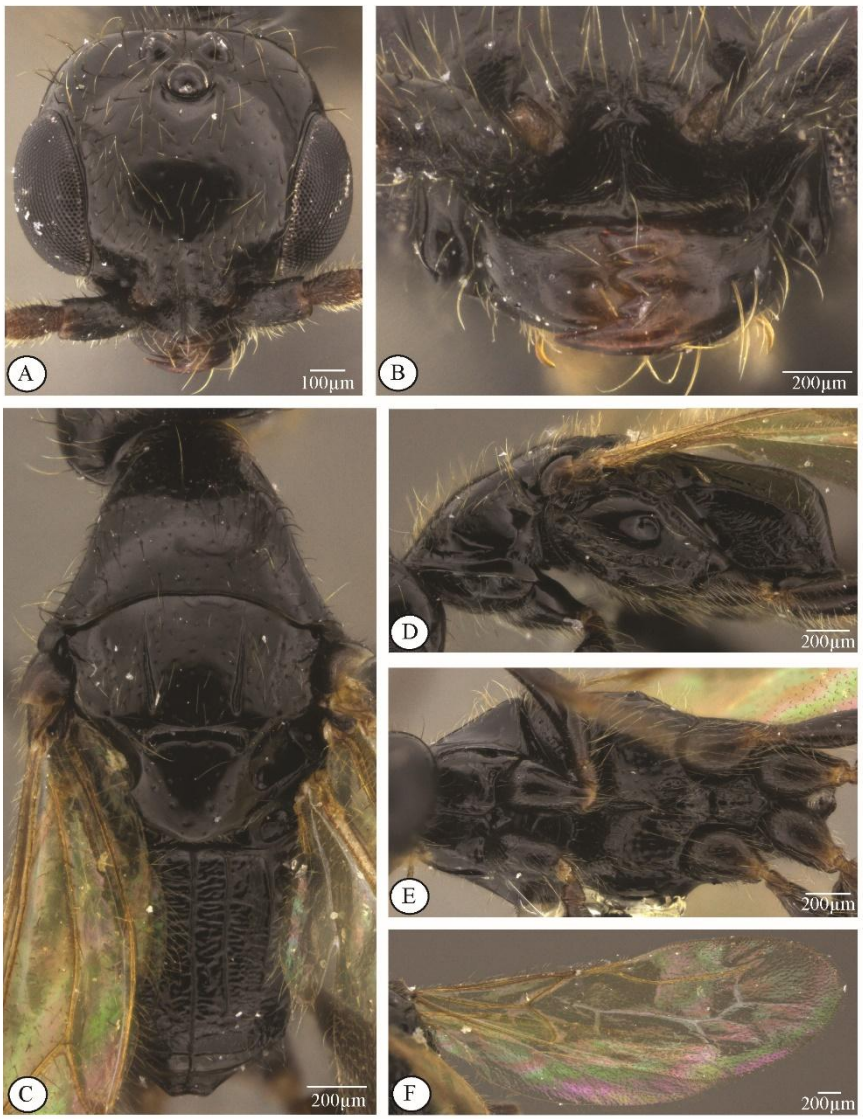

FIGURE 39. *Chlorepyris huli* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

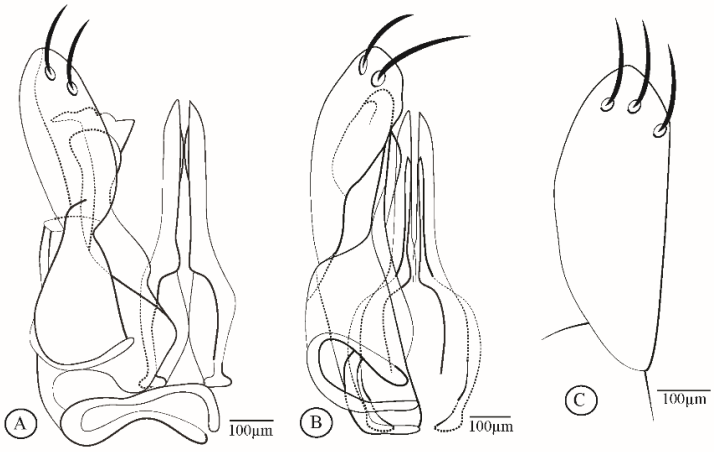

FIGURE 40. *Chlorepyris huli* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

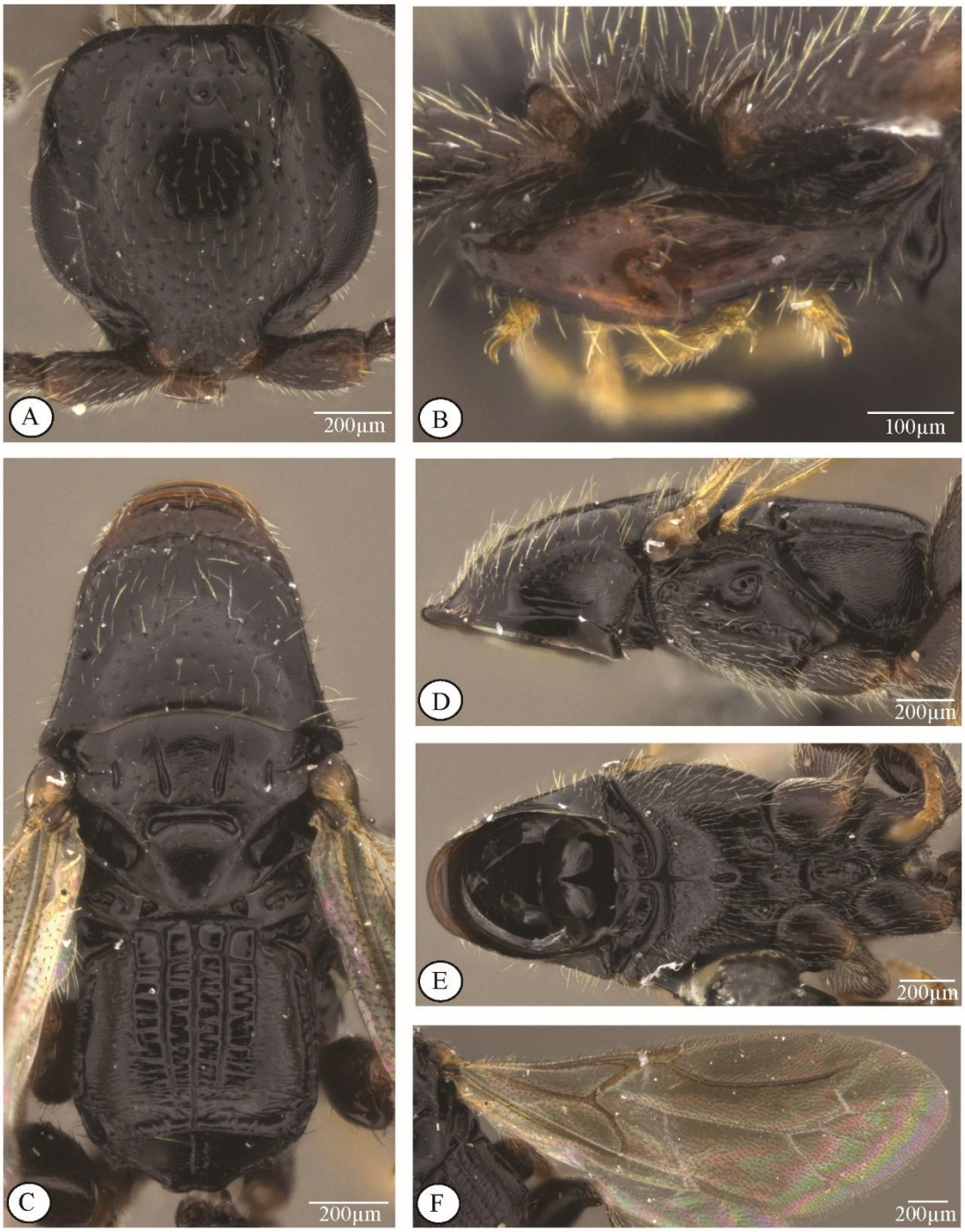

FIGURE 41. *Chlorepyris iatmul* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

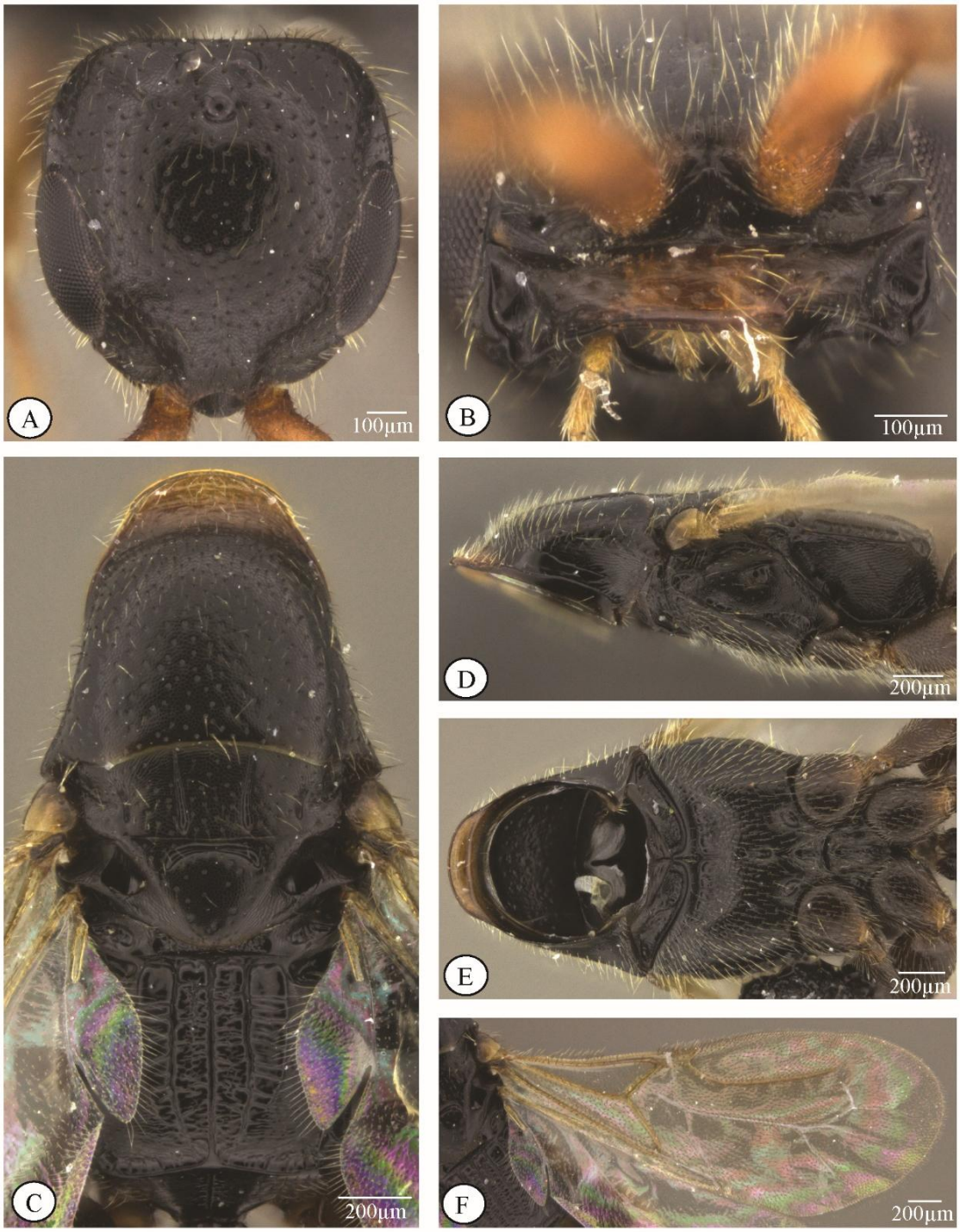

FIGURE 42. *Chlorepyris kaluli* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

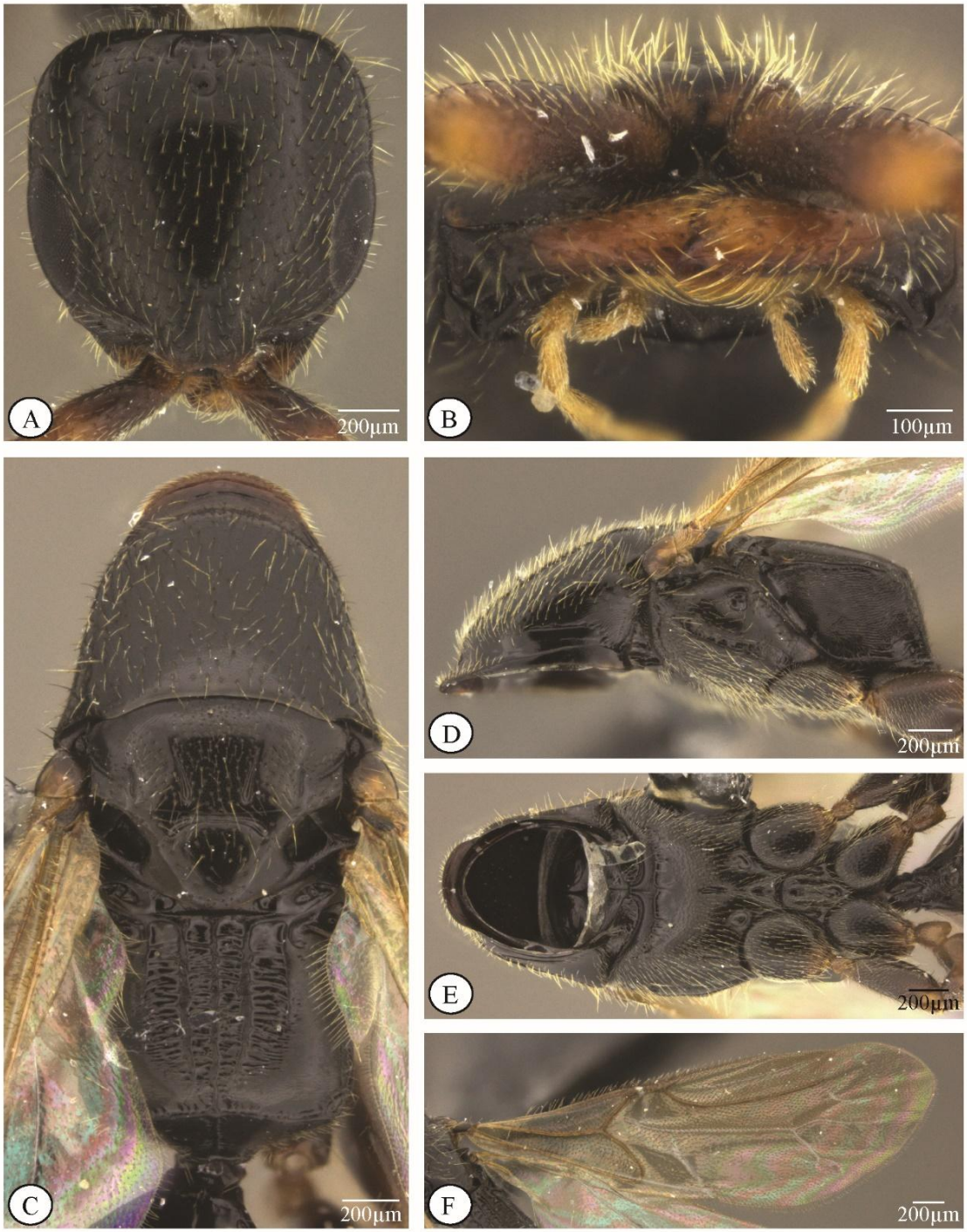

FIGURE 43. *Chlorepyris koteka* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

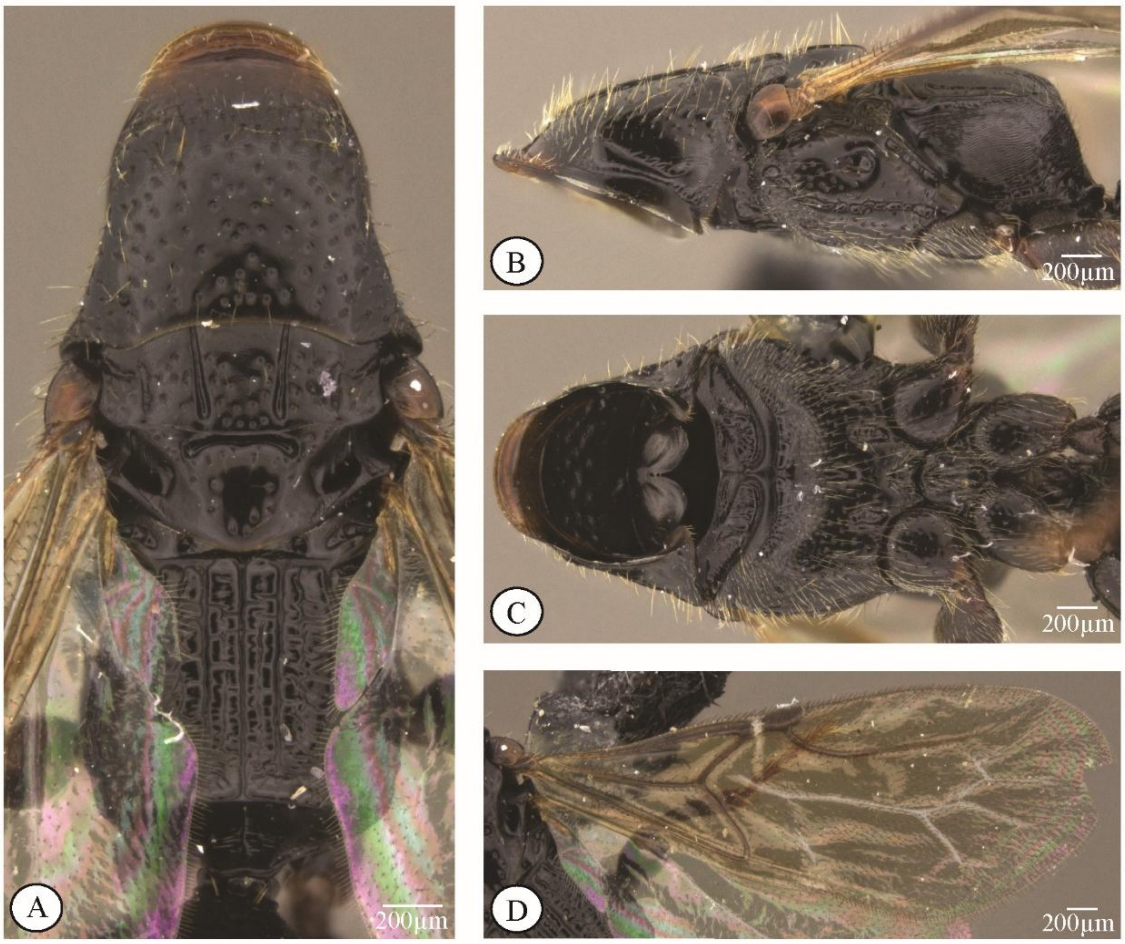

FIGURE 44. *Chlorepyris kwoma* Colombo & Azevedo n. sp., female. **A**, mesosoma in dorsal view; **B**, mesosoma in lateral view; **C**, mesosoma in ventral view; **D**, forewing in dorsal view.

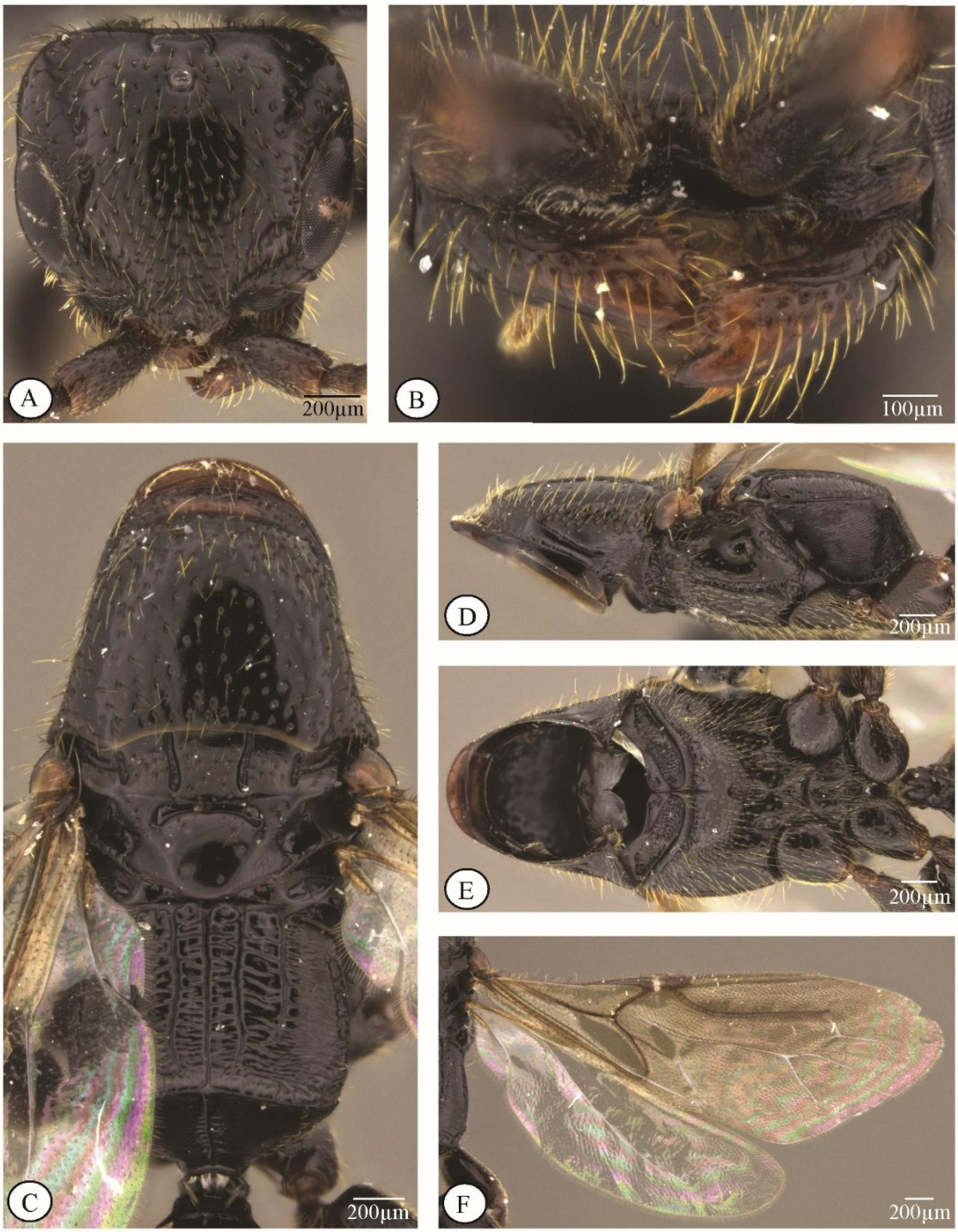

FIGURE 45. *Chlorepyris maisin* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

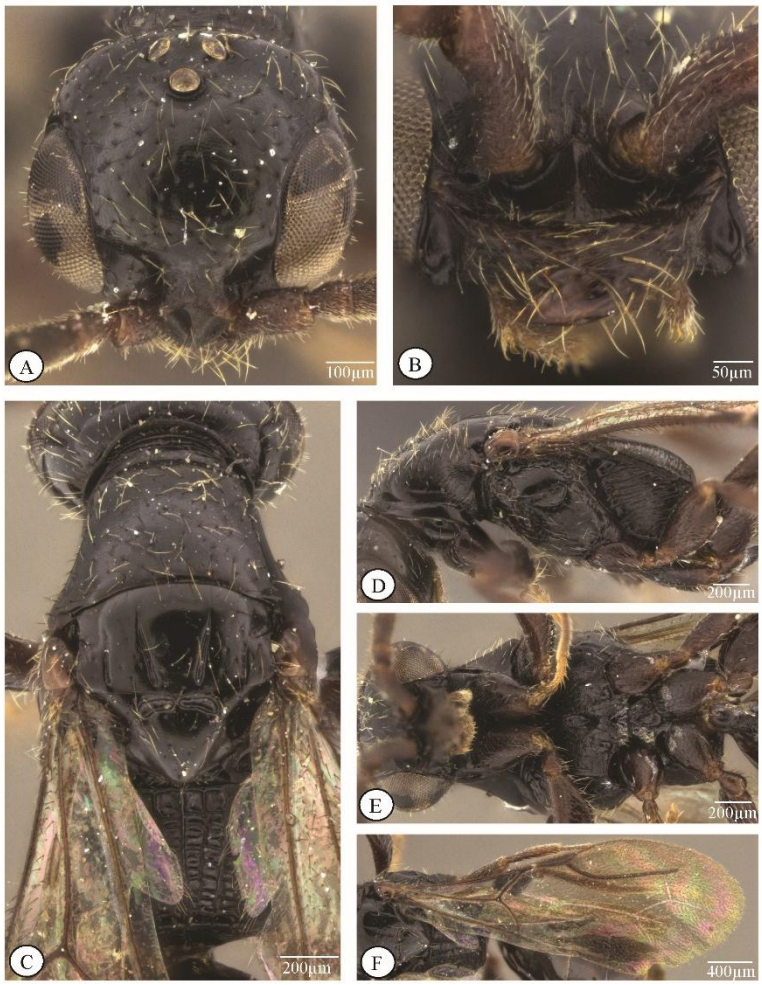

FIGURE 46. *Epyris interruptus* Kieffer, male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

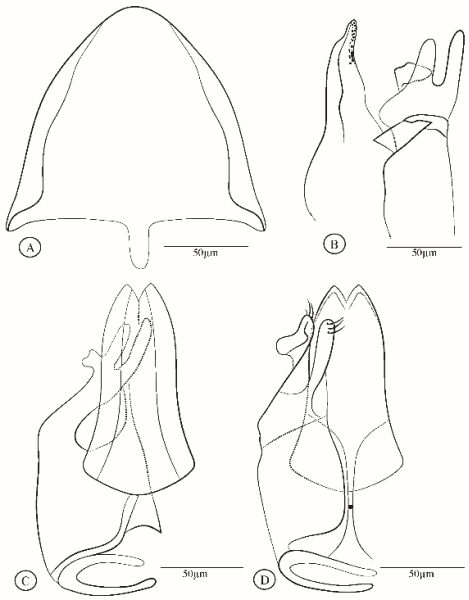

FIGURE 47. *Epyris interruptus* Kieffer, male. **A**, hypopygium in dorsal view; **B**, genitalia in lateral view; **C**, genitalia in dorsal view; **D**, genitalia in ventral view.

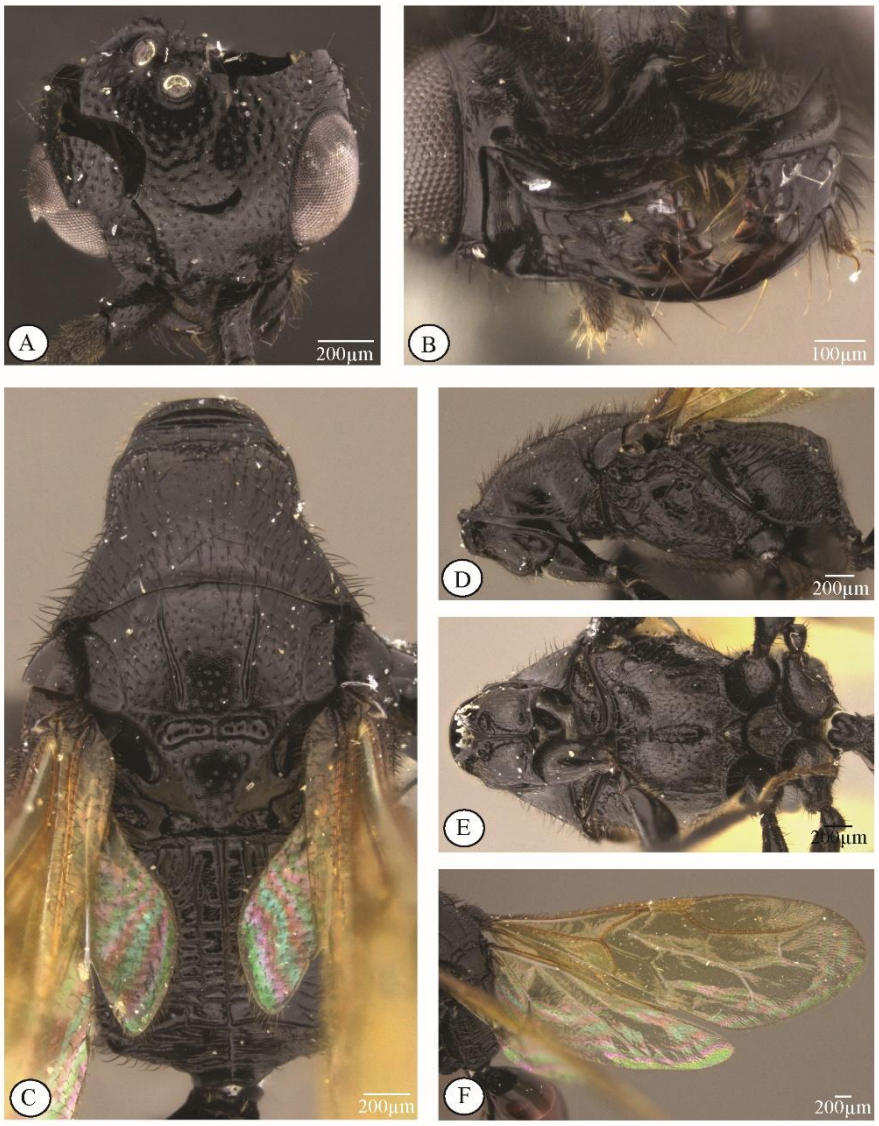

FIGURE 48. *Epyris melpa* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

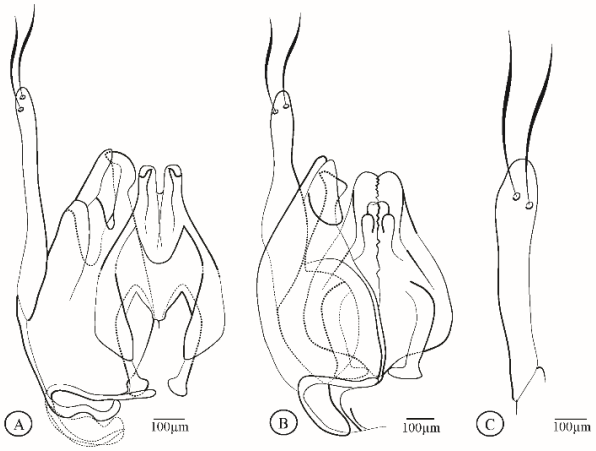

FIGURE 49. *Epyris melpa* Colombo & Azevedo n. sp., male. **A,** genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

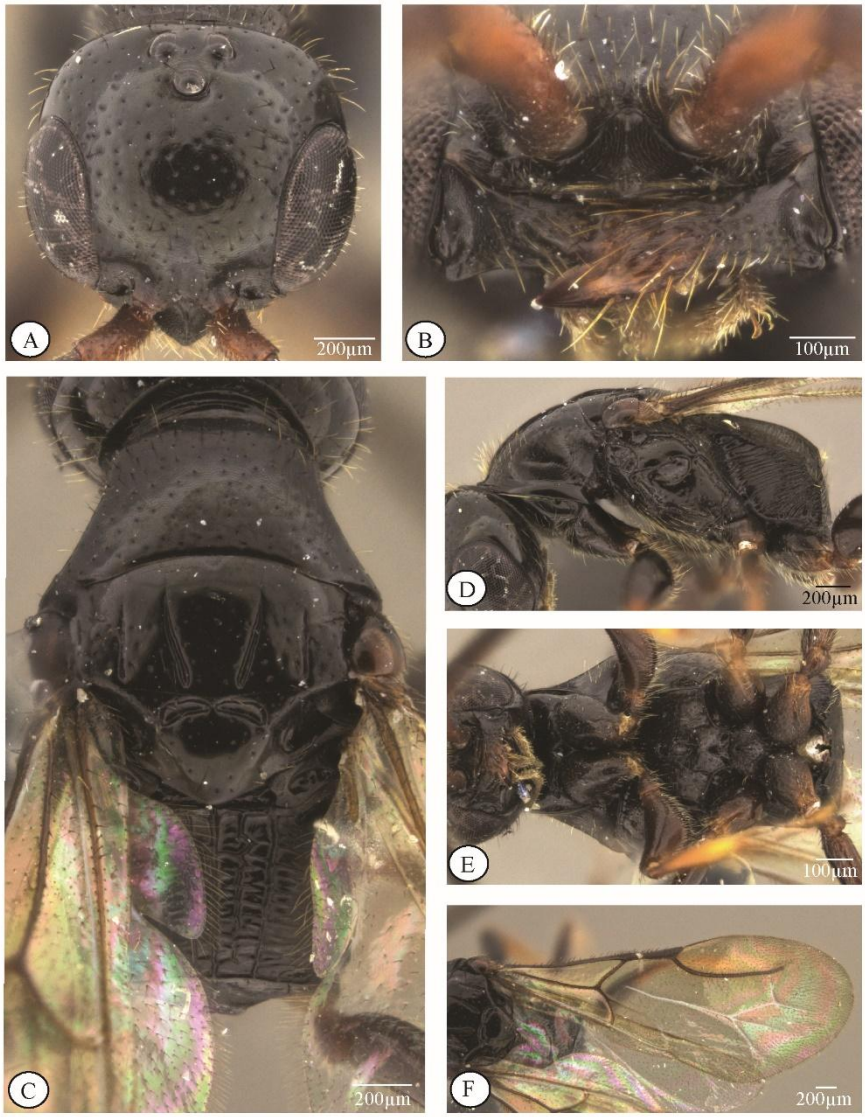

FIGURE 50. *Epyris mian* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

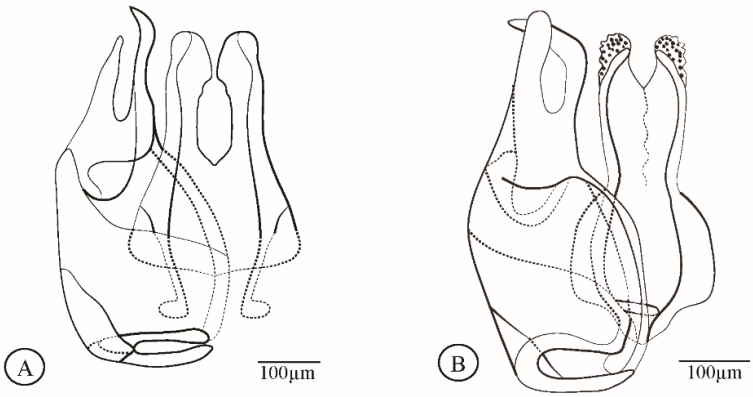

FIGURE 51. *Epyris mian* Colombo & Azevedo n. sp., male. **A,** genitalia in dorsal view; **B**, genitalia in ventral view.

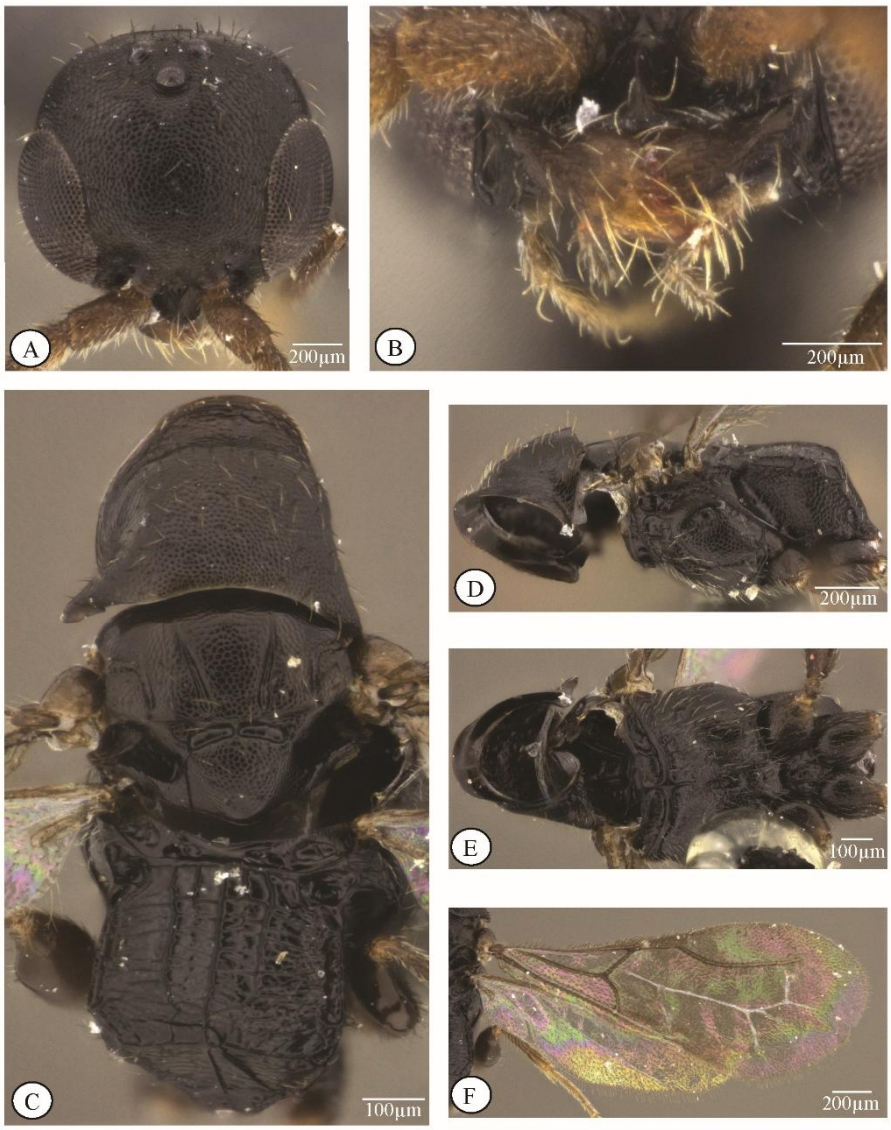

FIGURE 52. *Epyris min* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; F, forewing in dorsal view.

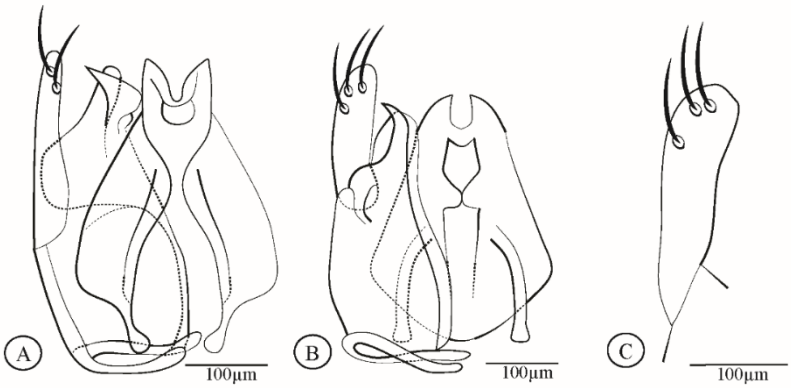

FIGURE 53. *Epyris min* Colombo & Azevedo n. sp., male. **A,** genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view.

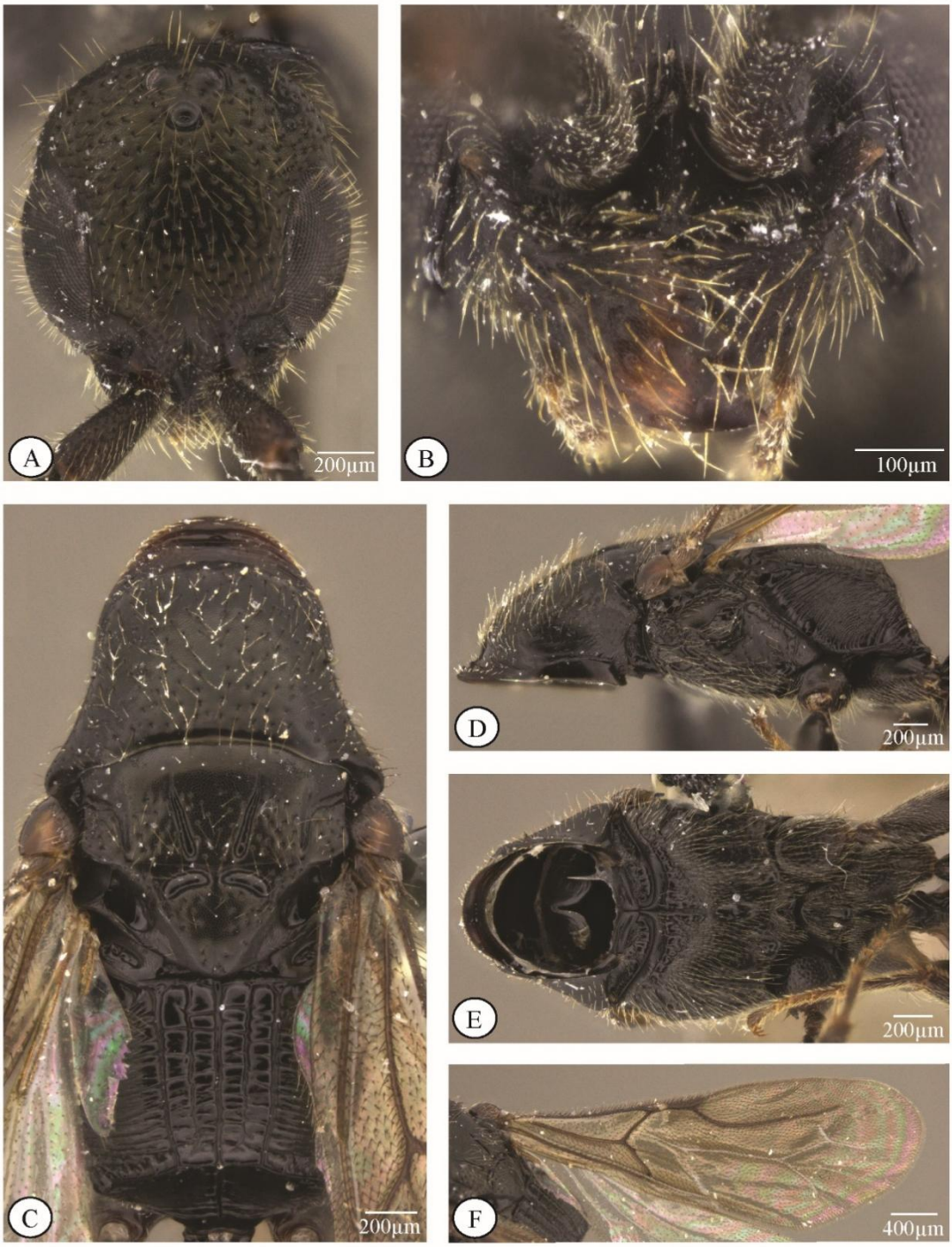

FIGURE 54. *Epyris motu* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

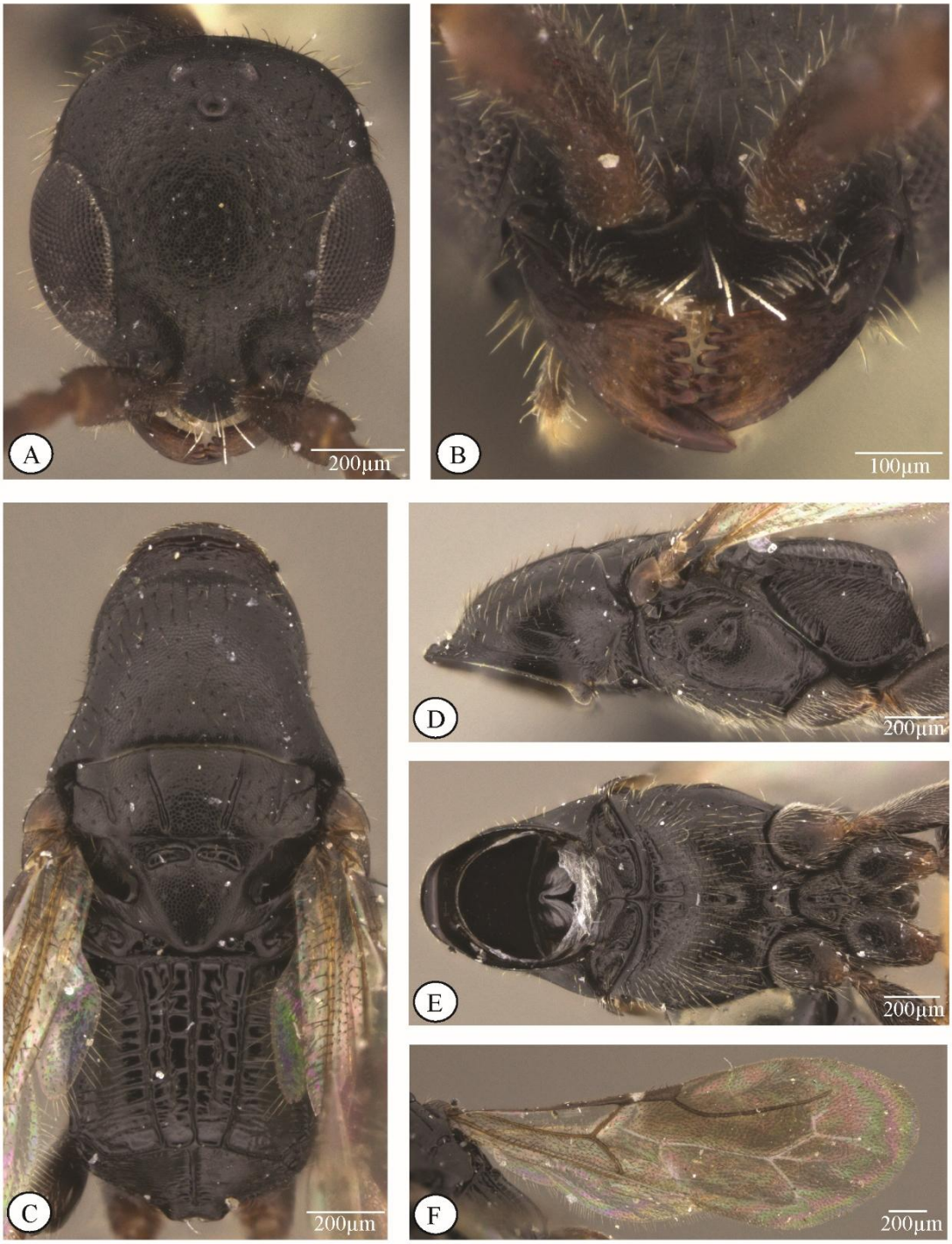

FIGURE 55. *Epyris mundugumor* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

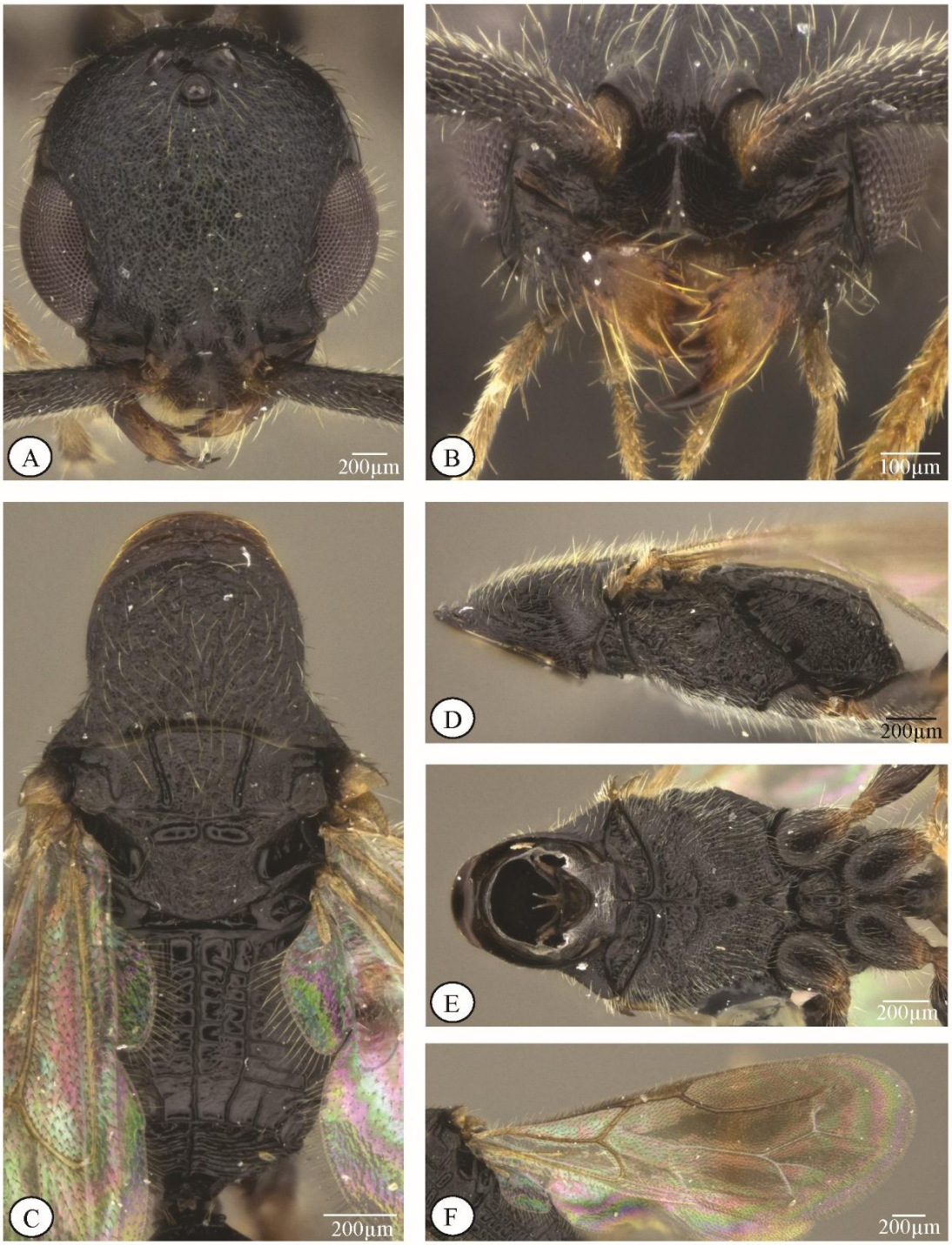

FIGURE 56. *Epyris ogea* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

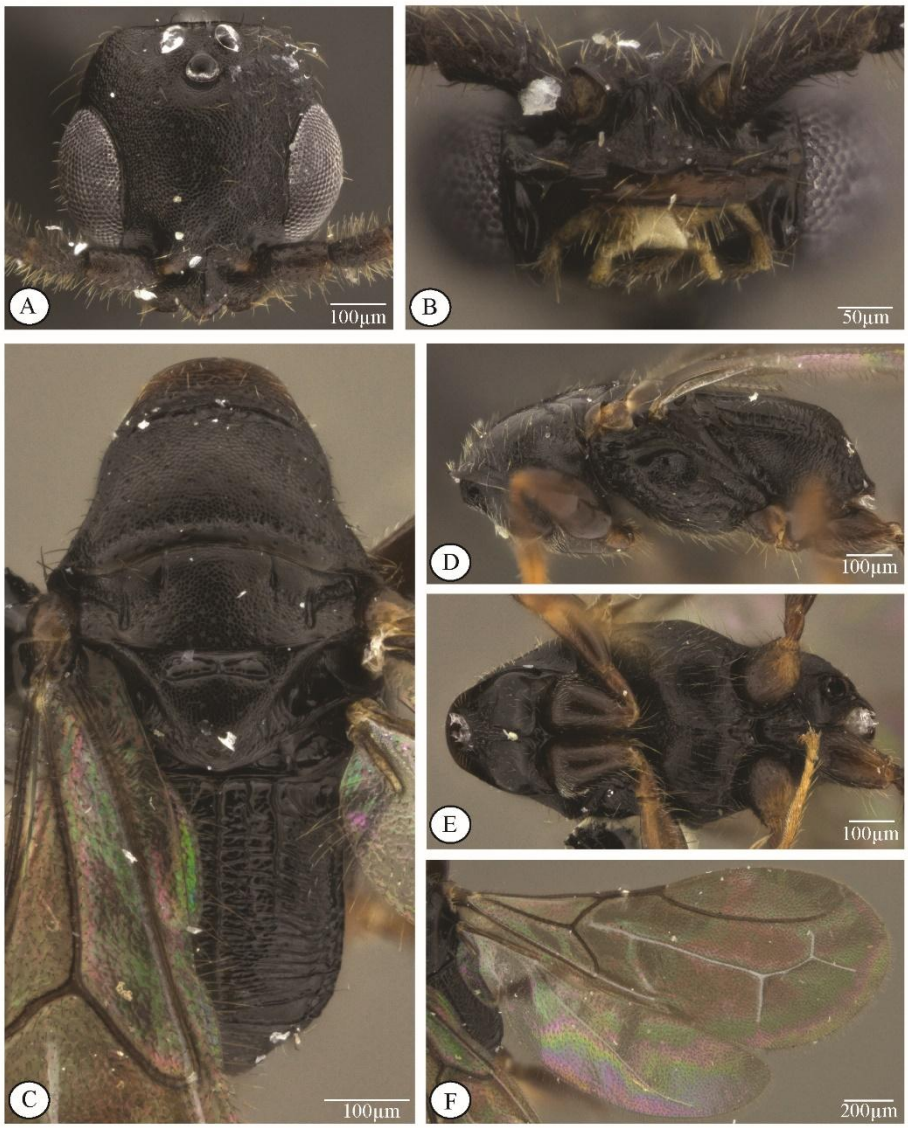

FIGURE 57. *Holepyris orokaiva* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

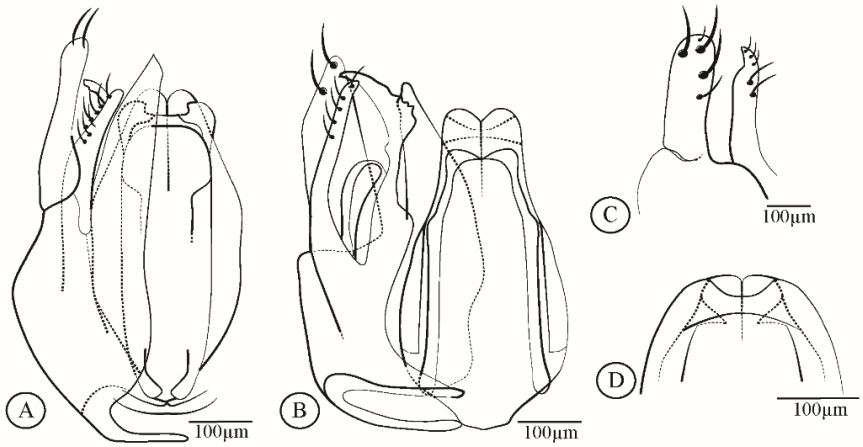

FIGURE 58. *Holepyris orokaiva* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view; **D**, apex of aedeagus in dorsal view.

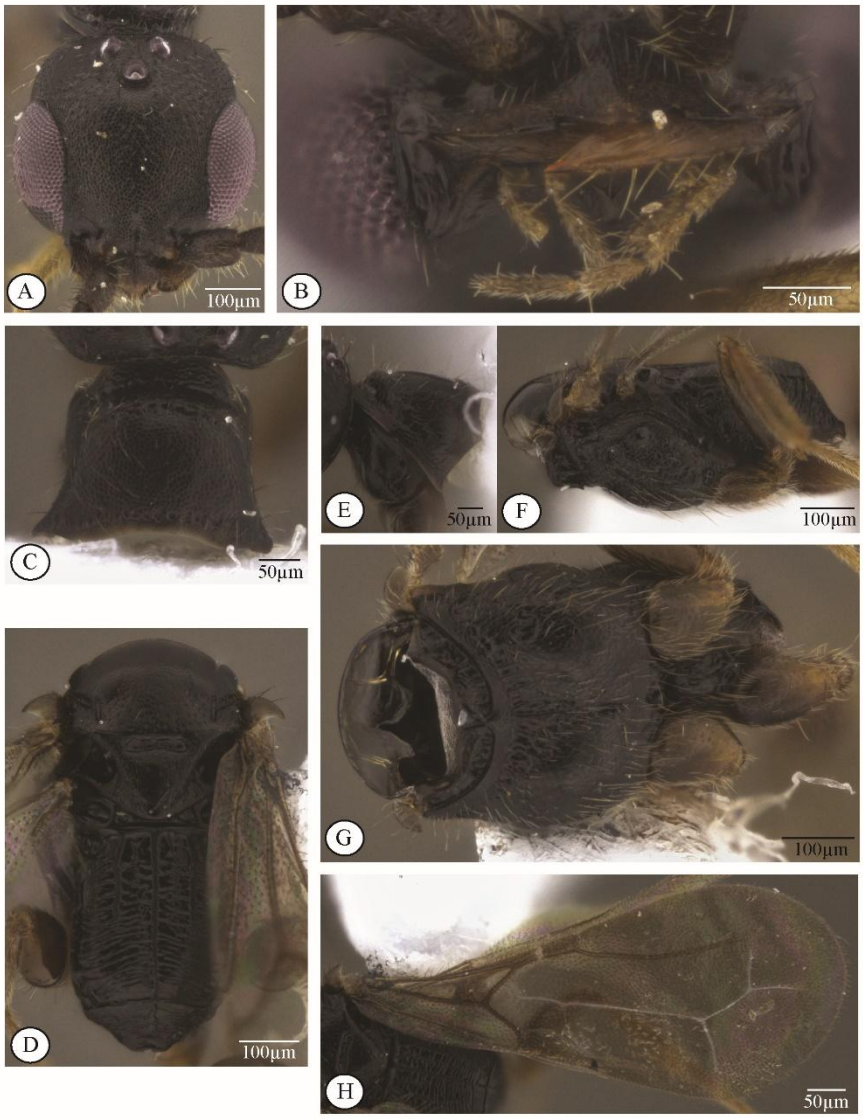

FIGURE 59. *Holepyris sambia* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

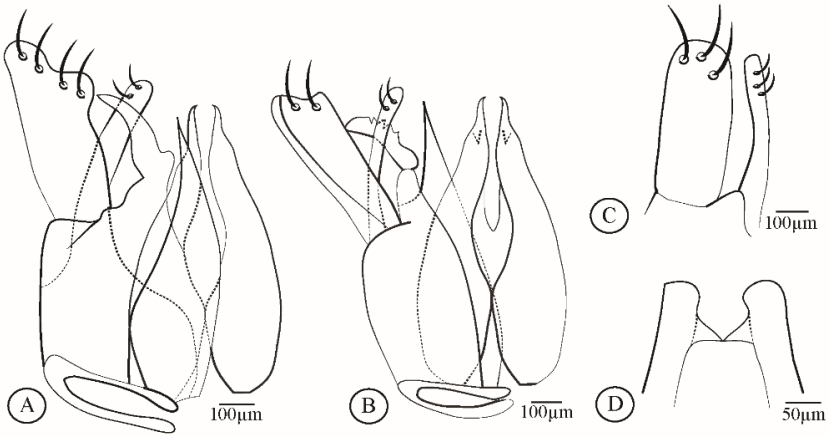

FIGURE 60. *Holepyris sambia* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view; **D**, apex of aedeagus in dorsal view.

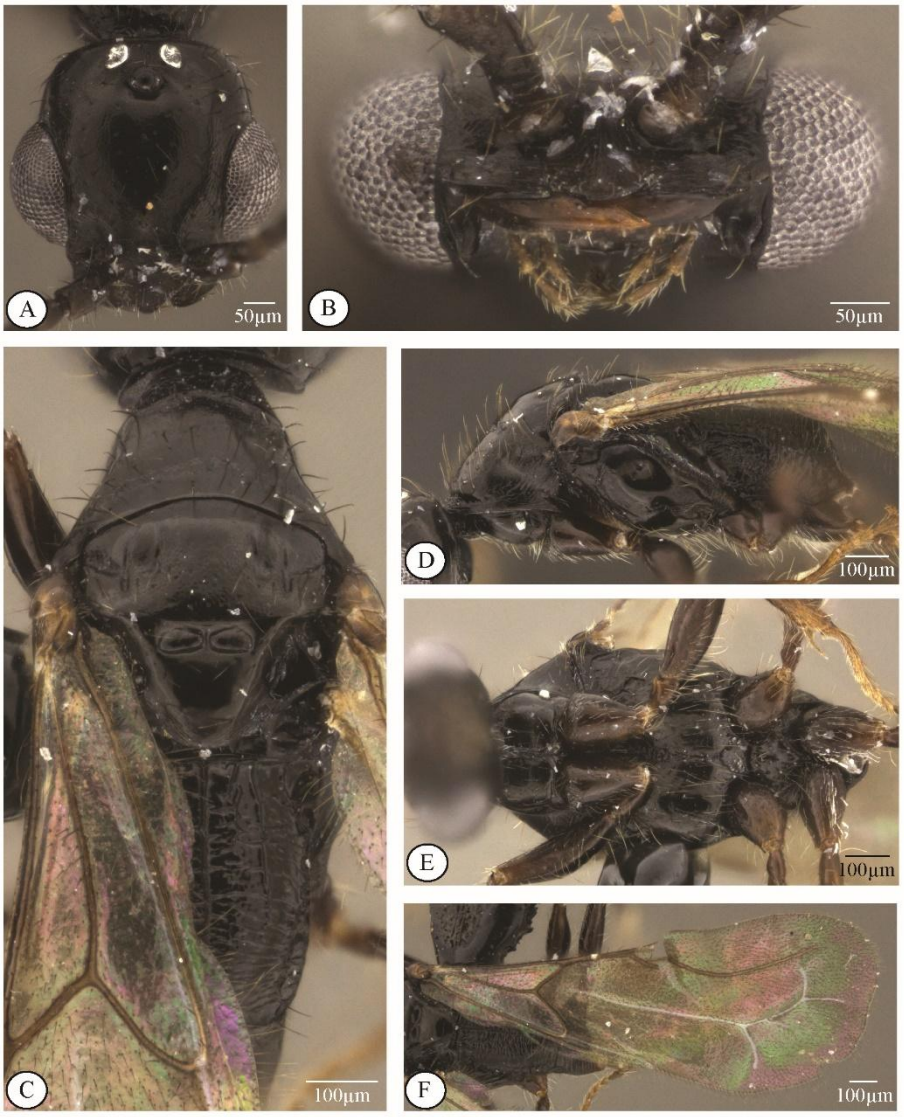

FIGURE 61. *Holepyris swagap* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

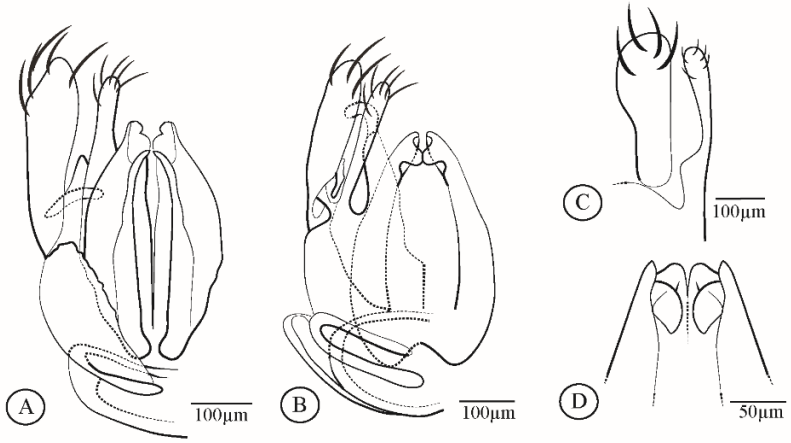

FIGURE 62. *Holepyris swagap* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view; **D**, apex of aedeagus in dorsal view.

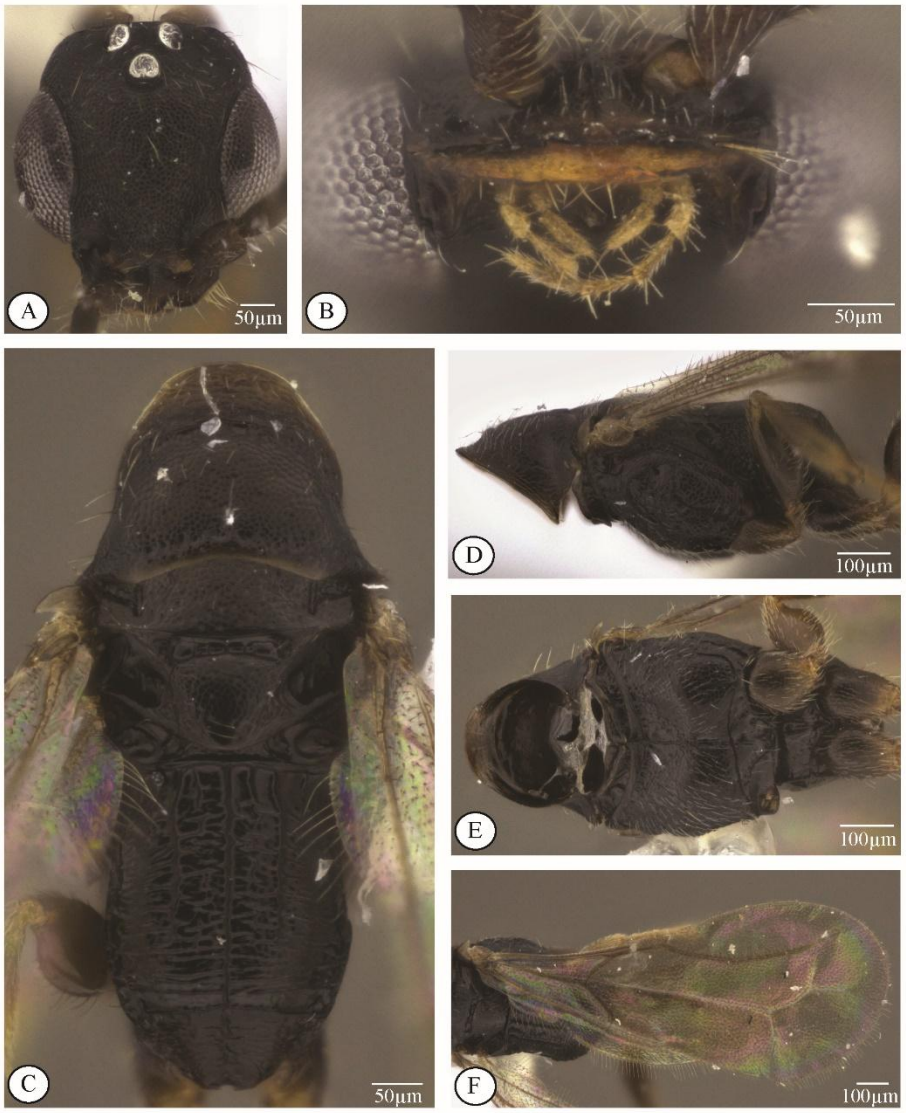

FIGURE 63. *Holepyris tairora* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

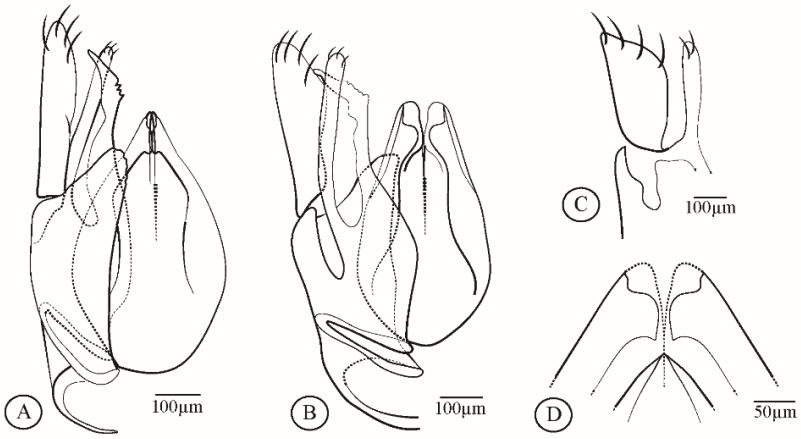

FIGURE 64. *Holepyris tairora* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view; **D**, apex of aedeagus in dorsal view.

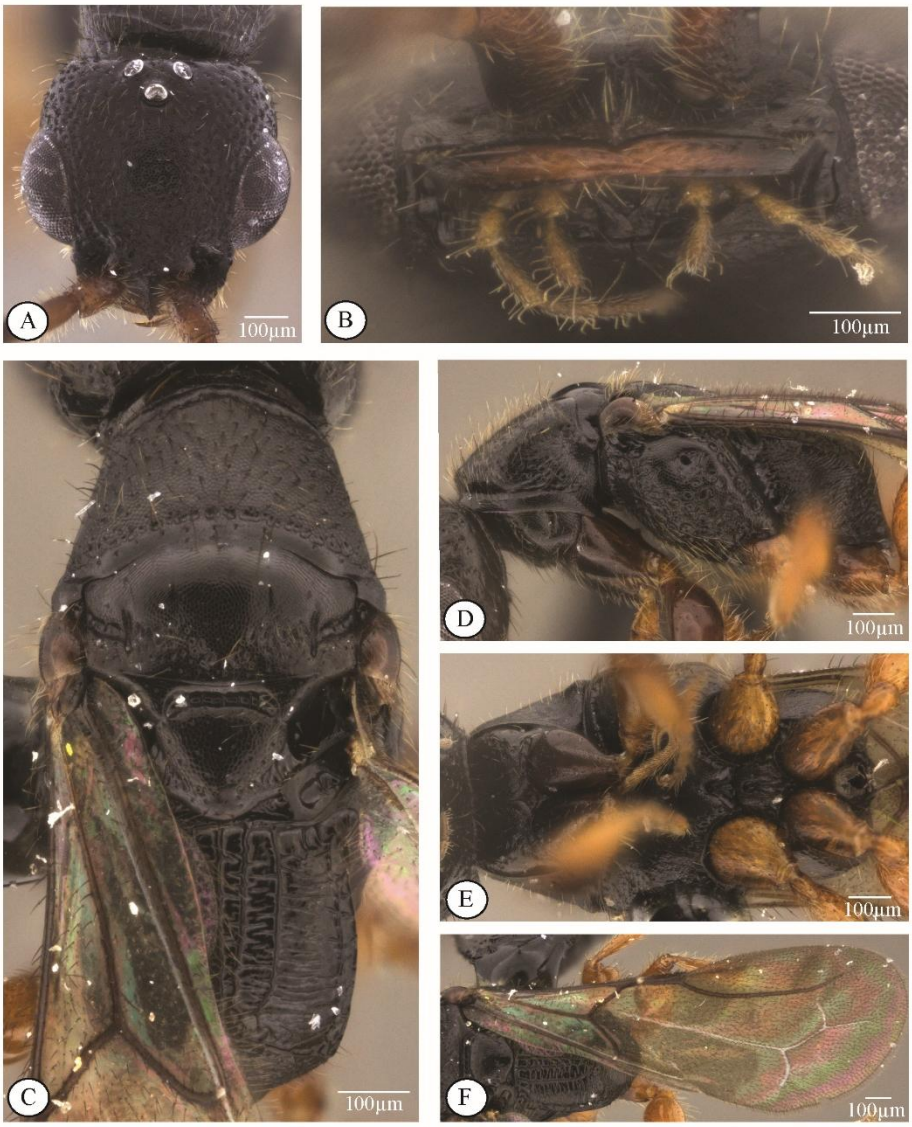

FIGURE 65. *Holepyris telefol* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

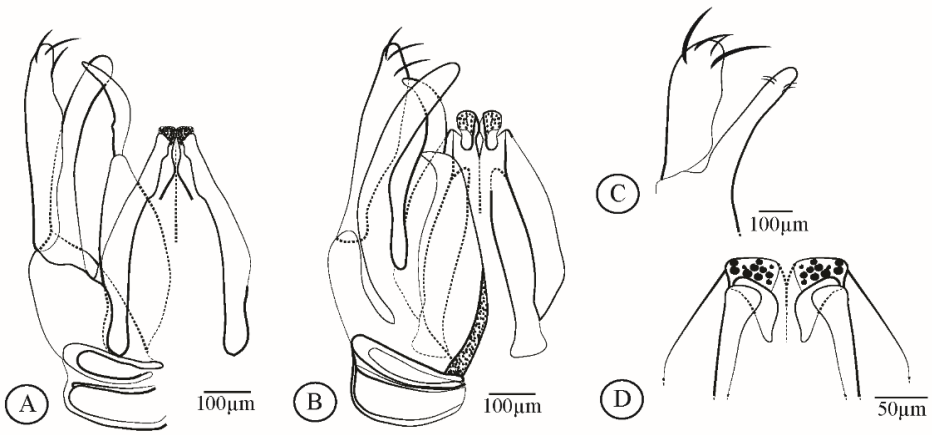

FIGURE 66. *Holepyris telefol* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view; **D**, apex of aedeagus in dorsal view.

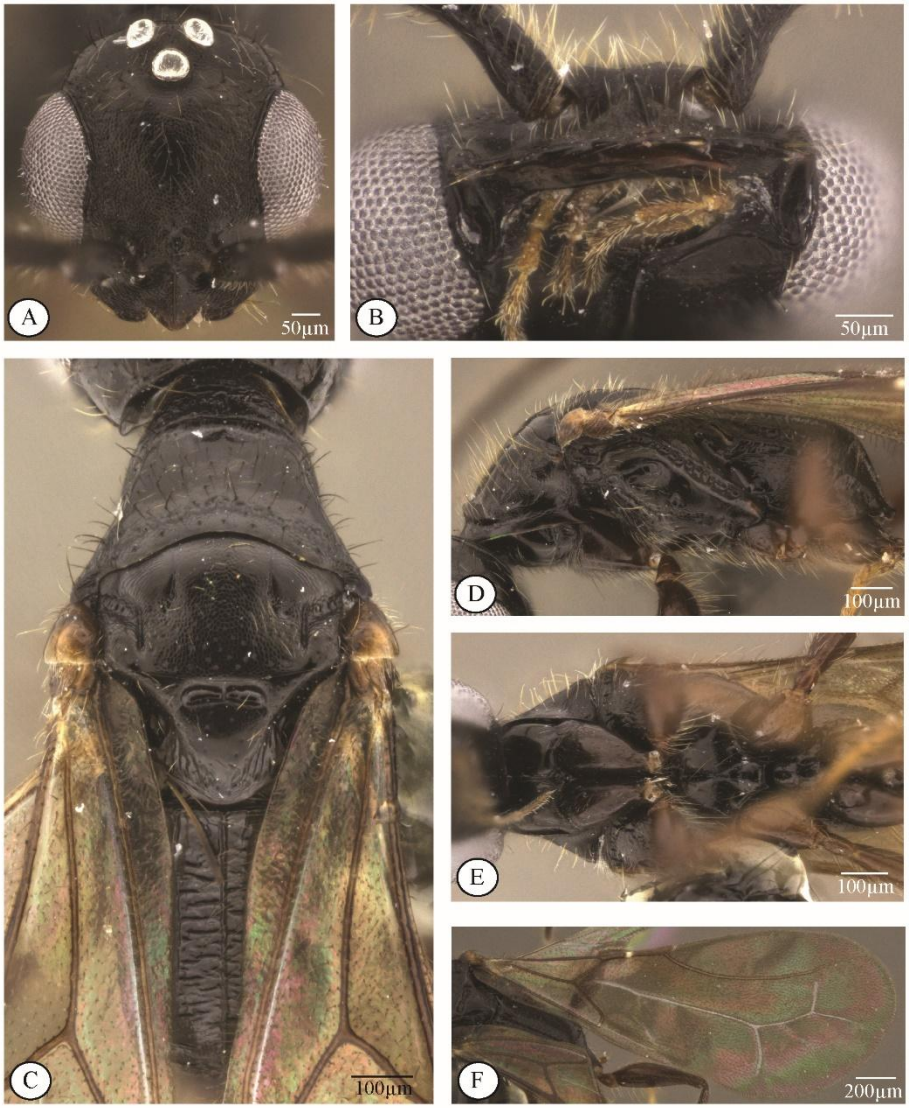

FIGURE 67. *Holepyris tsembaga* Colombo & Azevedo n. sp., male. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; F, forewing in dorsal view.

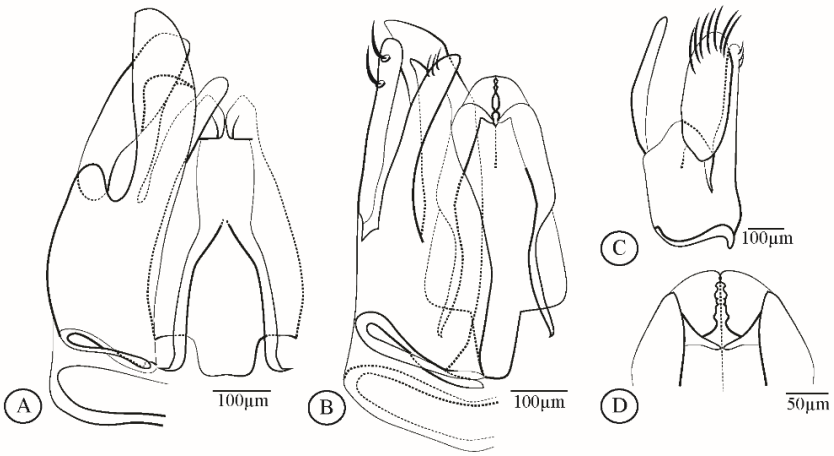

FIGURE 68. *Holepyris tsembaga* Colombo & Azevedo n. sp., male. **A**, genitalia in dorsal view; **B**, genitalia in ventral view; **C**, paramere in lateral view; **D**, apex of aedeagus in dorsal view.

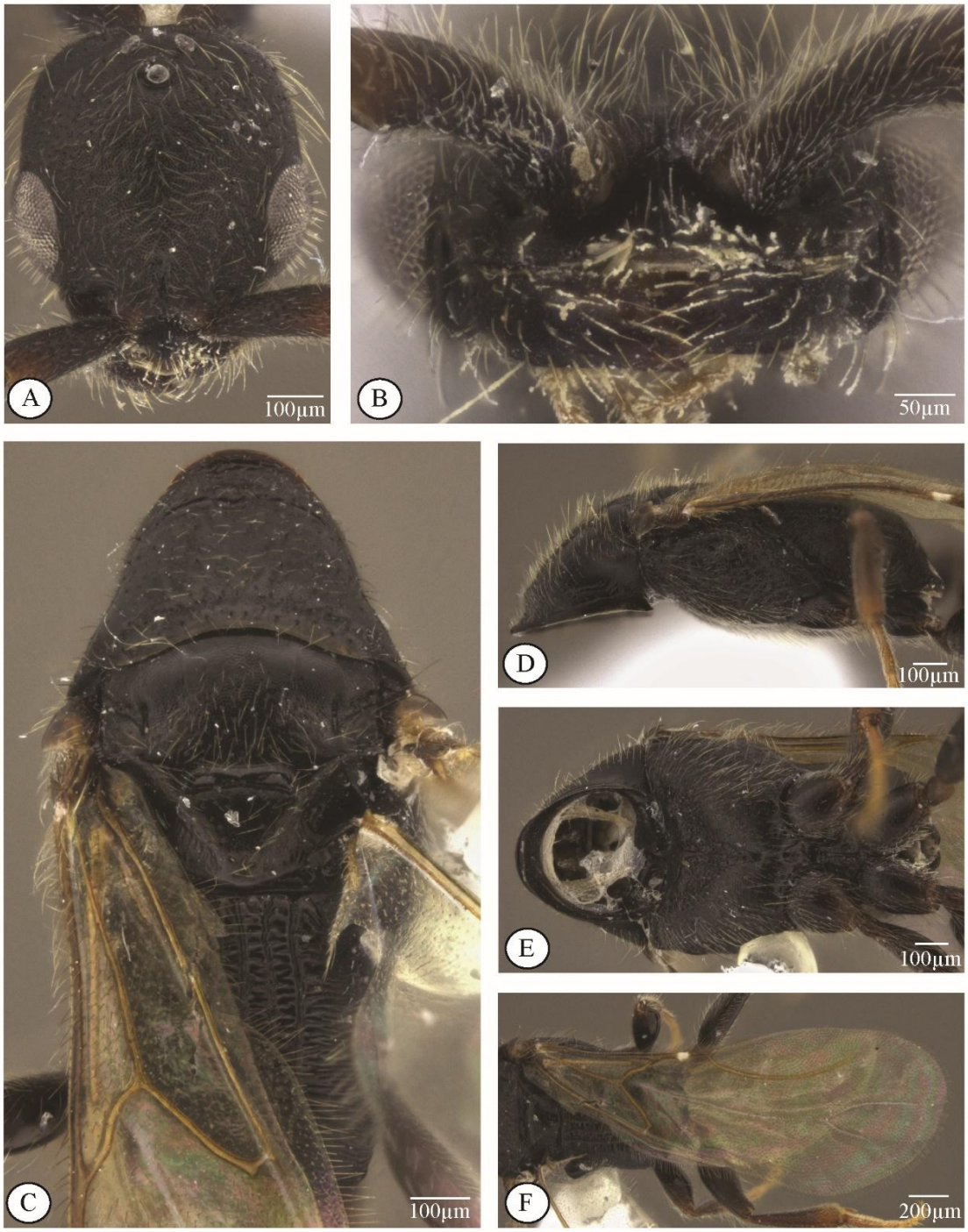

FIGURE 69. *Holepyris wiru* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

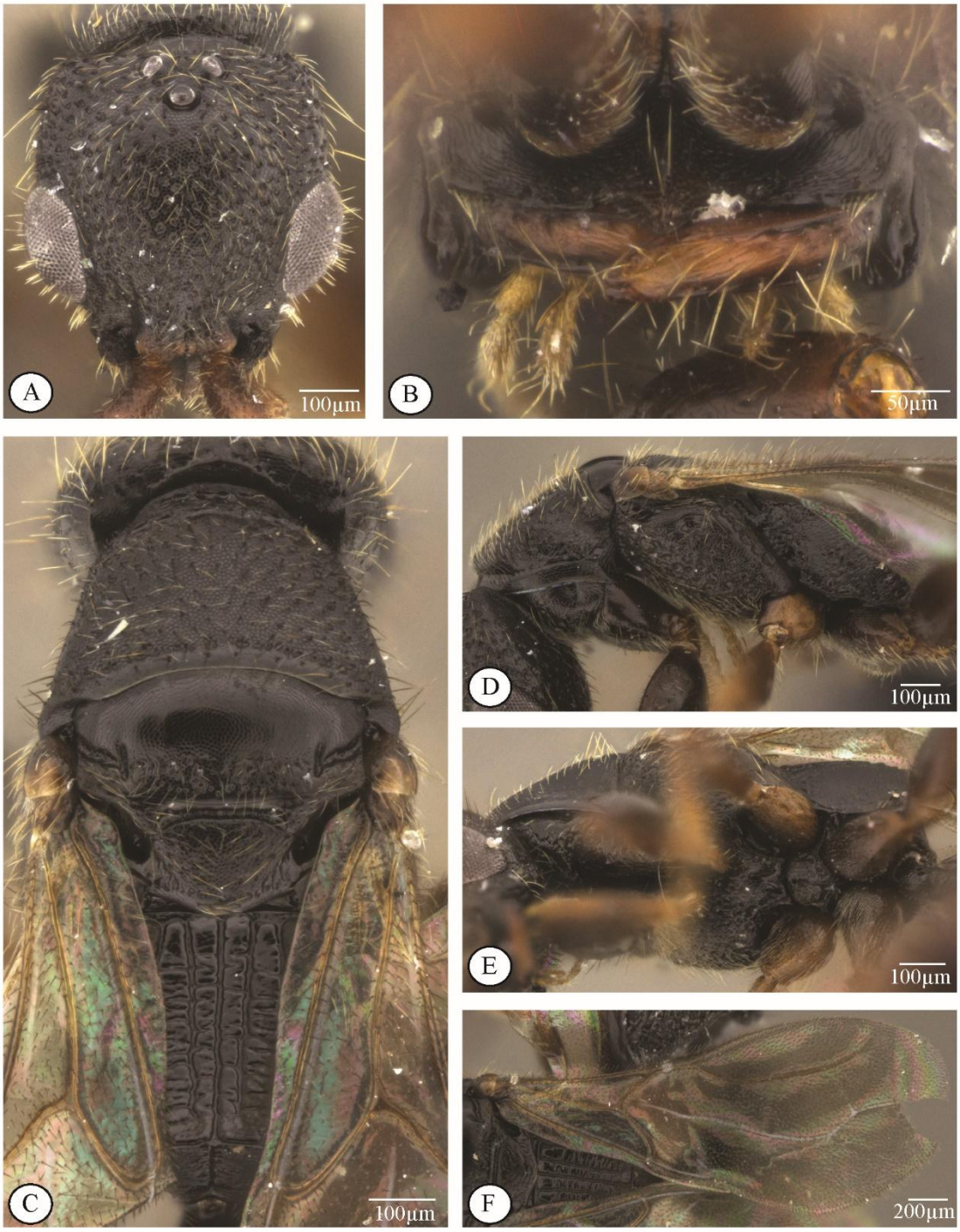

FIGURE 70. *Holepyris yaifo* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

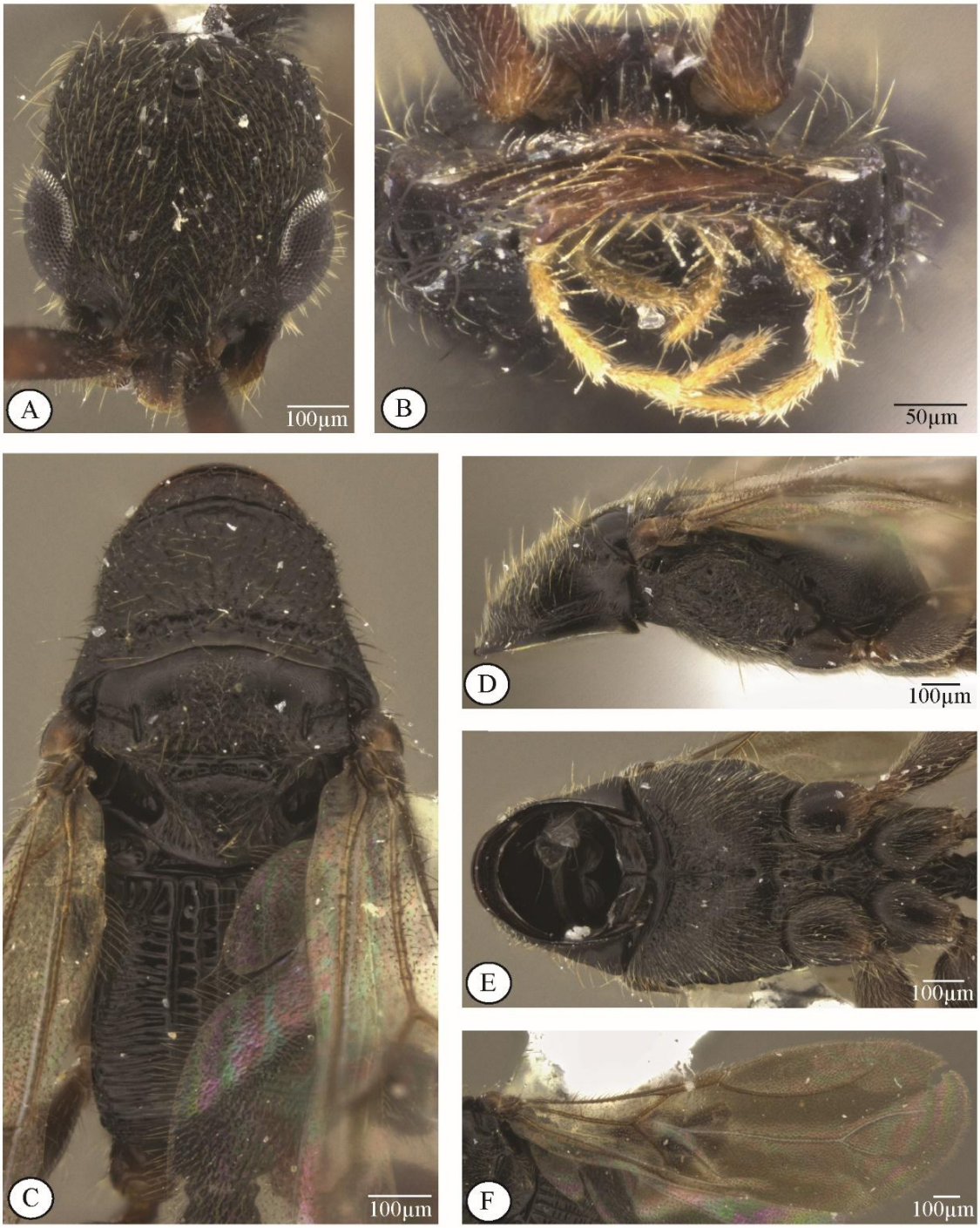

FIGURE 71. *Holepyris zia* Colombo & Azevedo n. sp., female. **A**, head in dorsal view; **B**, mandible in frontal view; **C**, mesosoma in dorsal view; **D**, mesosoma in lateral view; **E**, mesosoma in ventral view; **F**, forewing in dorsal view.

CAPÍTULO II

Phylogenetic overview of flat wasps (Hymenoptera, Bethylidae) reveals Elektroepyrinae, a new fossil subfamily[2]

ABSTRACT

The flat wasps, Bethylidae, are cosmopolitan and one of the most diverse families of Chrysidoidea. Bethylidae have 2,920 described extant species and almost 90 fossil species. The oldest geological record of the family is the Lower Cretaceous, from Lebanese and Spanish ambers and Transbaikalian rock fossils. Here we describe and illustrate one new fossil subfamily of Bethylidae: †Elektroepyrinae **subfam. nov.** represented by †*Elektroepyris* Perrichot & Nel from the lowermost Eocene Oise amber (France), which was cladistically assessed against all other eight subfamilies of Bethylidae. The new taxon is easily distinguished from other subfamilies by the forewing venation with the third abscissa of Cu present. Phylogenetic analyses support the monophyly of all subfamilies of Bethylidae, with a matrix with 69 morphological characters and 22 terminal taxa from where †Elektroepyrinae **subfam. nov.** emerged as independent lineage from all other subfamilies.

Keywords: Aculeata, Eocene, French amber, Oise amber

INTRODUCTION

The flat wasps, Bethylidae, belong to the Chrysidoidea (Hymenoptera) and have shown to be a monophyletic taxon (Brothers & Carpenter, 1993; Ronquist, 1999; Ronquist *et al.*, 1999; Carr *et al.*, 2010). Bethylidae are external gregarious parasitoids of the larval stage of Coleoptera and Lepidoptera (Evans, 1964). The family has 2,920 species, arranged in 96 genera (Azevedo *et al.*, 2018), which are currently divided into five extant subfamilies: Bethylinae, Epyrinae, Mesitiinae, Pristocerinae and Scleroderminae, and three extinct subfamilies: †Lancepyrinae, †Holopsenellinae and †Protopristocerinae.

The history of taxonomic assignment of bethylids is complex, but was recently summarized by Azevedo *et al.* (2018) and is not repeated here. Recently, many works on the fossil fauna of Bethylidae have been published, as in Azevedo & Azar (2012), Barbosa *et al.* (2013), Ramos *et al.* (2014), Engel *et al.* (2016), Engel (2019), Falières & Nel (2018, 2019a, 2019b, 2019c, 2020), Colombo & Azevedo (2019) and Colombo *et al.* (2020).

[2] Capítulo publicado e formatado seguindo as instruções para os autores da Revista *Palaeoentomology* (ISSN 2624-2826).

Many of these works have managed to detect new taxa and expand our knowledge about the evolution of bethylids. The family has hitherto almost 90 valid fossil species.

The main goals of this paper are to describe the new fossil subfamily †Elektroepyrinae, which is proposed to accommodate the extinct genus †*Elektroepyris* Perrichot & Nel, 2008 from the lowermost Eocene Oise amber (France), and to ascertain its phylogenetic position in the first phylogeny, which covers all subfamilies of Bethylidae.

MATERIAL AND METHODS

The amber piece containing the inclusion with the holotype of †*Elektroepyris magnificus* Perrichot & Nel, 2008 is deposited in the Museum National d'Histoire Naturelle, France (MNHN, curator: André Nel) and was examined by the photos and original description.

The terms applied to the integument sculpture follow Harris (1979) and those applied to the general morphology follow Lanes *et al.* (2020).

The material used in this study for phylogenetic analyses was provided by insect collection of the following institutions: California Academy of Sciences, U.S.A. (CAS), Iziko South African Museum, South Africa (ISAM), Queen Sirikit Botanical Garden, Thailand (QSBG), Universidad de Panama, Panama (MIUP) and Universidade Federal do Espírito Santo, Brazil (UFES).

For this purpose, the ingroup includes 21 terminals, representing all current eight subfamilies of Bethylidae, extant and extinct (Tab. 1). The outgroup is represented by the scolebythid wasp *Clystopsenella longiventris* Kieffer, 1910.

We worked on improving character-coding system, avoiding as much as possible the continuous quantitative characters. Several characters have been proposed from the codification of new features of the forewing, especially associated with venation. Sixty-nine morphological characters were analyzed, including one character from general body, 26 characters from the head, 22 from the mesosoma, 18 characters from the wing and two from the metasoma (Appendix 1).

The morphological dataset was analyzed using parsimony, considering the coherence with several groups generally accepted by previous research. The characters were treated as unordered and non-polarized. Inapplicable characters were treated as "-", and missing data were treated as "?" (Appendix 2).

The searches for the most parsimonious (MP) trees were carried out with the software TNT version 1.1 (Goloboff *et al.*, 2008). For the heuristic searches (Goloboff *et*

al., 2003, 2008), searches were performed under New Technology methods using the following parameters: memory with 99999 trees; collapsing rules as TBR; best score hits with 10 times; random seed as default (1); a sectorial search as default; ratchet perturbation phase (up-weighting prob and down-weighting prob = 10) and with 10000 iterations; tree-drifting of 10000 cycles and, tree-fusing of ten rounds. Implied weights analyses using a concavity function (K) that weights against homoplastic data (Goloboff *et al.*, 1993) were also conducted, using a TNT script (setk.run) written by Salvador Arias to calculate the appropriate value. A value of 2.343 was returned and subsequently used in the implied weighting scheme. Resampling support values were calculated using bootstrap and reported as absolute frequencies from 1000 replicates.

The cladogram recovered with the software TNT was manipulated with WinClada-ASADO version 1.61 (Nixon, 2002) and edited in Adobe Illustrator CS6 version 23.0.3.

RESULTS

For the search with equal weighting, 7.054.582.423 rearrangements were examined, and retrieved three MP trees, with a best score of 150. The strict consensus of equal weight analyses resulted in one cladogram with steps (L) of 165, consistency index (CI) of 0.42 and retention index (RI) of 0.60 (Fig. 1A). In the search with implied weighting, 7.389.707.320 rearrangements were examined, and retrieved three MP trees, with a best score of 16.43. The strict consensus of implied weight analyses resulted in one cladogram with L = 165, CI = 0.42 and RI = 0.60 (Fig. 1B).

In the topology of the tree obtained under both equal and implied weights, all subfamilies of Bethylidae are retrieved as monophyletic, and †Elektroepyrinae **subfam. nov.** as an independent clade as well. All five major groups of Bethylidae were recovered as monophyletic groups, and in all analyses †*Elektroepyris* failed to cluster within them. Because of that, we allocated it into a distinct subfamily, †Elektroepyrinae **subfam. nov.** One autapomorphy supports this clade, namely, the forewing venation with the third abscissa of Cu (57:0, Fig. 2D).

Systematic palaeontology

Family Bethylidae Haliday, 1839

Subfamily †Elektroepyrinae Colombo & Azevedo subfam. nov.

Type genus. †*Elektroepyris* Perrichot & Nel, 2008.

Included genus. †Elektroepyris Perrichot & Nel, 2008.

Diagnosis. Female holotype (Fig. 2). Antenna with 11 flagellomeres. Eye very large, much longer than frons width, bulging. Frons strongly coriaceous. Frontal angle of ocellar triangle acute. Median clypeal carina not extending posterad into frons. Anterior ocellus anterior to supra-ocular line. Dorsal pronotal area longer than wide, ecarinate. Macropterous, forewing with C, R, 1Cu closed cells, Rs+M vein fully absent, distal flexion lines not visible, 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein, third abscissa of Cu tubular, and indistinct to claval flexion line. Pterostigma subcircular. Mesoscutum-mesoscutellar sulcus apparently absent, fovea large, circular. Metanotum undeveloped medially, not overlapping mesoscutellum. Claws slightly curved.

Male. Unknown.

Genus †*Elektroepyris* Perrichot & Nel, 2008

Type species. †*Elektroepyris magnificus* Perrichot & Nel, 2008.

Included species. †*Elektroepyris magnificus* Perrichot & Nel, 2008.

Diagnosis. As in subfamily because of monotypy.

Locality and horizon. Oise amber, Le Quesnoy, Chevrière, region of Creil, Oise Department, France. Ypresian, 53 million years ago (Nel & Brasero 2010); lowermost Eocene.

†*Elektroepyris magnificus* Perrichot & Nel, 2008

Type material. Holotype, female, piece code PA-6470, deposited in MNHN collection, examined by photos.

Diagnosis. As in subfamily because of monotypy.

Description. Female holotype (Fig. 2). Body length ~3.78 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head as long as wide and quadrate, not globoid in lateral view. Flagellomere about as long as wide; flagellar pubescence appressed; pedicel longer than flagellomere I, rectangular. Clypeus with median lobe not visible. Median clypeal carina not visible. Eye glabrous, located close to mandibular base. Frons strongly coriaceous, punctures large, very close one to another. Frontal line inconspicuous. Frontal angle of ocellar triangle acute. Anterior ocellus anterior to supra-ocular line. Dorsal pronotal area without posterior sulcus, lateral surface strongly concave. Posterior mesofurcal pit drop-shaped. Metafurcal pit drop-shaped. Notaulus present, very narrow. Parapsidal signum absent. Mesoscutum-mesoscutellar sulcus absent, fovea large, circular and aligned with notaulus. Metapectal-propodeal disc apparently longer than wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae not visible. Mesotibia without spines. Metasoma polished, weakly setose.

Male. Unknown.

DISCUSSION

Oise amber deposit provides the best studied Eocene amber fauna (Nel *et al.*, 1999, Nel & Brasero, 2010) that is older than Baltic amber; although data on the fauna of early and middle Eocene fossil resins are common (Wang *et al.*, 2014; Nadein & Perkovsky, 2019; Dietrich & Perkovsky, 2019 and references therein) still, other bethylids with similar age are known only from Fushun amber (see below). Bethylids are the best known chrysidoids in Oise amber (Martynova *et al.*, 2019). Other known Oise amber chrysidoids are Scolebythidae with "Gondwanan" extant distribution (Zhang *et al.*, 2020 and references therein) and a single dryinid species from the genus *Pseudodryinus* Olmi, 1991 (Peinado *et al.*, 2006, Martynova *et al.*, 2019) with an extant tropical distribution (four Oriental species, two Afrotropical species, two species from Queensland and New Guinea, one species from western Honshu (Japan) and South Korea). Apparently †*Pseudodryinus parisiensis* Peinado *et al.*, 2006 belongs to a different evolutionary lineage from recent species; at least it is not close to the species from western Honshu and South Korea (M. Olmi, pers. comm.).

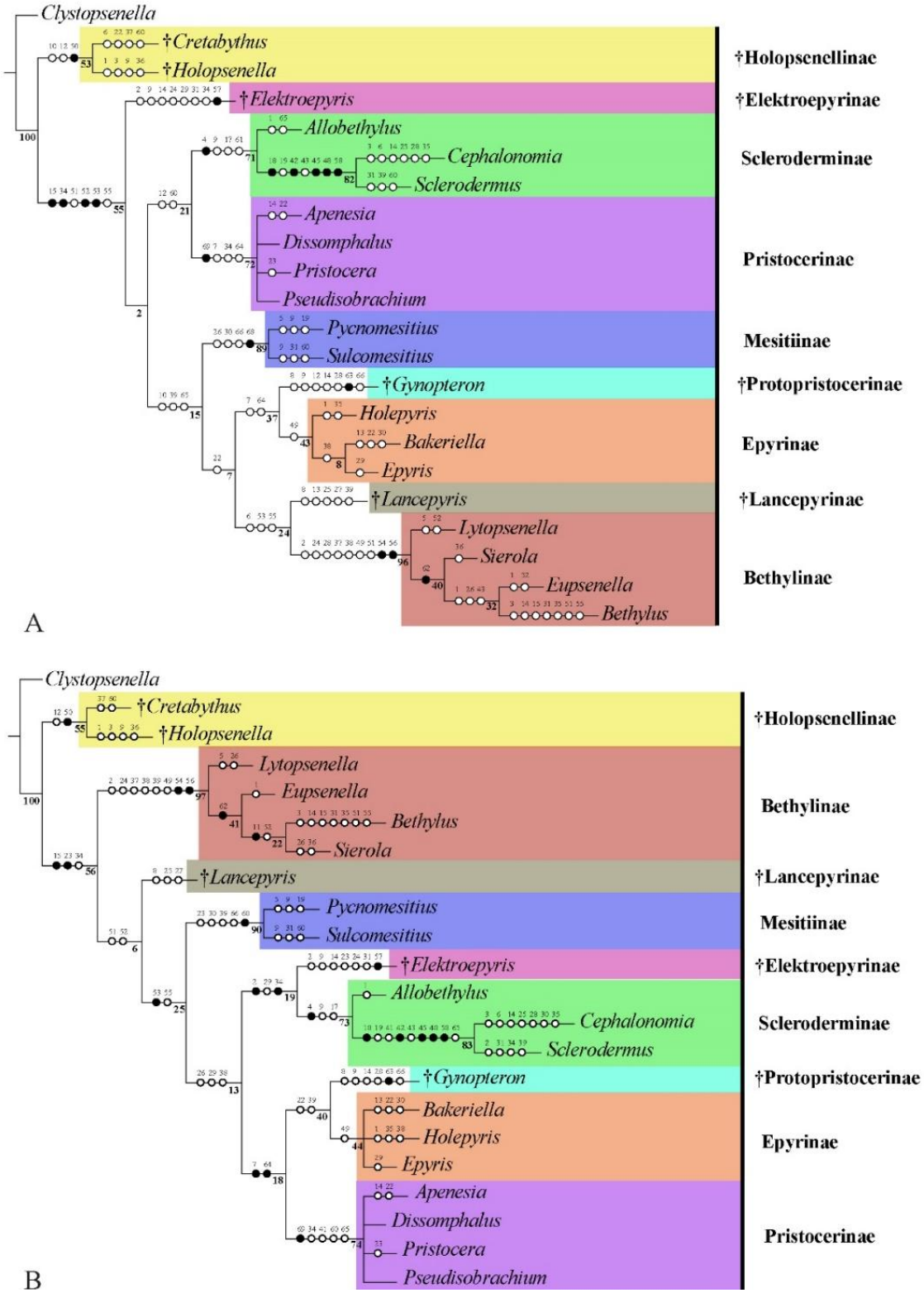

FIGURE 1. Parsimonious trees. **A**, Equal weighting analyses. **B**, Implied weighting analyses. Black circles represent homologies and

Oise amber hymenopterans are very diverse (14 families, 23 genera and 25 species); ants (except one species) and chalcidoids from Oise fauna are still undescribed (A. Nel, pers. comm.). Very uncommon is the bethylid overrepresentation in Oise hymenopteran

fauna (nine from 25 species); one of the reasons can be the very abundant and diverse Oise coleopteran fauna (Kirejtshuk & Nel, 2013), many of Oise beetles could be the bethylid hosts. Even if we will count the known percentage of Oise bethylids in all hymenopteran species except ants and chalcidoids, the bethylids (35%) will be evidently higher than in the next bethylid diversity hotspot, Rovno amber. In the Rovno amber, 14 bethylid species are found (Ramos *et al.*, 2014; Colombo *et al.*, 2020; our unpublished data) representing 26% of 54 Rovno hymenopteran species (ants and chalcidoids not included) (Perkovsky, 2018; Martynova *et al.*, 2019; Perkovsky *et al.*, 2020). High bethylid percentage and diversity (it includes three subfamilies unknown from Priabonian ambers) can be explained by paratropical climate of Oise amber forest, favourable for bethylids and their hosts. However, we must use caution in affirming any biological trends, because there are many wasps still undescribed from Oise amber, so that the relative abundance of flat wasps can be different.

Half of the Oise bethylid subfamilies and three from nine genera are common with Baltic amber (see below). The single known bethyline genus from Oise amber is *Eupsenella* with 45 extant species limited to Australia and New Zealand (Ramos & Azevedo, 2012); and seven fossil species, including four Priabonian species evenly distributed between Rovno and Baltic amber (Ramos *et al.*, 2014), one from Oise amber (De Ploëg & Nel, 2004) and two from Fushun amber (Hong, 2002). The extinction of *Eupsenella* in the Northern Hemisphere can be associated with the transition from an equable climate to a more pronounced seasonality in high and middle latitudes after the end of Eocene (Archibald & Farrell, 2003). At least half of extant *Eupsenella* are thermophiles: only 24 of 45 extant species are unknown from tropical regions in Australasia. All known early Eocene *Eupsenella* were thermophiles as well. The Oise species *Eupsenella neoeocenica* Ramos & Azevedo, 2018 in Azevedo *et al.* (2019), as new name for *Eupsenella eocenica* (De Ploëg & Nel, 2004), is morphological similar to the Fushun genus †*Fushunochrysites* Hong, 2002, synonymized with *Eupsenella* by Azevedo *et al.* (2018), mainly because both have the forewing with 1M cell almost elliptical and, the extant species are similar to the Priabonian species. *Eupsenella* is known from four different ambers and is the single bethylid genus known from Eocene of Europe and Asia. The genus *Lytopsenella* Kieffer, 1911 has the largest number of fossil species compared to the other Bethylinae, but has not been found in Oise amber and this does not seem surprising. One possible explanation for this is that all fossil *Lytopsenella* species are from

the Baltic and Rovno ambers (one species in common to both ambers and all other exclusive for Baltic) and all extant *Lytopsenella* species are distributed in the subtropical regions of Chile. The climate of this latter region is somewhat similar to the past equable climate of Baltic and Rovno amber forests (Perkovsky *et al.*, 2020), but differs from paratropical climate of Oise amber. Two groups can be especially good indicators of these climatic differences: in equable climate of Baltic and Rovno amber forests, with winters warm and summers not hot (Archibald & Farrell, 2003), aphids were nearly as abundant (Perkovsky & Wegierek, 2018 and references therein) as in the Cretaceous *Baeomorpha* realm. In contrast, the Oise amber forest with hot summers was as unfavorable for aphids (still not reported for Oise amber) as the paratropical or tropical climate of the Cretaceous Isoptera realm (Gumovsky *et al.*, 2018). The Priabonian amber forests were too cold for thermophile mastotermitids, but in Oise amber they are nearly as common as kalotermitids (Nel & Bourguet, 2006).

Regarding the Pristocerinae, †*Eopristocera bilobata* Falières & Nel, 2019 was discussed in our previous paper (Colombo *et al.*, 2020). *Pristocera* is reported from both Oise and Baltic amber (Colombo *et al.*, 2020). Still, it was argued that †*Pristocera alaini* Falières & Nel, 2019 may belongs to the thermophile genus *Pseudisobrachium* Kieffer, 1904 (Colombo *et al.*, 2020). The latter genus is unknown from Baltic amber, but is represented by two species in the more southern Rovno amber (Colombo *et al.*, 2020) and the reason for it is that the warmer Rovno amber climate (Sokoloff *et al.*, 2018) results in a larger "tropical" share in the Rovno fauna vs. the Baltic fauna (Legalov *et al.*, 2018, 2019). Recently, the first fossil species of *Dissomphalus* (*D. schubnelli* Falières & Nel, 2020) was published from Oise amber, its possible association with Micromalthidae (Coleoptera) and Cecidomyiidae (Diptera) is specially discussed (Falières & Nel, 2020).

Micromalthidae are still not described from Baltic amber, but is not rare in Rovno amber (Perkovsky, 2016 and our unpublished data), and Rovno amber gall midges are very common and diverse (90 named species in 20 genera: Fedotova & Perkovsky, 2009, 2017; Perkovsky & Fedotova, 2016 and references therein). It seems that Priabonian amber records of *Dissomphalus* could be limited by Rovno amber.

Epyrinae present the biggest paleodiversity of Bethylidae. The genus *Chlorepyris* Kieffer, 1913 was known in Europe by one extinct species, †*C. gallicus* (Perrichot & Nel, 2008), but we know many undescribed Priabonian species from succinites; and the Oise *Epyris* supposedly belongs to this genus as well (data in prep.). *Chlorepyris* has no extant

species in the Palaearctic region (Azevedo *et al.*, 2018) but it is the most diverse genus in the number of fossil species: 13 Priabonian species (four from Rovno and nine from Baltic amber) were found (data in prep.). Currently, the genus has 65 species and was revalidated by Waichert & Azevedo (2009) but this genus is probably polyphyletic (Alencar & Azevedo, 2013).

There are nine sclerodermines are registered (Colombo & Azevedo, 2019), and the only genus and species, †*Paleoscleroderma lamarrei* Falières & Nel, 2019 has been registered for Oise amber. In comparison, five species and five genera are reported for Baltic amber, including a single fossil representative of the thermophilic *Glenosema* Kieffer, 1905 and the Neotropical genus *Nothepyris* Evans, 1973 (Colombo & Azevedo, 2019). Scleroderminae were presumably abundant in the Eocene, with ~66% of all fossil species, and for this reason we assume that the Oise sclerodermines diversity is mostly unknown.

Differences between bethylids, and other chrysidoids, from succinites, Rovno and Baltic ambers, and Oise amber can be explained by differences between the paratropical climate of Oise amber forest and the equable climate of Baltic and Rovno amber forests. Abundance and diversity of bethylids in the representative Oise and Rovno amber collections predict their great unstudied diversity in much more abundant equable Baltic.

Perrichot & Nel (2008) provided a detailed discussion for †*Elektroepyris* and concluded that this genus shares the following synapomorphies with the clade (Epyrinae + Mesitiinae + Galodoxinae) sensu Terayama (2003): pterostigma located in basal half of forewing length, metanotum undeveloped medially, and dorsal pronotal area longer than anteromesoscutum. Terayama (2003) treated Epyrinae as an independent subfamily, although without any cladistic support. Galodoxinae were synonymized with the tribe Sclerodermini (Azevedo & Lanes, 2009). Later in the cladistic analyses performed by Alencar & Azevedo (2013), the genus †*Elektroepyris* was excluded, and was transferred to Epyrinae sensu Alencar & Azevedo (2013). The reasons of this genus transfer were not discussed by Alencar & Azevedo (2013).

We performed new cladistic analyses and included for the first time †*Elektroepyris*. We found that this genus is a distinct lineage from all other subfamilies of Bethylidae and for this reason, we are proposing †Elektroepyrinae as new subfamily.

Recently, several morphological studies have cladistically analyzed the subfamilies and genera of Bethylidae (e.g., Lanes & Azevedo, 2008; Azevedo & Azar, 2012) but this is

the first to include representatives from all subfamilies. The †Holopsenellinae were recovered as sister-group for all other Bethylidae (Fig. 1A, B) and the first lineage to diverge as was hypothesized by Engel *et al.* (2016). Bethylinae were the second subfamily to diverge, as recovered by our implied weighting analysis (Fig. 1B) and previous works (Carr *et al.*, 2010 and Azevedo & Azar, 2012). This subfamily was recovered as monophyletic (Ramos & Azevedo, 2018). †Lancepyrinae were the third subfamily to diverge (Fig. 1B) emerging immediately after Bethylinae, as also found by Azevedo & Azar (2012). We were not able to find any synapomorphy for this group, probably because of the inclusion of more fossil terminals. This procedure increases the gaps in analyses since many structures are not visible. A characteristic shared by †Holopsenellinae, Bethylinae and †Lancepyrinae is the presence of the forewing with a tubular RS+M vein, at least as stub and for this reason, we hypothesized that this group diverged before the remaining subfamilies. The positioning of the other subfamilies varied in the analyses, however, all of them were recovered as monophyletic. For more details about the extant subfamilies, see Lanes & Azevedo (2008) and Vargas *et al.* (2020) for Scleroderminae, Alencar & Azevedo (2013) for Epyrinae, Alencar *et al.* (2018) for Pristocerinae. †Protopristocerinae were included in a cladistic analysis for the first time, and have been recovered as sister-group of Epyrinae. As in Mesitiinae, these subfamilies lack phylogenetic inferences that seek to explore the positioning of their genera.

The positioning of †Elektroepyrinae varied between the two analyzes and were supported by an autapomorphy in both analyzes: the forewing with the third abscissa of Cu tubular (57:0). Among the flat wasps, this character is present only in this taxon, and this vein is unusually long. This character is present in some species of Chrysidini (Chrysididae), but and in other chrysidids are not present (Kimsey & Bohart, 1991). In the topology of equal weighting †*Elektroepyris* is recovered as a sister-group of all other subfamilies of Bethylidae, with the exception of †Holopsenellinae (Fig. 1A). However, in the topology of implied weighting †Elektroepyrinae share with Scleroderminae two synapomorphies: head shape in lateral view and anteromesoscutum short (Fig. 1B). Scleroderminae were diagnosed by Azevedo *et al.* (2018) as wasps with the body slender, sometimes strongly flat and forewing of the macropterous forms with anterior margin incurved and various configurations of cells and veins, but never with the third abscissa of Cu present, whereas †Elektroepyrinae have the body robust and forewing with anterior margin straight and with the third abscissa of Cu present.

Chrysidoids were confirmed as the sister-group of all remaining Aculeata by phylogenomic data and whose early diversification occurred 224–160 Ma (Peters *et al.*, 2017), probably during the Jurassic (Branstetter *et al.*, 2017). Among the ten families of Chrysidoidea, Chrysididae have the oldest representative, †*Dahurochrysis veta* Rasnitsyn, 1990, an imprint from Turga, Russian Federation (Berriasian-Valangian, Lower Cretaceous) (Rasnitsyn, 1990). For Embolemidae, the oldest representatives are the genera †*Baissobius* Rasnitsyn, 1975 and †*Embolemopsis* Olmi, Rasnitsyn & Guglielmino, 2010, from Aptian of Russian Federation and Mongolia (Rasnitsyn, 1975, 1996; Olmi *et al.*, 2010). In Dryinidae, the oldest representative is †*Archaeodryinus palaeophoenicius* (Olmi, 2000), from lower Barremian Lebanese amber, Lower Cretaceous (Olmi *et al.*, 2020). For Scolebythidae, the oldest representatives are three genera from lower Barremian Lebanese amber, Lower Cretaceous: †*Libanobythus* Prentice & Poinar, 1996, †*Uliobythus* Engel & Grimaldi, 2007 and †*Zapenesia* Engel & Grimaldi, 2007 (Prentice & Poinar, 1996; Engel & Grimaldi, 2007). In Sclerogibbidae, the oldest is †*Sclerogibbodes embioleia* Engel & Grimaldi, 2006, from lower Barremian Lebanese amber, Lower Cretaceous (Engel & Grimaldi, 2006). About the other four families, Plumariidae are represented only by extant species (Rasnitsyn, 1975; Brothers 2011; Perrichot *et al.*, 2014) and †Falsiformicidae, †Plumalexiidae and †Chrysobythidae are known for the Upper Cretaceous (Evans, 1973; Rasnitsyn, 1975; Brothers, 2011; Lucena & Melo, 2018; Melo & Lucena, 2019).

In flat wasps, the fossil evidence suggests that this group began to diverge in the Early Cretaceous, and during the Barremian were already well established, given the presence of †*Lancepyris* and †*Holopsenella* in this period and their cladistic positions in our analyses. The Eocene was an important setting in generating the currently recognized generic diversity of extant bethylid subfamilies, as the majority of genera appear to have evolved between 34 and 56 Ma. A few genera are estimated as being of very young crown-group age, such as *Anisepyris* Kieffer, 1905 (15–20 Ma) and *Apenesia* Westwood, 1874 (15–20 Ma). These estimates must be viewed with prudence as incomplete taxon sampling could influence them.

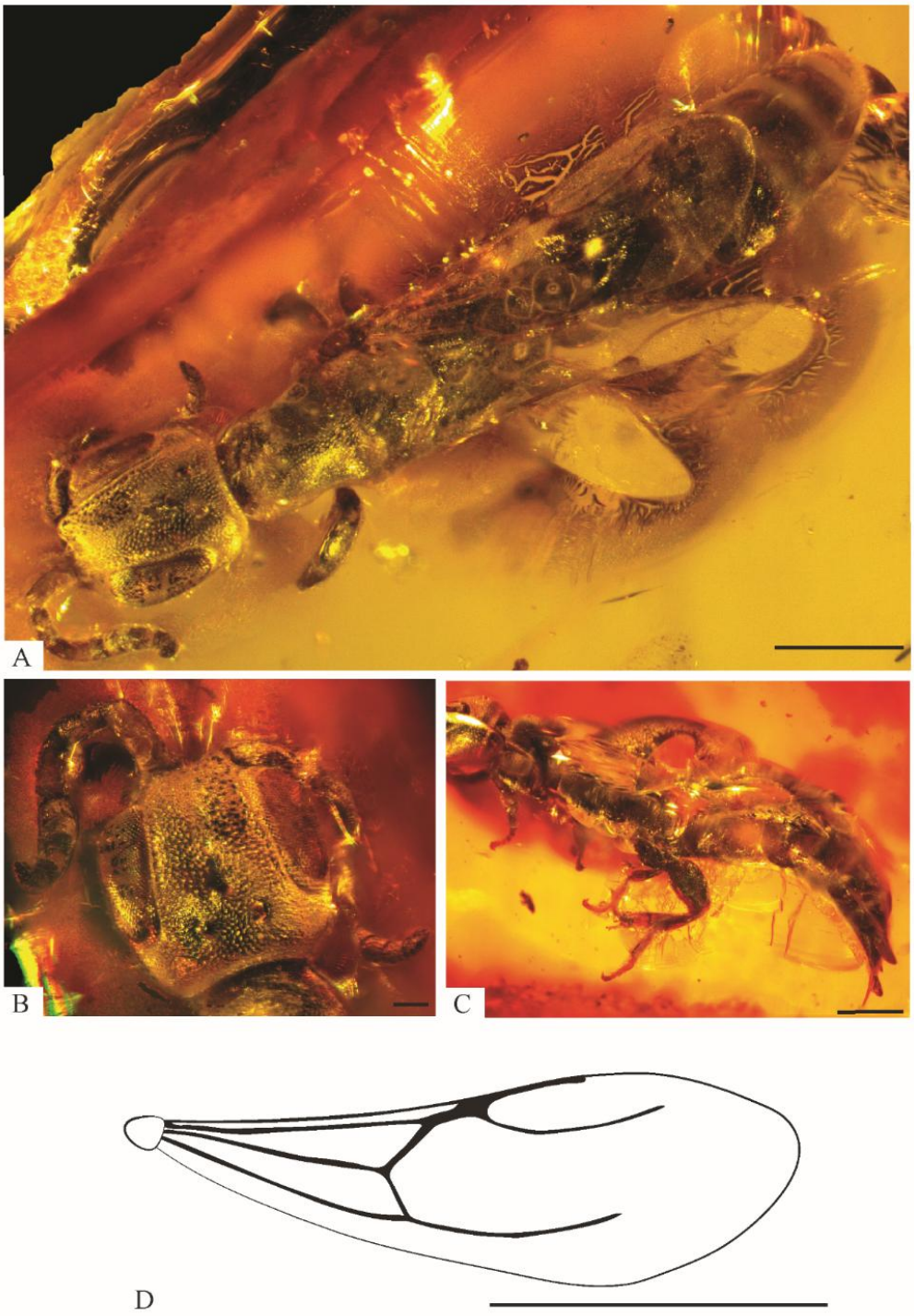

FIGURE 2. †*Elektroepyris magnificus* Perrichot & Nel, piece code PA-6470, female holotype. **A**, Habitus, dorsal view. **B**, Head, dorsal view. **C**, Habitus, lateral view. **D**, Forewing, dorsal view. Scale bars = 0.5 mm. ©MNHN.

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REFERENCES

Alencar, I.D.C.C. & Azevedo, C.O. (2013) Reclassification of Epyrini (Hymenoptera: Bethylidae): A tribal approach with commentary on their genera. *Systematic Entomology*, 38 (1), 45–80. https://doi.org/10.1111/j.1365-3113.2012.00648.x

Alencar, I.D.C.C., Waichert, C. & Azevedo, C.O. (2018) Opening Pandora's box of Pristocerinae: molecular and morphological phylogenies of *Apenesia* (Hymenoptera, Bethylidae) reveal several hidden genera. *Systematic Entomology*, 43, 481–509. https://doi.org/10.1111/syen.12295

Archibald, B. & Farrell, B.D. (2003) Wheeler's dilemma. *Acta zoologica cracoviensia*, 46, 17–23.

Azevedo, C.O. & Azar, D. (2012) A new fossil subfamily of Bethylidae (Hymenoptera) from the Early Cretaceous Lebanese amber and its phylogenetic position. *Zoologia*, 29, 210–218. https://doi.org/10.1590/S1984-46702012000300004

Azevedo, C.O. & Lanes, G.O. (2009) Cladistic assessment and redescription of *Galodoxa torquata* Nagy (Hymenoptera, Bethylidae), a striking species with swallow tailed metasomal sternite. *Zoologische Mededelingen*, 83, 841–851.

Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas, J.M. & Lim, J. (2018) Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, 4489, 1–294. https://doi.org/10.11646/zootaxa.4489.1.1

Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas, J.M. & Lim, J. (2019) Erratum, Global guide of the flat wasps (Hymenoptera, Bethylidae) (vol. 4489, 1-294, 2018). *Zootaxa*, 4559 (3), 598–600. http://dx.doi.org/10.11646/zootaxa.4559.3.13

Barbosa, D.N., Perkovsky, E.E. & Azevedo, C.O. (2013) Two new species of *Laelius* Ashmead (Hymenoptera: Bethylidae) from Upper Eocene Rovno amber. *Neues Jahrbuch fur Geologie und Paläontologie*, 267, 67–73. https://doi.org/10.1127/0077-7749/2012/0297

Branstetter, M.G., Danforth, B.N., Pitts, J.P., Faircloth, B.C., Ward, P.S., Buffington, M.L., Gates, M.W., Kula, R.R. & Brady, S.G. (2017) Phylogenomic Insights into the Evolution of Stinging Wasps and the Origins of Ants and Bees. *Current Biology*, 27, 1019–1025. https://doi.org/10.1016/j.cub.2017.03.027

Brothers, D.J. (2011) A new Late Cretaceous family of Hymenoptera, and phylogeny of the Plumariidae and Chrysidoidea (Aculeata). *ZooKeys*, 130, 515–542. https://doi.org/10.3897/zookeys.130.1591

Brothers, D.J. & Carpenter, J.M. (1993) Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera*). Journal of Hymenoptera Research*, 2, 227–304. https://doi.org/10.5281/zenodo.17378

Carr, M., Young, J.P.W. & Mayhew, P.J. (2010) Phylogeny of bethylid wasps (Hymenoptera: Bethylidae) inferred from 28S and 16S rRNA genes. *Insect Systematic and Evolution*, 41, 55–73. https://doi.org/10.1163/187631210X486995

Colombo, W.D. & Azevedo, C.O. (2019) Synopsis of the fossil Scleroderminae (Hymenoptera, Bethylidae) with description of a new genus and four new species from Baltic amber. *Historical Biology*, 1–10. [online only] https://doi.org/10.1080/08912963.2019.1650275

Colombo, W.D., Gobbi, F.T., Perkovsky, E.E. & Azevedo, C.O. (2020) Synopsis of the fossil Pristocerinae (Hymenoptera, Bethylidae), with description of two new genera and species from Burmese, Taimyr, Baltic and Rovno ambers. *Historical Biology*, 1–17. [online only] https://doi.org/10.1080/08912963.2020.1733551

De Ploëg, G. & Nel, A. (2004) A new bethylid wasp from the Lowermost Eocene amber of France (Hymenoptera: Bethylidae: Bethylinae). *Geologica Acta*, 2, 1–10. https://doi.org/10.1344/105.000001637

Dietrich, C.H. & Perkovsky, E.E. (2019) First record of Cicadellidae (Insecta: Hemiptera: Auchenorrhyncha) from Eocene Sakhalinian amber. *ZooKeys*, 886, 127–134.

https://doi.org/10.3897/zookeys.886.3882.

Engel, M.S. (2019) A holopsenelline wasp in mid-Cretaceous amber from Myanmar (Hymenoptera: Bethylidae). *Palaeoentomology*, 2, 199–204. https://doi.org/10.11646/palaeoentomology.2.2.10

Engel, M.S. & Grimaldi, D.A. (2006) The first Cretaceous sclerogibbid wasp (Hymenoptera: Sclerogibbidae). *American Museum Novitates*, 3515, 1–7. https://doi.org/10.1206/0003-0082(2006)3515[1:TFCSWH]2.0.CO;2

Engel, M.S. & Grimaldi, D.A. (2007) Cretaceous Scolebythidae and phylogeny of the family (Hymenoptera: Chrysidoidea). *American Museum Novitates*, 3568, 1–16. https://doi.org/10.1206/0003-0082(2007)475[1:CSAPOT]2.0.CO;2

Engel, M.S., Ortega-B., J. & Azevedo, C.O. (2016) A new bethylid wasp in Lebanese Early Cretaceous amber (Hymenoptera: Chrysidoidea), with comments on other Mesozoic taxa. *American Museum Novitates*, 3855, 1–14. https://doi.org/10.1206/3855.1

Evans, H.E. (1964) A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology*, 132, 1–222.

Evans, H.E. (1973) Cretaceous Aculeate wasps from Taimyr, Siberia (Hymenoptera). *Psyche*, 80 (3), 166–178. https://doi.org/10.1155/1973/16876

Falières, E. & Nel, A. (2018) The oldest representative of the extant genus *Epyris* in the Lowermost Eocene amber of France (Hymenoptera: Bethylidae: Epyrinae). *Palaeoentomology*, 1, 32–36. https://doi.org/10.11646/palaeoentomology.1.1.3

Falières, E. & Nel, A. (2019a) The first sclerodermine and pristocerine flat wasps in Lowermost Eocene amber of France (Hymenoptera: Bethylidae). *Comptes Rendus Palevol*, 18, 509–515. https://doi.org/10.1016/j.crpv.2019.04.007

Falières, E. & Nel, A. (2019b) A new bethylid wasp from the Lowermost Eocene Oise amber, France (Insecta: Hymenoptera). *Palaeoentomology*, 2, 211–214. https://doi.org/10.11646/palaeoentomology.2.3.2

Falières, E. & Nel, A. (2019c) The first representative of the extinct flat wasp subfamily Protopristocerinae (Insecta: Hymenoptera, Bethylidae). *Palaeoentomology*, 2, 322–326.

https://doi.org/10.11646/palaeoentomology.2.4.4

Falières, E. & Nel, A. (2020) First fossil of the extant flat wasp genus *Dissomphalus* Ashmead, 1893 (Hymenoptera: Bethylidae: Pristocerinae). *Zoosystema*, 42 (15), 207–213.
https://doi.org/10.5252/zoosystema2020v42a15

Fedotova, Z.A. & Perkovsky, E.E. (2009) New gall midges of the tribe Leptosynini (Diptera, Cecidomyiidae) from the Late Eocene ambers and the classification of the supertribe Heteropezidi. *Paleontological Journal*, 43 (9), 1101–1179.
https://doi.org/10.1134/S0031030109090111

Fedotova, Z.A. & Perkovsky, E.E. (2017) New genus and species of gall midges (Diptera, Cecidomyiidae, Porricondylinae, Holoneurini) from the Late Eocene amber of Olevsk (Zhitomir Region, Ukraine). *Vestnik Zoologii*, 51 (1), 23–30.
https://doi.org/10.1515/vzoo-2017-0004

Goloboff, P.A. (1993) Character optimization and calculation of tree lengths. *Cladistics*, 9, 433–436.
https://doi.org/10.1111/j.1096-0031.1993.tb00236.x

Goloboff, P.A., Farris, J.S., Källersjö, M, Oxelman, B., Ramírez, M.J. & Szumik, C.A. (2003) Improvements to resampling measures of group support. *Cladistics*, 19, 324–332.
https://doi.org/10.1111/j.1096-0031.2003.tb00376.x

Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.
https://doi.org/10.1111/j.1096-0031.2008.00217.x

Gumovsky, A., Perkovsky, E. & Rasnitsyn, A. (2018) Laurasian ancestors and "Gondwanan" descendants of Rotoitidae (Hymenoptera: Chalcidoidea): What a review of Late Cretaceous *Baeomorpha* revealed. *Cretaceous Research*, 84, 286–322.
https://doi.org/10.1016/j.cretres.2017.10.027

Harris, R.A. (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology*, 28, 1–31.

Hong, Y.C. (2002) *Atlas of amber insects of China*. Henan Scientific and Technological Publishing House, 394 pp.

Kimsey, L.S. & Bohart, R.M. (1990) *The chrysidid wasps of the world*. Oxford Science Publications, New York, 652 pp.

Kirejtshuk A.G. & Nel A. (2013) Current knowledge of Coleoptera (Insecta) from the Lowermost Eocene Oise amber. *Insect Systematics & Evolution*, 44, 175–201. https://doi.org/10.1163/1876312X-04402007

Lanes, G.O. & Azevedo, C.O. (2008) Phylogeny and Taxonomy of Sclerodermini (Hymenoptera, Bethylidae, Epyrinae). *Insect Systematics and Evolution*, 39, 55–86. https://doi.org/10.1163/187631208788784165

Lanes, G.O., Kawada, R., Azevedo, C.O. & Brothers, D. (2020) Revisited morphology applied for Systematic of flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, 4752 (1), 1–127. https://doi.org/10.11646/zootaxa.4752.1.1

Legalov, A.A., Nazarenko, V.Y. & Perkovsky, E.E. (2018) A new genus of fungus weevils (Coleoptera: Anthribidae) in Rovno amber. *Fossil Record*, 21, 207–212. https://doi.org/10.5194/fr-21-207-2018

Legalov, A.A., Nazarenko, V.Y. & Perkovsky, E.E. (2019) New weevils (Coleoptera: Curculionidae) from Rovno Amber. *Paleontological Journal*, 53(10), 63–77. https://doi.org/10.1134/S0031030119100101

Lucena, D.A.A. & Melo, G.A.R. (2018) Chrysidid wasps (Hymenoptera: Chrysididae) from Cretaceous Burmese amber: phylogenetic affinities and classification. *Cretaceous Research*, 89, 279–291. https://doi.org/10.1016/j.cretres.2018.03.018

Martynova, K.V., Perkovsky, E.E., Olmi, M. & Vasilenko, D.V. (2019) New records of Upper Eocene chrysidoid wasps (Hymenoptera: Chrysidoidea) from basins of Styr and Stokhod rivers (Rovno Amber). *Paleontological Journal*, 53(10), 998–1023. https://doi.org/10.1134/S0031030119100125

Melo, G.A.R. & Lucena, D.A.A. (2019) †Chrysobythidae, a new family of chrysidoid wasps from Cretaceous Burmese amber (Hymenoptera, Aculeata). *Historical Biology*, 1–13. https://doi.org/10.1080/08912963.2019.1570184

Nadein, K.S. & Perkovsky, E.E. (2019) Small and common: the oldest tropical Chrysomelidae (Insecta: Coleoptera) from the lower Eocene Cambay amber of India. *Alcheringa: An Australasian Journal of Palaeontology*, 43 (4), 597-611

https://doi.org/10.1080/03115518.2019.1622780

Nel, A. & Brasero N. (2010) Oise amber. *In*: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 137–148.

Nel, A. & Bourguet, E. (2006) Termite of the Early Eocene amber of France (Isoptera: Mastotermitidae, Kalotermitidae). *Neues Jahrbuch fur Geologie und Paläontologie*, 2006 (2), 101–115.
https://doi.org/10.1127/njgpm/2006/2006/101

Nel, A., De Ploëg, G., Dejax, J., Dutheil, D., Franceschi, D., Gheerbrant, E., Godinot, M., Hervet, S., Menier, J.-J., Augé, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J., Hua, S., Jossang, A., Lapparent de Broin, F., Pozzi, J.-P., Paicheler, J.-C., Bouchet, F. & Rage, J.-C. (1999) An exceptional Sparnacian locality with plants, arthropods and vertebrates (Earliest Eocene, MP7): Le Quesnoy (Oise, France). *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science*, 329, 65–72.
https://doi.org/10.1016/S1251-8050(99)80229-8

Nixon, K. C. (2002) WinClada, version 1.00.08. Published by the author, Ithaca, New York.

Olmi, M., Rasnitsyn, A.P. & Guglielmino, A. (2010) Revision of rock fossils of Dryinidae and Embolemidae (Hymenoptera: Chrysidoidea). *Zootaxa*, 2499, 21–38.
https://doi.org/10.11646/zootaxa.2499.1.2

Olmi, M., Perkovsky, E. E., Martynova, K. V., Contarini, M., Bückle, C. & Guglielmino, A. (2020) An important intermediate step in the evolution of pincer wasps: an extraordinary new type of chela from mid-Cretaceous Burmese amber (Hymenoptera, Dryinidae). *Cretaceous Research*, 104420.
https://doi.org/10.1016/j.cretres.2020.104420

Peinado, J., Nel, A. & Waller, A. (2006). A dryinid wasp in Early Eocene amber from the Paris Basin (Hymenoptera: Dryinidae). *Zootaxa*, 1168, 31–41.
https://doi.org/10.11646/zootaxa.1168.1.3

Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Peterse, M., Lanfear, R., Diez, P.A., Heraty, J., Kjer, K.M., Klopfstein, S., Meier, R., Polidori, C., Schmitt, T., Liu, S., Zhou, X., Wappler, T., Rust, J., Misof, B. & Niehuis, O. Evolutionary History of the Hymenoptera. *Current Biology*, 27, 1013–1018.

https://doi.org/10.1016/j.cub.2017.01.027

Perkovsky, E.E. (2016) A new species of Micromalthidae (Coleoptera) from the Rovno amber: 1. Adult morphology. *Paleontological Journal*, 50 (3), 293–296. https://doi.org/10.1134/S0031030116030047

Perkovsky, E.E. (2018) Only a half of species of Hymenoptera in Rovno amber is common with Baltic amber. *Vestnik Zoologii*, 52, 353–360. https://doi.org/10.2478/vzoo-2018-0037

Perkovsky, E.E. & Fedotova, Z.A. (2016) *Rovnodiplosis eduardi* gen. et sp. nov., the first record of a fossil gall midge of the supertribe Mycodiplosidi (Diptera, Cecidomyioidea, Cecidomyiidae) in the Late Eocene of the Rovno amber. *Paleontological Journal*, 50, 1027–1032. https://doi.org/10.1134/S0031030116090124

Perkovsky, E.E. & Wegierek, P. (2018 [2017]). Aphid-*Buchnera*-Ant symbiosis, or why are aphids rare in the tropics and very rare further south? *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 107 (2–3), 297–310. https://doi.org/10.1017/S1755691017000147

Perrichot, V., Engel, M.S., Nel, A., Ortega-Blanco, J., Delclòs, X., Soriano, C., Lohrmann, V. & Tafforeau, P. (2014) "False ants" from the Cretaceous (Hymenoptera: Chrysidoidea: Falsiformicidae). *Mitteilungen des Entomologischen Vereins Stuttgart*, 49, 26.

Perrichot, V. & Nel, A. (2008) Eocene bethylid wasps from French amber (Hymenoptera: Bethylidae). *Neues Jahrbuch für Geologie und Paläontologie*, 248 (1), 91–101. https://doi.org/10.1127/0077-7749/2008/0248-0091

Prentice, M.A., Poinar, G.O., Jr. & Milki, R. (1996) Fossil scolebythids (Hymenoptera: Scolebythidae) from Lebanese and Dominican amber. *Proceedings of the Entomological Society of Washington*, 98 (4), 802–811.

Ramos, M.S. & Azevedo, C.O. (2012) Revision of *Eupsenella* Westwood, 1874 (Hymenoptera, Bethylidae). *Zootaxa*, 3539, 1–80. https://doi.org/10.11646/zootaxa.3539.1.1

Ramos, M.S. & Azevedo, C.O. (2018) Revisited phylogeny of Bethylinae (Hymenoptera, Bethylidae) solves basal polytomy. *Insect Systematics and Evolution*, 2018, 1–51. [online only] https://doi.org/10.1163/1876312X-00002202

Ramos, M.S., Perkovsky, E.E., Rasnitsyn, A.P. & Azevedo, C.O. (2014) Revision of Bethylinae fossils (Hymenoptera: Bethylidae) from Baltic, Rovno and Oise amber, with comments on the Tertiary fauna of the subfamily. *Neues Jahrbuch fur Geologie und Paläontologie*, 271, 203–228. https://doi.org/10.1127/0077-7749/2014/0385

Rasnitsyn, A.P. (1975) Hymenoptera Apocrita of Mesozoic. *Transactions of the Palaeontological Institute, Akademii Nauk SSSR*, 147, 1–134.

Rasnitsyn, A.P. (1990) Hymenopterans. Vespida. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta*, 239, 177–205 (In Russian).

Rasnitsyn, A.P. (1996) New Early Cretaceous Embolemidae (Vespida = Hymenoptera: Chrysidoidea). *Memoirs of the Entomological Society of Washington*, 17, 183–187.

Ronquist, F. (1999) Phylogeny of the Hymenoptera (Insecta): The state of the art. *Zoologica Scripta*, 28, 3–11. https://doi.org/10.1046/j.1463-6409.1999.00019.x

Ronquist, F., Rasnitsyn, A.P., Roy, A., Eriksson, K. & Lindgren, M. (1999) Phylogeny of the Hymenoptera: a cladistic reanalysis of Rasnitsyn's (1988) data. *Zoologica Scripta*, 28, 13–50. https://doi.org/10.1046/j.1463-6409.1999.00023.x

Sokoloff, D.D, Ignatov, M.S., Remizowa, M.V, Nuraliev, M.S., Blagoderov, V., Garbout, A. & Perkovsky, E.E. (2018) Staminate flower of *Prunus s. l.* (Rosaceae) from Eocene Rovno amber (Ukraine). *Journal of Plant Research*, 131, 925–943. https://doi.org/10.1007/s10265-018-1057-2

Terayama, M. (2003) Phylogenetic Systematics of the Family Bethylidae (Insecta: Hymenoptera) Part I. Higher classification. *Academic Reports of the Faculty of Engineering of Tokyo Polytechnic University*, 26, 1–14.

Wang, B., Rust, J., Engel, M.S., Szwedo, J., Dutta, S., Nel, A., Fan, Y., Meng, F.W., Shi, G.L., Jarzembowski, E.A., Wappler, T., Stebner, F., Fang, Y., Mao, L.M., Zheng, D.R. & Zhang, H.C. (2014) A diverse paleobiota in early Eocene Fushun amber from China. *Current Biology*, 24, 1606-1610. https://doi.org/10.1016/j.cub.2014.05.048

Zhang, Q., Rasnitsyn, A.P., Olmi, M., Martynova, K.V. & Perkovsky, E.E. (2020) First scolebythid wasp (Hymenoptera: Chrysidoidea, Scolebythidae) in mid-Cretaceous Burmese amber. *Palaeoentomology*, 3 (1), 41–45.

APPENDIX 1. Character list.

1. Head, ratio LH/WH: (0) wider than long; (1) longer than wide; (2) as long as wide.

2. Head shape, lateral view: (0) oval; (1) rectangular; (2) triangular.

3. Number of antennomeres: (0) 12; (1) 13.

4. Torulus: (0) projected; (1) reduced.

5. Scape length: (0) short, ≤ than 2 × pedicel length; (1) long, > than 2 × pedicel length.

6. Scape apical width: (0) wider than base; (1) as wide as base.

7. Pedicel shape: (0) progressively widening apicad; (1) evenly wide.

8. Pedicel length: (0) wider than long; (1) about as long as wide; (2) longer than wide.

9. Flagellomere I length: (0) shorter than pedicel; (1) about as long as pedicel; (2) longer than pedicel.

10. Length of antenna: (0) long, reaching at least posterior half of dorsal pronotal area; (1) short, reaching at most anterior half of dorsal pronotal area.

11. Relative size of ventral tooth: (0) distinctly larger than others; (1) equally-sized.

12. Exposition of clypeal base, dorsal view: (0) covered by frons; (1) not covered by frons.

13. Median clypeal carina: (0) high, in lateral view; (1) short, in lateral view.

14. Number of maxillar palpomeres: (0) 6; (1) 5; (2) 4; (3) 3; (4) 2; (5) 1.

15. Number of labial palpomeres: (0) 4; (1) 3; (2) 2; (3) 1.

16. Eye: (0) multifaceted; (1) with very few facets.

17. Eye outline: (0) protuberant; (1) not protuberant.

18. Eye length, dorsal view: (0) long, HE > 0.38 × LH; (1) short, HE < 0.33 × LH.

19. Eye shape in lateral view: (0) elongate; (1) circular.

20. Eye setation: (0) scarce or nearly so; (1) abundant.

21. Ocelli: (0) present; (1) absent.

22. Position of posterior ocelli: (0) far from vertex crest, posterior ocelli distant from vertex crest at least DAO; (1) closed to vertex crest, posterior ocelli distant from vertex crest less than DAO.

23. Position of anterior margin of anterior ocellus: (0) posterior to supra-ocular line; (1) anterior to supra-ocular line.

24. Ventral profile of gena in lateral view: (0) curved; (1) angled.

25. Frontal line: (0) present; (1) absent.

26. Frontal line: (0) long, touching anterior ocellus; (1) short, not touching anterior ocellus.

27. Shape of dorsal pronotal area: (0) narrow anteriorly; (1) wide anteriorly.

28. Length of anterior region of pronotal collar: (0) long, pronotal collar more than 0.16 × pronotal disc length, visible dorsally; (1) short, pronotal collar less than 0.14 × pronotal disc length, not visible dorsally.

29. Length of dorsal pronotal area, dorsal view: (0) short, when median width more than median length; (1) median-sized, when median width and length are equally-sized; (2) elongate, when median width less than median length.

30. Humeral angle of dorsal pronotal area, dorsal view: (0) rounded; (1) angulate.

31. Posterior margin of dorsal pronotal area, dorsal view: (0) incurved; (1) outcurved; (2) almost straight.

32. Prosternum length, maximum length/maximum width ratio, ventral view: (0) long, at least 1.5 × longer than wide; (1) short, at most as long as wide.

33. Mesoscutum: (0) anteromesoscutum and mesoscutellum undivided; (1) anteromesoscutum and mesoscutellum clearly outlined.

34. Length of anteromesoscutum: (0) long, when longer than dorsal pronotal area; (1) medium-sized, as long as half of dorsal pronotal area; (2) short, when shorter than half of dorsal pronotal area.

35. Notaulus: (0) present; (1) absent.

36. Parapsidal signum: (0) present; (1) absent.

37. Length of mesoscutellum: (0) long, at least 0.60 × longer than basal width; (1) short, less than 0.50 × basal width.

38. Mesoscutum-mesoscutellar sulcus: (0) present; (1) absent.

39. Mesopleuron profile, dorsal view: (0) flat; (1) bulging.

40. Tegula: (0) present; (1) absent.

41. Aptery: (0) present; (1) absent.

42. Microptery: (0) present; (1) absent.

43. Brachyptery: (0) present; (1) absent.

44. Macroptery: (0) present; (1) absent.

45. Costal cell (C) of forewing: (0) present; (1) absent.

46. Costal cell (C) of forewing, size: (0) wide; (1) narrow.

47. Radial cell (R) of forewing: (0) closed; (1) opened.

48. First cubital cell (1Cu) of forewing: (0) opened; (1) closed.

49. First cubital cell (1Cu) of forewing, size: (0) as long as Radial cell; (1) shorter than Radial cell.

50. Second cubital cell (2Cu) of forewing: (0) opened; (1) closed.

51. First medial cell (1M) of forewing: (0) closed; (1) opened.

52. First radial 1 cell (1R1) of forewing: (0) closed; (1) opened.

53. Rs+M vein of forewing: (0) present; (1) absent.

54. Rs+M vein of forewing, shape: (0) angled; (1) straight.

55. Second radial 1 cell (2R1) of forewing: (0) closed; (1) opened.

56. Second radial 1 cell (2R1) of forewing: (0) lanceolate; (1) subcircular.

57. Third abscissa of Cu of forewing: (0) present; (1) absent.

58. Jugal lobe of hind wing: (0) large; (1) reduced.

59. Protrochanter insertion at coxa: (0) medially; (1) apically.

60. Profemur width, lateral view: (0) wide, more than 0.6 × as wide as long; (1) narrow, less than 0.45 × as wide as long.

61. Tarsal claws: (0) simple; (1) bifid; (2) trifid.

62. Claw shape, frontal or lateral views: (0) curved; (1) angled.

63. Metanotum median length: (0) developed; (1) reduced.

64. Metapectal-propodeal complex: (0) long, longer than wide; (1) short, wider than long.

65. Propodeal spiracle position: (0) on lateral surface of metapectal-propodeal complex; (1) on dorsal surface of metapectal-propodeal complex.

66. Spine of posterior corner of metapectal-propodeal complex: (0) present; (1) absent.

67. Petiole: (0) root and body fused; (1) root and body divided.

68. Metasomal segment II: (0) as long as other segments; (1) distinctly longer than other segments.

69. Dimorphism sexual: (0) strong; (1) absent or nearly so.

APPENDIX 2. Data matrix of 69 characters used in the cladistic analyses.

										1										2			
Taxa/Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**
Clystopsenella	2	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1
Bethylus	1	2	0	0	1	1	1	1	1	0	1	0	0	1	2	0	0	0	0	0	0	1	0
Eupsenella	0	2	1	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Lytopsenella	2	2	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Sierola	2	2	1	0	1	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0
Bakeriella	2	0	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Epyris	2	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Holepyris	1	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
†*Elektroepyris*	2	2	1	0	1	0	1	1	2	1	0	0	1	1	1	0	0	0	0	0	0	0	1
†*Cretabythus*	2	0	1	?	1	1	1	1	0	0	0	1	1	0	?	0	0	0	0	?	0	1	?
†*Holopsenella*	0	0	0	0	1	0	1	1	2	0	0	1	1	0	0	0	0	0	0	0	0	0	1
†*Lancepyris*	2	0	1	0	1	1	1	2	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Pycnomesitius	2	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Sulcomesitius	2	0	1	0	1	0	1	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Apenesia	0/2	0	1	0	1	0	0	1	1	1	0	1	1	2	1	0/1	0	0	0	0	0/1	1	0
Dissomphalus	1/2	0	1	0	1	0	0	1	0/1	0/1	0	1	1	0	1	0/1	0	0	0	0/1	0/1	0	0
Pristocera	1/2	0	1	0	1	0	0	1	1/2	1	0	1	0	0	1	0/1	0	0	0	0	0/1	0	1
Pseudisobrachium	1/2	0	1	0	1	0	0	1	1	0/1	0	1	0/1	0	1	0/1	0	0	0	0/1	0/1	0	0
†*Gynopteron*	2	0	1	0	1	0	0	2	0	0	0	1	0	2	1	0	0	0	0	0	0	1	0
Allobethylus	1	1	1	1	1	0	1	1	0	1	0	1	0	0	2	0	1	0	0	0	0	0	0
Cephalonomia	2	1	0	1	1	1	1	1	0	1	0	1	0	1/2	2/3	0	1	1	1	0	0/1	0	0
Sclerodermus	2	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	1	1	1	0	0/1	0	0

	2						3										4						
Taxa/Characters	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**
Clystopsenella	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Bethylus	1	0	0	1	1	0	0	1	1	1	1	1	0	0	1	1	0	0	0	1	0	0	1
Eupsenella	1	0	0	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0	0	1	0	0	1
Lytopsenella	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	1
Sierola	1	0	1	1	1	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	1
Bakeriella	0	0	1	1	0	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1
Epyris	0	0	1	1	0	2	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1
Holepyris	0	0	1	1	0	1	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1
†*Elektroepyris*	1	0	1	1	0	2	0	2	1	1	2	0	?	1	?	0	0	0	0	0	0	0	1
†*Cretabythus*	0	0	?	?	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
†*Holopsenella*	0	?	?	1	0	0	0	0	1	1	0	0	1	1	?	0	0	0	0	0	0	0	1
†*Lancepyris*	0	1	-	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1
Pycnomesitius	0	0	0	1	0	0	1	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1
Sulcomesitius	0	0	0	1	0	0	1	2	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1
Apenesia	0	0/1	1	1	0	0/1	0	0/2	1	0/1	0	0/1	0/1	1	0/1	0	0/1	1	0	0	0	0	1
Dissomphalus	0	0/1	1	1	0	0/1	0	0/2	1	0/1	0	0/1	0/1	1	0/1	0	0/1	1	0	0	0	0	1
Pristocera	0	0/1	1	1	0	0/1	0	2	1	0/1	0	0/1	0/1	1	0/1	0	0/1	1	0	0	0	0	1
Pseudisobrachium	0	0/1	1	1	0	0/2	0	0/2	1	0/1	0	1	0/1	1	0/1	0	0/1	1	0	0	0	0	1
†*Gynopteron*	0	0	1	1	1	1	0	0	1	1	1	0	0	?	?	1	0	0	0	0	0	0	1
Allobethylus	0	0	1	1	0	2	0	0	1	1	2	0	0	1	1	0	0	0	0	0	0	0	1
Cephalonomia	0	1	-	1	1	1	0	0	1	0/1	2	1	0	1	0/1	0	0/1	1	1	1	0	1	-
Sclerodermus	0	0	1	1	0	2	0	2	1	0/1	1	0	0	1	0/1	1	0/1	1	1	1	0	1	-

	4			5										6									
Taxa/Characters	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Clystopsenella	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	1	0	1
Bethylus	0	1	1	0	1	1	0	0	1	-	1	0	0	0	1	1	1	1	1	1	1	0	1
Eupsenella	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	0	1
Lytopsenella	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	1	1	0	1
Sierola	0	1	1	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	0	1
Bakeriella	0	1	1	0	1	1	1	-	1	-	1	0	0	0	1	0	1	0	1	1	0	0	1
Epyris	0	1	1	0	1	1	1	-	1	-	1	0	0	0	1	0	1	0	1	1	0	0	1
Holepyris	0	1	1	0	1	1	1	-	1	-	1	0	0	0	1	0	1	0	1	1	0	0	1
†*Elektroepyris*	0	1	0	0	1	1	1	-	1	-	0	0	0	0	?	0	1	1	?	1	?	0	?
†*Cretabythus*	0	1	0	1	0	0	0	1	0	0	1	?	0	1	?	0	1	1	?	1	1	0	?
†*Holopsenella*	0	1	0	1	0	0	0	1	0	0	1	?	0	0	1	0	1	1	?	1	1	0	?
†*Lancepyris*	0	1	0	0	1	1	0	1	0	0	1	0	0	0	1	0	1	1	?	1	1	0	?
Pycnomesitius	0	1	0	0	1	1	1	-	1	-	1	0	0	0	1	0	1	1	1	0	1	1	1
Sulcomesitius	0	1	0	0	1	1	1	-	1	-	1	0	0	1	1	0	1	1	1	0	1	1	1
Apenesia	0	1	0	0	1	1	1	-	1	-	1	0	0	1	1	0	0/1	0	0	1	1	0	0
Dissomphalus	0	1	0	0	1	1	1	-	1	-	1	0	0	1	1	0	0/1	0	0	1	1	0	0
Pristocera	0	1	0	0	1	1	1	-	1	-	1	0	0	1	0/1	0	0/1	0	0	1	1	0	0
Pseudisobrachium	0	1	0	0	1	1	1	-	1	-	1	0	0	1	1	0	0/1	0	0/1	1	1	0	0
†*Gynopteron*	0	1	0	0	1	1	1	-	1	-	1	?	0	0	?	?	0	0	?	0	?	0	?
Allobethylus	0	1	0	0	1	1	1	-	1	-	1	0	0	1	0	0	1	1	1	1	1	0	?
Cephalonomia	0/1	0	-	0	1	1	1	-	1	-	1	1	0	1	0	0	1	1	0	1	1	0	1
Sclerodermus	0	0	-	0	1	1	1	-	1	-	1	1	0	0	0	0	1	1	0	1	1	0	1

CAPÍTULO III

Synopsis of the fossil flat wasps Epyrinae (Hymenoptera, Bethylidae), with description of three new genera and ten new species[3]

ABSTRACT

The subfamily Epyrinae is the most common in the bethylid fossil record. Its geological history ranges from the Eocene to the Pleistocene and it is the only subfamily that has no records in the Cretaceous. Here we revise, diagnose, and illustrate known epyrine fossil wasps. A new genus is proposed, †*Gloxinius* Colombo & Azevedo gen. nov., to contain the species †*Gloxinius bifossatus* (Brues, 1939) comb. nov., transferred from *Epyris* Westwood, 1832. The species †*Chlorepyris concaptus* (Brues, 1933) comb. nov., †*Chlorepyris invelatus* (Brues, 1933) comb. nov., and †*Chlorepyris setosus* (Brues, 1933) comb. nov. are transferred from *Epyris* Westwood, 1832 to *Chlorepyris* Kieffer, 1913. Three species are transferred from *Epyris* Westwood, 1832 to Pristocerinae: †*Merascylla* Colombo & Azevedo gen. nov. is proposed to contain †*Merascylla atavella* (Cockerell, 1920) comb. nov. †*Pseudisobrachium elatus* (Brues, 1933) comb. nov., and †*Pseudisobrachium inhabilis* (Brues, 1923) comb. nov. are transferred to *Pseudisobrachium* Kieffer, 1904. One species is transferred from *Epyris* Westwood, 1832 to Scleroderminae: †*Mael* Colombo & Azevedo gen. nov. is proposed to contain †*Mael longiceps* (Brues, 1923) comb. nov. Ten new species are described from Baltic and Rovno ambers: †*Chlorepyris deploegi* Colombo & Azevedo sp. nov., †*Chlorepyris engeli* Colombo & Azevedo sp. nov., †*Chlorepyris hopei* Colombo & Azevedo sp. nov., †*Chlorepyris jouaulti* Colombo & Azevedo sp. nov., †*Chlorepyris mckellari* Colombo & Azevedo sp. nov., †*Chlorepyris meunieri* Colombo & Azevedo sp. nov., †*Chlorepyris neli* Colombo & Azevedo sp. nov., †*Chlorepyris perrichoti* Colombo & Azevedo sp. nov., †*Holepyris rasnitsyni* Colombo & Azevedo sp. nov., and †*Holepyris terayamai* Colombo & Azevedo sp. nov. The species †*Laelius nudipennis* Brues, 1933 is no longer classified as Bethylidae and it is transferred to Platygastroidea *incertae sedis*. Eighty-one fossil species are now recognised in Bethylidae, with 30 belonging to Epyrinae and distributed within six genera. A key for fossil epyrines is provided.

Keywords: Aculeata, amber; Chrysidoidea; Platygastroidea; revisionary Systematics.

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INTRODUCTION

Epyrinae have a complex taxonomic history. The classification of this group has varied from the tribe (Kieffer 1914; Evans 1964) to the subfamily level (Berland 1928; Alencar & Azevedo 2013). Currently, it is proposed as a subfamily based on phylogenetic analyses of morphological data (Alencar & Azevedo 2013) and recovered as a monophyletic group by molecular (Carr *et al.* 2011).

Epyrinae are the second most diverse subfamily in Bethylidae, with c. 930 described species worldwide distributed into 12 valid genera (Azevedo *et al.* 2018; Colombo *et al.* 2020*b*). They are also the most diverse subfamily in terms of known fossil species (see Table 1 in Azevedo *et al.* 2018, p. 9–10). The status and relationships between the genera were reviewed by Alencar and Azevedo (2013) and we adopt their subfamily concept, which is similar to the one proposed by Evans (1964) for Epyrini.

Epyrinae represent the first described fossils of flat wasps. *Epyris staphylinoides* (Hope, 1837) was described by Hope (1837) based on Pleistocene copal resin and "animé" gum from Zanzibar or Madagascar copal. Since then, the epyrine fossil record has been considerably increased, currently encompassing 25 species. Most fossil species of Epyrinae, 14 in total, were described by Brues (1910, 1923, 1933, 1939). Of these, 13 species were found in the Priabonian Baltic amber (succinite), and one was based on exoskeleton impression from the late Priabonian lacustrine, shale in the Florissant Formation of Colorado, U.S.A. (Brues 1910).

The fossil species of Epyrinae are distributed into six genera, of which five have extant species (*Anisepyris* Kieffer, 1905; *Chlorepyris* Kieffer, 1913; *Epyris* Westwood, 1832; *Holepyris* Kieffer, 1904; and *Laelius* Ashmead, 1893), while a sixth is based exclusively on fossils (†*Gloxinius* Colombo & Azevedo **gen. nov.**). Among these genera, *Chlorepyris* Kieffer, 1913 is the most diverse, with twelve fossil species, followed by *Holepyris* Kieffer, 1904, with seven species.

Despite changes in the taxonomy of the family (Azevedo *et al.* 2018), the classification and revision of diagnostic characters in the epyrine fossil records have never been challenged. This study aims to revise all previously described fossils of epyrine wasps, providing redescriptions and illustrations. We describe and illustrate three new genera and ten new species and provide the first key for all fossil species of Epyrinae. This study represents the first comprehensive taxonomic revision of fossil Epyrinae.

MATERIAL AND METHODS

The new pieces in this study are from Baltic and Rovno ambers. The Rovno amber pieces were mined from the Pugach quarry, Klesiv, Rivne Oblast (Klesov, Rovno region) except SIZK UA-68, which was mined in either the Pugach or Volnoje quarry, Dubrovytsia, Rivne Oblast, Ukraine (Dubrovitsa, Rovno region) and obtained from the state-owned Ukramber factory (Rovno). All Rovno amber material belongs to Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine in Kiev (SIZK), as assigned in the text. The Baltic amber pieces, described here for the first time, were extracted from an amber mine in Yantarny (Kaliningrad Oblast, Russia), in the Prussian Formation dating to the upper Eocene, and belong to the Paleontological Institute, Russian Academy of Sciences (PIN).

Photos of holotypes were provided by curators from the following collections: American Museum of Natural History, U.S.A. (AMNH), Los Angeles County Museum of Natural History, U.S.A. (LACM), Museum of Comparative Zoology, U.S.A. (MCZ), Muséum National d'Histoire Naturelle, France (MNHN), the Natural History Museum, United Kingdom (NHM), Oxford University Museum of Natural History (OUMNH), Schmalhausen Institute of Zoology of National Academy of Sciences, Ukraine (SIZK), and the Forschungsinstitut und Naturmuseum Senckenberg, Germany (SMF). Some material, which was said to be deposited in the Evers, Königsberg and Strong collections is unavailable and probably lost. In this study, we examine their records and original descriptions, which we discuss in the text. We tried to find all types assigned to be deposited in the Geological Institution and Amber Collection of the University of Königsberg. Nevertheless, because of World War II, parts of the collection of Baltic Amber from the Кенигсбергский университет (University of Königsberg) were transferred to the Volpriehausen potash mine near Göttingen (Gehler *et al.* 2018). The former Königsberg Amber Collection (Baltic amber) has now been incorporated into Göttingen's Geoscience Museum (Reich *et al.* 2015). When contacted, the curators of Göttingen's amber collections confirmed that the types of Bethylidae from Königsberg must be considered to have been lost during World War II.

The stratigraphic distribution of the fossils follows Iturralde-Vinent & MacPhee (1996) for Dominican amber from the Miocene, Cohen *et al*. (2020) for Rovno amber from the Priabonian upper Eocene and for Baltic amber from the Priabonian upper Eocene, Nel

& Brasero (2010) for Oise amber from Ypresian lowermost Eocene, Prothero & Sanchez (2004) for Florissant Formation from the Priabonian upper Eocene, Ross & Self (2014) for the Bouldnor Formation from the Priabonian upper Eocene, Petrulevičius *et al.* (2011) for the Rott Formation from the Chattian upper Oligocene, Geirnaert (2002) for Zanzibar copal from the Pleistocene and Shi *et al.* (2012) for Burmese amber from the Cenomanian mid-Cretaceous.

The terms applied to the integument sculpture follow Harris (1979) and those applied to general morphology follow Lanes *et al.* (2020).

The generic names are an allusion to the characters of the Japanese fantasy manga *The Seven Deadly Sins* (*Nanatsu no Taizai*) written and illustrated by Nakaba Suzuki, as specified in the etymologies. All new species are named after taxonomists who have described at least one fossil species of flat wasps, and whose names have never previously been used for any species of this family.

The key proposed here is modified from Azevedo *et al.* (2018). The species †*Epyris deletus* Brues, 1910, †*Epyris rectinervis* (Cockerell, 1921), and †*Epyris tenellus* Statz, 1938 were excluded from the key because of their poorly preserved fossils, which lack reliable characteristics to key them.

The drawings were made with a camera lucida adapted to a Leica DM 2500 microscope, then scanned into Adobe Illustrator CS6 version 23.0.3. The images were taken under a Leica Z16 APO stereomicroscope coupled to a Leica DFC 2 video camera by Leica Microsystems (Switzerland) using a modular dome illumination system per Kawada & Buffington (2016). Helicon Focus was used to combine the images obtained at different focal heights (HeliconSoft).

RESULTS

Systematic palaeontology

Family **Bethylidae** Haliday, 1839

Subfamily **Epyrinae** Kieffer, 1914

Genus ***Anisepyris*** Kieffer, 1905

†***Anisepyris gradatus*** Sorg, 1988

Figure 1

Holotype. Female, piece code SMF-Be 559, deposited in the SMF collection.

Diagnosis (based on the original description and illustration provided by the curator). Body length ~6.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma castaneous; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Mandible apparently tetradentate. Clypeus with rounded median lobe, visible dorsally, lateral lobe reduced. Median clypeal carina outlined, higher than frons. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomere as long as wide; flagellar pubescence appressed; pedicel as long as flagellomere I, rectangular, apex dilated. Eye located far from mandibular base, setose, bulging. Frons coriaceous, punctures large. Frontal line not visible. Frontal angle of ocellar triangle acute. Anterior ocellus anterior to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina complete; posterior pronotal sulcus present, bearing sequence of foveae. Posterior mesofurcal pit drop-shaped. Metafurcal pit not visible. Notauli present, narrow, converging posteriorly. Parapsidal signum shorter than notaulus. Fore wing with four distal flexion lines; 2r-rs&Rs vein tubular, long, well pigmented, straight, not converging posteriorly to R1 vein. Pterostigma subcircular. Mesoscutum-mesoscutellar sulcus present, incurved medially. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. This species was proposed by Sorg (1988, Figs. 23a, 23b, and 41a) and is hitherto the sole fossil species known in *Anisepyris* Kieffer, 1905. Barbosa & Azevedo (2018, p. 132) redescribed it and allocated it into the *cupreolus* species-group. This species, however, is missing in their key for females of the *cupreolus* species-group (p. 111). Moreover, †*A. gradatus* Sorg, 1988 keys out to the *amazonicus* species-group (Barbosa & Azevedo 2018, p. 12) since it has tetradentate mandibles (see Fig. 1B and Sorg 1988, Fig. 23a, p. 90) with the distal teeth not equally sized and the posterior mesopleural foveae absent.

†*Anisepyris gradatus* Sorg, 1988 is morphologically similar to *A. beori* Barbosa & Azevedo, 2018, and *A. beori* Barbosa & Azevedo, 2018 and *A. analis* (Cresson, 1872) are morphologically similar (Barbosa & Azevedo 2018, p. 45). Indeed, †*A. gradatus* Sorg, 1988, *A. beori* Barbosa & Azevedo, 2018 and *A. analis* (Cresson, 1872) are morphologically similar in sharing tetradentate mandibles; a median clypeal carina; very

long scapes, and pedicels as long as flagellomere I, with appressed flagellar pubescence; extremely large and setose eyes; a dorsal pronotal area wider than long, with the transverse pronotal carina complete and the posterior pronotal sulcus present, with a sequence of foveae; narrow notauli, converging posteriorly; fore wings with four distal flexion lines, as well as a tubular, long, well pigmented and straight 2r-rs&Rs vein, not converging posteriorly to the R1 vein; non-spinose mesotibiae.

The main differences between these three species are that the median clypeal lobe has a median carina shorter than the frons in *A. analis* (Cresson, 1872), and higher than the frons in †*A. gradatus* Sorg, 1988 and *A. beori* Barbosa & Azevedo, 2018 when seen in the lateral view; and the pterostigma is elongated in *A. analis* (Cresson, 1872) and subcircular in †*A. gradatus* Sorg, 1988 and *A. beori* Barbosa & Azevedo, 2018. Finally, †*A. gradatus* Sorg, 1988 occurred 15–20 million years ago, which, given the typical duration of insect species, adds further support to the conclusion that †*A. gradatus* Sorg, 1988 is a valid species.

Locality and age. Dominican amber, Burdigalian/Langhian terrestrial amber in the Dominican Republic. Miocene, 15 to 20 million years ago.

Genus ***Chlorepyris*** Kieffer, 1913

†***Chlorepyris deploegi*** Colombo & Azevedo **sp. nov.**

Figure 2

Derivation of name. This species is named after Gael De Ploëg, who described a fossil bethylid species.

Holotype. Male, piece code SIZK K-364. The sample was found in the piece and weighed 3.1 grams after primary treatment. Deposited in the SIZK collection.

Diagnosis. Body length ~4.7 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head as long as wide and subcircular, not globoid in lateral view. Mandible tetradentate. Clypeus with median lobe angular, lateral lobe reduced. Antenna long, surpassing posterior margin of metapectal-propodeal complex. Flagellomere longer than wide; flagellar pubescence erect; pedicel longer than flagellomere I, rectangular. Eye located far from mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small, very sparse. Frontal line not visible. Frontal angle of ocellar triangle obtuse. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior

pronotal sulcus absent. Posterior mesofurcal pit elongated. Metafurcal pit apparently circular. Notauli present, wide, converging posteriorly. Parapsidal signum shorter than notaulus. Fore wing with four distal flexion lines; 2r-rs&Rs vein tubular, long, well pigmented, angled, not converging posteriorly to R1 vein. Pterostigma rectangular. Mesopleuron with subalar impression connected with mesopleural suture, trabeculate; mesopleural suture connected with mesopleural epicoxal sulcus; lower mesopleural foveae delimited, not connected with mesopleural suture; transepisternal line present; mesopleural pit evident. Mesoscutum-mesoscutellar sulcus present, weakly incurved medially, wide, foveae indistinct. Metapectal-propodeal disc as long as wide; poorly preserved. Mesotibia without spines. Metasoma polished, weakly setose. Genitalia: paramere with apex straight, not arched inward, dorsal margin straight; basiparamere not visible; basivolsella not visible; aedeagus bottle-shaped, poorly preserved. Female unknown.

Remarks. This species is similar to †*Chlorepyris mckellari* **sp. nov.** in the presence of mandibles with four teeth, angular median clypeal lobe, pedicel longer than flagellomere I, eyes far from mandibular bases, anterior ocellus positioned posterior to supra-ocular line, and notauli. However, †*C. deploegi* **sp. nov.** has long antennae, surpassing the posterior margin of the metapectal-propodeal complex, as well as a dorsal pronotal area as long as wide, and fore wings with the 2r-rs&Rs vein angled. Conversely, †*C. mckellari* **sp. nov.** has short antennae, not surpassing the posterior margin of the mesoscuto-scutellar suture, a dorsal pronotal area longer than wide, and fore wings with the 2r-rs&Rs vein curved.

Locality and age. Klesiv, Rovno amber, Ukraine. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris concaptus*** (Brues, 1933)

Figure 3

Holotype. Female, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description and illustration). Body length 3.6 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black or dark castaneous; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Mandible tetradentate. Clypeus not visible. Antenna mid-sized, not surpassing posterior margin of metapectal-propodeal complex. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel as long as flagellomere I, apex dilated. Eye

apparently located far from mandibular base, glabrous, bulging. Frons weakly coriaceous. Frontal line not visible. Frontal angle of ocellar triangle acute. Anterior ocellus anterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum present. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma rectangular. Mesoscutum-mesoscutellar sulcus present, incurved medially. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished, setose. Male unknown.

Remarks. This species was originally placed in *Isobrachium* Förster, 1856 and later transferred to *Epyris* Westwood, 1832 by Azevedo *et al.* (2018). Brues (1933, p. 138–139) provided a detailed description of the holotype, as well as a drawing (Pl. 12, Fig. 77). He described the species as having the 'scutellum with a very small fovea at each side, connected by a narrow groove that bends sharply backward at each end'. He is referring to the presence of a mesoscutum-mesoscutellar sulcus, which is absent in *Epyris* Westwood, 1832. Among the extant genera of Epyrinae, only *Anisepyris* Kieffer, 1905 and *Chlorepyris* Kieffer, 1913 have a mesoscutum-mesoscutellar sulcus, which resembles the shape mentioned by Brues. We note that other characters support the attribution of this species to *Chlorepyris* Kieffer, 1913, including glabrous eyes, an ecarinate dorsal pronotal area without angulate anterior corners, and fore wings with 2r-rs&Rs present as a tubular vein.

The original description of this species was based on one specimen, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*C. concaptus* (Brues, 1933) does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris engeli*** Colombo & Azevedo **sp. nov.**

Figure 4

Derivation of name. This species is named after Michael Engel, who described various bethylid fossil species, genera, and subfamilies.

Holotype. female, piece code PIN 964/122. Deposited in the PIN collection.

Diagnosis. Body length ~3.6 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma light to dark castaneous; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Mandible with dorso-apical margin denticulate. Clypeus with median lobe apparently trapezoidal, lateral lobe reduced. Median clypeal carina well delimited, higher than frons, in lateral view. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres as long as wide; flagellar pubescence appressed; pedicel longer than flagellomere I, rectangular in dorsal view, apex dilated. Eye located far from mandibular base, glabrous, flat. Frons coriaceous, punctures absent. Frontal line narrow. Frontal angle of ocellar triangle obtuse. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus apparently absent. Parapsidal signum present. Fore wing with three distal flexion lines; 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma rectangular. Mesoscutum-mesoscutellar sulcus present, strongly incurved medially, inconspicuous, circular foveae distinct. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished.

Male unknown.

Remarks. *Chlorepyris engeli* is distinguished from its fossil congeners by its mandibles with denticulate dorso-apical margins and its mesoscutum-mesoscutellar sulcus, which is strongly incurved medially.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris gallicus*** (Perrichot & Nel, 2008)

Figure 5

Holotype. Male, piece code MNHN.F.A30297, deposited in the MNHN collection.

Diagnosis (based on original description and new illustration provided by the curator). Body length 1.3 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex,

petiole, antenna, and metasoma castaneous; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Mandibular teeth not visible. Clypeus with rounded median lobe, weakly visible dorsally, lateral lobe reduced. Median clypeal carina outlined, shorter than frons. Antenna long, surpassing posterior margin of metapectal-propodeal complex. Flagellomeres as long as wide; flagellar pubescence erect; pedicel as long as flagellomere I, rectangular. Eye located far from mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small, very sparse. Frontal line not visible. Frontal angle of ocellar triangle obtuse. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit drop-shaped. Metafurcal pit not visible. Notaulus apparently present, incomplete posteriorly. Parapsidal signum shorter than notaulus. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma rectangular. Mesoscutum-mesoscutellar sulcus present, incurved medially. Metapectal-propodeal disc longer than wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae not visible. Mesotibia without spines. Metasoma polished, setose. Genitalia not visible. Female unknown.

Remarks. This species was originally allocated in *Rhabdepyris* Kieffer, 1904 (Perrichot & Nel 2008) and was transferred to *Chlorepyris* Kieffer, 1913 by Azevedo *et al.* (2018). *Chlorepyris gallicus* (Perrichot & Nel, 2008) has glabrous eyes. Moreover, the male has antennae with a rather long flagellomere I, which is well separated from flagellomere II (Perrichot & Nel 2008), and the mesoscutum-mesoscutellar sulcus is present (absent in *Epyris* Westwood, 1832). These characteristics are diagnostic for *Chlorepyris* Kieffer, 1913 (see Azevedo *et al.* 2018).

Locality and age. Le Quesnoy, in Chevrières, Oise Department, France. Ypresian, 53 million years ago, lowermost Eocene.

†***Chlorepyris hopei*** Colombo & Azevedo **sp. nov.**

Figure 6

Derivation of name. This species is named after Frederick William Hope, who described the first fossil bethylid species.

Holotype. Female, piece code PIN 964/118. Deposited in the PIN collection.

Diagnosis. Body length ~2.3 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head as long as wide and subcircular, not globoid in lateral view. Mandible not visible. Clypeus not visible. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres as long as wide; flagellar pubescence appressed; pedicel longer than flagellomere I, rectangular. Eye located far from mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small, very sparse. Frontal line not visible. Frontal angle of ocellar triangle acute. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum not visible. Fore wing apparently with four distal flexion lines; 2r-rs&Rs vein tubular, long, weakly pigmented, curved, not converging posteriorly to R1 vein. Pterostigma subcircular. Mesopleuron not visible. Mesoscutum-mesoscutellar sulcus present, weakly incurved medially, wide, foveae distinct. Metapectal-propodeal disc as long as wide; poorly visible. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. This species is similar to †*Chlorepyris invelatus* (Brues, 1933) in sharing a pedicel longer than flagellomere I, lacking notauli, possessing fore wings with 2r-rs&Rs present as a tubular, long and curved vein, and possessing a mesoscutum-mesoscutellar sulcus that is incurved medially. However, †*C. hopei* **sp. nov.** has the anterior ocellus positioned posterior to the supra-ocular line and its dorsal pronotal area is as long as it is wide, whereas the anterior ocellus of †*C. invelatus* (Brues, 1933) is positioned anterior to the supra-ocular line and the dorsal pronotal area is longer than it is wide.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†*Chlorepyris invelatus* (Brues, 1933) **comb. nov.**

Holotype. Female, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description). Body length 4.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black or dark castaneous; wings hyaline. Head as long as wide, not globoid in lateral view. Mandible not visible. Clypeus not visible. Flagellomeres longer than wide; flagellar pubescence not

visible; pedicel longer than flagellomere I. Eye of moderate size. Frons weakly coriaceous. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Anterior ocellus situated anterior to supra-ocular line. Dorsal pronotal area longer than wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum present. Fore wing with distal flexion lines not visible and 2r-rs&Rs vein present. Pterostigma small. Mesoscutum-mesoscutellar sulcus present, straight medially. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished, setose. Male unknown.

Remarks. This species was originally placed in *Isobrachium* Förster, 1856. Azevedo *et al.* (2018) synonymised *Isobrachium* Förster, 1856 with *Epyris* Westwood, 1832 and transferred *E. invelatus* (Brues, 1933) to *Epyris* Westwood, 1832. Brues (1933, p. 139) provided a detailed description of the holotype, though unfortunately without drawings. He described the species as having a 'scutellum with a pair of small, deeply impressed foveae at base, connected by a straight transverse furrow'. Therefore, we conclude that this species does not belong to *Epyris* Westwood, 1832 due to the presence of the mesoscutum-mesoscutellar sulcus, uncommon in the latter genus. Moreover, Brues (1933) described the species as having a body covered with tiny-polished punctations, which support its classification as *Chlorepyris* Kieffer, 1913.

The original description of this species was based on three specimens, but they are all lost, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*C. invelatus* (Brues, 1933) does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris jouaulti*** Colombo & Azevedo **sp. nov.**

Figure 7

Derivation of name. This species is named after Corentin Jouault, who described various bethylid fossil species and genera.

Holotype. Male, piece code SIZK K-7725: a complete flat wasp embedded in a amber piece; air bubbles present, over the mesosoma and metasoma. The sample was cut from a clear amber piece and weighed 26.65 grams after primary treatment (Perkovsky *et al.* 2012). Deposited in the SIZK collection.

Syninclusions. SIZK K-7720 Ceratopogonidae [female of *Ceratopogon* Meigen, 1803]; SIZK K-7721 Formicidae [worker of *Lasius schiefferdeckeri* Mayr, 1868]; SIZK K-7722 Thripidae [*Praedendrothrips avus* Priesner, 1924, see Shmakov & Perkovsky 2009]; SIZK K-7723 Miridae; SIZK K-7724 Empididae, Collembola (Entomobryomorpha); SIZK K-7725 stellate trichomes; SIZK K-7726 Ceratopogonidae [male of *Monohelea clunipes* (Loew, 1850)]; SIZK K-7727 Encyrtidae [holotype of *Archaeocercus schuvachinae* Simutnik in Simutnik & Perkovsky 2018]; SIZK K-7728 Ceratopogonidae [female of *Brachypogon* Kieffer, 1899]. Legs of other arthropods and stellate trichomes present.

Diagnosis. Body length ~2.1 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head as long as wide and subcircular, not globoid in lateral view. Mandible apparently tetradentate. Clypeus not visible. Antenna mid-sized, not surpassing posterior margin of metapectal-propodeal complex. Flagellomeres as long as wide; flagellar pubescence appressed; pedicel longer than flagellomere I, rectangular. Eye located close to mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small, very sparse. Frontal line not visible. Ocelli not visible. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal not visible. Metafurcal not visible. Notaulus absent. Parapsidal signum present. Fore wing poorly preserved. Mesopleuron not visible. Mesoscutum-mesoscutellar sulcus present, weakly incurved medially, wide, foveae distinct. Metapectal-propodeal disc as long as wide, poorly preserved. Mesotibia without spines. Metasoma polished, glabrous. Genitalia not visible. Female unknown.

Remarks. This species is similar to †*Chlorepyris meunieri* **sp. nov.** by in having the antennae mid-sized and not surpassing the posterior margin of metapectal-propodeal complex, the dorsal pronotal area wider than long, lacking notauli, and possessing fore wings with a tubular and long 2r-rs&Rs vein. †*Chlorepyris jouaulti* **sp. nov.,** however, has tetradentate mandibles, eyes that are located close to the mandibular bases and a mesoscutum-mesoscutellar sulcus that is incurved medially, whereas †*C. meunieri* has pentadentate mandibles, eyes that are located far from the mandibular bases and a mesoscutum-mesoscutellar sulcus that is straight medially.

Locality and age. Klesiv, Rovno amber, Ukraine. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris mckellari*** Colombo & Azevedo **sp. nov.**

Figure 8

Derivation of name. This species is named after Ryan McKellar, who described various bethylid fossil species and genera.

Holotype. Female, piece code SIZK K-24565. Deposited in the SIZK collection.

Syninclusions. SIZK K-24566, Sciaridae.

Diagnosis. Body length ~2.5 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Mandible tetradentate. Clypeus with median lobe apparently angular, lateral lobe reduced. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres longer than wide; flagellar pubescence appressed; pedicel longer than flagellomere I, with cross-section subcircular. Eye located far from mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small, very sparse. Frontal line inconspicuous. Frontal angle of ocellar triangle obtuse. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area longer than wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit drop-shaped. Metafurcal pit circular. Notaulus present, wide. Parapsidal signum shorter than notaulus. Fore wing with four distal flexion lines, 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma subrectangular. Mesopleuron with subalar impression not connected with mesopleural suture, smooth; mesopleural suture not connected with mesopleural epicoxal sulcus; lower mesopleural foveae not delimited; transepisternal line absent; mesopleural pit as puncture. Mesoscutum-mesoscutellar sulcus present, weakly incurved medially, wide, circular foveae distinct. Metapectal-propodeal disc longer than wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished, glabrous. Male unknown.

Remarks. This species is similar to †*Chlorepyris neli* **sp. nov.** in having short antennae that do not surpass the posterior margin of mesoscuto-scutellar suture, the pedicels longer than flagellomeres I, the eyes located far from the mandibular bases, notauli present, parapsidal signum shorter than notauli, and fore wings with tubular, long and curved 2r-

rs&Rs vein. However, the dorsal pronotal area of †*Chlorepyris mckellari* **sp. nov.** is longer than it is wide and its mesoscutum-mesoscutellar sulcus is incurved medially, whereas the dorsal pronotal area of †*C. neli* **sp. nov.** is wider than it is long and its mesoscutum-mesoscutellar sulcus is straight medially.

Locality and age. Klesiv, Rovno amber, Ukraine. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris setosus*** (Brues, 1933) **comb. nov.**

Holotype. Female, piece code 13919, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description). Body length 4.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna black, and metasoma probably greenish metallic; wings hyaline. Head as long as wide, not globoid in lateral view. Mandible not visible. Clypeus not visible. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel as long as flagellomere I. Eye elongate, not bulging. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Anterior ocellus probably posterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notauli present, narrow, converging posteriorly. Parapsidal signum shorter than notaulus. Fore wing with distal flexion lines not visible, 2r-rs&Rs vein present. Pterostigma small, rectangular. Mesoscutum-mesoscutellar sulcus present, incurved medially. Metapectal-propodeal disc probably as long as wide; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished, setose. Male unknown.

Remarks. This species was originally allocated in *Rhabdepyris* Kieffer, 1904 and later transferred to *Epyris* Westwood, 1832 by Azevedo *et al.* (2018). Brues (1933, p. 140–141) provided a detailed description of the holotype, though without drawings. We note that the presence of a mesoscutum-mesoscutellar sulcus, which is incurved medially in †*C. setosus* (Brues, 1933), is diagnostic for *Chlorepyris* Kieffer, 1913, suggesting that the species should be to that genus.

Brues (1933, p. 141) commented that this species is similar to *Trachepyris* Kieffer, 1905, mainly due to the arrangement of the bristles along the body. However, *Trachepyris*

Kieffer, 1905, like *Epyris* Westwood, 1832, does not have a mesoscutum-mesoscutellar sulcus.

The original description of this species was based on four specimens, but they are all lost, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*C. setosus* (Brues, 1933) does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris meunieri*** Colombo & Azevedo **sp. nov.**

Figure 9

Derivation of name. This species is named after Fernand Meunier, who described a fossil bethylid species.

Holotype. Female, piece code PIN 964/121; air bubbles present over the metasoma. Deposited in the PIN collection.

Diagnosis. Body length ~4.8 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Mandible apparently pentadentate. Clypeus with median lobe weakly incurved, lateral lobe reduced. Antenna mid-sized, surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres longer than wide; flagellar pubescence appressed; pedicel as long as flagellomere I, quadrate. Eye located far from mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small, very sparse. Frontal line inconspicuous. Frontal angle of ocellar triangle acute. Anterior ocellus crossing to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum present. Fore wing with three distal flexion lines; 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma subrectangular. Mesopleuron with subalar impression connected with mesopleural suture, foveolate; mesopleural suture not visible posteriorly; lower mesopleural foveae not delimited; transepisternal line absent; mesopleural pit present, circular. Mesoscutum-mesoscutellar sulcus present, straight

medially, narrow, circular foveae distinct. Metapectal-propodeal disc poorly preserved. Mesotibia without spines. Metasoma polished, weakly setose. Male unknown.

Remarks. This species is similar to †*Chlorepyris jouaulti* **sp. nov.** in sharing mid-sized antennae that do not surpass the posterior margin of the metapectal-propodeal complex, a dorsal pronotal area wider than long, lacking notauli, and possessing fore wings with a tubular and long 2r-rs&Rs vein. However, †*C. meunieri* **sp. nov.** has pentadentate mandibles, its eyes are located far from the mandibular bases, and its mesoscutum-mesoscutellar sulcus is straight medially; whereas, †*C. jouaulti* **sp. nov.** has tetradentate mandibles, its eyes are located close to the mandibular bases, and its mesoscutum-mesoscutellar sulcus is incurved medially.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris neli*** Colombo & Azevedo **sp. nov.**

Figure 10

Derivation of name. This species is named after André Nel, who described various bethylid fossil species and genera.

Holotype. Female, piece code SIZK UA-68, a complete flat wasp is embedded in a amber piece. The piece weighed 1.35 grams after primary treatment. Deposited in the SIZK collection.

Syninclusions. stellate trichomes.

Diagnosis. Body length ~3.0 mm. Head, dorsal pronotal area, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head as long as wide and subcircular, weakly globoid in lateral view. Mandible not visible. Clypeus not visible. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres as long as wide; flagellar pubescence appressed; pedicel longer than flagellomere I, rectangular. Eye located far from mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small, very sparse. Frontal line not visible. Ocelli not visible. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notauli present, narrow, converging posteriorly. Parapsidal signum shorter than notaulus. Fore wing with four distal flexion lines; 2r-rs&Rs vein tubular, long, weakly pigmented, curved, not converging posteriorly to R1 vein. Pterostigma subcircular. Mesopleuron not visible.

Mesoscutum-mesoscutellar sulcus present, straight medially, wide, foveae distinct. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina incurved; metapostnotal median carina present; metapostnotal carinae not visible. Mesotibia without spines. Metasoma polished, setose. Male unknown.

Remarks. This species is similar to †*Chlorepyris mckellari* **sp. nov.** in sharing short antennae that do not surpass the posterior margin of the mesoscuto-scutellar suture, pedicels longer than flagellomeres I, eyes located distant from the mandibular bases, notauli present, parapsidal signum shorter than notauli, and fore wings with tubular, long and curved 2r-rs&Rs veins. However, the dorsal pronotal area of †*C. neli* **sp. nov.** is wider than it is long and its mesoscutum-mesoscutellar sulcus is straight medially, whereas the dorsal pronotal area of †*C. mckellari* **sp. nov.** is longer than it is wide and its mesoscutum-mesoscutellar sulcus is incurved medially.

Locality and age. Klesiv, Rovno amber, Ukraine and Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Chlorepyris perrichoti*** Colombo & Azevedo **sp. nov.**

Figure 11

Derivation of name. This species is named after Vincent Perrichot, who described various bethylid fossil species and one genus.

Holotype. Female, piece code PIN 964/116. Deposited in the PIN collection.

Diagnosis. Body length ~4.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Head longer than wide and subquadrate, not globoid in lateral view. Mandible tetradentate. Clypeus poorly preserved. Antenna mid-sized, surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres longer than wide; flagellar pubescence appressed; pedicel longer than flagellomere I, rectangular. Eye poorly preserved. Frons weakly coriaceous, punctures small, very sparse. Frontal line not visible. Frontal angle of ocellar triangle obtuse. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit drop-shaped. Metafurcal pit circular. Notauli present, narrow. Parapsidal signum as long as notaulus. Fore wing with four distal flexion lines; 2r-rs&Rs vein tubular, long, well pigmented, angled, not converging posteriorly to R1 vein. Pterostigma subrectangular.

Mesopleuron with subalar impression connected with mesopleural suture, trabeculate; mesopleural suture connected with mesopleural epicoxal sulcus; lower mesopleural foveae delimited, connected with mesopleural suture; transepisternal line present; mesopleural pit not evident. Mesoscutum-mesoscutellar sulcus present, incurved medially, narrow, foveae indistinct. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished, weakly setose. Male unknown.

Remarks. This species differs from all other congeners since its head is longer than it is wide and its parapsidal signum is as long as the notauli, which makes it easily to distinguish from other fossil species of *Chlorepyris* Kieffer, 1913.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

Genus ***Epyris*** Westwood, 1832

†***Epyris deletus*** Brues, 1910

Figure 12

Holotype. Female, piece code AMNH-FI 18891. Deposited in the AMNH collection.

Diagnosis (based on original description and illustration provided by the curator). Body length 5.5 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma back or dark castaneous. Head slightly wider than long, not globoid in lateral view. Mandible not visible. Clypeus not visible. Antenna poorly preserved. Eye not visible. Frons not visible. Frontal line not visible. Frontal angle of ocellar triangle not visible. Dorsal pronotal area longer than wide; transverse pronotal carina apparently present; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus not visible. Parapsidal signum not visible. Fore wing with distal flexion lines not visible, 2r-rs&Rs vein long. Pterostigma subrectangular. Mesoscutum-mesoscutellar sulcus not visible. Metapectal-propodeal disc poorly preserved. Mesotibia not preserved. Metasoma elongate. Male unknown.

Remarks. The original description of †*Epyris deletus* Brues, 1910 was based on a poorly preserved fossil. Brues (1910, p. 9) commented on the similarity of this species with *Epyris* Westwood, 1832 and *Mesitius* Spinola, 1853 and reaffirmed its classification as *Epyris* Westwood, 1832. However, we were not able to find any diagnostic character to place this species in *Epyris* Westwood, 1832 or any other genera of Epyrinae and will therefore

abstain from a nomenclatural act until more information comes to light, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Florissant Formation of Colorado, U.S.A. Priabonian, 34 to 35 million years ago, upper Eocene.

†***Epyris kiefferi*** Brues, 1910

Holotype. Male, piece code 9026, supposed to be deposited in Königsberg collection, lost (see Methods section).

Diagnosis (based on original description). Body length 2.2 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black or dark castaneous; wings hyaline. Head wider than long, not globoid in lateral view. Flagellomere shorter than long; pedicel as long as flagellomere I. Eye glabrous, bulging. Frons weakly coriaceous. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notauli probably absent. Parapsidal signum present. Fore wing with distal flexion lines not visible, 2r-rs&Rs vein present. Pterostigma rectangular. Mesoscutum-mesoscutellar sulcus present, foveae distinct. Metapectal-propodeal disc poorly preserved. Mesotibia without spines. Metasoma polished, setose. Genitalia not visible. Female unknown.

Remarks. This species was originally allocated in *Artiepyris* Kieffer, 1913 and transferred to *Epyris* Westwood, 1832 by Evans (1964, p. 111). Brues (1933, p. 131) provided a detailed description of the holotype, though it lacked illustrations. He described the "scutellum with two small, widely separated foveae connected by a straight impressed line or groove". The presence of the mesoscutum-mesoscutellar sulcus therefore suggests that this species does not belong to *Epyris* Westwood, 1832. Brues (1933) suggested that this species belongs to *Artiepyris* Kieffer, 1913 since its antennae have twelve antennomeres. Although *Artiepyris* Kieffer, 1913 had been described with this characteristic (Kieffer 1913*a*), Evans (1964) indicated that *Artiepyris* Kieffer, 1913 actually has an extremely reduced flagellomere I, so *Artiepyris* Kieffer, 1913 actually has 13 antennomeres, and has subsequently been synonymized into *Epyris* Westwood, 1832.

Moreover, the description suggests this species does not belong to *Epyris* Westwood, 1832 or even to *Artiepyris* Kieffer, 1913 in the old sense, since its body length is less than 2.2 mm and it has a mesoscutum-mesoscutellar sulcus, while the body length of *Artiepyris* Kieffer, 1913 is usually around 5.0 mm at least, and the mesoscutum-mesoscutellar sulcus is absent. The antennae with twelve antennomeres and the small size of the specimen seem to imply that this species should be allocated in Sclerodermatinae. Nevertheless, we do not have illustrations, and the holotype has been lost. We therefore abstain from a nomenclatural act here.

The original description of this species was based on one specimen, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*E. kiefferi* Brues, 1910 does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Epyris moulyi*** Falières & Nel, 2018

Figure 13

Holotype. Male, piece code MNHN.F.A70620 (PA-16149), deposited in the MNHN collection.

Diagnosis (based on original description and new illustration provided by the curator). Body length 3.8 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma castaneous; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Mandible pentadentate. Clypeus with angular median lobe, weakly visible dorsally, lateral lobe reduced. Median clypeal carina outlined, shorter than frons. Antenna mid-sized, not surpassing posterior margin of metapectal-propodeal complex. Flagellomeres as long as wide; flagellar pubescence appressed; pedicel longer than flagellomere I, rectangular. Eye located far from mandibular base, glabrous, bulging. Frons strongly coriaceous, punctures large, very closely space. Frontal line not visible. Frontal angle of ocellar triangle acute. Anterior ocellus positioned anterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not

visible. Notauli present, converging posteriorly. Parapsidal signum shorter than notaulus. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein tubular, long, well pigmented, angled, not converging posteriorly to R1 vein. Pterostigma rectangular. Mesoscutum-mesoscutellar sulcus absent, foveae large, subrectangular, apparently trabeculate. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae not visible. Mesotibia without spines. Metasoma polished, setose. Genitalia not visible. Female unknown.

Remarks. This species was assigned to *Epyris* Westwood, 1832 by Falières & Nel (2018), who provided detailed comments, high-quality photos, and justification for addressing this species in *Epyris* Westwood, 1832. The authors, however, described the mesoscuto-scutellar suture as being comprised of three pairs of pits not connected by a continuous sulcus. We analysed the figures provided by Falières & Nel (2018, Figs. 1D, 1F and 2A, p. 33–34) and concluded that the mesoscuto-scutellar suture has two large foveae that are probably trabeculate or which were deformed during the formation of the fossil. The authors therefore interpreted it as having three pairs of pits, which does not occur in Bethylidae.

The presence of a trabeculate mesoscuto-scutellar suture is common in *Holepyris* Kieffer, 1904, *Formosiepyris* Terayama, 2004 and *Disepyris* Kieffer, 1905 (Azevedo *et al.* 2018). This specimen clearly does not belong to these genera, mainly because the mesoscutum-mesoscutellar sulcus is absent in the fossil and present in these genera. Moreover, the lateral clypeal lobes are reduced in †*E. moulyi* Falières & Nel, 2018, whereas *Holepyris* Kieffer, 1904 has lateral clypeal lobes that are as long as the median lobe. The eyes of †*E. moulyi* Falières & Nel, 2018 are of moderate size and its fore wings have a long 2r-rs&Rs vein, whereas *Disepyris* Kieffer, 1905 has very large eyes and the 2r-rs&Rs vein of the fore wing is usually short. Finally, in †*E. moulyi* Falières & Nel, 2018, the dorsal pronotal area is not posteriorly foveolate and the anteromesoscutum lacks a foveolate transverse groove, whereas the dorsal pronotal area in *Formosiepyris* Terayama, 2004 is posteriorly foveolate and the anteromesoscutum has a foveolate transverse groove.

Furthermore, we note that dorsal pronotal area of this species is ecarinate with the anterior corner not angular (see Fig. 1D in Falières & Nel 2018), the mandibles are pentadentate, the median clypeal lobe is well-projected forward, the notauli are present, the parapsidal signum is present, the 2r-rs&Rs vein of the fore wings is long, and the mesoscutum-mesoscutellar sulcus is absent.

Locality and age. Le Quesnoy, in Chevrières, Oise Department, France. Ypresian, 53 million years ago; lowermost Eocene.

†***Epyris rectinervis*** (Cockerell, 1921)

Figure 14

Holotype. Indeterminate sex, piece code NHMUK I.9352. Deposited in the NHM collection.

Diagnosis (based on original description and illustration provided by the curator). Wing length 3.0 mm. Integument castaneous. Head not preserved. Dorsal pronotal area apparently wider than long; transverse pronotal carina apparently absent; posterior pronotal sulcus absent. Notaulus not preserved. Parapsidal signum not preserved. Fore wing with two distal flexion lines, 2r-rs&Rs vein long. Pterostigma subrectangular. Mesoscuto-scutellar suture not preserved. Metapectal-propodeal disc longer than wide. Mesotibia not preserved. Metasoma not preserved.

Remarks. †*Epyris rectinervis* (Cockerell, 1921) was first published as *Mesitius* Spinola, 1853 (?). Brues (1933, p. 168) listed the species as *Epyris* Westwood, 1832 but did not provide any information or a nomenclatural act. Gordh & Móczar (1990, p. 103) considered that Brues' (1933) listing had transferred the species to *Epyris* Westwood, 1832, an assessment that was followed by Perrichot & Nel (2008, p. 101) and Azevedo & Azar (2012, p. 217), who likewise listed it in *Epyris* Westwood, 1832. Later, Antropov *et al.* (2014, p. 394) cited the species as *Mesitius? rectinervis* Cockerell, 1921, providing an image of the holotype and reporting that 'the type was not re-studied, and its taxonomic position is not confirmed'. Finally, Azevedo *et al.* (2018), Falières & Nel (2018) and Martynova *et al.* (2019) cited the species as *Epyris* Westwood, 1832 following Brues' classification.

We highlight the shape of metapectal-propodeal disc, with corners angular, and the fore wing with three cells closed (C, R, 1Cu) as characteristics that place this species within Epyrinae. However, the specimen lacks diagnostic characters that would place it more narrowly in *Epyris* Westwood, 1832 or any other genera of Epyrinae; therefore, we will abstain from a nomenclatural act until more information comes to light and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Bembridge Marls, Bouldnor Formation, Isle of Wight, United Kingdom. Priabonian, 34 million years ago, upper Eocene.

†***Epyris tenellus*** Statz, 1938

Figure 15

Holotype. Female, piece code LACMIP-2533.790. Deposited in the LACM collection.

Diagnosis (based on original description and new illustration provided by the curator). Body length 4.8 mm. Integument castaneous to black. Head as long as wide. Mandible tridentate. Eye large, circular. Antenna mid-sized, not surpassing posterior margin of metapectal-propodeal complex, with 11 flagellomeres. Dorsal pronotal area as long as wide. Fore wing with apparently three cells closed (C, R, 1Cu), poorly preserved, 2r-rs&Rs vein long. Pterostigma rectangular. Mesoscuto-scutellar suture not preserved. Metapectal-propodeal disc apparently as long as wide. Mesotibia not spinose. Metasoma with subequals tergites. Male unknown.

Remarks. The description of †*Epyris tenellus* Statz, 1938 was based on a poorly preserved fossil. The general morphology of the specimen is similar to *Chlorepyris* Kieffer, 1913, though we abstain from any nomenclatural act because of the lack of observable characteristics and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Rott Formation, Germany. Chattian, 23 to 24 million years ago, upper Oligocene.

Epyris staphylinoides (Hope, 1837)

1901 *Calyoza Ashmeadi* Enderlein; Synonymy by Krombein 1992, 94: 347.

1906 †*Calyoza ramosa* Meunier; Synonymy by Krombein 1992, 94: 348.

Holotype. Male, piece without code, deposited in Strong collection, examined based on literature, lost.

Neotype. Male, deposited in the OUMNH collection.

Diagnosis (based on original description and illustration from Krombein,1992). Male neotype. Body length 6.5 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole and antenna black; last three metasomal segments reddish; wings hyaline.

Head as long as wide, not globoid in lateral view. Mandible tetradentate. Clypeus with rounded median lobe, weakly visible dorsally, lateral lobe reduced. Median clypeal carina outlined, as long as frons. Antenna pectinate; flagellar pubescence appressed; pedicel longer than flagellomere I, apex strongly dilated; flagellomere I reduced into ring-shape. Eye large, elongate, glabrous. Frontal line inconspicuous. Frontal angle of ocellar triangle probably acute. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus present, drop-shaped. Parapsidal signum longer than notaulus. Fore wing with one distal flexion line; 2r-rs&Rs vein present, short. Pterostigma large, rectangular. Mesoscutum-mesoscutellar sulcus absent, foveae oval. Metapectal-propodeal disc wider than long; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia with short spines. Metasoma polished. Genitalia: paramere longer than basiparamere in dorsal view, apex straight, not arched inward, tubular.

Female. Body length 7.7 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole; mandible, antenna, all tarsi and last three metasomal segments reddish; wings hyaline. Head as long as wide, not globoid in lateral view. Mandible pentadentate. Clypeus with rounded median lobe, weakly visible dorsally, lateral lobe reduced. Median clypeal carina outlined, as long as frons. Antenna filiform; flagellar pubescence appressed; pedicel as long as flagellomere I, apex dilated; flagellomere I not reduced into ring-shape. Eye large, elongate, glabrous. Frontal line inconspicuous. Frontal angle of ocellar triangle probably acute. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus present, drop-shaped. Parapsidal signum longer than notaulus. Fore wing with one distal flexion line; 2r-rs&Rs vein present, short. Pterostigma large, rectangular. Mesoscutum-mesoscutellar sulcus absent, foveae oval. Metapectal-propodeal disc wider than long; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia with spines. Metasoma polished.

Remarks. This is the type species of *Calyoza* Hope, 1837, designated by monotypy. Krombein (1992) designated a neotype, synonymised *Calyoza* Hope, 1837 with *Epyris* Westwood, 1832, and provided a detailed and illustrated description of this taxon.

Locality and age. Holotype from ‘Animé gum’, corresponding to East African (Zanzibar) or Madagascar copal; precise age unknown, likely Holocene. Neotype from Port Natal, South Africa (Recent).

Genus ***Holepyris*** Kieffer, 1904

†***Holepyris neodubius*** Azevedo, 2018

Holotype. Male, piece without code, supposed to be deposited at the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description). Body length 3.5 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide, not globoid in lateral view. Mandible not visible. Clypeus not visible. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel as long as flagellomere I. Eye elongate, bulging. Frontal line not visible. Frontal angle of ocellar triangle probably obtuse. Anterior ocellus probably anterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notauli present, converging posteriorly. Parapsidal signum shorter than notaulus. Fore wing with distal flexion lines not visible, 2r-rs&Rs vein present. Pterostigma small, rectangular. Mesoscutum-mesoscutellar sulcus present, foveae indistinct. Metapectal-propodeal disc probably as long as wide; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished, setose. Female unknown.

Remarks. This species was originally placed in *Misepyris* Kieffer, 1913. Evans (1964, p. 140) transferred this species to *Holepyris* Kieffer, 1904. The original description of this species was based on one specimen, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*H. neodubius* Azevedo, 2018 does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Holepyris rasnitsyni*** Colombo & Azevedo **sp. nov.**

Figure 16

Derivation of name. This species is named after Alexandr P. Rasnitsyni, who described a bethylid fossil species and genus.

Holotype. Male, piece code PIN 964/115. Deposited in the PIN collection.

Diagnosis. Body length ~3.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide and subcircular, not globoid in lateral view. Mandible tetradentate. Clypeus with median lobe trapezoidal, well-developed, lateral lobes shorter than median lobe. Antenna long, surpassing posterior margin of metapectal-propodeal complex. Flagellomeres longer than wide; flagellar pubescence appressed; pedicel shorter than flagellomere I, subrectangular. Eye located far from mandibular base, glabrous, bulging. Frons coriaceous. Frontal line present, narrow. Ocelli poorly preserved. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus present, containing sequence of foveae. Posterior mesofurcal pit drop-shaped. Metafurcal pit elongated. Notaulus absent. Parapsidal signum present. Fore wing with four distal flexion lines; 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma rectangular. Mesopleuron with subalar impression connected with mesopleural suture, trabeculate; mesopleural suture connected with mesopleural epicoxal sulcus; lower mesopleural foveae not delimited, not connected with mesopleural suture; transepisternal line absent; mesopleural pit evident. Mesoscutum-mesoscutellar sulcus present, incurved medially, narrow, foveae distinct, smooth. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished, weakly setose. Genitalia: paramere with apex acute, not arched inward, dorsal margin straight; basiparamere not visible; cuspis longer than wide; aedeagus subtrapezoidal, apical margins converging. Female unknown.

Remarks. †*Holepyris rasnitsyni*, along with †*Holepyris neodubius* Azevedo, 2018, is described based on a male specimen. †*Holepyris rasnitsyni* **sp. nov.** has the pronotal sulcus partially comprised of a sequence of foveae, lacks notauli, and its mesoscutum-mesoscutellar sulcus has distinct foveae; whereas †*H. neodubius* Azevedo, 2018 lacks a pronotal sulcus, has notauli, and its mesoscutum-mesoscutellar sulcus has indistinct foveae.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Holepyris terayamai*** Colombo & Azevedo **sp. nov.**

Figure 17

Derivation of name. This species is named after Mamoru Terayama, who described one bethylid fossil species in addition to hundreds of extant species.

Holotype. Female, piece code SIZK K-797. The sample was cut from a clear amber piece, which weighed 11.2 grams after primary treatment (Perkovsky *et al.* 2012).

Syninclusions. SIZK K-796 Mycetophilidae (*Synapha* Meigen, 1818); SIZK K-797 [male of Chironomidae (Orthocladiinae)], Collembola (Entomobryomorpha); SIZK K-798 Collembola (Entomobryomorpha); SIZK K-799 Acari (Bdellidae). The amber was not subjected to any fixation. Deposited in the SIZK collection.

Diagnosis. Body length ~4.4 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide and subcircular, not globoid in lateral view. Mandible bidentate. Clypeus with median lobe rounded, well-developed, lateral lobes shorter than median lobe. Antenna mid-sized, not surpassing posterior margin of metapectal-propodeal complex. Flagellomeres longer than wide; flagellar pubescence appressed; pedicel shorter than flagellomere I, subrectangular. Eye located far from mandibular base, glabrous, bulging. Frons coriaceous. Frontal line present, narrow. Frontal angle of ocellar triangle apparently obtuse. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit elongated. Metafurcal pit apparently circular. Notauli present, narrow, converging posteriorly. Parapsidal signum shorter than notaulus. Fore wing with four distal flexion lines; 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma rectangular. Mesopleuron with subalar impression apparently connected with mesopleural suture, smooth; mesopleural suture not visible posteriorly; lower mesopleural foveae delimited, connected with mesopleural suture; transepisternal line present; mesopleural pit evident. Mesoscutum-mesoscutellar sulcus present, straight, narrow, with foveae distinct, trabeculate. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished, weakly setose. Male unknown.

Remarks. This species is similar to †*Holepyris planiceps* Brues, 1933 in possessing pedicels shorter than flagellomere I, bidentate mandibles, eyes far from the mandibular bases, and anterior ocellus posterior to the supra-ocular line. However, the mesoscutum-mesoscutellar sulcus of †*Holepyris terayamai* **sp. nov.** is trabeculate with distinct foveae, whereas the mesoscutum-mesoscutellar sulcus of †*H. planiceps* Brues, 1933 is smooth with indistinct foveae.

Locality and age. Klesiv, Rovno amber, Ukraine. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Holepyris minor*** (Brues, 1939)

Figure 18

Holotype. Female, piece code PALE-6634. Deposited in the MCZ collection.

Diagnosis (based on original description and illustration provided by the curator). Body length 1.8 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black, antenna and legs castaneous; wings hyaline. Head as long as wide, not globoid in lateral view. Mandible not visible. Clypeus not visible. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel longer than flagellomere I. Eye elongate, bulging, close to mandibular base. Frontal line not visible. Frontal angle of ocellar triangle acute. Anterior ocellus crossing to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus present, narrow, diverging posteriorly. Parapsidal signum absent. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein long, curved. Pterostigma small, subcircular. Mesoscutum-mesoscutellar sulcus present, incurved medially, smooth. Metapectal-propodeal disc longer than wide; metapostnotal median carina present; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. This species was originally proposed in the genus *Misepyris* Kieffer, 1913 and later transferred to *Holepyris* Kieffer, 1904 (Evans 1964, p. 140).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Holepyris planiceps*** Brues, 1933

Figure 19A

Holotype. Female, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description and illustration). Body length 2.2 mm. Wings hyaline. Head longer than wide, not globoid in lateral view. Mandible bidentate. Clypeus not visible. Antenna mid-sized, not surpassing posterior margin of metapectal-propodeal complex. Flagellomeres longer than wide; flagellar pubescence not visible; pedicel as long as flagellomere I. Eye elongate, not bulging, far from mandibular base. Frontal line not visible. Frontal angle of ocellar triangle oblique. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum present. Fore wing with two distal flexion lines; 2r-rs&Rs vein long, curved. Pterostigma small, subcircular. Mesoscutum-mesoscutellar sulcus present, with indistinct foveae, smooth. Metapectal-propodeal disc longer than wide; metapostnotal median carina present; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. The original description of this species was based on one specimen, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*H. planiceps* Brues, 1933 does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Holepyris precursor*** Brues, 1933

Figure 19B

Holotype. Female, piece code B14174, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description and illustration). Body length 2.3 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex and petiole black; legs and metasoma castaneous; wings hyaline. Head as long as wide, not globoid in lateral view. Mandible tridentate. Clypeus not visible. Antenna long, surpassing posterior margin of

metapectal-propodeal complex. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel longer than flagellomere I. Eye oval, not bulging, glabrous, far from mandibular base. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Anterior ocellus posterior to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum present. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein long, almost touching the R1 vein. Pterostigma small, subcircular. Mesoscutum-mesoscutellar sulcus present, with indistinct foveae, smooth. Metapectal-propodeal disc longer than wide; metapostnotal median carina present; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. The original description of this species was based on one specimen, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*H. precursor* Brues, 1933 does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Holepyris robustus*** (Brues, 1933)

Figure 20

Holotype. Female, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description and illustration). Body length 3.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole; legs and metasoma black; wings hyaline. Head as long as wide. Mandible not visible. Clypeus not visible. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel longer than flagellomere I. Eye oval, not bulging, glabrous, far from mandibular base. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notauli present, converging posteriorly. Parapsidal signum

present. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein long, almost touching the R1 vein. Pterostigma small. Mesoscutum-mesoscutellar sulcus present, with indistinct foveae, smooth. Metapectal-propodeal disc longer than wide; metapostnotal median carina present; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. This species was originally placed in *Misepyris* Kieffer, 1913 and later transferred to *Holepyris* Kieffer, 1904 by Evans (1964, p.140).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

Genus ***Laelius*** Ashmead, 1893

†***Laelius pallidus*** Brues, 1933

Holotype. Female, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description). Body length 2.5 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide, globoid in lateral view. Mandible not visible. Clypeus not visible. Flagellomeres as long as wide; pedicel longer than flagellomere I. Eye large, elongate, glabrous. Frontal line inconspicuous. Frontal angle of ocellar triangle obtuse. Anterior ocellus anterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum absent. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein present, very short. Pterostigma indistinct. Mesoscutum-mesoscutellar sulcus present, foveae apparently distinct. Metapectal-propodeal wider than long; metapostnotal anterior carina absent; metapostnotal median carina absent; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. The original description of this species was based on one specimen, so that no other specimen is candidate to be lectotype. Besides, we were not able to find any additional material that could be used as neotype. Given that the original description of †*L. pallidus* Brues, 1933 does not provide enough information to propose any nomenclatural act, its taxonomic identity is uncertain, and this species should be omitted from phylogenetic time-calibration analysis (see Discussion section).

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Laelius preteritus*** Barbosa & Azevedo, 2013

Figure 21

Holotype. Female, piece code K-4207, deposited in the SIZK collection, type examined.

Diagnosis. Body length 4.32 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide, globoid in lateral view. Mandible pentadentate. Clypeus with trapezoidal median lobe, visible dorsally, lateral lobe reduced. Median clypeal carina outlined, shorter than frons. Antenna short, not surpassing posterior margin of mesoscuto-scutellar suture. Flagellomeres as long as wide; flagellar pubescence appressed; pedicel as long as flagellomere I, apex weakly dilated. Eye large, elongate, glabrous. Frontal line inconspicuous. Frontal angle of ocellar triangle probably obtuse. Anterior ocellus crossing to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit drop-shaped. Metafurcal pit circular. Notauli absent. Parapsidal signum present. Fore wing with four distal flexion lines; 2r-rs&Rs vein present, very long. Pterostigma small, subcircular. Mesoscutum-mesoscutellar sulcus present, foveae apparently distinct. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished. Male unknown.

Locality and age. Klesiv, Rovno amber, Ukraine. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Laelius rovnensis*** Barbosa & Azevedo, 2013

Figure 22

Holotype. Female, piece code K-3672. Deposited in the SIZK collection, type examined.

Syninclusions. Anystidae (Erythracarinae), piece code K-3671, SIZK collection.

Diagnosis. Body length 4.71 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide, globoid in lateral view. Mandible pentadentate. Clypeus with angular median lobe, visible dorsally, lateral lobe reduced. Median clypeal carina outlined, shorter than frons. Antenna

mid-sized, not surpassing posterior margin of metapectal-propodeal complex. Flagellomeres as long as wide; flagellar pubescence appressed; pedicel longer than flagellomere I, apex weakly dilated. Eye large, elongate, glabrous. Frontal line inconspicuous. Frontal angle of ocellar triangle obtuse. Anterior ocellus crossing to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus present, with sequence of foveae. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus present, incomplete anteriorly. Parapsidal signum shorter than notaulus. Fore wing with two distal flexion lines; 2r-rs&Rs vein present, very long. Pterostigma small, subcircular. Mesoscutum-mesoscutellar sulcus present, foveae apparently distinct. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished. Male unknown.

Locality and age. Klesiv, Rovno amber, Ukraine. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

Genus †***Gloxinius*** Colombo & Azevedo **gen. nov.**

Derivation of name. The generic epithet *Gloxinius* refers to the Gloxinia, the first king of the Fairy King's Forest. Gender masculine.

Type species. †*Epyris bifossatus* Brues, 1939 by original designation.

Diagnosis (based on original description and new illustrations provided by the curator). Male holotype. Head as long as wide and subquadrate, not globoid in lateral view. Mandible pentadentate. Clypeus with rounded median lobe, weakly visible dorsally, lateral lobe reduced. Median clypeal carina outlined, as long as frons. Antenna long, surpassing posterior margin of metapectal-propodeal complex. Flagellomeres longer than wide; flagellar pubescence appressed; pedicel as long as flagellomere I, rectangular. Eye located close to mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures small and very sparse. Frontal line not visible. Frontal angle of ocellar triangle obtuse. Anterior ocellus situated posterior to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit drop-shaped. Metafurcal pit drop-shaped. Notaulus absent. Parapsidal signum longer than notaulus. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein tubular, long, well pigmented, curved, not converging posteriorly to R1 vein. Pterostigma subcircular. Mesoscutum-mesoscutellar sulcus present, incurved medially. Metapectal-propodeal disc

as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished. Female unknown.

Remarks. †*Gloxinius* **gen. nov.** is morphologically related to *Chlorepyris* Kieffer, 1913 and keys out to couplet 7 (metapostnotal carina usually long, not incurved medially) in Azevedo *et al.* (2018, p. 135–136). However, the dorsal pronotal area of †*Gloxinius* **gen. nov.** is much wider than it is long and almost angulate, which is more similar to the pristocerine genera *Dissomphalus* Ashmead, 1893 and *Trichiscus* Benoit, 1956 than to epyrine taxa. †*Gloxinius* **gen. nov.** also shares the following similarities with *Anisepyris* Kieffer, 1905: usually with long antennae, surpassing the posterior margin of metapectal-propodeal complex; anteromesoscutum longer than the dorsal pronotal area; and clypeus with an angulated median lobe and median clypeal carina outlined. However, the eyes of †*Gloxinius* **gen. nov.** are glabrous, its pronotal dorsal area is ecarinate, it lacks notauli, and the genitalia have a subtrapezoidal aedeagus; whereas the eyes of *Anisepyris* Kieffer, 1905 are densely setose, the pronotal dorsal area is usually carinate, notauli are present, and the genitalia have a bottle-shaped aedeagus.

†***Gloxinius bifossatus*** (Brues, 1939) **comb. nov.**

Figure 23

Holotype. Male, piece code PALE-7679, deposited in the MCZ collection.

Diagnosis (based on original description and new illustrations provided by the curator). Similar to the genus description, and with the following additional species-level characteristics: body length 2.75 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous; wings hyaline. Genitalia: paramere longer than basiparamere in dorsal view, apex straight, not arched inward, dorsal margin straight; basiparamere wide, not covering aedeagal base; apex of cuspis anterior to apex of paramere; digitus with apex apparently aligned to apex of cuspis; aedeagus subtrapezoidal, its apex aligned to apex of digitus, base of apodeme not visible. Female unknown.

Remarks. This species was originally erected in *Homoglenus* Kieffer, 1905. Terayama (2003) synonymised *Homoglenus* Kieffer, 1905 with *Epyris* Westwood, 1832 and transferred this species to *Epyris* Westwood, 1832. We analysed the holotype of this species using high-quality images herein. We note that a mesoscutum-mesoscutellar sulcus

is present (Fig. 3C) in *E. bifossatus* (Brues, 1939), which is absent in *Epyris* Westwood, 1832. The specimen was preserved with the genitalia exposed (Figs. 3E-3F), and we were able to observe that the aedeagus progressively narrows apically, the basivolsella is long, and the paramere is wide. These characteristics are missing in *Epyris* Westwood, 1832. We therefore transfer *E. bifossatus* (Brues, 1939) to *Gloxinius* **gen. nov.**

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

Species transferred to Pristocerinae:

Subfamily **Pristocerinae** Mocsáry, 1881

Genus †***Merascylla*** Colombo & Azevedo **gen. nov.**

Derivation of name. The generic epithet *Merascylla* refers to the Merascylla (Malascula), an elite warrior of the Demon Clan, serving directly under the Demon King as the Faith of the Ten Commandments. Gender feminine.

Type species. †*Epyris atavellus* Cockerell, 1920 by original designation

Description (based on original description and new illustrations provided by the curator). Male holotype (Fig. 24). Head longer than wide, not globoid in lateral view. Mandible tetradentate. Clypeus with rounded median lobe. Antenna long, surpassing posterior margin of metapectal-propodeal complex. Pedicel shorter than flagellomere I, flagellomeres longer than wide; flagellar pubescence appressed. Eye apparently small. Propleuron extremely elongate. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein angled, long. Pterostigma subrectangular. Mesotibia without spines. Metasoma polished. Genitalia not visible. Female unknown.

Remarks. †*Merascylla* **gen. nov.** is morphologically related to *Foenobethylus* Kieffer, 1913 due to the presence of an apparently flat and elongated body, strongly elongated propleuron, enlarged and accentuatedly curved metafemur, arched protrochanter, and fore wing without a poststigmal abscissa of R1. However, †*Merascylla* **gen. nov.** has fore wings with the intersection of the Rs&M and Sc+R veins almost touching the pterostigma, and the metafemora without a spine and sharply narrowing distally; whereas, *Foenobethylus* Kieffer, 1913 has fore wings with the intersection of the Rs&M and Sc+R veins far from the pterostigma, and the metafemora with a spine and smoothly narrowing distally.

†***Merascylla atavella*** (Cockerell, 1920) **comb. nov.**

Figure 24

Holotype. Male, piece code NHMUK In.20149(1). Deposited in the NHM collection.

Diagnosis (based on original description and new illustrations provided by the curator). Similar to the genus description, and with the following additional species-level characteristics: body length 3.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma castaneous; wings hyaline. Female unknown.

Locality and age. Burmese amber, Myanmar. Cenomanian, approximately 99 million years ago, mid-Cretaceous.

Genus ***Pseudisobrachium*** Kieffer, 1904

†***Pseudisobrachium elatus*** (Brues, 1933) **comb. nov.**

Holotype. Male, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description). Body length 5.0 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide, not globoid in lateral view. Mandible not visible. Clypeus not visible. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel not visible. Eye small, elongate, setose. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus present. Parapsidal signum present. Fore wing with distal flexion lines not visible, 2r-rs&Rs vein present. Pterostigma small. Mesoscutum-mesoscutellar sulcus present, foveae indistinct. Metapectal-propodeal disc as long as wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae present. Mesotibia without spines. Metasoma polished. Genitalia not visible. Female unknown.

Remarks. This species was originally proposed in the genus *Rhabdepyris* Kieffer, 1904. Azevedo *et al.* (2018) synonymised *Rhabdepyris* Kieffer, 1904 with *Epyris* Westwood, 1832 and transferred it to *Epyris* Westwood, 1832. Brues (1933, p. 141) provided a detailed description of the holotype, but without drawings. In remarks on this species, Brues (1933) commented ‘In Kieffer's key this species will fall in the subgenus *Xestobethylus* Cameron, 1909 which is represented by a single living species from South

America'. Evans (1973) synonymised *Xestobethylus* Cameron, 1909 with *Pseudisobrachium* Kieffer, 1904.

Characteristics such small and setose eyes, flagellomeres that are as long as they are wide, and a mesoscutum-mesoscutellar sulcus with indistinct foveae are found in species of *Pseudisobrachium* Kieffer, 1904. Based on these characters and Brues' observations about morphological similarity to *Xestobethylus* Cameron, 1909, as well as recent records of *Pseudisobrachium* Kieffer, 1904 from Rovno and Baltic ambers (Colombo *et al.* 2020*a*), we transfer *E. elatus* (Brues, 1933) to *Pseudisobrachium* Kieffer, 1904 here.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

†***Pseudisobrachium inhabilis*** (Brues, 1923) **comb. nov.**

Holotype. Male, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description). Body length 5.0 mm. Head longer than wide. Mandibular teeth not visible. Clypeus not visible. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel longer than flagellomere I, rectangular. Eye glabrous. Frons weakly coriaceous, punctures small, very sparse. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus apparently present, complete. Parapsidal signum present. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein tubular, long. Pterostigma subcircular. Mesoscutum-mesoscutellar sulcus probably present. Metapectal-propodeal disc longer than wide; metapostnotal anterior carina straight; metapostnotal median carina present; metapostnotal carinae not visible. Mesotibia without spines. Metasoma polished, setose. Genitalia not visible. Female unknown.

Remarks. The original description of this species lacks any illustration. Brues (1922, p. 339) commented:

> this species may possibly belong to one of the groups recently segregated from *Epyris* Westwood, 1832, agreeing well with *Monepyris* Kieffer, 1905 except that there is no third closed basal cell in the wing. As it does not agree perfectly with any of these, I have preferred to let it remain in the old genus.

The genus *Monepyris* Kieffer, 1905 was synonymised with *Pseudisobrachium* Kieffer, 1904 by Kieffer (1906, in Kieffer & Marshall 1904-1906).

Later, Brues (1933, p. 130) noted that there "are two amber species which will have to be left in this genus as formerly constituted as I have been unable to assign them to any more definite positions". He was referring to the genus *Epyris* Westwood, 1832 and the species *E. inhabilis* (Brues, 1923) and *E. longiceps* (Brues, 1923) (=*Epyris neolongiceps* Azevedo, 2018). Given Brues' observations on the similarity of this species to *Xestobethylus* Cameron, 1909 and the recent records of *Pseudisobrachium* Kieffer, 1904 from Rovno and Baltic ambers (Colombo *et al.* 2020*a*), we transfer *E. inhabilis* (Brues, 1923) to *Pseudisobrachium* Kieffer, 1904.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

Species transferred to Scleroderminae:

Subfamily **Scleroderminae** Kieffer, 1914

Genus †***Mael*** Colombo & Azevedo **gen. nov.**

Derivation of name. The generic epithet *Mael* refers to the Mael, one of the Four Archangels of the Goddess Clans.

Type species. †*Calyoza longiceps* Brues, 1923 by original designation

Description (based on original description). Head longer than wide, not globoid in lateral view. Mandible pentadentate. Clypeus not visible. Flagellomeres as long as wide; flagellar pubescence not visible; pedicel longer than flagellomere I. Eye located close to mandibular base, oval. Frontal line not visible. Frontal angle of ocellar triangle probably acute. Anterior ocellus probably posterior to supra-ocular line. Dorsal pronotal area wider than long; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus present. Parapsidal signum absent. Fore wing with apparently two cells closed (R, 1Cu), distal flexion lines not visible, 2r-rs&Rs vein long. Pterostigma small, rectangular. Mesoscuto-scutellar suture absent. Metapectal-propodeal disc wider than long; metapostnotal median carina present;

metapostnotal carinae present. Mesotibia without spines. Metasoma polished, setose. Male unknown.

Remarks. This species was originally allocated in *Calyoza* Hope, 1837 as *C. longiceps* Brues, 1923. Later, Brues (1933, p. 130) compared it with living species of *Calyoza* Hope, 1837 and transferred it to *Epyris* Westwood, 1832. Azevedo *et al.* (2018) synonymised *Rhabdepyris* Kieffer, 1904 with *Epyris* Westwood, 1832 and consequently transferred the species from the former genus. *Rhabdepyris longiceps* Kieffer, 1913 was also transferred, giving rise to a secondary homonymy. For this reason, a new name was proposed for *Epyris longiceps* (Brues, 1923): *Epyris neolongiceps* Azevedo, 2018.

Brues (1923, p. 336–337) provided a good description of the holotype, but without drawings. Three features described by Brues (1923) are unusual for epyrine wasps, namely the head being much longer than it is wide, the complete lack of a mesoscuto-scutellar suture, and the fore wing with only two closed cells.

On the fore wing, the costal vein (C) was poorly preserved and the author either did not describe it, or the species only has two closed cells. Brues (1933) commented that the head is very long. Finally, the absence of a mesoscuto-scutellar suture (comprised of foveae or a sulcus) confirms that this species does not belong to Epyrinae and would be better addressed to Sclerodermatinae.

†*Mael* **gen. nov.** is morphologically similar to *Megaprosternum* Azevedo, 2006 and *Allobethylus* Kieffer, 1905 since its head is much longer than it is wide. *Mael* **gen. nov.** does not have the mesoscuto-scutellar suture and costal cell in the fore wing, whereas *Allobethylus* Kieffer, 1905 has the mesoscuto-scutellar suture and costal cell in the fore wing. In *Megaprosternum* Azevedo, 2006, females are apterous and only the males are macropterous.

†***Mael longiceps*** (Brues, 1923) **comb. nov. et rev. nom.**

Reinstalled name of *Calyoza longiceps* Brues, 1923 from *Epyris neolongiceps* Azevedo, 2018 (*in* Azevedo *et al.* 2018).

Holotype. Female, piece without code, deposited in the Königsberg collection, lost (see Methods section).

Diagnosis. Similar to the genus description, for species level characteristics, which include: body length 2.7 mm. Male unknown.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

Species transferred to Platygastroidea *incertae sedis:*

Superfamily **Platygastroidea** Haliday, 1833

†***Laelius nudipennis*** Brues, 1933

Figure 25

Holotype. Female, piece without code, supposed to be deposited in the Königsberg collection, lost (see Methods section).

Diagnosis (based on original description and illustration). Body length 2.6 mm. Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma black; wings hyaline. Head as long as wide, globoid in lateral view. Mandible not visible. Clypeus not visible. Flagellomeres as long as wide; pedicel longer than flagellomere I. Eye large, elongate, glabrous. Frontal line inconspicuous. Frontal angle of ocellar triangle obtuse. Anterior ocellus anterior to supra-ocular line. Dorsal pronotal area as long as wide; transverse pronotal carina absent; posterior pronotal sulcus absent. Posterior mesofurcal pit not visible. Metafurcal pit not visible. Notaulus absent. Parapsidal signum absent. Fore wing with distal flexion lines not visible; 2r-rs&Rs vein present, very short. Pterostigma poorly visible. Mesoscutum-mesoscutellar sulcus present, foveae apparently distinct. Metapectal-propodeal wider than long; metapostnotal anterior carina absent; metapostnotal median carina absent; metapostnotal carinae absent. Mesotibia without spines. Metasoma polished. Male unknown.

Remarks. The original description and illustration (Brues 1933) do not allow a precise classification of this species because some parts of the body seem to be distorted, crushed, or artificially flattened. Even so, the reported characteristics are sufficient to affirm that this species does not belong to Bethylidae, because of the different style of wing venation and the antennae.

We initially believed that it belonged to Pteromalidae or Platygastridae, because these traits somewhat resemble the pattern found in these groups. Certainly, the wing venation does bear a greater resemblance to some Platygastroidea than it does to a chalcidoid, since its submarginal vein goes directly into a punctiform marginal vein from which the stigmal vein originates. In a typical chalcidoid, there would also be a distinct marginal vein resulting in a venation pattern that extends further along the length of the

wing with the apex of the postmarginal vein extending at least halfway along the wing (Gary Gibson, *pers. comm.*). Furthermore, the body structure does not match that of a chalcid neither in its pronotal structure nor its head, while no notauli or axillae have been described or illustrated.

The illustration does seem problematic, especially since the specimen's stigma are more similar to those typical of Platygastroidea. However, including it in the latter group would be incorrect if the specimen is a female with exposed and normal ovipositor sheaths, which the drawings suggest is the case (Roger Burks, *pers. comm.*). Furthermore, it seems clear that there are no defined lateral margins on the metasoma which would rule out the core Scelionidae as a possibility, though it does not preclude the specimen from belonging to Telenominae, particularly if the metasoma has been laterally flattened in the preservation process (Simon van Noort, *pers. comm.*).

The presence of ovipositor sheaths could preclude this species from being classified as a platygastroid. Indeed, the drawings do appear to show very distinct, exserted ovipositor sheaths, while no slender lancets are visible (Gary Gibson, *pers. comm.*). However, there are a few platygastroids that have unextruded ovipositors as well as distinct and elongate gonoplacs. Species of *Phanuromyia* Dodd, 1914, especially those found in South Africa, have protective sheaths, though their degree of exsertion does differ (Norman Johnson, *pers. comm.*). If this specimen is, in fact, a bethylid, the exserted genital structures could be the male harpe rather than the third valvulae of a female.

According to Gary Gibson (*pers. comm.*), this species is likely not a chalcidoid because of the following features: the flagellum is filiform rather than clavate; there is no evidence of a prepectus, with the posterior limit of the pronotum extends much closer to the tegula than typical for chalcidoids; the mesonotum lacks both notauli and axillae, the former of which are often absent or so weak in some chalcidoids that they might not be apparent in a fossil, while evident axillae would be expected if the specimen was a chalcidoid. Finally, there is evidence of a petiole, while the gaster has too few segments.

We should also note that many platygastroids, especially those at the base of the phylogeny, do not have clearly clavate antennae and the scape is relatively shorter than is typical for most species today (Norman Johnson, *pers. comm.*).

If the specimen is, in fact, a platygastrid, it does not fit into any described genus. Norman Johnson (*pers. comm.*) suggests that the strongly depressed body may indicate either †*Proplatyscelio* or *Janzenella*, the former described by Brues (1940) from Baltic

amber and the latter by Masner & Johnson (2007) from extant material and Dominican amber. However, †*Proplatyscelio* has distinct notauli, though small, and the wing venation of *Janzenella* is quite different from that of the specimen. Further conclusions on the classification of †*Laelius nudipennis* Brues, 1933 would require an examination of whether the fossil (which is lost) has papillary sensilla on the antennal clava.

Given the uncertainty discussed above and the fact that the material is lost, it is prudent to address it to Platygastroidea *incertae sedis* until the fossil is found.

Locality and age. Baltic amber, Russian Federation. Priabonian, 33,9 to 37,7 million years ago, upper Eocene.

Key to Epyrinae from fossil and subfossil resins

1. Mesoscuto-scutellar suture with pits not connected by sulcus … 2
- Mesoscuto-scutellar suture with pits connected by sulcus … 3

2. Flagellomere I very reduced, ring-shaped … *Epyris staphylinoides* (Hope, 1837)
- Flagellomere I as long as wide, quadrate … †*Epyris moulyi* Falières & Nel, 2018

3. Transverse pronotal carina present … †*Anisepyris gradatus* Sorg, 1988
- Transverse pronotal carina absent … 4

4. Lateral clypeal lobe developed, as long as median lobe … 5
- Lateral clypeal lobe reduced, shorter than median lobe … 11

5. Metapectal-propodeal disc as long as wide … 6
Metapectal-propodeal disc longer than wide … 8

6. Posterior pronotal sulcus present … †*Holepyris rasnitsyni* **sp. nov.**
- Posterior pronotal sulcus absent … 7

7. Pedicel shorter than flagellomere I; anterior ocellus posterior to supra-ocular line … †*Holepyris terayamai* **sp. nov.**
- Pedicel as long as flagellomere I; anterior ocellus anterior to supra-ocular line … †*Holepyris neodubius* Azevedo, 2018

8. Head longer than wide; pedicel as long as flagellomere I … †*Holepyris planiceps* Brues, 1933
- Head as long as wide; pedicel longer than flagellomere I … 9

9. Dorsal pronotal area as long as wide … †*Holepyris robustus* (Brues, 1933)
- Dorsal pronotal area wider than long … 10

10. Anterior ocellus posterior to supra-ocular line; notaulus absent; mesoscutum-mesoscutellar sulcus straight medially … †*Holepyris precursor* Brues, 1933
- Anterior ocellus crossing to supra-ocular line; notaulus present; mesoscutum-mesoscutellar sulcus incurved medially … †*Holepyris minor* (Brues, 1939)

11. Body with black setae; head globoid in lateral view … 12
- Body with setae; head triangular or subtriangular in lateral view … 14

12. Fore wing with 2r-rs&Rs vein absent or reduced … †*Laelius pallidus* Brues, 1933
- Fore wing with 2r-rs&Rs vein developed … 13

13. Median clypeal lobe angular; notaulus present … †*Laelius rovnensis* Barbosa & Azevedo, 2013
- Median clypeal lobe straight; notaulus absent … †*Laelius preteritus* Barbosa & Azevedo, 2013

14. Anteromesoscutum 2 × longer than dorsal pronotal area … †*Gloxinius bifossatus* (Brues, 1939)
- Anteromesoscutum as long as dorsal pronotal area … 15

15. Dorso-apical margin of mandible denticulate … †*Chlorepyris engeli* **sp. nov.**
- Dorso-apical margin of mandible not denticulate … 16

16. Dorsal pronotal area as long as or longer than wide … 17
- Dorsal pronotal area wider than long … 23

17. Head longer than wide; mesoscutum-mesoscutellar sulcus with indistinct foveae … †*Chlorepyris perrichoti* **sp. nov.**
- Head as long as wide; mesoscutum-mesoscutellar sulcus with distinct foveae … 18

18. Anterior ocellus anterior to supra-ocular line … 19
- Anterior ocellus posterior to supra-ocular line … 20

19. Pedicel longer than flagellomere I; dorsal pronotal area longer than wide … †*Chlorepyris invelatus* (Brues, 1933)
- Pedicel as long as flagellomere I; dorsal pronotal area as long as wide … †*Chlorepyris concaptus* (Brues, 1933)

20. Notaulus absent … †*Chlorepyris hopei* **sp. nov.**
- Notaulus present … 21

21. Pedicel as long as flagellomere I … †*Chlorepyris setosus* (Brues, 1933)
- Pedicel longer than flagellomere I … 22

22. Dorsal pronotal area longer than wide; fore wing with 2r-rs&Rs vein curved … †*Chlorepyris mckellari* **sp. nov.**
- Dorsal pronotal area as long as wide; fore wing with 2r-rs&Rs vein angled … †*Chlorepyris deploegi* **sp. nov.**

23. Mesoscutum-mesoscutellar sulcus straight medially … 24
- Mesoscutum-mesoscutellar sulcus incurved medially … 25

24. Pedicel as long as flagellomere I; notaulus absent … †*Chlorepyris meunieri* **sp. nov.**
- Pedicel longer than flagellomere I; notaulus present … †*Chlorepyris neli* **sp. nov.**

25. Pedicel as long as flagellomere I; eye not touching mandibular base; notaulus present … †*Chlorepyris gallicus* (Perrichot and Nel, 2008)

- Pedicel longer than flagellomere I; eye touching mandibular base; notaulus absent … †*Chlorepyris jouaulti* **sp. nov.**

DISCUSSION

Epyrine wasps are easily identified in amber pieces, generally because the current generic classification in Epyrinae is based mostly on the mesoscuto-scutellar suture with sulcus and/or foveae. Luckily, these characters are usually visible in amber-preserved specimens, permitting reliable identification. This is not the case in other subfamilies, with identification in groups such as Pristocerinae relying on male genitalic characters (Azevedo *et al.* 2018).

The fossil fauna of Epyrinae has hitherto consisted of 25 species belonging to six genera. Our study adds ten species to the fossil fauna of Epyrinae and transfers four species to other subfamilies, resulting in a group now containing 30 fossil species (Figure 26). More than 50% of the species are from the Baltic amber, contrasting with findings by Perkovsky *et al.* (2007), who reported a higher diversity of arthropod fauna in Rovno amber. The difference in fauna between sites is an indication of their different geographic origin (Perkovsky *et al.* 2007). The difference in the number of samples between mine sites can also be associated with the levels of exploitation of each mine. In a discussion of the legal mining activities in each site, Perkovsky *et al.* (2010) noted that output at the Ukrainian site averaged c. 32,000 kg per year over a 16-year period, while the mining permit for the Kaliningrad Oblast covers c. 310,000 kg per year. Since mining in the Kaliningrad region is c. 150 × higher than in Ukraine, the probability of finding inclusions with flat wasps is considerably higher. Furthermore, legal mining in Ukraine started in 1993, while it began over a century earlier in the Samland peninsula, Kaliningrad Oblast (Weitshat & Wichard 2002). The effect is seen in the historical records of fossils of flat wasps, with the first recorded fossil species found in the Baltics and described by Brues (1923), with the first species record from Ukraine following 90 years later by Barbosa & Azevedo (2013).

A comprehensive taxonomy of epyrine fossils is severely hindered by lost holotypes. Epyrinae have ten missing types, eight of which come from the Baltic amber (Königsberg collection), and two from the Zanzibar copal resin (it is possible that one is from Madagascar copal). The latter two types correspond to †*Epyris ramosus* Meunier, 1906 and †*Epyris staphylinoides* (Hope, 1837) from the Evers and Strong collections, respectively.

Krombein (1992) designated a neotype for †*E. staphylinoides* (Hope, 1837) and synonymised †*E. ramosus* Meunier, 1906 as a junior synonym, partially solving the problem. Unfortunately, almost 30% of all fossil epyrine types remain lost. The lost types comprise three species of *Chlorepyris* Kieffer, 1913, †*C. concaptus* (Brues, 1933), †*C. invelatus* (Brues, 1933), and †*C. setosus* (Brues, 1933), one species of *Epyris* Westwood, 1832 (†*E. kiefferi* Brues, 1910), three species of *Holepyris* Kieffer, 1904 (†*H. neodubius* Azevedo, 2018, †*H. planiceps* Brues, 1933, and †*H. precursor* Brues, 1933), and one species of *Laelius* Ashmead, 1893 (†*L. pallidus* Brues, 1933). Brues provided detailed descriptions of the mesoscutum-mesoscutellar sulcus, which was decisive for transferring the first three species to *Chlorepyris* Kieffer, 1913, as noted in the remarks of each species. Nevertheless, the descriptions and drawings of the species of *Epyris* Westwood, 1832, *Holepyris* Kieffer, 1904 and *Laelius* Ashmead, 1893 whose types have been lost lack sufficient taxonomic information to accurately identify these taxa, making generic and suprageneric classifications doubtful. These species should therefore be omitted from phylogenetic time-calibration analysis.

Among the genera of Epyrinae, *Chlorepyris* Kieffer, 1913 is noteworthy for its fossil diversity and current disjunct distribution. The genus has been found in the Neotropics and Australia, with morphological dissimilarities between species from these regions. The Australian species are morphologically similar to those of *Trachepyris* Kieffer, 1905 with respect to features such as a narrow 2r-rs&Rs vein in the fore wing. Meanwhile, the Neotropical species are morphologically similar to *Epyris* Westwood, 1832. The only known occurrence of this genus in northern Eurasia was the extinct species †*C. gallicus* (Perrichot & Nel, 2008) (Azevedo *et al.* 2018). Our analysis adds ten extinct species of *Chlorepyris* Kieffer, 1913 from this region, making it the most diverse genus in terms of number of fossil species in Bethylidae. Our findings show that *Chlorepyris* Kieffer, 1913 has been present as a lineage and was presumably abundant in Europe during the Eocene.

The Eurasian fossil species of *Chlorepyris* Kieffer, 1913 show similarity to both morphological patterns found in the group. The striking morphological distinction between extant and extinct species suggests that *Chlorepyris* Kieffer, 1913 was very morphologically diverse during the Eocene and indicates a broader distribution of the genus in the past. Extinction likely played a role in the biogeographic history of the group and the fixation of a phenotype in the current disjunct distribution. *Chlorepyris* Kieffer, 1913 has 65 described species, most of which are found in the tropics, with no species

found in temperate regions, though about one third have distributions that include subtropical areas (Azevedo *et al.* 2018). Similar current and past distributions have been observed in other warm-adapted bethylids, such as the pristocerine *Pseudisobrachium* Kieffer, 1904 (see Colombo *et al.* 2020*a*, 2020*b*) and the sclerodermine *Glenosema* Kieffer, 1905 (see Azevedo & van Noort 2019, Colombo & Azevedo 2019). The Eocene was the terminal phase of transition from the warm to cold biosphere (Akhmet'ev & Beniamovski 2006). The cooling trend following the Eocene may have caused local extinction or dispersal to warmer areas. Molecular dating analyses should provide further support to elucidate the historical distribution of the group. Finally, *Chlorepyris* Kieffer, 1913 was revalidated as a genus by Waichert & Azevedo (2009). The species are reliably identified, and an Eocene origin can be used to constrain the stem group *Chlorepyris* Kieffer, 1913 in phylogenetic time-calibrations.

Epyris Westwood, 1832 is other genus that needs discussion. Historically, several fossil species were mistakenly classified as *Epyris* Westwood, 1832, likely due to an inability to identify the specimen at the genus level. *Epyris* Westwood, 1832 is currently the largest taxonomic problem in Bethylidae and is considered a major taxonomic wastebasket. The type-species, *Epyris niger* Westwood, 1832, has been lost and several synonymies have been proposed without cladistic analyses. In this study, we propose new combinations within Epyrinae for eight species previously identified as *Epyris* Westwood, 1832. For example, when the genera *Isobrachium* Förster, 1856, *Rhabdepyris* Kieffer, 1904 and *Calyoza* Hope, 1837 were synonymised with *Epyris* Westwood, 1832, their fossil species were reassigned as well, at times without careful fossil examination. It is important to point out that although five species have been allocated in *Epyris* Westwood, 1832, the only species that has well-preserved and conclusive diagnostic characteristics is *E. moulyi* Falières & Nel, 2018, from the Oise amber, making it a good candidate for time-calibration in phylogenetic analyses. The other five species are poorly preserved and remain in *Epyris* Westwood, 1832 due to a lack of information, as explained in the specific remarks.

Our results contribute to the fauna of different deposits. The Bethylidae fauna for Rovno amber comprises three subfamilies (Bethylinae, Pristocerinae and Epyrinae). *Laelius* Ashmead, 1893 was hitherto the only genus of Epyrinae recorded in Rovno amber (Barbosa & Azevedo 2013). We have added two genera, *Chlorepyris* Kieffer, 1913 and *Holepyris* Kieffer, 1904, to its fauna, suggesting a broad diversity of Bethylidae in this region's past. The extant species of *Holepyris* Kieffer, 1904 thrive in cold temperatures,

with nearly half of the known species occurring in the Holarctic region. Past distribution patterns are consistent with this trend, with six species recorded from Baltic amber and one from Rovno amber. Finally, the Priabonian distribution of *Laelius* Ashmead, 1893, with one species from Baltic and two from Rovno amber, is consistent with the distribution of its dermestid host. Dermestids are abundant and diverse in Baltic amber, though they have not been as thoroughly explored Rovno amber (Perkovsky *et al.* 2021). However, scolytines, another host of *Laelius* Ashmead, 1893, have been found in the Rovno amber (Petrov & Perkovsky 2008, 2018).

We add two new genera (†*Gloxinius* **gen. nov.** and *Chlorepyris* Kieffer, 1913) to the fauna of Bethylidae from Baltic amber, which now represents 20 genera. *Lytopsenella kerneggeri* Ohl, 1995 (Bethylinae) is the only species found in multiple deposits: Rovno, Hamburg-Harburg, and the Kaliningrad Oblast (Ramos *et al.* 2014). The other species have single records. The established north-eastern Eocene fauna of flat wasps differs in that *Sierola* Cameron, 1881 and *Pseudisobrachium* Kieffer, 1904 have been recorded in Rovno amber, though they are unknown in Baltic amber (Ramos *et al.* 2014; Perkovsky 2018, Colombo *et al.* 2020*a*). Additionally, the Florissant Formation of Colorado in the U.S.A. (†*Epyris deletus* Brues, 1910) and Bembridge Marls in England (†*Epyris rectinervis* (Cockerell, 1921)) have recorded confirmed occurrences of epyrine flat wasps. We can therefore conclude that, during the Eocene, Epyrinae were already quite diverse, abundant, and established (Fig. 26). The Eocene was an important setting in generating the currently recognised generic diversity of extant bethylid subfamilies, as the majority of genera appear to have evolved between 56 and 34 Ma (Colombo *et al.* 2020*b*). A single record of the group exists from the Miocene, †*Anisepyris gradatus* Sorg, 1988, which was found in Dominican amber in the Dominican Republic. The youngest fossil in the family, *Epyris staphylinoides* (Hope, 1837), likely dates to the Holocene and was found in the Zanzibar copal resin of Tanzania, also known as East African "animé" or Madagascar copal. East African "animé" is derived almost entirely from the trees of *Hymenaea verrucosa* Gaertner, 1971 (Fabaceae), the natural range of which was recently restricted to East Africa and Zanzibar (Poinar 1992; Geirnaert 2002; Langenheim 2003). The age of "résine animé" from East Africa is still a matter of debate. Following radiocarbon analysis, Burleigh & Whalley (1983) did not determine a minimum age, describing this resin as a very modern one. Meanwhile, Schlüter & Von Gnielinski (1987) claim that it stems from the Pleistocene and is no older than the Upper Pliocene (based on the stratigraphy of

Tanzanian mainland and Zanzibar). Kosmowska-Ceranowicz (2001) discussed the age of copals (young semifossilised resins) and assigned them to the Pleistocene period (radiocarbon dating). Geirnaert (2002) suggested that East African copal was about 100,000 years old. The ambiguous definitions and age of copal resins were recently summarised by Matuszewska (2010) and Solórzano-Kraemer *et al*. (2020). However, all we can presently conclude is that this resin is much younger than Baltic amber, the age of which ranges between several thousands of years (Feist *et al.* 2007), likely Holocene. It must be pointed out that most recent discussions and investigations on "animé" (copal) pertain to Madagascar (Penney *et al.* 2005; Feist *et al.* 2007; Bosselaers *et al.* 2010), rather than Zanzibar or the East African coast.

The bethylid fauna of Oise is represented by nine species belonging to six subfamilies. The amber deposit of Oise was discovered by Gael De Ploëg in 1996 (Nel *et al.* 1999). Among the Epyrinae, the occurrence of *Chlorepyris* Kieffer, 1913 (†*C. gallicus* (Perrichot & Nel, 2008)) and *Epyris* Westwood, 1832 (†*E. moulyi* Falières & Nel, 2018) has been recorded. Flat wasps from Oise are extensively discussed by Colombo *et al.* (2020*b*) and not repeated here.

Hymenoptera represent a significant part of global biodiversity and have done so since at least the Cretaceous (Zhang *et al.* 2018). Flat wasps began to diverge in the Early Cretaceous and were already well established during the Barremian (Colombo *et al.* 2020*b*). Thus, the lack of representatives of Epyrinae from the Cretaceous is probably a gap in sampling or a lack of preserved specimens. The subfamilies with the greatest representation in the fossil record (Epyrinae and Bethylinae) are not present in Burmese amber. The only species of Epyrinae from that region is transferred to Pristocerinae, †*Merascylla atavella* (Cockerell, 1920) in this analysis. It is important to note that the known fauna of Bethylidae may well increase significantly. Zhang *et al.* (2018) report 124 pieces (almost 7% of all Hymenoptera), including bethylids, in a collection of Burmese amber kept at the Nanjing Institute of Geology and Palaeontology, China Academy of Sciences (NIGPCAS).

With this line of research, revisions of the fossils of the five largest subfamilies of Bethylidae will be completed. This will allow future paleostudies to advance further in the evolutionary history of this family. In addition, phylogenetic studies will be able to use the taxa reviewed here more reliably, as well as other review works (Ramos *et al*. 2014; Colombo & Azevedo, 2019; Colombo *et al*. 2020*a*, 2020*b*) focused on molecular clock

analysis, for example. Finally, it is likely that further exploration in major deposits, such as Burmese, Oise and Rovno, will lead to the emergence of new Bethylidae and help to clarify their evolutionary gaps and the current configuration of extant fauna.

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REFERENCES

Akhmet'ev, M. A. & **Beniamovski, V. N.** 2006. The Paleocene and Eocene in the Russian Part of West Eurasia. *Stratigraphy and Geological Correlation*, **14**, 49–72.

Alencar, I. D. C. C. & **Azevedo, C. O.** 2013. Reclassification of Epyrini (Hymenoptera: Bethylidae): a tribal approach with commentary on their genera. *Systematic Entomology*, **38**, 45–80. doi:10.1111/j.1365-3113.2012.00648.x

Antropov, A. V., Belokobylskij, S. A., Compton, S. G., Dlussky, G. M., Khalaim, A. I., Kolyada, V. A., Kozlov, M. A., Perfilieva, K. S. & **Rasnitsyn, A. P.** 2014. The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the Insect Limestone (Late Eocene) of the Isle of Wight, UK. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **104**, 335–446. doi:10.1017/S1755691014000103

Ashmead, W. H. 1893. A monograph of the North American Proctotrypidae. *Bulletin of the United States National Museum*, **45**, 1–472. doi:10.5479/si.03629236.45.1

Azevedo, C. O. 2006. Two new genera of Sclerodermini (Hymenoptera: Bethylidae: Epyrinae) with large, scolebythid-like prosternums. *Zootaxa*, **1191**, 35–47. doi:10.11646/zootaxa.1191.1.3

Azevedo, C. O., Alencar, I. D. C. C., Ramos, M. S., Barbosa, D. N., Colombo, W. D., Vargas, J. M. & **Lim, J.** 2018. Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, **4489**, 1–294. doi:10.11646/zootaxa.4489.1.1

Azevedo, C. O. & **Azar, D.** 2012. A new fossil subfamily of Bethylidae (Hymenoptera) from the Early Cretaceous Lebanese amber and its phylogenetic position. *Zoologia*, **29**, 210–218. doi:10.1590/S1984-46702012000300004

Azevedo, C. O. & **van Noort, S.** 2019. Review of Afrotropical *Glenosema* Kieffer (Hymenoptera, Bethylidae) with description of 13 new species. *Zootaxa*, **4585**, 401–437. doi:10.11646/zootaxa.4585.3.1.

Barbosa, D. N. & **Azevedo, C. O.** 2018. Revision of *Anisepyris* Kieffer (Hymenoptera, Bethylidae), with description of 135 new species. *Zootaxa*, **4416**, 001–258. doi:10.11646/zootaxa.4416.1.1

Barbosa, D. N., Perkovsky, E. E. & **Azevedo, C. O.** 2013. Two new species of *Laelius* Ashmead (Hymenoptera: Bethylidae) from upper Eocene Rovno amber. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, **267**, 67–73. doi:10.1127/0077-7749/2012/0297

Berland, L. 1928. *Faune de France 19. Hyménoptères Vespiformes II.* Office Central de Faunistique, Paris, 215 pp.

Bosselaers, J., Dierick, M., Cnudde, V., Masschaele, B., Van Hoorebeke, L. & **Jacobs, P.** 2010. High resolution X-ray computed tomography of an extant new *Donuea* (Araneae: Liocranidae) species in Madagascan copal. *Zootaxa*, **2427**, 25–35. doi:10.11646/zootaxa.2427.1.3

Brues, C. T. 1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. *Bulletin of the Museum of Comparative Zoology*, **54**, 1–125.

Brues, C. T. 1923. Some new fossil parasitic Hymenoptera from Baltic amber. *Proceedings of the American Academy of Arts and Sciences*, **58**, 327–346. doi:10.2307/20025999

Brues, C. T. 1933. The parasitic Hymenoptera of the Baltic amber. Part I. *Bernstein-Forschungen*, **3**, 4–172.

Brues, C. T. 1939. New Oligocene Braconidae and Bethylidae from Baltic amber. *Annals of the Entomological Society of America*, **31**, 251–263. doi:10.1093/aesa/32.2.251

Brues, C. T. 1940. Fossil parasitic Hymenoptera of the family Scelionidae from Baltic amber. *Proceedings of the America Academy of Arts and Sciences*, **74**, 69–90.

Burleigh, R. & **Whalley, P.** 1983. On the relative geological ages of amber and copal. *Journal of Natural History*, **17**, 919–921. doi:10.1080/00222938300770721

Cameron, P. 1881. Notes on Hymenoptera, with descriptions of new species. *Transactions of the Entomological Society of London*, **1881**, 555–577.

Cameron, P. 1909. A contribution to the knowledgeof the parasitic Hymenoptera of Argentina. *Transactions of the American Entomological Society*, **35**, 419–450.

Carr, M., Young, J. P. W. & **Mayhew, P. J.** 2010. Phylogeny of bethylid wasps (Hymenoptera: Bethylidae) inferred from 28S and 16S rRNA genes. *Insect Systematics and Evolution*, **41**, 55–73. doi:10.1163/187631210X486995

Cockerell, T. D. A. 1920. Fossil arthropods in the British Museum, I. *Annals and Magazine of Natural History*, **5**, 273–279. doi:10.1080/00222932008632376

Cockerell, T. D. A. 1921. Fossil arthropods in the British Museum, V. Oligocene Hymenoptera from the Isle of Wight. *Annals and Magazine of Natural History*, **7**, 1–25. doi:10.1080/00222932108632485

Cohen, K. M., Harper, D. A. T. & **Gibbard, P. L.** 2020. ICS International Chronostratigraphic Chart 2020/03. International Commission on Stratigraphy, IUGS. www.stratigraphy.org (visited: 2020/10/20)

Colombo, W. D. & **Azevedo, C. O.** 2019. Synopsis of the fossil Scleroderminae (Hymenoptera, Bethylidae) with description of a new genus and four new species from Baltic amber. *Historical Biology*, published online 08 August 2019. doi:10.1080/08912963.2019.1650275

Colombo, W. D., Gobbi, F. T., Perkovsky, E. E. & **Azevedo, C. O.** 2020*a*. Synopsis of the fossil Pristocerinae (Hymenoptera, Bethylidae), with description of two new genera and species from Burmese, Taimyr, Baltic and Rovno ambers. *Historical Biology*, published online 13 March 2020. doi:10.1080/08912963.2020.1733551

Colombo, W. D., Perkovsky, E. E. & **Azevedo, C. O.** 2020*b*. Phylogenetic overview of flat wasps (Hymenoptera, Bethylidae) reveals Elektroepyrinae, a new fossil subfamily. *Palaeoentomology*, **3**, 269–283. doi:10.11646/palaeoentomology.3.3.8

Cresson, E. T. 1872. Hymenoptera Texana. *Transactions of the American Entomological Society*, **4**, 153–292. doi:10.2307/25076272

Dodd, A. P. 1914. Further new genera and species of Australian Proctotrypoidea. *Proceedings of the Royal Society of Queensland*, **26**, 91–140. doi:10.5281/zenodo.23758

Enderlein, G. 1901. Neue Evaniiden, Stephaniden, Mutilliden (Apterogyna), Proctotrupiden Und Chalcididen: Mit Einer Bestimmungstabelle Der Afrikanischen Stephaniden. *Archiv für Naturgeschichte*, **1**, 187–220.

Evans, H. E. 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology*, **132**, 1–222.

Evans, H. E. 1973. Further studies on South American Bethylidae (Hymenoptera). *Proceedings of the Entomological Society of Washington*, **75**, 194–204.

Falières, E. & **Nel, A.** 2018. The oldest representative of the extant genus *Epyris* in the lowermost Eocene amber of France (Hymenoptera: Bethylidae: Epyrinae). *Palaeoentomology*, **1**, 32–36. doi:10.11646/palaeoentomology.1.1.3

Feist, M., Lamprecht, I. & **Müller, F.** 2007. Thermal investigations of amber and copal. *Thermochimica Acta*, **458**, 162–170. doi:10.1016/j.tca.2007.01.029

Förster, A. 1856. *Hymenopterologische studien: Chalcidiae und Proctotrupii*. Ernst ter Meer, Aachen, 152 pp. doi:10.5962/bhl.title.8795

Gaertner, J. 1791. *De fructibus et seminibus plantarum*. Sumtibus Auctoris, Typis Academiae Carolinae, Stutgardiae, 306 pp. doi:10.5962/bhl.title.53838

Gehler, A., Reich, M. & **Reitner, J.** 2018. Göttingen: The Palaeontological Collections of the Geoscience Museum at the Georg-August University in Göttingen. Pp. 261–270 in L. A. & U. Joger (eds) *Paleontological Collections of Germany, Austria and Switzerland*. Springer, Cham, 573 pp. doi:10.1007/978-3-319-77401-5

Geirnaert, E. 2002. *L'Ambre: Miel de Fortune et Memoire de Vie*. Les Editions du Piat, Monistrol-sur-Loire, 176 pp.

Gordh, G. & Móczár, L. 1990. A catalog of the world Bethylidae (Hymenoptera: Aculeata). *Memoirs of the American Entomological Institute*, **46**, 1–364.

Haliday, A. H. 1833. An essay on the classification of the parasitic Hymenoptera of Britain, which correspond with the *Ichneumones minuti* of Linnaeus. *Entomological Magazine*, **1**, 259–276.

Haliday, A. H. 1839. *Hymenoptera Britannica: Oxyura*. Hippolytus Bailliere, London, 16 pp.

Harris, R. 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology*, **28**, 1–31.

Hope, F. W. 1837. Description of various new species of insects found in gum animè. *Transaction of Entomological Society of London*, **2**, 52–57.

Iturralde-Vinent, M. A. & **MacPhee, R. D. E.** 1996. Age and paleogeographical origin of Dominican amber. *Science*, **273**, 1850–1852. doi:10.1126/science.273.5283.1850

Kawada, R. & **Buffington, M. L.** 2016. A scalable and modular dome illumination system for scientific microphotography on a budget. *PLoS ONE*, **11**, e0153426. doi:10.1371/journal.pone.0153426

Kieffer, J. J. 1899. Description d'un genre nouveau et tableau des genres européens de la famille des Chironomides [Dipt.]. *Bulletin de la Société entomologique de France*, **4**, 66–70.

Kieffer, J. J. 1904*a*. Descriptions de nouveaux Dryinidae et Bethylidae du Musée Civique de Gênes. *Annali del Museo Civico di Storia Naturale di genova*, **41**, 351–412.

Kieffer, J. J. 1904*b*. Nouveaux proctotrypides myrmécophiles. *Bulletin de la Société d'Histoire Naturelle de Metz*, **23**, 31–58. doi:10.5281/zenodo.24240

Kieffer, J. J. 1905. Description de nouveaux Proctotrypides exotiques avec une planche et une figure dans le texte. *Annales de la Société Scientifique de Bruxelles*, **29**, 95–142.

Kieffer, J. J. 1913*a*. Nouveaux microhyménoptères de l'Afrique équatoriale. *Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricultura*, **7**, 105–112. doi:10.5281/zenodo.23805

Kieffer, J. J. 1913*b*. Serphides des Iles Philippines. *Insecta*, **3**, 317–324. doi:10.5281/zenodo.23750

Kieffer, J. J. 1914. Bethylidae. *Das Tierreich*, **41**, 228–595.

Kieffer, J. J. & **Marshall, T. A.** 1904–1906. Proctotrypides. [Publication dates of the different parts: Pp. 1–64 1st January 1904; Pp. 65–144 1st April 1905; Pp. 145–288 1st November 1905; Pp. 289–368 31st January 1906; Pp. 369 until the end 1st October 1906] in E. André (ed) *Species des Hyménoptères d'Europe et d'Algérie.* Librairie Scientifique, A. Hermann, Paris, **9**, 551 pp.

Kosmowska-Ceranowicz, B. 2001. Bursztyn i inne żywice kopalne świata. Kopale i żywice sztuczne – imitacje lub fałszerstwa bursztynu. *Polski Jubiler*, **1**, 24–27. [In Polish].

Krombein, K. V. 1992. Systematics of the genera of Epyrinae with ramose male antennae (Hymenoptera: Bethylidae). *Proceedings of the Entomological Society of Washington*, **94**, 345–360.

Lanes, G.O., Kawada, R., Azevedo, C.O. & **Brothers, D.J.** 2020. Revisited morphology applied for systematics of flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, **4752**, 001–127. doi:10.11646/zootaxa.4752.1.1

Langenheim, J. H. 2003. *Plant resins: chemistry, evolution, ecology and ethnobotany*. Timber Press, Portland, Cambridge, 586 pp.

Loew, H. 1850. Ueber den Bernstein und die Bernsteinfauna. *Programm Der Königlichen Realschule Zu Meseritz*, **1850**, 1–44. doi:10.5962/bhl.title.98386

Martynova, K. V., Perkovsky, E. E., Olmi, M. & **Vasilenko, D. V.** 2019. New records of upper Eocene Chrysidoid wasps (Hymenoptera: Chrysidoidea) from basins of Styr and Stokhod Rivers (Rovno Amber). *Paleontological Journal*, **53**, 16–41.

Masner, L. & **Johnson, N. F.** 2007. *Janzenella*, an enigmatic new genus of scelionid wasp from Costa Rica (Hymenoptera, Platygastroidea, Scelionidae). *American Museum Novitates*, **3574**, 1–7. doi:10.1206/3574.1

Matuszewska, A. 2010. *Bursztyn i inne żywice kopalne, subfossylne i współczesne*. Uniwersytet Śląski, Oficyna Wydawnicza Wacław Walasek, Katowice, 234 pp. [In Polish].

Mayr, G. 1868. *Die Ameisen des Baltischen Bernstein*. Beiträge zur Naturkunde Preussens Physikalische-Ökonomischen Gesellschaft, Königsberg, 102 pp.

Meigen, J. W. 1803. Versuch einer neuen Gattungs Einteilung der europäischen zweiflügeligen Insekten. *Magazin für Insektenkunde (Illiger)*, **2**, 259–281.

Meigen, J. W. 1818. *Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten*. Bei Friedrich Wilhelm Forstmann, Gedrukt bei Beaufort Sohn, Aachen, 332 pp. doi:10.5962/bhl.title.12464

Meunier, F. 1906. Sur deux insectes (Hyménoptère et Diptère) du copal fossile de Zanzibar et sur un "Asilidae" (Diptère) du Copal récent de Zanzibar. *Revue Scientifique du Bourbonnais et du Centre de la France*, **19**, 59–63.

Nel, A. & **Brasero, N.** 2010. Oise amber. Pp. 137–148 in D. Penney (ed) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, 304 pp.

Nel, A., De Plöeg, G., Dejax, J., Dutheil, D., Franceschi, D., Gheerbrant, E., Godinot, M., Hervet, S., Menier, J. -J., Augé, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J., Hua, S., Jossang, A., Lapparent De Broin, F., Pozzi, J. -P., Paicheler, J. -C., Bouchet, F. & **Rage, J. -C.** 1999. An exceptional Sparnacian locality with plants, arthropods and vertebrates (Earliest Eocene, MP7): Le Quesnoy (Oise, France). *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science*, **329**, 65–72. doi: 10.1016/S1251-8050(99)80229-8

Ohl, M. 1995. Eine neue Bethylidae der Gattung *Lytopsenella* Kieffer 1911 aus dem Baltischen Bernstein (Hymenoptera: Chrysidoidea). *Palaeontologische Zeitschrift*, **69**, 409–416.

Penney, D., Ono, H. & **Selden, P. A.** 2005. A new synonymy for the Madagascan copal spider fauna (Araneae, Selenopidae). *Journal of Afrotropical Zoology*, **2**, 41–44.

Perkovsky, E. E. 2018. Only a half of species of Hymenoptera in Rovno amber is common with Baltic Amber. *Vestnik Zoologii*, **52**, 353–360. doi:10.2478/vzoo-2018-0037

Perkovsky, E. E., Hava, J. & **Zaitsev, A. A.** 2021. First finding of skin beetle (Coleoptera, Dermestidae) from Sakhalinian amber. *Paleontological Journal*, **55**, in press.

Perkovsky, E. E., Rasnitsyn, A. P., Vlaskin, A. P. & **Rasnitsyn, S. P.** 2012. Contribution to the study of the structure of amber forest communities based on analysis of syninclusions in the Rovno amber (Late Eocene of Ukraine). *Paleontological Journal*, **46**, 293–301. doi:10.1134/S0031030112030136

Perkovsky, E. E., Rasnitsyn, A. P., Vlaskin, A. P. & **Taraschuk, M. V.** 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates*, **48**, 229–245.

Perkovsky, E. E., Zosimovich, V. Yu. & **Vlaskin, A. P.** 2010. Rovno amber. Pp. 116–136 in D. Penney (ed) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, 304 pp.

Perrichot, V. & **Nel, A.** 2008. Eocene bethylid wasps from French amber (Hymenoptera: Bethylidae). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, **248**, 91–101. doi:10.1127/0077-7749/2008/0248-0091

Petrov, A. V. & **Perkovsky, E. E.** 2008. New species of bark beetles from the Rovno amber (Insecta: Coleoptera: Scolytidae). *Paleontological Journal*, **42**, 406–408.

Petrov, A. V. & **Perkovsky, E. E.** 2018. A new genus and species of Scolytinae (Coleoptera: Curculionidae) from the Rovno amber. *Paleontological Journal*, **52**, 164–167.

Petrulevičius, J. F., Wappler, T., Nel, A. & **Rust, J.** 2011. The diversity of Odonata and their endophytic ovipositions from the upper Oligocene Fossillagerstätte of Rott (Rhineland, Germany). *ZooKeys*, **130**, 67–89. doi:10.3897/zookeys.130.1441

Poinar, G. O. Jr. 1992. *Life in amber*. Stanford University Press, Palo Alto, California, 350 pp.

Priesner, H. A. 1924. Bernstein-Thysanopteren I. *Entomologische Mitteilungen*, **13**, 130–151.

Prothero, D. R. & **Sanchez, F.** 2004. Magnetic stratigraphy of the upper Eocene Florissant Formation, Teller County, Colorado. *New Mexico Museum of Natural History and Science Bulletin*, **26**, 129–135.

Ramos, M. S., Perkovsky, E. E., Rasnitsyn, A. P. & **Azevedo, C. O.** 2014. Revision of Bethylinae fossils (Hymenoptera: Bethylidae) from Baltic, Rovno and Oise amber, with comments on the Tertiary fauna of the subfamily. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, **271**, 203–228. doi:10.1127/0077-7749/2014/0385

Reich, M., Gehler, A. & **Stegemann, T. R.** 2015. Amber Collections [Göttingen University, Germany]. Pp. 84–85 in Göttingen University (ed) *The Collections, Museums and Gardens of Göttingen University*. Universitätsbibliothek Göttingen, Germany, 121 pp.

Ross, A. J. & **Self, A.** 2014. The fauna and flora of the Insect Limestone (Late Eocene), Isle of Wight, UK: introduction, history and geology. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **104**, 232–44. doi:10.1017/S1755691014000073

Schlüter, T. & **Von Gnielinski, F.** 1987. The East African copal: its geologic, stratigraphic paleontologic significance and comparison with fossil resins of similar age. *National Museums of Tanzania Occasional Paper*, **8**, 1–32.

Shi, G., Grimaldi, D. A., Harlow, G. E., Wang, J., Wang, J., Yand, M., LEI, W., Li, Q. & **Li, X.** 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, **37**, 155–163. doi:10.1016/j.cretres.2012.03.014

Shmakov, A. S. & **Perkovsky, E. E.** 2009. Thrips (Thysanoptera, Insecta) from the Rovno amber, Eocene of Ukraine. *Paleontological Journal*, **43**, 669–674.

Simutnik, S. A. & **Perkovsky, E. E.** 2018. *Archaeocercus* gen. nov. (Hymenoptera, Chalcidoidea, Encyrtidae) from Late Eocene Rovno Amber. *Zootaxa*, **4441**, 543–548. doi:10.11646/zootaxa.4441.3.8

Solórzano-Kraemer, M. M., Delclòs, X., Engel, M. S. & **Peñalver, E.** 2020. A revised definition for copal and its significance for palaeontological and Anthropocene biodiversity-loss studies. *Scientific reports*, **10**, 1–12. doi:10.1038/s41598-020-76808-6

Sorg, M. 1988. Zur Phylogenie und Systematik der Bethylidae (Insecta: Hymenoptera, Chrysidoidea). *Sonderveröffentlichungen des Geologischen Instituts der Universität Köln*, **63**, 1–146.

Spinola, M. 1853. Compte rendu des Hyménoptères inédits provenants du voyage entomologique de M. Ghiliani dans la Para en 1846. *Memorie della Reale Accademia Delle Scienze di Torino*, **13**, 19–94. doi: 10.5281/zenodo.24751

Statz, G. 1938. Neue funde parasitischer Hymenopteren aus dem Tertiär von Rott am Siebengebirge. *Decheniana*, **98**, 71–151.

Terayama, M. 2003. Phylogenetic systematics of the family Bethylidae (Insecta: Hymenoptera) part I. Higher classification. *Academic Reports of the Faculty of Engineering of Tokyo Polytechnic University*, **26**, 1–14.

Terayama, M. 2004. *Formosiepyris*, a new genus of the family Bethylidae (Hymenoptera, Chrysidoidea) from the Oriental Region, with a proposal of a new synonymy of genus. *Liberal Arts*, **12**, 91–99.

Waichert, C. & **Azevedo, C. O.** 2009. Phylogenetic analysis of *Rhabdepyris* (Hymenoptera: Bethylidae) and redefinition of generic limits based on morphological characters. *Zootaxa*, **2284**, 1–29. doi: 10.5281/zenodo.191239

Weitschat W. & **Wichard W.** 2002. *Atlas of plants and animals in Baltic amber*. Verlag Dr. Friedrich Pfeil, München, 256 pp.

Westwood, J. O. 1832. Descriptions of several new British forms amongst the parasitic hymenopterous insects. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, **1**, 127–129. doi:10.1080/14786443208647849

Zhang, Q., Rasnitsyn, A. P., Wang, B. & **Zhang, H.** 2018. Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: A review of the fauna. *Proceedings of the Geologists Association*, **129**, 736–747. doi:10.1016/j.pgeola.2018.06.004

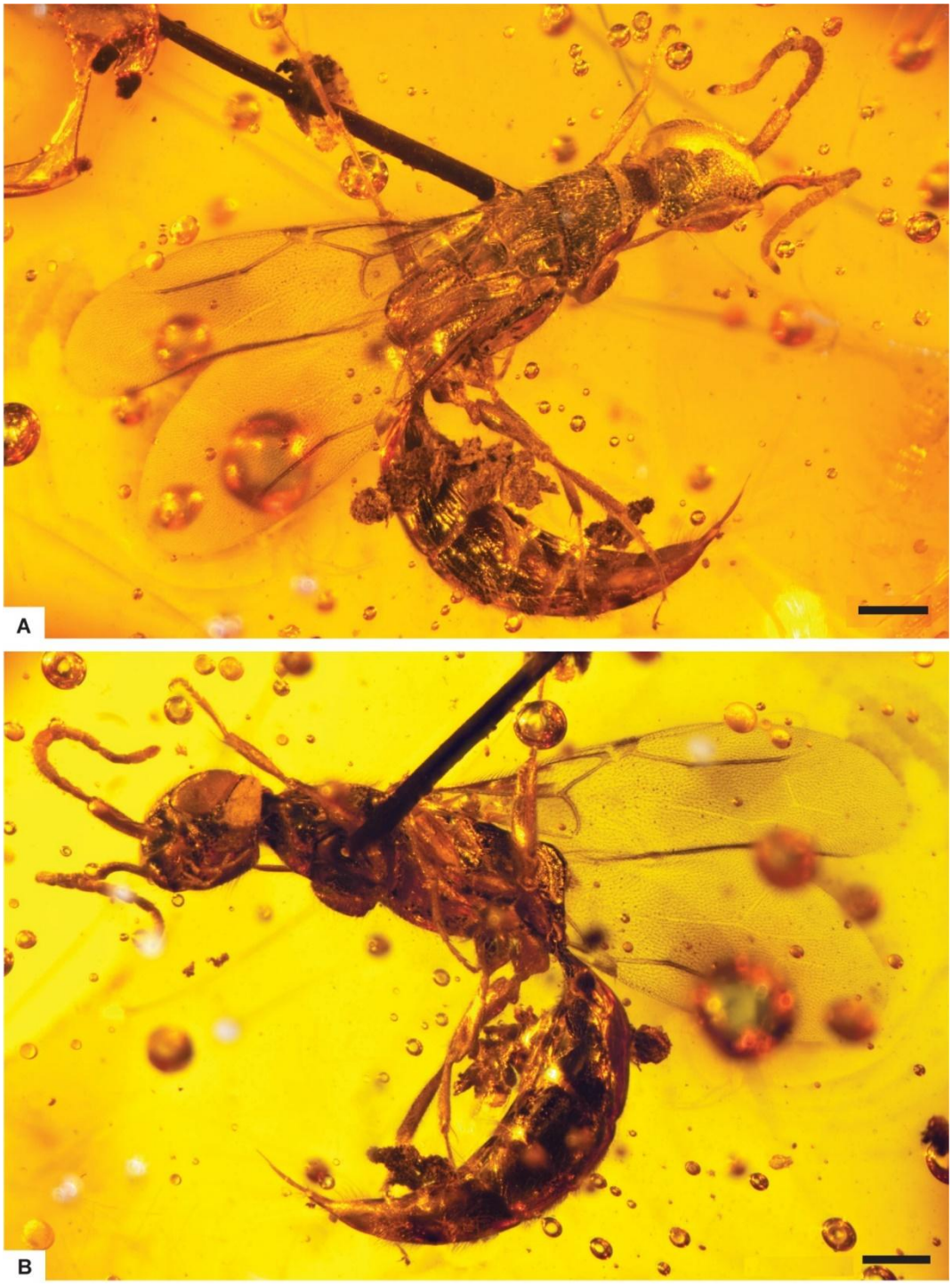

FIGURE 1. †*Anisepyris gradatus* Sorg, 1988, piece code SMF-Be 559, female holotype. **A**, Habitus, dorsolateral view; **B**, Habitus, ventrolateral view. Scales: 0.5 mm. Reproduced with permission of SMF.

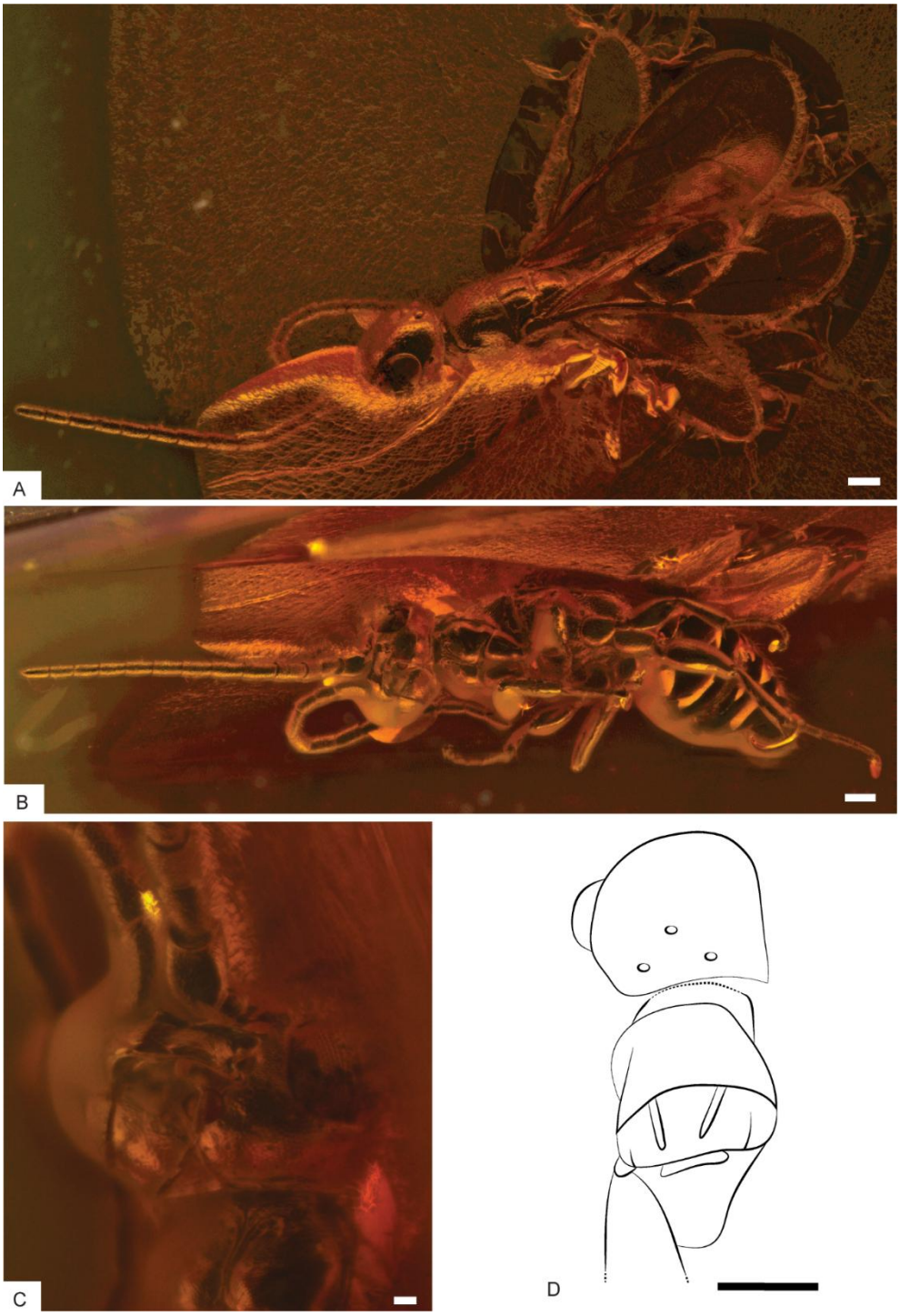

FIGURE 2. †*Chlorepyris deploegi* **sp. nov.**, piece code SIZK K-364, male holotype. **A**, Habitus, lateral view; **B**, Habitus, ventral view; **C**, Head, frontal view; **D**, Head and mesosoma, dorsal view. Scales: 0.2 mm for A–C, 0.5 mm for D.

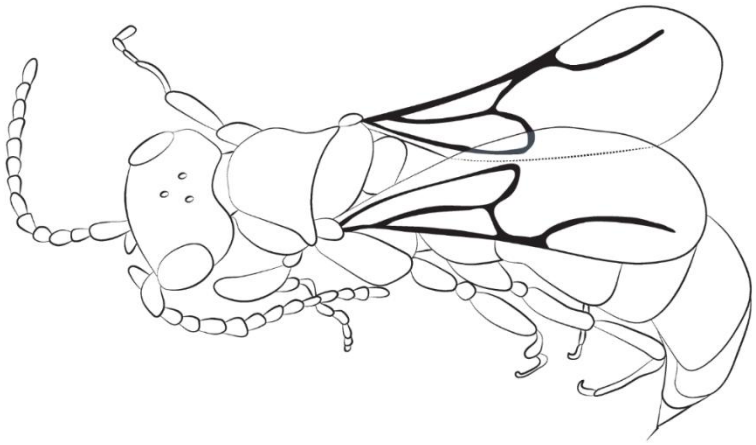

FIGURE 3. †*Chlorepyris concaptus* (Brues, 1933), piece without code, female holotype, habitus, dorsolateral view [redrawn digitally from Brues 1933].

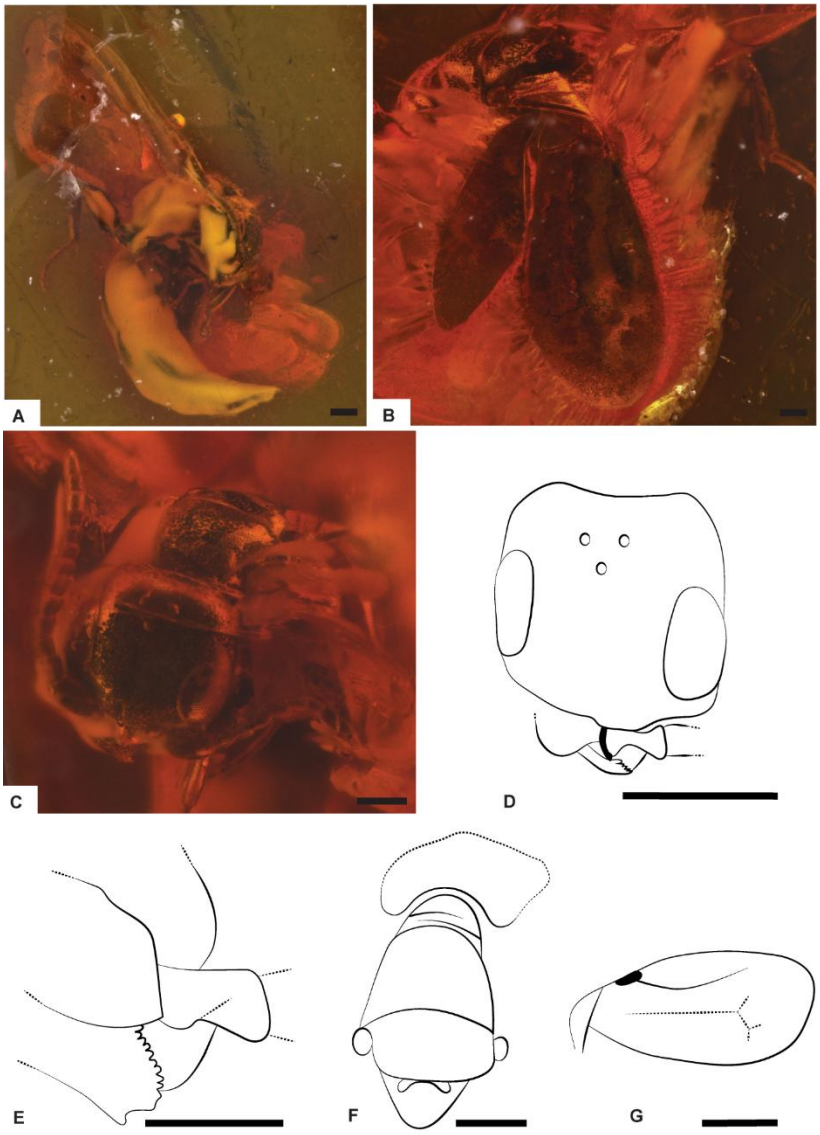

FIGURE 4. †*Chlorepyris engeli* **sp. nov.**, piece code PIN 964/122, female holotype. **A**, Habitus, lateral view; **B**, Habitus, dorsolateral view; **C**, Head, frontal view; **D**, Head, dorsal view; **E**, Mandible, frontal view; **F**, Mesosoma, dorsal view; **G**, Fore wing, dorsal view. Scales: 0.5 mm for D and G, 0.2 mm for A–C.

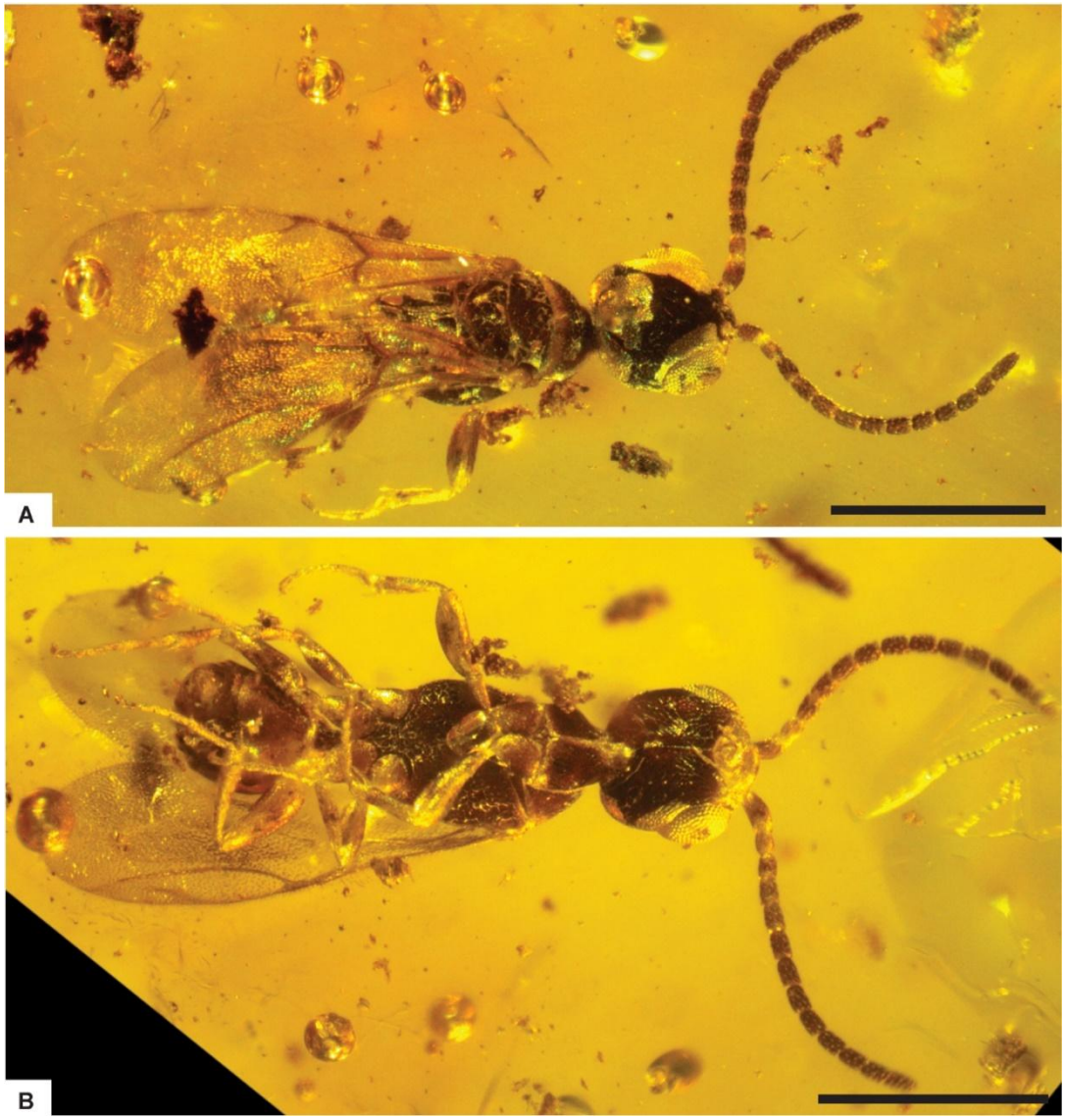

FIGURE 5. †*Chlorepyris gallicus* (Perrichot & Nel, 2008), piece code MNHN.F.A30297, male holotype. **A**, Habitus, dorsal view; **B**, Habitus, ventral view. Scales: 0.5 mm. Reproduced with permission of MNHN.

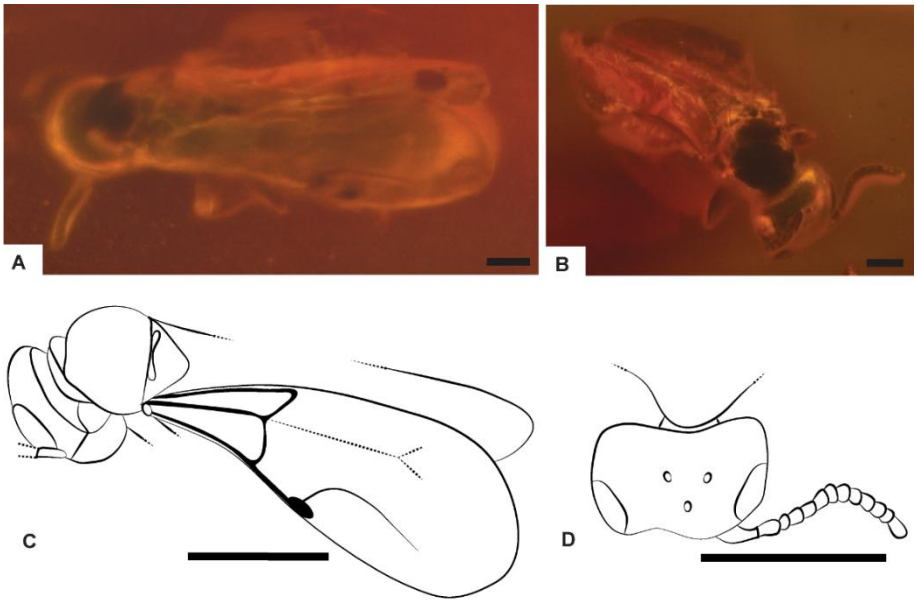

FIGURE 6. †*Chlorepyris hopei* **sp. nov.**, piece code PIN 964/118, female holotype. **A**, Habitus, dorsal view; **B**, Habitus, frontal view; **C**, Habitus, dorsolateral view; **D**, Head, dorsal view. Scales: 1.0 mm for C and D, 0.2 mm for A and B.

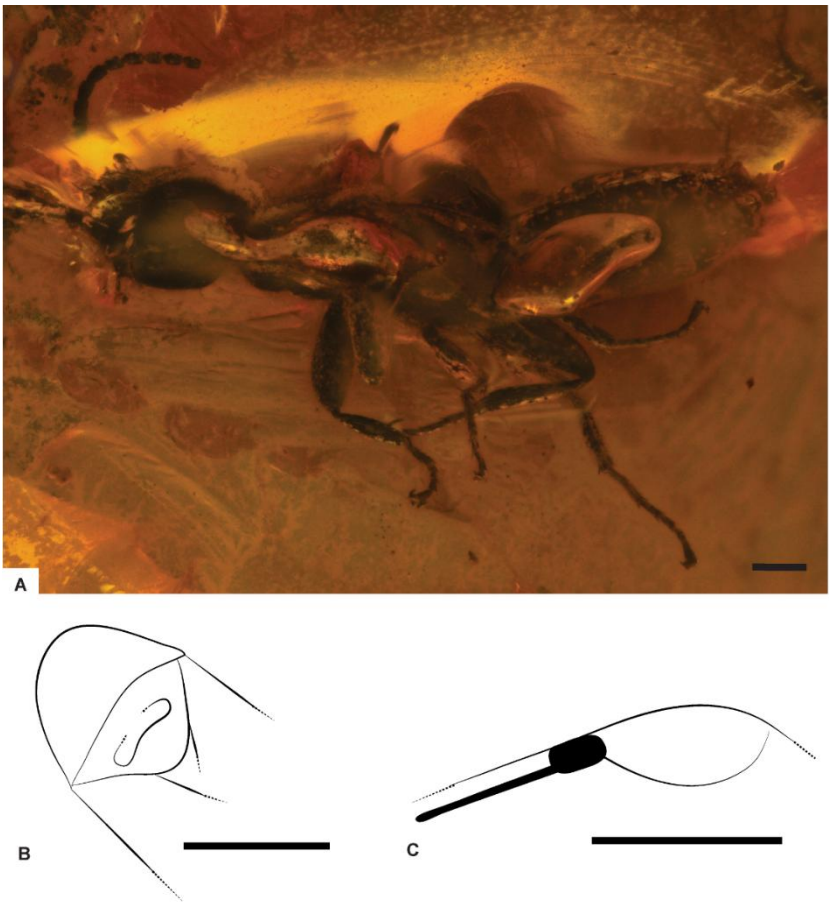

FIGURE 7. †*Chlorepyris jouaulti* **sp. nov.**, piece code SIZK K-7725, male holotype. **A**, Habitus, lateral view; **B**, Mesoscutellum, dorsal view; **C**, Fore wing, dorsal view. Scales: 1.0 mm for B and C, 0.2 mm for A.

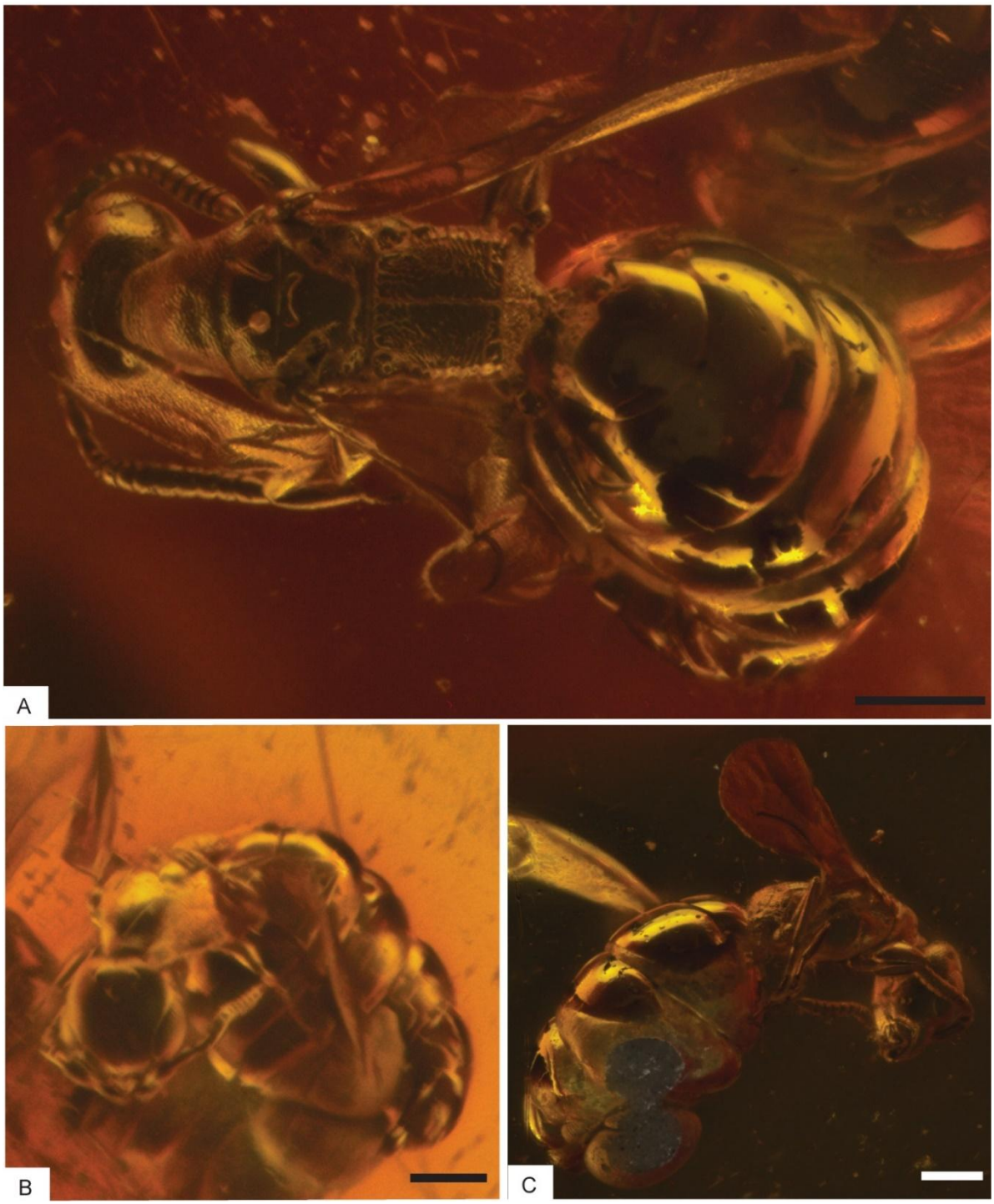

FIGURE 8. †*Chlorepyris mckellari* **sp. nov.**, piece code SIZK K-24565, female holotype. **A**, Habitus, dorsal view; **B**, Habitus, frontal view. **C**, Habitus, posterolateral view. Scales: 0.2 mm.

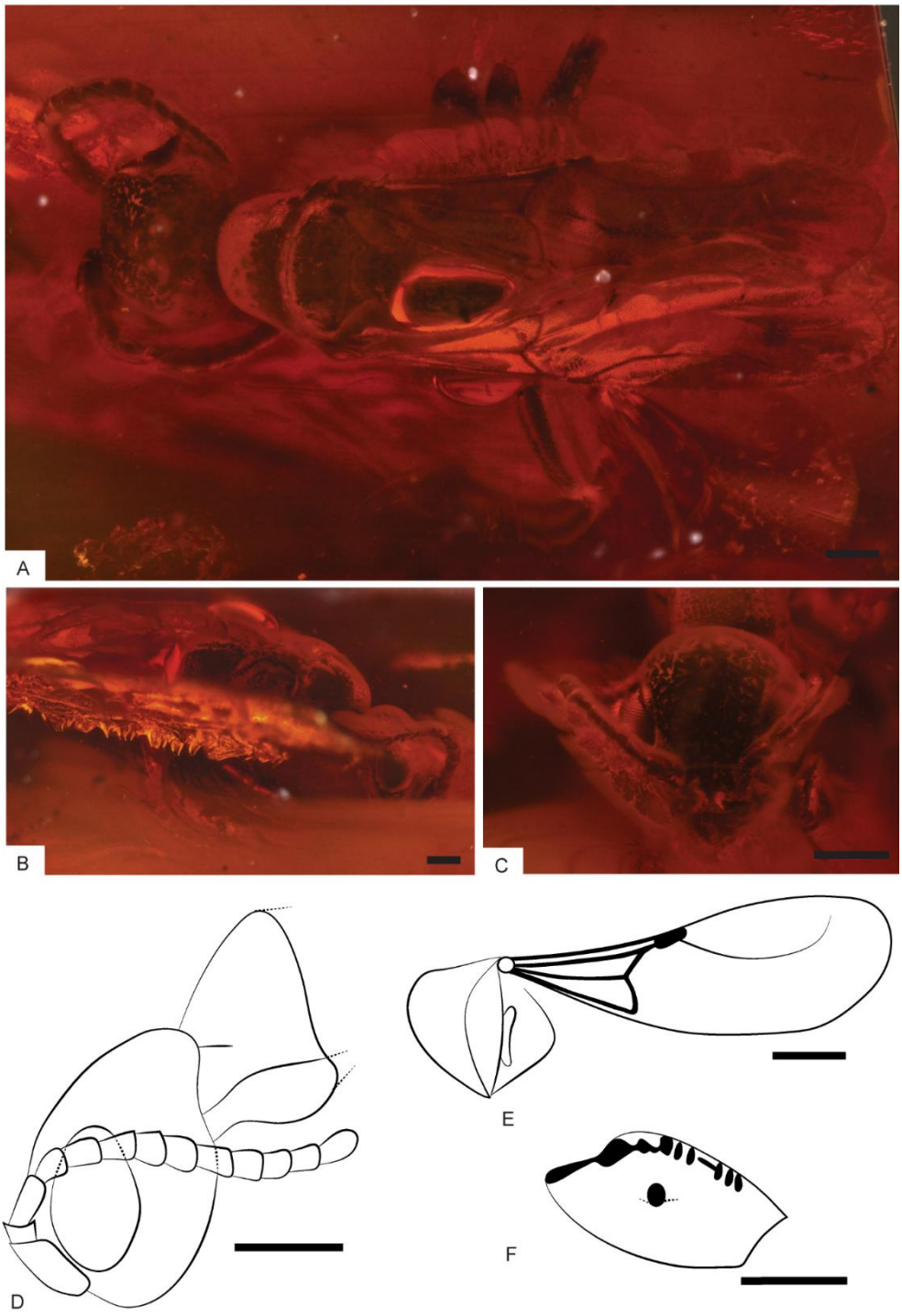

FIGURE 9. †*Chlorepyris meunieri* **sp. nov.**, piece code PIN 964/121, female holotype. **A**, Habitus, dorsal view; **B**, Habitus, lateral view; **C**, Head, dorsal view; **D**, Head and pronotum, lateral view; **E**, Mesosoma and fore wing, dorsal view; **F**, Mesopleuron, lateral view. Scales: 0.5 mm for D–F, 0.2 mm for A–C.

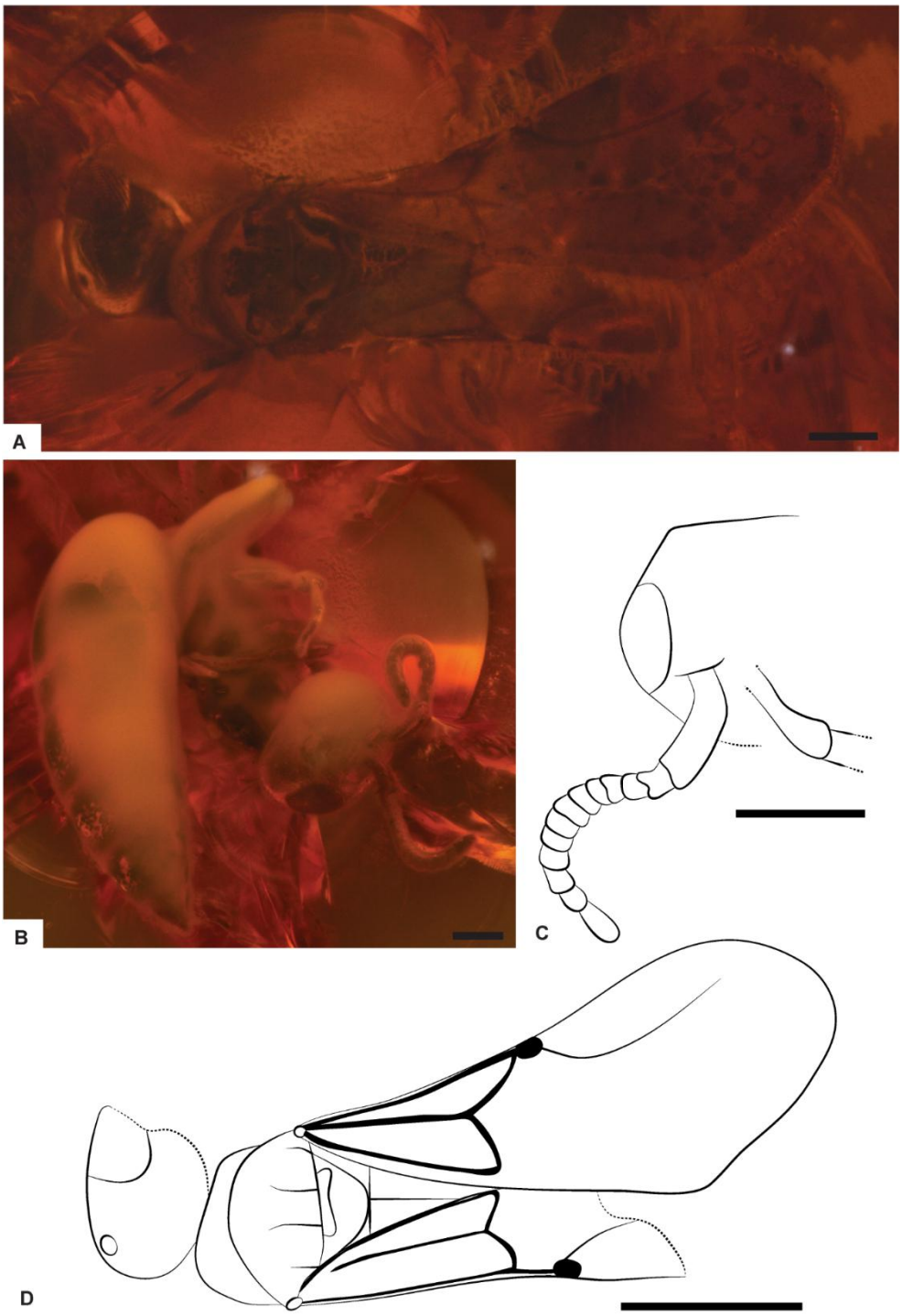

FIGURE 10. †*Chlorepyris neli* **sp. nov.**, piece code SIZK UA-68, female holotype. **A**, Habitus, dorsal view; **B**, Habitus, posterolateral view; **C**, Head, dorsal view; **D**, Habitus, dorsal view. Scales: 1.0 mm for D, 0.5 mm for C and 0.2 mm for A and B.

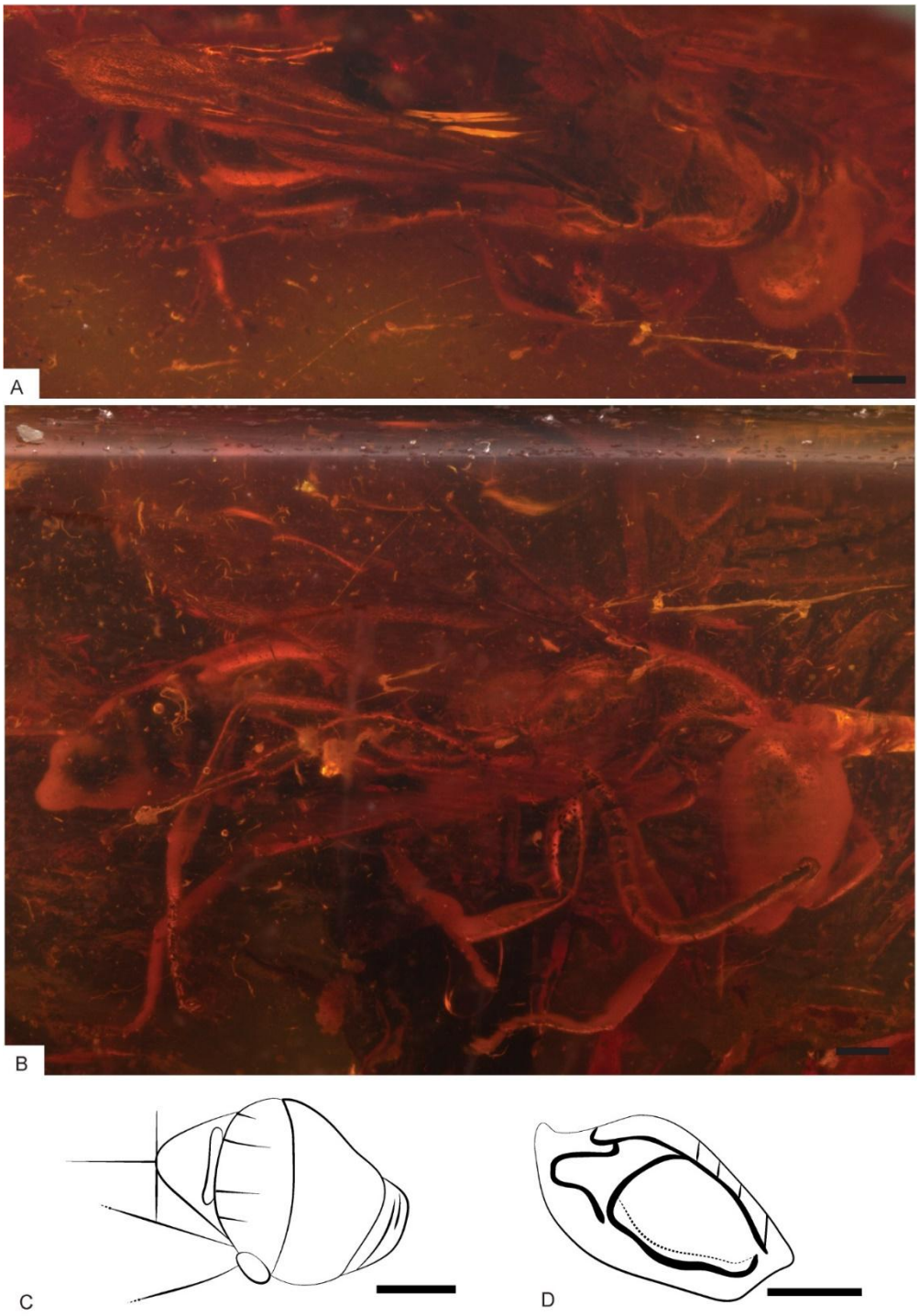

FIGURE 11. †*Chlorepyris perrichoti* **sp. nov.**, piece code PIN 964/116, female holotype. **A**, Habitus, dorsal view; **B**, Habitus, lateral view; **C**, Mesosoma, dorsal view; **D**, Mesopleuron, lateral view. Scales: 0.5 mm for C and D, 0.2 mm for A and B.

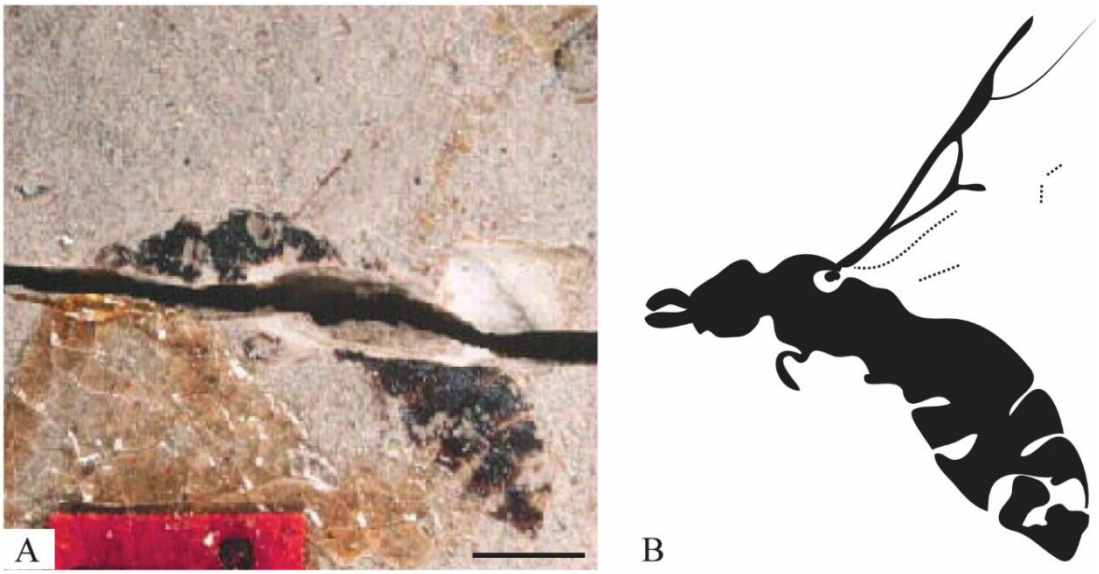

FIGURE 12. †*Epyris deletus* Brues, 1910, piece code AMNH-FI 18891, female holotype. **A** and **B**, Habitus, lateral view. Scales: 0.5 mm. Reproduced with permission of AMNH, Paleontology.

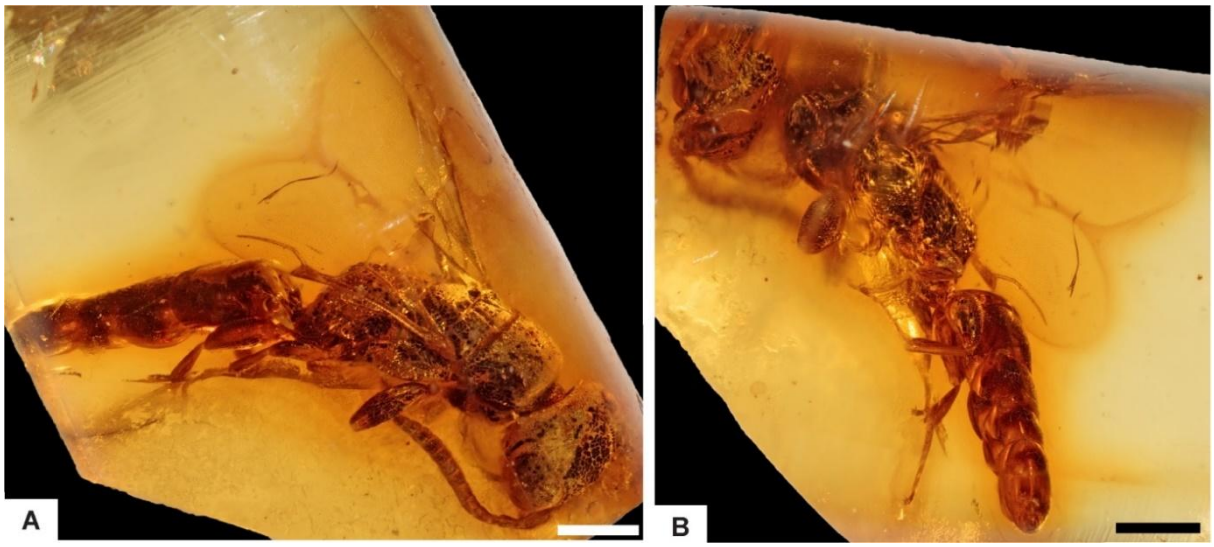

FIGURE 13. †*Epyris moulyi* Falières & Nel, 2018, piece code PA 16149, male holotype. **A**, Habitus, dorsolateral view; **B**, Habitus, ventrolateral view. Scales: 0.5 mm. Reproduced with permission of MNHN.

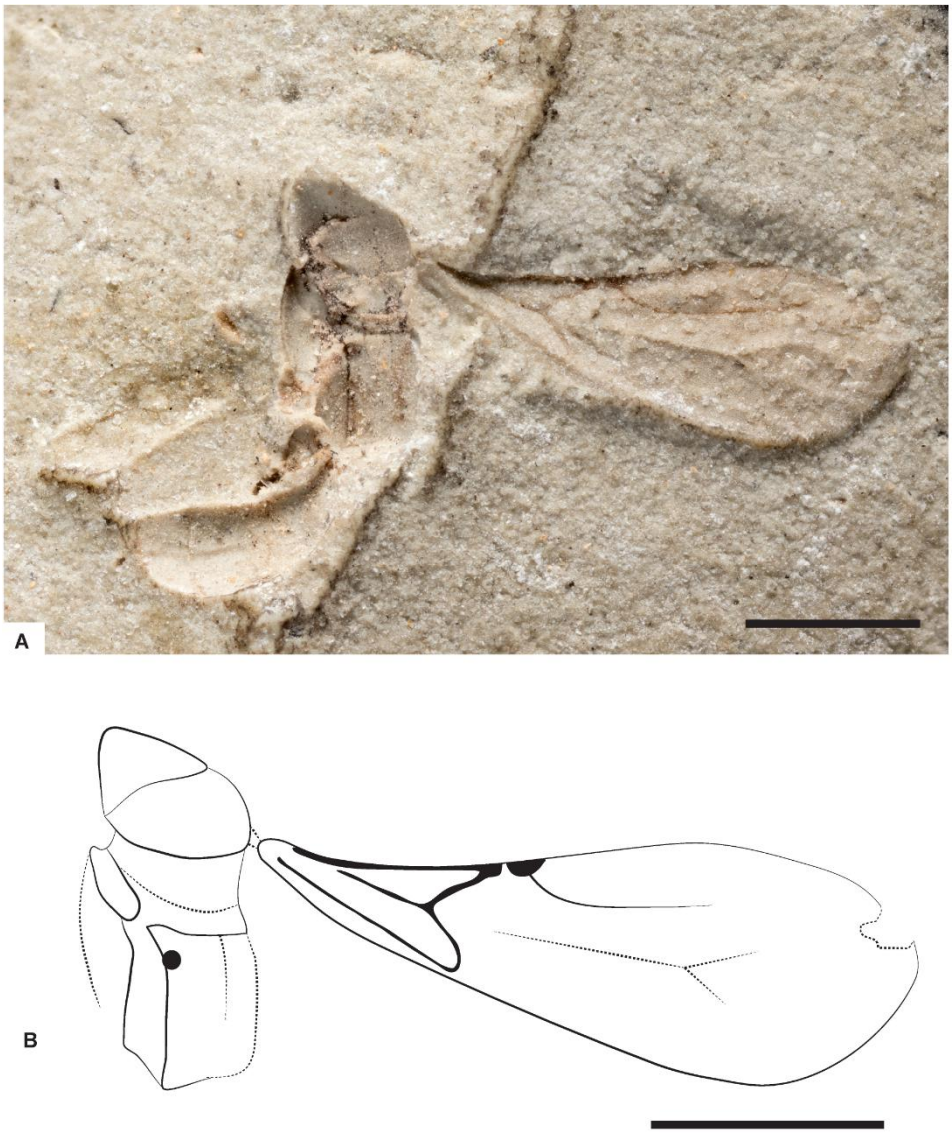

FIGURE 14. †*Epyris rectinervis* (Cockerell, 1921), piece code NHMUK I.9352, holotype. **A** and **B**, Mesosoma and fore wing, dorsolateral view. Scales: 0.5 mm. Reproduced with permission of NHM, London.

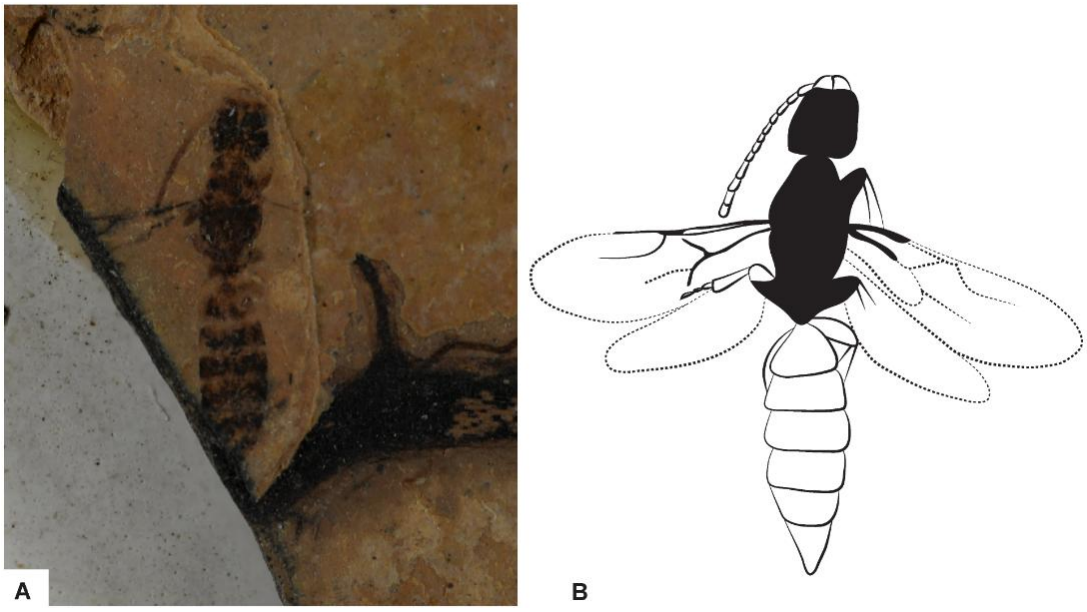

FIGURE 15. †*Epyris tenellus* Statz, 1938, piece code LACMIP-2533.790, female holotype. **A** and **B**, Habitus, dorsal view. Reproduced with permission of LACMIP, GBIF: https://www.gbif.org/occurrence/1851091819.

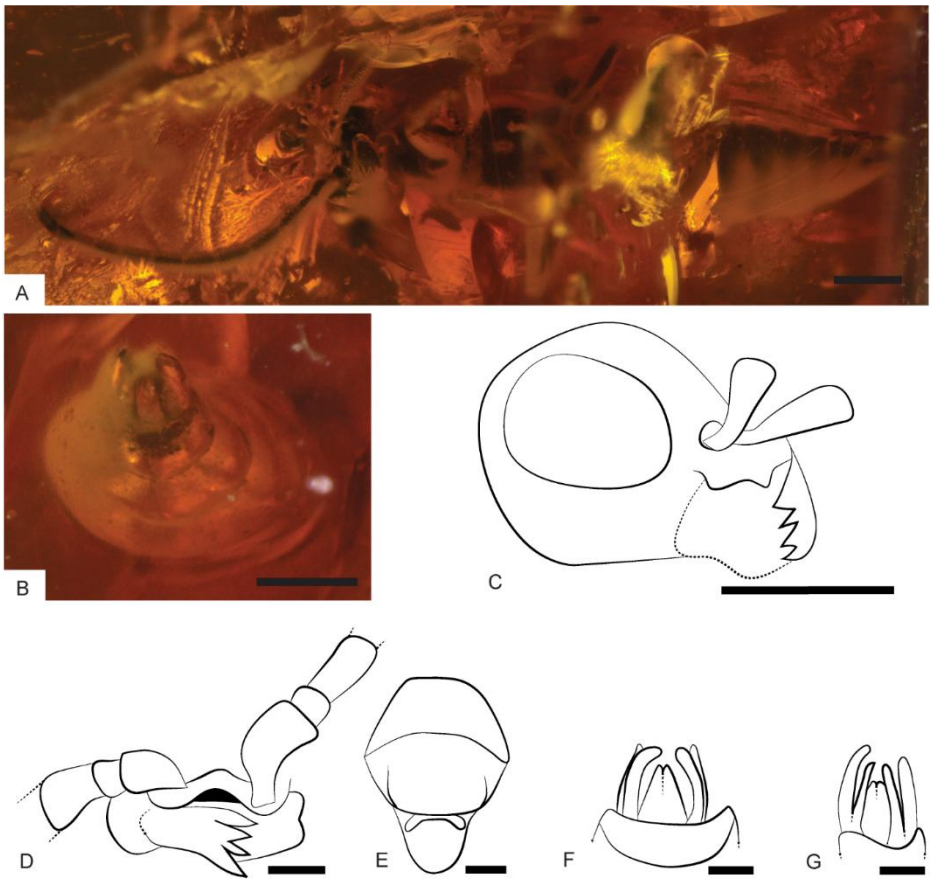

FIGURE 16. †*Holepyris rasnitsyni* **sp. nov.**, piece code PIN 964/115, male holotype. **A**, Habitus, ventral view; **B**, Genitalia, dorsal view; **C**, Head, lateral view; **D**, Mandible, frontal view; **E**, Mesosoma, dorsal view; **F**, Genitalia, dorsal view; **G**, Genitalia, ventral view. Scales: 0.3 mm for D–G, 0.5 mm for C and 0.2 mm for A and B.

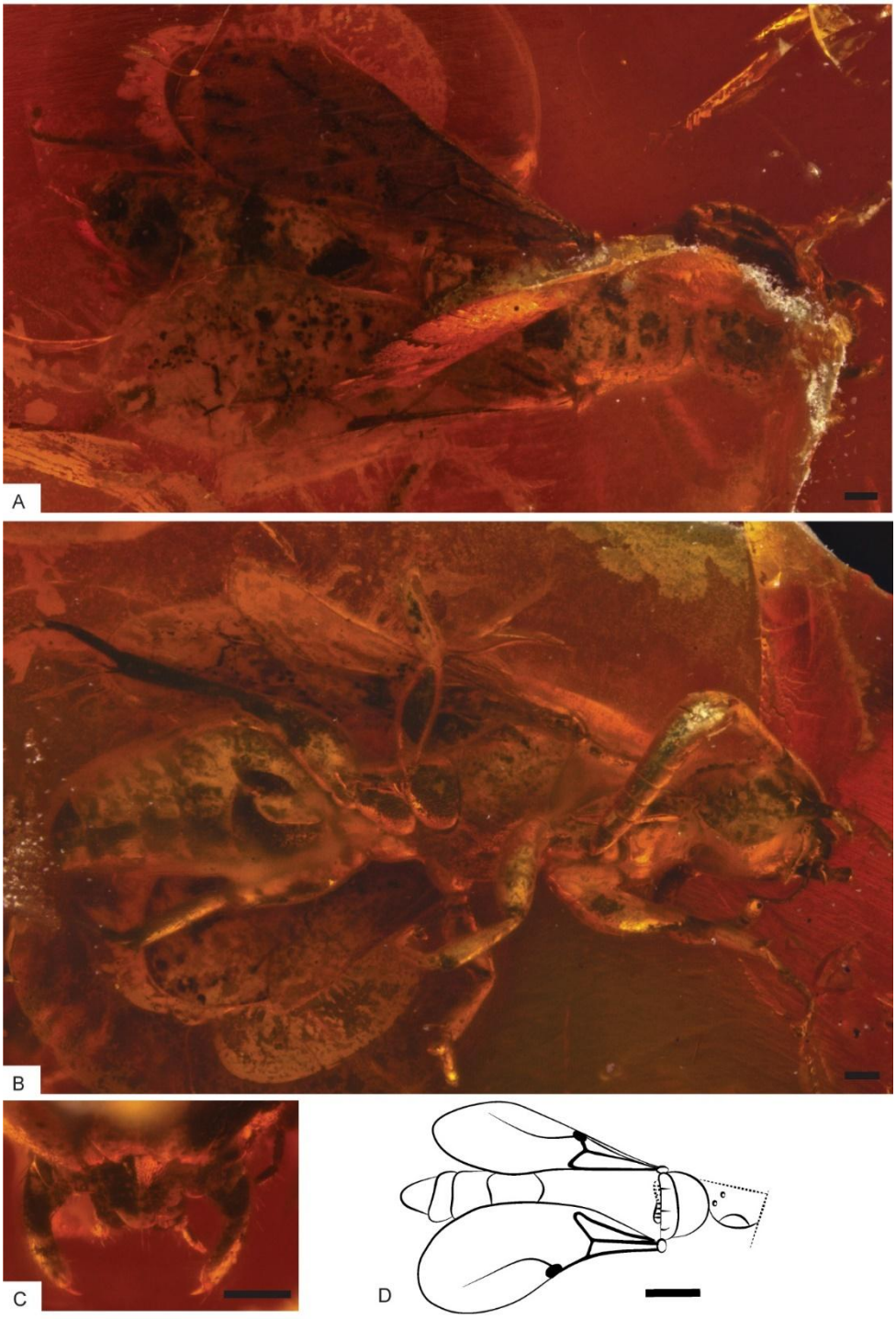

FIGURE 17. †*Holepyris terayamai* **sp. nov.**, piece code SIZK K-797, female holotype. **A**, Habitus, dorsal view; **B**, Habitus, ventrolateral view; **C**, Clypeus and mandible, dorsal view; **D**, Habitus, dorsal view. Scales: 0.2 mm for A–C, 1.0 mm for D.

FIGURE 18. †*Holepyris minor* (Brues, 1939), piece code PALE-6634, female holotype, habitus, dorsal view. Scales: 0.5 mm. Reproduced with permission of President and Fellows of Harvard College.

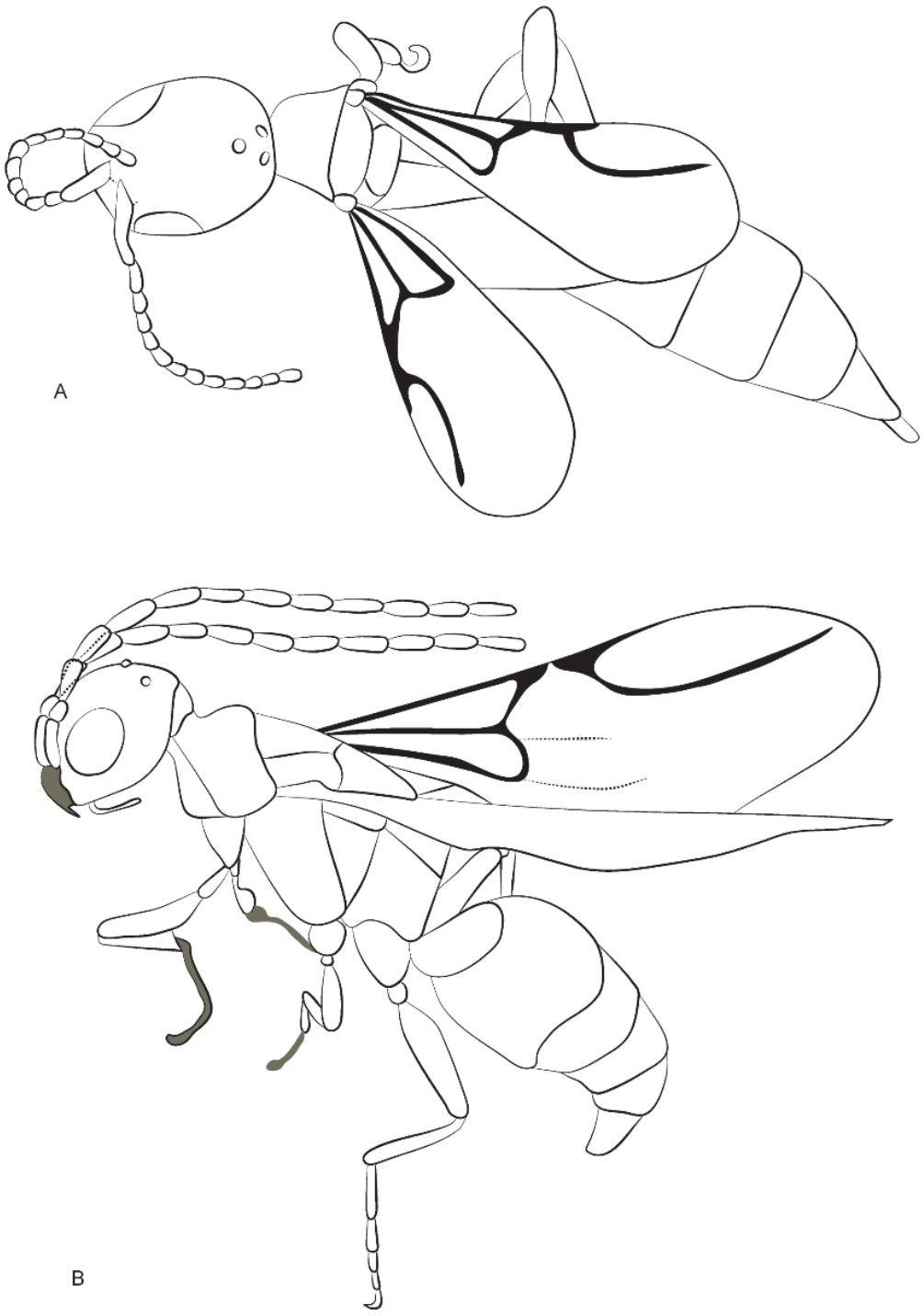

FIGURE 19. A, †*Holepyris planiceps* Brues, 1933, piece without code, female holotype, habitus in dorsal view; **B**, †*Holepyris precursor* Brues, 1933, piece code B14174, female holotype, habitus in lateral view. [redrawn digitally from Brues 1933].

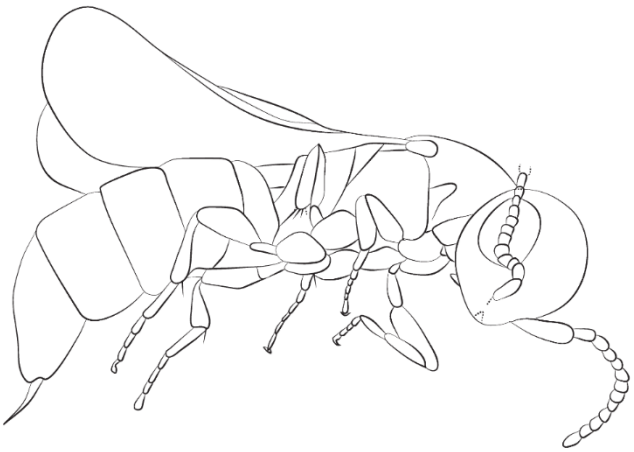

FIGURE 20. †*Holepyris robustus* (Brues, 1933), piece without code, female holotype, habitus in ventrolateral view. [redrawn digitally from Brues 1933].

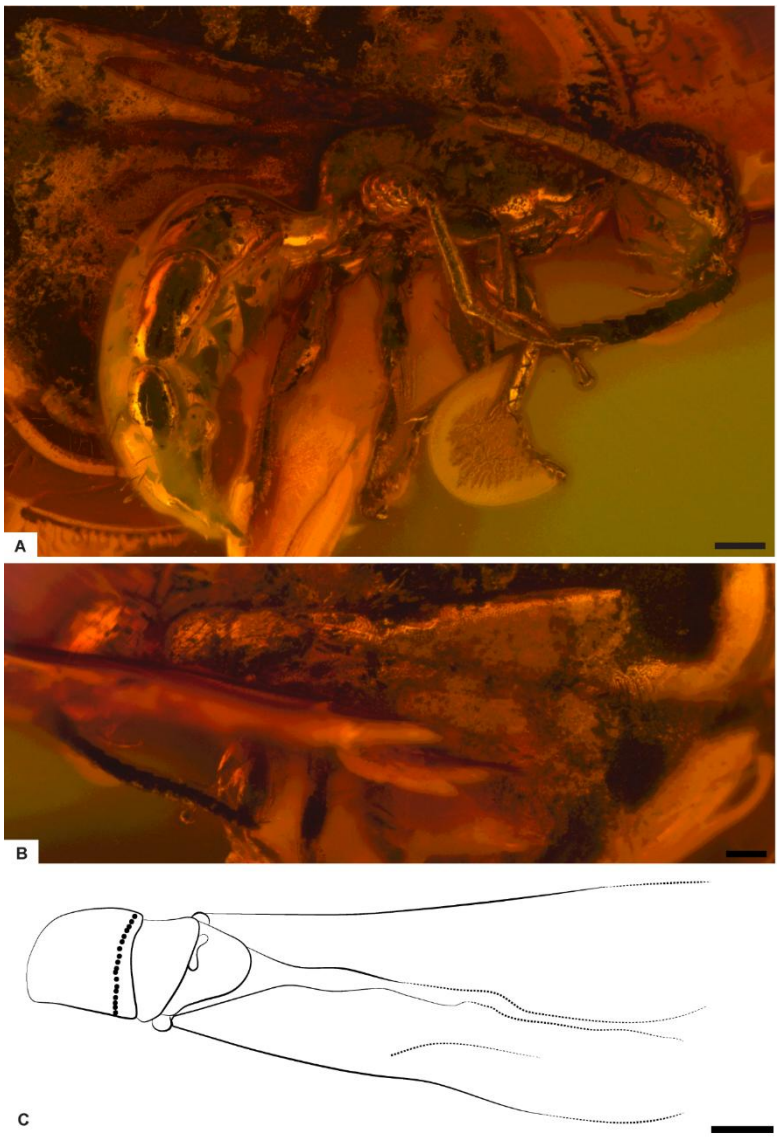

FIGURE 21. †*Laelius preteritus* Barbosa & Azevedo, 2013, piece code K-4207, female holotype. **A**, Habitus, ventrolateral view; **B**, Habitus, dorsal view; **C**, Mesosoma and fore wings, dorsal view. Scales: 0.2 mm.

FIGURE 22. †*Laelius rovnensis* Barbosa & Azevedo, 2013, piece code K-3672, female holotype. **A**, Habitus, dorsolateral view; **B**, Habitus, ventral view. Scales: 0.2 mm.

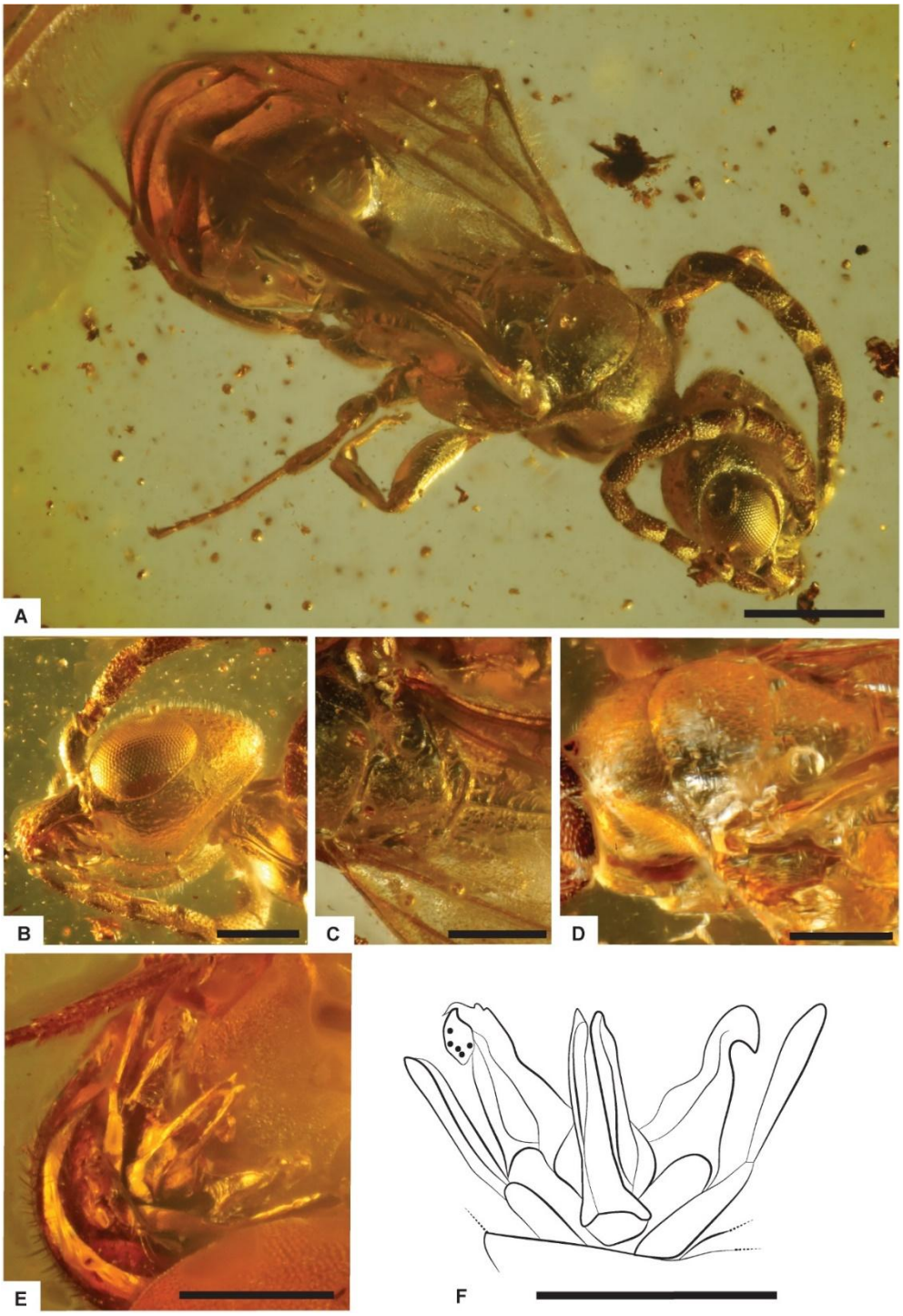

FIGURE 23. †*Gloxinius bifossatus* (Brues, 1939), piece code PALE-7679, male holotype. **A**, Habitus, dorsolateral view; **B**, Head, lateral view; **C**, Mesoscutellum, dorsal view; **D**, Mesosoma, dorsolateral view; **E** and **F**, Genitalia, dorsal view. Scales: 0.25 mm for B–F, 0.5 mm for A. Reproduced with permission of President and Fellows of Harvard College.

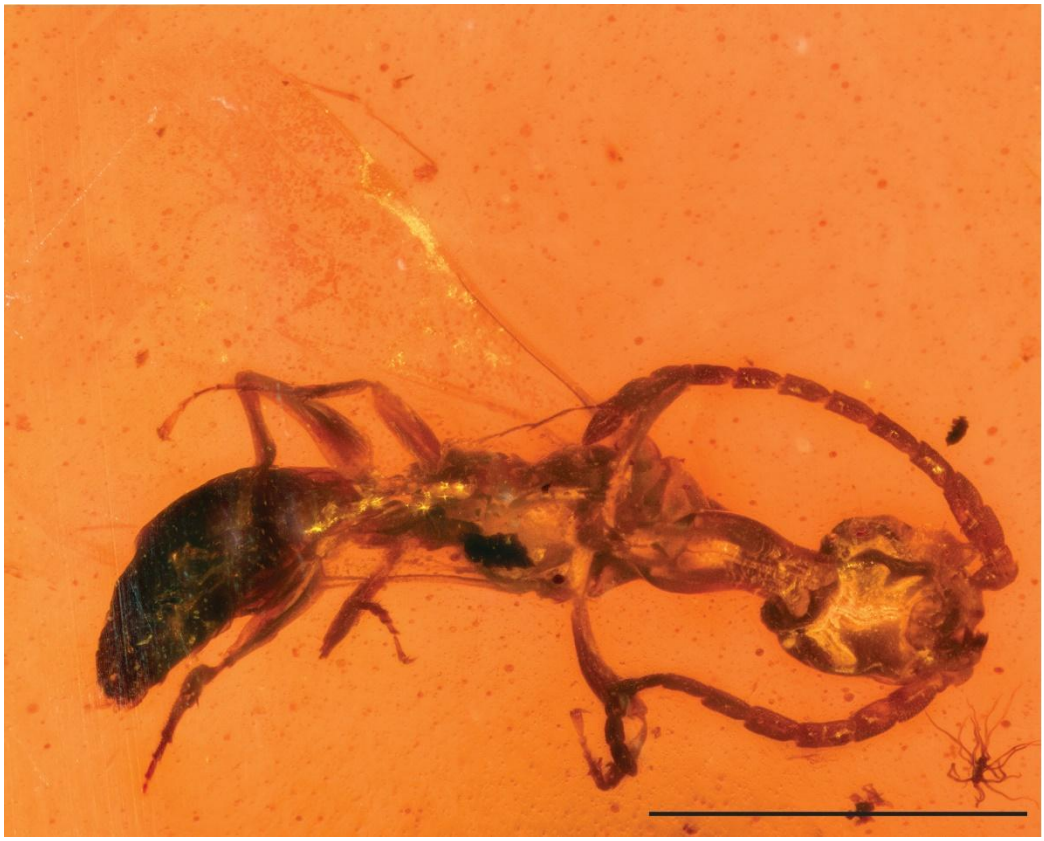

FIGURE 24. †*Merascylla atavella* (Cockerell, 1920), piece code NHMUK In.20149(1), male holotype, habitus, ventral view. Scales: 1.0 mm. Reproduced with permission of NHM, London.

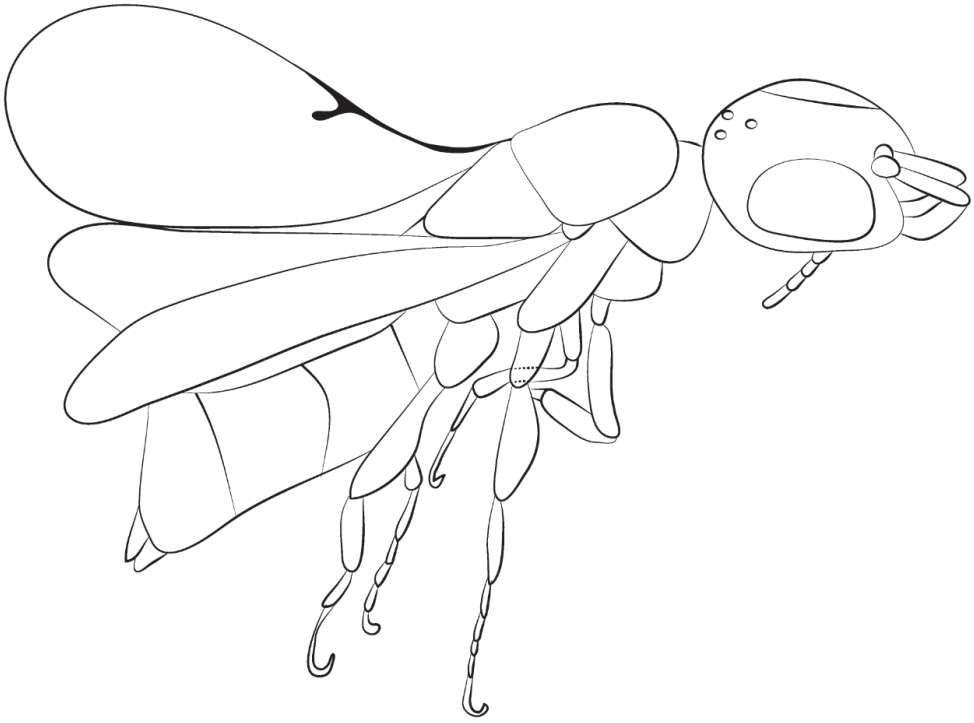

FIGURE 25. †*Laelius nudipennis* Brues, 1933, piece without code, female holotype. [redrawn digitally from Brues 1933].

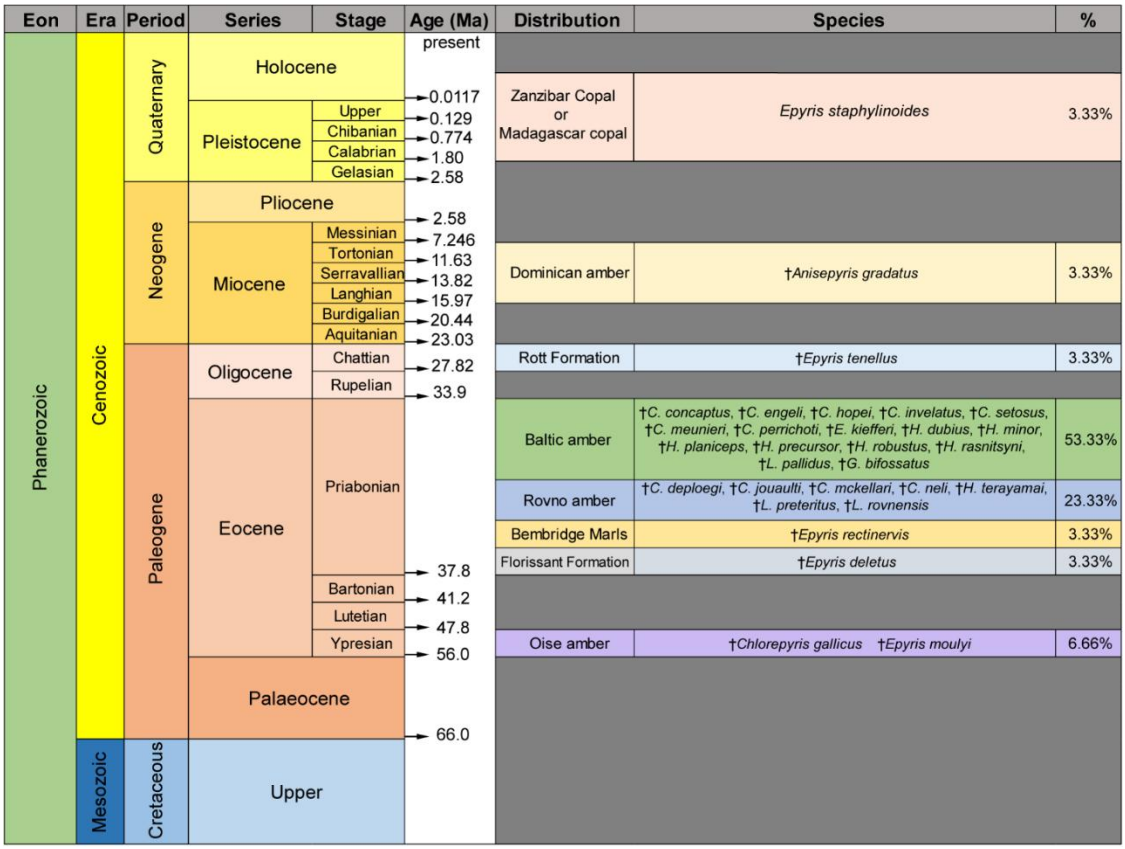

FIGURE 26. Chronostratigraphic chart of Epyrinae fossils. Numerical dates attached to each time interval by Cohen *et al*. (2020).

CAPÍTULO IV

Systematics of Epyrinae (Hymenoptera, Bethylidae) with a worldwide phylogeny using total evidence[4]

ABSTRACT

Epyrinae are one of most species-rich subfamily in Bethylidae. A phylogeny of Epyrinae is reconstructed with parsimony, likelihood, and Bayesian inferences using the nuclear markers 18S and 28S, the mitochondrial genes 16S, Cytochrome Oxidase Subunit I, and Cytochrome B, and 232 morphological characters. This is the first phylogenetic study to examine all 42 epyrine genera, including junior synonyms and extinct taxa. In total, this study considered 195 terminal taxa, with 175 as ingroup taxa and 20 as outgroup. The resulting tree of total evidence recovered *Anisepyris*, *Bakeriella*, *Calyozina*, *Chlorepyris*, *Disepyris*, *Laelius*, and *Trachepyris* as monophyletic; *Formosiepyris*, *Epyris*, and *Holepyris* are non-monophyletic. Here, we describe two new genera: *GenusA* to be proposed as **gen.n.** and *GenusB* to be proposed as **gen.n.**; we revalidate six genera, five of them junior synonyms of *Epyris* and one of *Holepyris*, they are: *Calyoza* to be proposed as **stat. rev.**, *Dolus* to be proposed as **stat. rev.**, *Muellerella* to be proposed as **stat. rev.**, *Psilepyris* to be proposed as **stat. rev.**, *Rysepyris* to be proposed as **stat. rev.** and *Trissepyris* to be proposed as **stat. rev.** The genera *Artiepyris*, *Calyozella*, *Paracalyoza*, *Peudocalyoza*, and *Xenepyris* will be proposed as junior synonyms of *Calyoza* to be proposed as **stat. rev.**; *Homoglenus* and *Neodisepyris* will be proposed as junior synonyms of *Dolus* to be proposed as **stat. rev.**; *Disepyris*, *Formosiepyris* and *Lytepyris* will be proposed as junior synonyms of *Holepyris*; *Acanthepyris*, *Planepyris*, *Pristobethylus* and *Trachepyris* will be proposed as junior synonyms of *Muellerella* to be proposed as **stat. rev.**; *Misepyris* and *Parepyris* will be proposed as junior synonyms of *Rysepyris* to be proposed as **stat. rev.** In addition, we provide a checklist of all species of Epyrinae, analysed via direct observation of the type, illustrations, or literature. Finally, we split Epyrinae into 17 genera: *Anisepyris*, *Aspidepyris*, *Bakeriella*, *Calyoza* to be proposed as **stat. rev.**, *Calyozina*, *Chlorepyris*, *Dolus* to be proposed as **stat. rev.**, *Epyris*, †*Gloxinius*, *GenusA* to be proposed as **gen.n.**, *Holepyris*, *GenusB* to be proposed as **gen.n.**, *Laelius*, *Muellerella* to be proposed as **stat. rev.**, *Psilepyris* to be proposed as **stat. rev.**, *Rysepyris*

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to be proposed as **stat. rev.** and *Trissepyris* to be proposed as **stat. rev.**, allocating 962 species within them.

Key words. Integrative taxonomy, *Epyris*, molecular, morphology evolution.

INTRODUCTION

Bethylidae are external gregarian parasitoids, mainly of larval Coleoptera and Lepidoptera (Evans, 1964; Gordh & Móczár, 1990; Azevedo *et al*., 2018). The family belongs to Chrysidoidea (Hymenoptera) and has been shown to be a monophyletic taxon and sister-group of Chrysididae (Peter *et al*., 2017; Branstetter *et al*., 2017). Bethylidae contain about 3,000 species, which are divided into four extinct subfamilies: †Elektroepyrinae, †Holopsenellinae, †Lancepyrinae, and †Protopristocerinae, and five living subfamilies: Bethylinae, Pristocerinae, Mesitiinae, Scleroderminae, and Epyrinae (Azevedo *et al*., 2018; Colombo *et al*., 2020). The latter is the subject of this present study.

Epyrinae, one of the larger subfamilies of Bethylidae, contain about 962 species in 13 genera: *Anisepyris* Kieffer, *Aspidepyris* Evans, *Bakeriella* Kieffer, *Calyozina* Enderlein, *Chlorepyris* Kieffer, *Disepyris* Kieffer, *Epyris* Westwood, *Formosiepyris* Terayama, †*Gloxinius* Colombo & Azevedo, *Holepyris* Kieffer, *Laelius* Ashmead, *Trachepyris* Kieffer, and *Xenepyris* Kieffer.

In their original form, Epyrinae were composed of two tribes, Epyrini and Sclerodermini, as proposed by Kieffer (1914). Both tribes were raised to subfamily rank by Berland (1928), but were collapsed back to tribal status by Evans (1964), with the addition of a third tribe, Cephalonomiini. Epyrini were the largest and most morphologically diverse of the tribes. Evans (1964) proposed that Sclerodermini and Cephalonomiini were related to Epyrini by a series of "intermediate genera" (e.g., *Laelius* and *Plastanoxus* Kieffer) without phylogenetic investigation. Evans (1964) diagnosed Epyrini by having 13 antennomeres, eyes laterally placed, a median projecting lobe on the clypeus, well-defined notauli, and the metapectal-propodeal disc bordered by a transverse carina. However, these characters are highly variable within the group, and are present in other subfamilies of Bethylidae (Sorg, 1988; Carpenter, 1999; Terayama, 2003; Alencar & Azevedo, 2013).

Taxonomic revisions based on phylogenetic reconstructions of Epyrinae and their tribes began with Lanes & Azevedo (2008). The authors recovered Sclerodermini as monophyletic only when they contained Cephalonomiini, proposing that both tribes should be merged into Sclerodermini. Carr *et al*. (2010) reconstructed the first molecular

phylogeny using mitochondrial 16S and nuclear 28S genes, and reconstructed Epyrini and Sclerodermini as monophyletic, but not the subfamily. Sclerodermini were retrieved sister to Mesitiinae, although a small sampling number prevented the authors from proposing taxonomic changes (Carr *et al*., 2010). In Alencar & Azevedo (2013), Epyrini and Sclerodermini were subjected to a thorough morphological analysis in which characters from genitalia were examined. Sampling throughout Bethylidae, they found that Epyrinae *sensu* Evans (1964) were non-monophyletic, recovering the topology (Bethylinae + (Sclerodermini ((Mesitiinae + Pristocerinae) + Epyrini))). For the first time, synapomorphies were attributed to Epyrini: posterior pronotal sulcus punctate, propleural epicoxal sulcus circular, radial 1 vein of the forewing short, anterior area of the second abdominal sternum with anterior margin outcurved and median margin with narrow emargination, second abdominal segment not divided, with anterior area and posterior area fused, and aedeagus short with apex not reaching the cuspis maximum height. Thus, Epyrini and Sclerodermini were re-elevated to the subfamily status (Alencar & Azevedo, 2013).

While Epyrinae are well defined as a subfamily, several taxonomic questions remained, mainly about the limits of genera and their relationships. Only two phylogenetic analyses within Epyrinae have been published. Waichert & Azevedo (2009) analysed *Rhabdepyris* Kieffer, 1904 based on morphological characters, finding that the genus was paraphyletic, and transferred many species to *Laelius*, *Anisepyris*, and *Chlorepyris*. Azevedo *et al.* (2018) then synonymized the genus *Rhabdepyris* with *Epyris*. Barbosa & Azevedo (2011) synonymized *Allepyris* Kieffer, 1905, *Paralaelius* Kieffer, 1906, and *Prolaelius* Kieffer, 1905 with *Laelius* based on the results of a similar morphological phylogenetic approach.

Several genera in Epyrinae described by Kieffer (1905, 1913a), such as *Melanepyris* Kieffer, 1913, *Pristepyris* Kieffer, 1905, *Trissepyris* Kieffer, 1905, and *Neurepyris* Kieffer, 1905, have been synonymized with other genera (Alencar & Azevedo, 2009; Azevedo & Alencar, 2009; Azevedo & Alencar, 2010a; Azevedo & Alencar, 2010b; Alencar & Azevedo, 2011). Azevedo *et al.* (2018) synonymized *Neodisepyris* and *Leptepyris* with *Epyris* based on the original descriptions, and discussed the taxonomic position of *Xenepyris*, but abstained from proposing a nomenclatural act for the latter. Alencar & Azevedo (2013) were also unable to locate specimens of *Neodisepyris*, as well as the Baker Collection in the Philippines, in which the single species of *Leptepyris* Kieffer, 1914 and

the two species of *Xenepyris* were deposited. Therefore, these taxa have never been analysed under phylogenetic approaches.

The most speciose genus within Epyrinae, with over 300 species described worldwide, is *Epyris*. It is likely a taxonomic wastebasket because it cannot be defined by synapomorphies (Carpenter, 1999; Alencar & Azevedo, 2013). Previous phylogenetic investigations of Bethylidae, only contained a small sample of *Epyris*. In a molecular analysis by Carr *et al.* (2010) using 16S and 28S genes, only four species of *Epyris* were analysed and the genus was not always recovered as monophyletic. In Alencar & Azevedo (2013) it was found as paraphyletic in all analyses, but represented by only three species.

Epyris has numerous generic synonyms. Evans (1964) synonymized *Muellerella* Saussure, 1892, *Parepyris* Kieffer, 1913, *Psilepyris* Kieffer, 1913, and *Artiepyris* Kieffer with *Epyris*. Later, Evans studied *Artiepyris* and associated it morphologically with the *dodecatomus* species group (Evans 1969). Evans (1969) also split the Nearctic and Neotropical species of *Epyris* into nine species groups, pointing out that some groups were easily defined by distinctive characters (Evans' *montivagus* and *depressigaster* groups for instance), whereas others were possibly arbitrary because of shown plasticity (*tricostatus* and *rufipes* groups). Evans (1969) also provided an intuitive dendrogram to display relationships among the genera, suggesting that they derived from *Rhabdepyris*. Evans (1979a) removed the *montivagus* species group and placed them in a separate genus, *Bakeriella* Kieffer, 1910. Outside of Evans' work, several other genera have been synonymized within *Epyris*, such as *Dolus* Motschulsky, 1863 (Krombein, 1987a), *Calyoza* Hope, *Paracalyoza* Cameron, *Pseudocalyoza* Turner and *Calyozella* Enderlein (Krombein, 1992), *Homoglenus* Kieffer (Terayama, 2003), *Melanepyris* Kieffer and *Trissepyris* Kieffer (Azevedo & Alencar, 2010a; 2010b), *Leptepyris*, *Isobrachium* Förster, *Rhabdepyris* and *Neodisepyris* (Azevedo *et al.*, 2018), totaling 16 junior synonyms of *Epyris*.

Bakeriella is represented by 31 species and has a wide range of phenotypic plasticity (Azevedo *et al*., 2018), which makes it difficult to place species within the genus. All species were revised, illustrated and keyed by Azevedo (2014). *Calyozina* and *Aspidepyris* are the least speciose extant genera in Epyrinae, rarely collected, but morphologically well distinguished. *Calyozina* is an Oriental genus, with only three species, distinguished by having the dorsal pronotal area with anterior, lateral and posterior margins incurved and anterolateral corners angularly shaped. *Aspidepyris* is a Neotropical genus with two

species, easily recognized by having the dorsal pronotal area with an elevation that is wide anteriorly and narrows progressively posterad, a unique configuration in Bethylidae.

Finally, the taxonomic history of Epyrinae and their genera combines numerous synonymizations, species groups that are likely arbitrary, and generic taxa poorly distinguished among the subfamilies. Moreover, *Epyris*, the second largest genus within Bethylidae is likely an unnatural genus and its delimitation overlaps with other genera. Herein, we aim to reconstruct the phylogenetic relationship and clarify the generic delimitation within Epyrinae by examining a large, representative sample of *Epyris*, molecular and morphological datasets, and a complete representation of the genera of Epyrinae.

MATERIAL AND METHODS

Material examined. We examined all 962 species hitherto classified as Epyrinae during collection visits, or loans, and by the original descriptions. The material was provided by the following institutions (curators at the time material was accessed): ACC – Instituto de Ecología y Sistemática de Cuba, Havana, Cuba (R.N. Aguilla); AEIC – American Entomological Institute, Logan, U.S.A. (D. Wahl, now in Utah); AMNH – American Museum of Natural History, New York, U.S.A. (J.M. Carpenter); BMNH – Natural History Museum, London, U.K. (K. Goodger); BPBM – Bernice Pauahi Bishop Museum, Honolulu, U.S.A. (A. Ramsdale); CAS – California Academy of Sciences, San Francisco, U.S.A. (R. Zuparko); CMNH – Carnegie Museum of Natural History, Pittsburgh, U.S.A. (J. Ashe); CNC – Canadian National Collection of Insects, Ontario, Canada (J. Huber); CUIC – Cornell University, Ithaca, U.S.A. (E. R. Hoebecke); CZMA – Coleção Zoológica do Maranhão, São Luis, Brazil (F. Limeira–de–Oliveira); DZUP – Universidade Federal do Paraná, Curitiba, Brazil (K. Zanol); FIFML – Fundación y Instituto Miguel Lillo, Tucumán, Argentina (V. Colomo); HNHM – Magyar Természettudományi Múzeum, Budapest, Hungary (S. Csõsz); IAVH – Instituto Alexander von Humboldt, Bogota, Colombia (M. Ospina); INHS – Illinois Natural History Survey, Chicago, U.S.A. (C. Favret); INPA – Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (J. A. Rafael); ISAM – Iziko South African Museum, Cape Town, South Africa (S. van Noort); LACM – Los Angeles County Museum of Natural History, Los Angeles, U.S.A. (B. Brown); MACN – Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos

Aires, Argentina (A. Roig Alsina); MCZC – Museum of Comparative Zoology, Cambridge, U.S.A. (S. Cover & P.D. Perkins); MCSN – 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, Belém, 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); OUMNH – Oxford University Museum of Natural History, Oxford, U.K. (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, Leiden, Netherlands (C. van Achterberg); SEMC – Snow Entomological Collection, The University of Kansas, Kansas, U.S.A. (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, Washington, U.S.A. (T. Schultz & D. Furth); YNU – Yeungnam University, Gyeongsan(-si), South Korea (J.W. Lee); ZMHB – Museum fur Naturkunde, Berlin, Germany (F. Koch).

Terminology and treatment. The terminology for general morphology follows Lanes *et al.* (2020), measurements and indices follows Evans (1964), Azevedo (1999a), Lanes & Azevedo (2008) and Alencar & Azevedo (2013). 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 dissection. Each dissected genitalia and hypopygium was diaphanized according to Martinelli *et al*. (2017). 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 (Germany).

Terminal taxa. Phylogenetic relationships were inferred from 175 specimens of Epyrinae with three specimens of Chrysididae (two from Chrysidinae and one from Cleptinae),

which are the sister group to Bethylidae (Grimaldi & Engel, 2005). Bethylids from the other subfamilies were also included as outgroups, as follows: three specimens of Bethylinae, five of Pristocerinae, four specimens of Mesitiinae, and five specimens of Scleroderminae. Our taxon sampling heavily focused on Epyrinae morphological and geographical diversity, including representatives from all genera (extant and extinct), a broad range of zoogeographical regions, and different species group representatives (for example *staphylinoides* and *depressigaster*) of *Epyris*, aiming to test the validity of some synonyms (Appendix 1).

The genus *Trachepyris* Kieffer, 1905 was recognized only from females because the synapomorphies diagnostic for the group are only found within females (with males indistinguishable from male representatives of *Epyris*). Features used to identify female representatives of *Trachepyris* prior to phylogenetic analyses were: 1) mandible with a horizontal apex, which could be well-developed (as in *Trachepyris* sp. 1 and *Trachepyris* sp. 2), or a more subtle expansion as in *Trachepyris* sp., and 3) protarsus with strong setae. Potential males of *Trachepyris* are elaborated upon in the conclusion, and are identified as *Epyris*/*Trachepyris*.

Molecular data sampling

The molecular analyses were performed on a selection of 186 terminal taxa (19 taxa as outgroup and 167 as ingroup). We sampled specimens from all epyrine genera, except *Xenepyris*, as follows: *Anisepyris* (nine specimens), *Aspidepyris* (one specimen), *Bakeriella* (four specimens), *Calyozina* (one specimen), *Chlorepyris* (20 specimens), *Disepyris* (three specimens), *Epyris* (83 specimens), *Formosiepyris* (two specimens), *Holepyris* (22 specimens), *Laelius* (eight specimens), *Trachepyris* (three specimens) and *Epyris*/*Trachepyris* (11 specimens). All terminal taxa information for molecular data and GenBank accession numbers are listed in Appendix 1.

Morphological data sampling

The morphological analyses were performed on a selection of 168 terminal taxa, which represent the greatest morphological diversity possible (eight taxa as outgroup and 160 as ingroup). We utilized many of the same terminal taxa from the molecular analysis and representatives of type species and holotype specimens whenever possible for potential nomenclatural acts (Appendix 1), as follows: *Anisepyris* (nine specimens), *Aspidepyris*

(one specimen), *Bakeriella* (five specimens), *Calyozina* (two specimens), *Chlorepyris* (20 specimens), *Disepyris* (three specimens), *Epyris* (75 specimens), *Formosiepyris* (three specimens), †*Gloxinius* (one specimen), *Holepyris* (20 specimens), *Laelius* (seven specimens), *Trachepyris* (three specimens), and *Epyris*/*Trachepyris* (11 specimens).

Total evidence data sampling

The total evidence analyses were performed on a selection of 194 terminal taxa (20 taxa as outgroup and 174 as ingroup). We sampled specimens from all epyrine genera, except *Xenepyris* and †*Gloxinius* (Appendix 1), as follow: *Anisepyris* (nine specimens), *Aspidepyris* (one specimen), *Bakeriella* (five specimens), *Calyozina* (two specimens), *Chlorepyris* (21 specimens), *Disepyris* (three specimens), *Epyris* (85 specimens), *Formosiepyris* (three specimens), *Holepyris* (23 specimens), *Laelius* (eight specimens), *Trachepyris* (three specimens), and *Epyris*/*Trachepyris* (11 specimens).

Morphological data. The characters were treated as hypotheses of primary homology following De Pinna (1991). We worked on improving character-coding systems, avoiding continuous quantitative characters as much as possible. Important characters have been proposed from the codification of new features, mainly of the mesoscutum-mesoscutellar suture (a morphological structure widely used in taxonomy of Epyrinae); several characters are used again or modified mostly from Lanes & Azevedo (2008) and Alencar & Azevedo (2013). A total of 232 morphological characters were analysed: two from the general body, 64 characters from the head, 91 from the mesosoma, 21 characters from the wings, 12 from the metasoma; six from male hypopygium and 36 from male genitalia (Appendix 2). All characters were coded using Leica M80 microscopes and we coded the character states through examination of the specimens or high-quality photographs.

All character states were treated as unordered and non-polarized. Inapplicable and unknown characters were represented as '–' (Supplementary material). The data were included in the matrix using the program DELTA EDITOR (Description Language Taxonomy) by Dallwitz (1980). We used DELTA to generate a nexus file from the matrix.

DNA extraction and molecular protocols. Specimens were stored in 95 percent ethanol and refrigerated prior to extraction. Genomic DNA was isolated using a QIAGEN DNeasy Tissue Kit and NucleoSpin Tissue, following the manufacturer's protocols, with the

exception of using non-destructive lysing techniques (Paquin & Vink, 2009). This allowed for specimens to be pinned, identified, and used in morphological analyses after DNA extraction.

PCR amplification was accomplished using General Electric PuReTaq Ready-To-Go beads with the following primers: the 16S region was amplified using 16SWb (5'-CAC CTG TTT ATC AAA AAC AT-3') and 16SWa (5'-CGT CGA TTT GAA CTC AAA TC-3') (Dowton & Austin, 1994), the 18S region was amplified using 18SF2 (5'-CTA CCA CAT CCA AGG AAG GCA G- 3') and 18SR2 (5'-AGA GTC TCG TTC GTT ATC GGA-3') (Rokas *et al*., 2002), the 28S D2-D3 region was amplified using For28Vesp (5'-AGA GAG AGT TCA AGA GTA CGT G-3') and Rev28SVesp (5'-GGA ACC AGC TAC TAG ATG G-3') (Hines *et al*., 2007), the Cytochrome Oxidase I (COI) was amplified for the Folmer/barcode region using LCO (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer *et al*., 1994) and the Cytochrome b (Cytb) region was amplified using CB1 (5'-TAT GTA CTA CCA TGA GGA CAA ATA TC-3') and CB2 (5'-ATT ACA CCT CCT AAT TTA TTA GGA AT-3') (Simon *et al*., 1994). Thermocycler protocols are detailed in Appendix 3 from adaptations of Alencar *et al*. (2018).

Amplified DNA fragments were purified with the ExoSAP-IT (USB Corporation, Cleveland, OH, U.S.A.) enzyme purification protocol kit. Sequencing was performed at the American Museum of Natural History (AMNH-USA) in the Sackler Institute for Comparative Genomics on an ABI 3730 and at the Universidade Federal do Espírito Santo (UFES-Brazil) in the Núcleo de Genética Aplicada à Conservação da Biodiversidade (NGACB) on an ABI 3500.

The sequences of each gene were analysed with the program MEGA 7 (Kumar *et al*., 2016) and the identity confirmed through the BLAST method (Altschul *et al*., 1997). The alignments were made through the online program MAFFT 7 (Katoh, 2013) with setting the algorithm to E-INS-I and the scoring matrix to 200PAM/*k* =2, subsequently refined manually. Finally, a molecular concatenated matrix was produced using the MESQUITE 3.61 (Maddison & Maddison, 2019), resulting in 3367 nucleotide base pairs.

Combined morphology and molecular data. The Total Evidence (TE) matrix was manually compiled using the program NOTEPAD++ with the morphological and combined molecular data sets, and consisted of 195 taxa and 3599 characters.

Phylogenetic analyses

Morphological analyses

The morphological dataset was analysed using maximum parsimony. The searches for the most parsimonious (MP) trees were carried out with the software TNT 1.1 (Goloboff *et al*., 2008). Characters were treated under implied weights (Goloboff, 1993; Goloboff *et al*. 2008). We used the parameter settings as follows: space for 99999 trees in memory; Wagner trees random seed 1; 1000 replications; TBR algorithm; 10 trees saved per replication; other parameter as in default mode. The tree was rooted with *Eupsenella diemenensis* Dodd.

Heuristic searches (Goloboff, 2003; Goloboff *et al*., 2008) were performed under New Technology methods using a *sectorial search*, *ratchet* weighting probability of 10% with 1000 iterations, *tree-drifting* of 1000 cycles and *tree-fusing* of ten rounds. These parameters were used to generate robust trees. Implied weights analyses using a concavity function (K) that weights against homoplastic data (Goloboff, 1993) were also conducted, using a TNT script (setk.run) written by Salvador Arias to calculate the appropriate value. A value of 33,447266 was returned and subsequently used in the implied weighting scheme. Branch support was investigated using resampling support values, which were calculated using bootstrap with New Technology (default parameters) and reported as absolute frequencies from 100 replicates. The cladograms recovered with the software TNT was manipulated with WINCLADA-ASADO 1.61 (Nixon, 2002) and further edited in ADOBE ILLUSTRATOR CS6 23.0.3. For the best results, the character mesoscutum-mesoscutellar suture was mapped onto the implied weighting tree using WINCLADA-ASADO, and edited in ADOBE ILLUSTRATOR CS6 23.0.3.

Molecular analyses

We applied Maximum Likelihood (ML) and Bayesian Inference (BI) approaches to reconstruct the molecular topologies. The gene trees were reconstructed through BI to check for topological incongruence. The BI was performed in MRBAYES (Ronquist & Huelsenbeck, 2003) using the Cipres Science Gateway service (Miller *et al*., 2010, https://www.phylo.org/), with the Bayesian Markov chain Monte Carlo (MCMC) chains

running simultaneously for a total of 10 million generations, with sampling every 1000 generations and burn-in of 25%.

For the concatenated matrix, the optimal partition strategy and models of molecular evolution for the data were determined in PARTITIONFINDER 1.01 (Lanfear *et al.*, 2012). The model selection analyses under Bayesian information Criterion (BIC) returned SYM+I+G (set as nst=6 rates=invgamma in MRBAYES) for eight partitions: 16S; 18S; 28S; COI, codons 1–3; Cytb, codons 1, 2; and returned SYM+G (set as nst=6 rates=gamma in MRBAYES) for one partition: Cytb, codon 3.

For the concatenated matrix, we carried out the BI in MRBAYES using Cipres with MCMC chains running simultaneously for a total of 60 million generations, sampling every 2000 generations and burn-in of 25%. Trace plots and effective sample size (ESS) were examined in TRACER 1.5 to determine MCMC mixing and convergence for the gene trees and concatenated matrix. All BI analyses were rooted with *Cleptes seoulensis* Tsuneki, 1959.

The ML analyses were conducted with RAXML 8 (Stamatakis, 2014) through the Cipres Science Gateway under the model GTR GAMMA for each gene. We performed 1000 bootstrap replications to assess node supports. The ML analyses were rooted with *Cleptes seoulensis*, *Chrysis cembricola* Krombein and *Chrysis principalis* Smith. Phylogenetic tree viewing was performed in FIGTREE 1.4.2 (Rambaut, 2014, http://tree.bio.ed.ac.uk/software/figtree/), and then edited in ADOBE ILLUSTRATOR CS6 23.0.3.

Total Evidence analyses

We carried out Bayesian Inference (BI) approaches to reconstruct the Total Evidence topology. The models of molecular evolution for the nine partitions were imported from the molecular matrix. The tenth partition (standard data) was added for the morphological characters (3368-3599). The evolutionary model MK- Jukes-Cantor (prset Symdirihyperpr = fixed(infinity)) was selected for this partition following Lewis (2001).

The analyses were rooted with *Cleptes seoulensis*, with 60 million generations, sampling every 2000 generations and burn-in of 25%. Trace plots and ESS were examined in TRACER 1.5. Phylogenetic tree viewing was performed in FIGTREE 1.4.2, and then edited in ADOBE ILLUSTRATOR CS6 23.0.3.

Illustrations

Specimens were photographed with a Leica Z16 APO stereomicroscope fitted with a camera adaptor coupled to a Leica DFC 295 video camera (Leica Microsystems, Switzerland, Germany). The software LEICA APPLICATION SUITE 3.6.0 and Microsystems by Leica Limited (LAS) were used to capture individual focal planes. We used a scaleable and modular LED illumination dome for microscopic scientific photography as described by Kawada & Buffington (2016). HELICON FOCUS (version 4.2.9; HeliconSoft, Dominica) software was used for stacking the layers into a single combined-focus image.

RESULTS

Subfamily topology

Total evidence (TE) (posterior probability (PP)=1) and molecular topologies recovered a monophyletic Epyrinae (Bootstrap (B)=100 and PP=1) (Fig. 1; Appendix 4–6), as well as Scleroderminae, Pristocerinae, Bethylinae, and Mesitiinae. The subfamilies most closely related to Epyrinae are (Mesitiinae + Scleroderminae), however, the relationship among bethylids subfamilies remain uncertain. Subfamily topologies in TE and molecular analyses were (Bethylinae + (Pristocerinae + (Mesitiinae + Scleroderminae) + Epyrinae)).

All datasets resulted in similar species clustering. The statistical support and the phylogenetic relationships among the internal clades varied within the reconstruction approaches. The parsimony tree differed not only from the phylogenetic relationship between the clades, but also in the taxonomic composition of the clades themselves (Appendix 7). For instance, *Aspidepyris* and *Calyozina* were recovered as sister group in the parsimony reconstruction, whereas they nested within *Epyris* group 6 and *Epyris* group 2, respectively, in the approaches using only molecular dataset. However, extinct species and holotype representatives from monotypic genera were excluded from the molecular analyses, which showed similar topology in BI and ML approaches. Moreover, the molecular and the TE trees were congruent.

Representatives of *Epyris* and *Holepyris* clustered with different genera and were divided into several independent lineages in the topology. In the TE and molecular phylogenies, species of *Epyris* split up within seven different lineages (*Epyris sensu stricto* and groups 1–6, Fig. 1; Appendix 4–6), however, in the morphology-only parsimony analysis, the genus was split in six clades (all linages with low statistical support) and only

Epyris sensu stricto had the same taxon composition as seen in the ML and BI approaches. Species of *Holepyris* split within two lineages (group 1 and *Holepyris sensu stricto*).

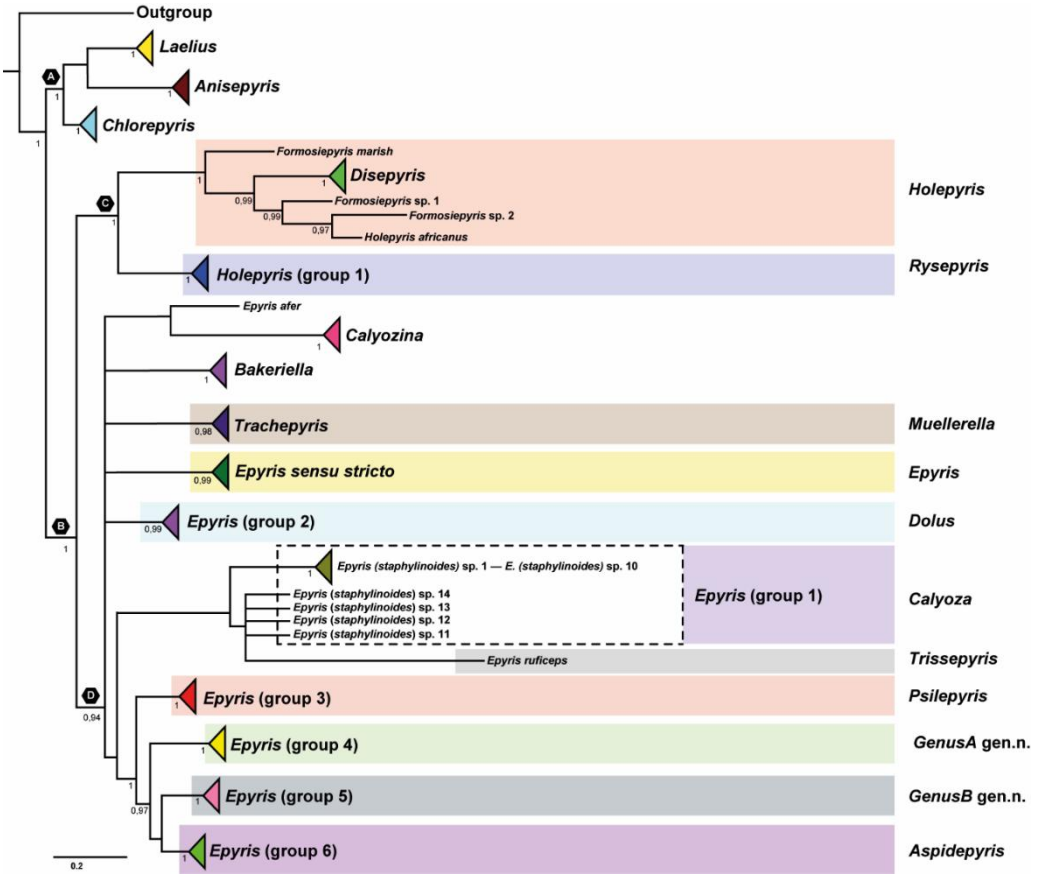

FIGURE 1. Bayesian topology of total evidence analysis with 232 morphological and 3367 molecular characters. Posterior probability values are shown above branches. Current classification as taxa terminal and new proposed classification at the ends.

The phylogenetic reconstruction of the TE retrieved 14 monophyletic groups within Epyrinae with good statistical supports: *Anisepyris* (PP=1), *Bakeriella* (PP=1), *Calyozina* (PP=1), *Chlorepyris* (PP=1), *Disepyris* (PP=1), *Epyris sensu stricto* (PP=0.99), *Epyris* (group 2) (PP=0.99), *Epyris* (group 3) (PP=1), *Epyris* (group 4) (PP=1), *Epyris* (group 5) (PP=1), *Epyris* (group 6) (PP=1), *Holepyris* (group 1) (PP=1), *Laelius* (PP=1) and *Trachepyris* (PP=0.98). *Aspidepyris* was sampled based on a single specimen, which clustered with species of *Epyris* (group 6). *Holepyris sensu stricto* had a single representative in the analyses, which clustered with *Formosiepyris* and *Disepyris*. *Formosipeyris* is a polyphyletic group.

Eleven of the lineages recovered in TE were reconstructed in the ML and BI analyses. Both topologies had similar clades: *Anisepyris* (PP=1; B=100), *Bakeriella* (PP=1; B=100), *Epyris sensu stricto* (PP=1; B=100), *Epyris* (group 1) (PP=1; B=100), *Epyris* (group 2) (PP=1; B=76), *Epyris* (group 3) (PP=1; B=100), *Epyris* (group 4) (PP=1; B=100), *Epyris* (group 5) (PP=1; B=100), *Epyris* (group 6) (PP=1; B=100), *Holepyris* (group 1) (PP=1; B=100) and *Trachepyris* (PP=1; B=100). *Aspidepyris* and *Calyozina* were sampled based on a single specimen. The first clustered with the *Epyris* (group 6 – similar to TE approach) and the second clustered with *Epyris* (group 2 – unlike TE approach). *Chlorepyris* was grouped with low statistical support (B=60) in the ML, and paraphyletic in the BI analysis.

The phylogenetic morphological reconstruction (Appendix 7) returned one parsimonious cladogram with 2433 steps (L) under implied weights. The consistency index (CI) was 12 and the retention index (RI) was 65. The subfamilial node was recovered with three synapomorphies: 131:0 (propleural epicoxal sulcus circular/subcircular, in lateral view); 180:0 (convex anterior margin with a narrow emargination of the anterior area of the S2, in ventral view); and 181:1 (anterior and posterior areas of the S2 fused). Six genera are recovered as monophyletic with good statistical support: *Anisepyris* (B=97), *Bakeriella* (B=89), *Calyozina* (B=100), *Disepyris* (B=100), *Laelius* (B=91) and *Holepyris* (group 1) (B=93). *Epyris* (groups 1–6) showed low statistical support (B<75) and, in addition, the lineages show a composition of terminal taxa different from all other topologies. *Chlorepyris*, *Epyris sensu stricto* and *Trachepyris* are grouped, but with low statistical support. *Holepyris sensu stricto* was sampled from a single representative and grouped with *Formosiepyris*. *Formosiepyris* is paraphyletic in our results.

Relationships within subfamily

Two major clades (A and B) were recovered within Epyrinae in all analyses, except the morphology-only parsimony topology (B≥97 (Appendix 5), PP=1 (Fig. 1; Appendix 4, 6)). Clade A includes *Anisepyris*, *Laelius*, and *Chlorepyris*, whereas clade B has representatives of *Aspidepyris*, *Bakeriella*, *Calyozina*, *Disepyris*, *Epyris sensu stricto*, *Epyris* (groups 1–6), *Formosiepyris*, *Holepyris sensu stricto*, *Holepyris* (group 1), and *Trachepyris*.

Topology of clade A varied in each of the four analyses. In TE, the relationship among genera was (*Chlorepyris* + (*Anisepyris* + *Laelius*)); in ML the outcome was

(*Anisepyris* + (*Laelius* + *Chlorepyris*)), in the Bayesian topology, *Chlorepyris* was paraphyletic and *Anisepyris* was the sister genus to all others. Species of *Chlorepyris* split into two clades. One composed entirely of species from Australia with the exception of a single species from Peru [hereby referred as Peru+Australia and another clade of *Chlorepyris* composed of exclusively Neotropical species [hereby referred to as Neotropical]. Finally, in the parsimony tree, *Laelius* and *Anisepyris* are sister-group and *Chlorepyris* is sister to *Laelius* + *Anisepyris*.

The second clade in Epyrinae (B) includes the remaining lineages. It is split into two subdivisions (C and D) in the total evidence tree. A small clade (PP=1) is composed of *Disepyris*, *Formosiepyris*, *Holepyris sensu stricto* and *Holepyris* (group 1), whereas a major clade (PP=94) includes *Aspidepyris*, *Bakeriella*, *Calyozina*, *Epyris sensu stricto*, *Epyris* (groups 1–6) and *Trachepyris*. The taxa included in clade C was similar in the different analyses. *Holepyris* (group 1) is the sister-group of *Disepyris*, *Formosiepyris* and *Holepyris sensu stricto*. *Disepyris* is monophyletic in all analyses, however, except in the parsimony, this genus is grouped with species of *Formosiepyris* and *Holepyris* and with this, the latter two are polyphyletic. Clade D shows polytomy within internal lineages in total evidence topology. In molecular topologies, however, *Epyris* (group 1) nested outside of clade D.

Morphological traits

Several of the morphological characters used in our analyses ended up being homoplasious. However, the most important alpha taxonomic character confirmed homologous in TE and parsimony topologies, e.g., the mesoscutum-mesoscutellar suture, with the evident loss of the sulcus between the foveae (Fig. 2).

The shape of the mesoscutum-mesoscutellar suture was also shown to be homologous between the lineages. In both topologies (parsimony and TE) the clade *Holepyris* (*sensu stricto* and group 1) + *Disepyris* +*Formosiepyris* share the mesoscutum-mesoscutellar suture sulcate, wide, transverse and usually trabeculate. The other major pattern of the mesoscutum-mesoscutellar suture present in the Epyrinae was recovered as homologous in the TE topology, but not in the parsimony analysis. The clade composed of *Laelius*, *Anisepyris* and *Chlorepyris* share a common mesoscutum-mesoscutellar suture sulcate, never trabeculate and with posterior margin incurved.

The mesoscutum-mesoscutellar suture without sulcus between foveae is homologous in Epyrinae, however its shapes and variations were presented with little resolution. In the TE topology, a major polytomy was recovered and in parsimony, at least 13 different patterns were identified on the tree. In the latter, the mesoscutum-mesoscutellar suture without sulcus were important characters in the delimitation of some linages, such as *Epyris sensu stricto*, for example.

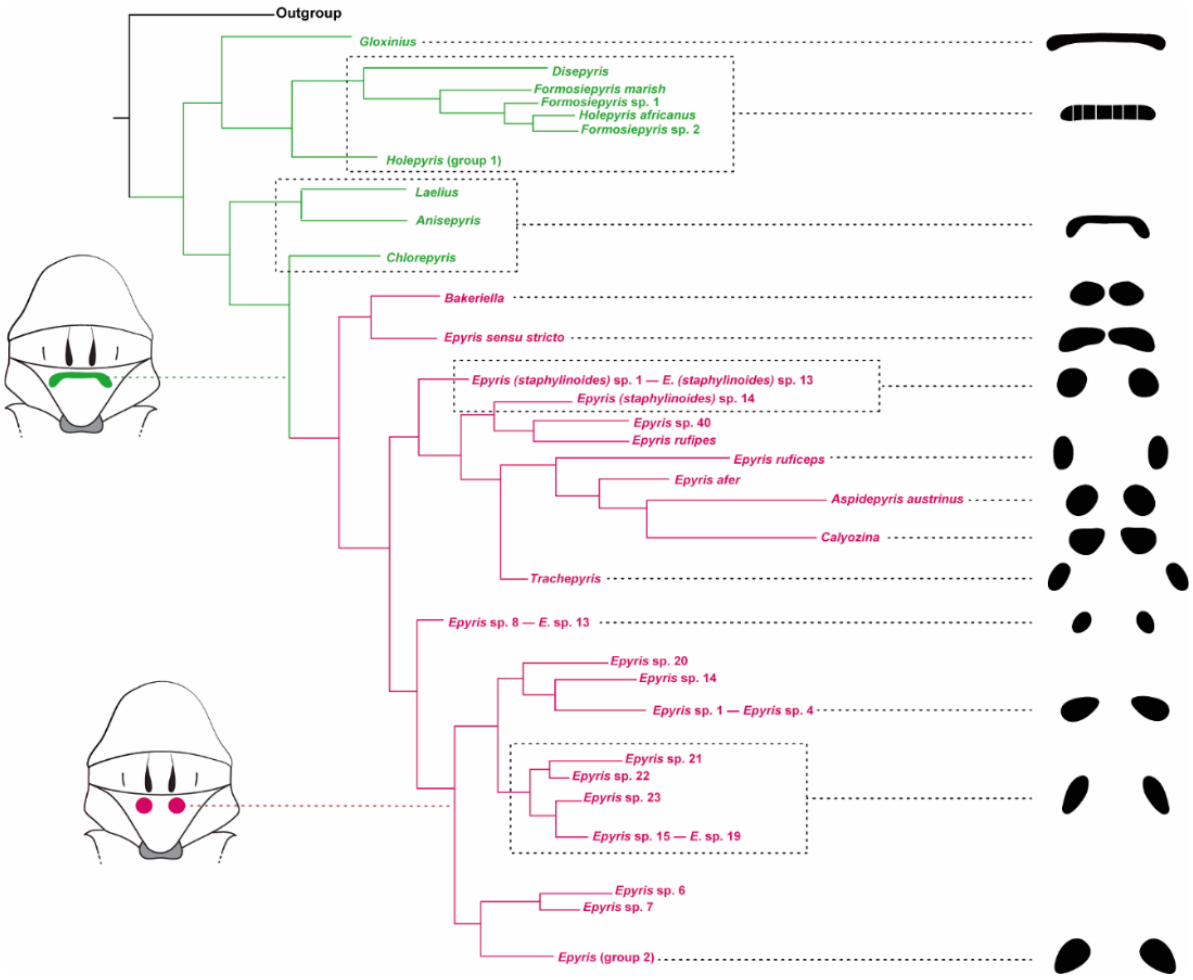

FIGURE 2. Phylogenetic character mapping: mesoscutum-mesoscutellar suture, based on Parsimony topology with 232 morphological characters.

Taxonomic implications

Based on the phylogenies recovered in our analyses, the generic delimitation in Epyrinae is incongruent with the evolutionary lineages. Here we propose a new classification for *Epyris sensu* Azevedo *et al.* (2018) based on phylogenetic relationship, describe two new genera, revalidate five genera and transfer species within epyrine taxa. We provide a checklist addressing each taxon in Appendix 5. Most of the species were

analysed directly from the holotype exemplar, and others were analysed using pictures and drawings from the literature. We divide Epyrinae into 17 genera: *Anisepyris*, *Aspidepyris* (=*Epyris* group 6), *Bakeriella*, *Calyoza* to be proposed as **stat. rev.** (=*Epyris* group 1), *Calyozina*, *Chlorepyris*, *Dolus* to be proposed as **stat. rev.** (=*Epyris* group 2), *Epyris* (=*Epyris sensu stricto*), †*Gloxinius*, *Holepyris* (=*Holepyris sensu stricto* + *Disepyris* + *Formosiepyris*), *GenusA* to be proposed as **gen.n.** (=*Epyris* group 4), *Laelius*, *Muellerella* to be proposed as **stat. rev.** (=*Trachepyris*), *GenusB* to be proposed as **gen.n.** (=*Epyris* group 5), *Psilepyris* to be proposed as **stat. rev.** (=*Epyris* group 3), *Rysepyris* to be proposed as **stat. rev.** (=*Holepyris* group 1) and *Trissepyris* to be proposed as **stat. rev.** (=*Epyris ruficeps*). The taxonomic implications, with the comparison between the classification of Epyrinae *sensu* previous studies and the current classification, that will be proposed here, are summarized in Fig. 3.

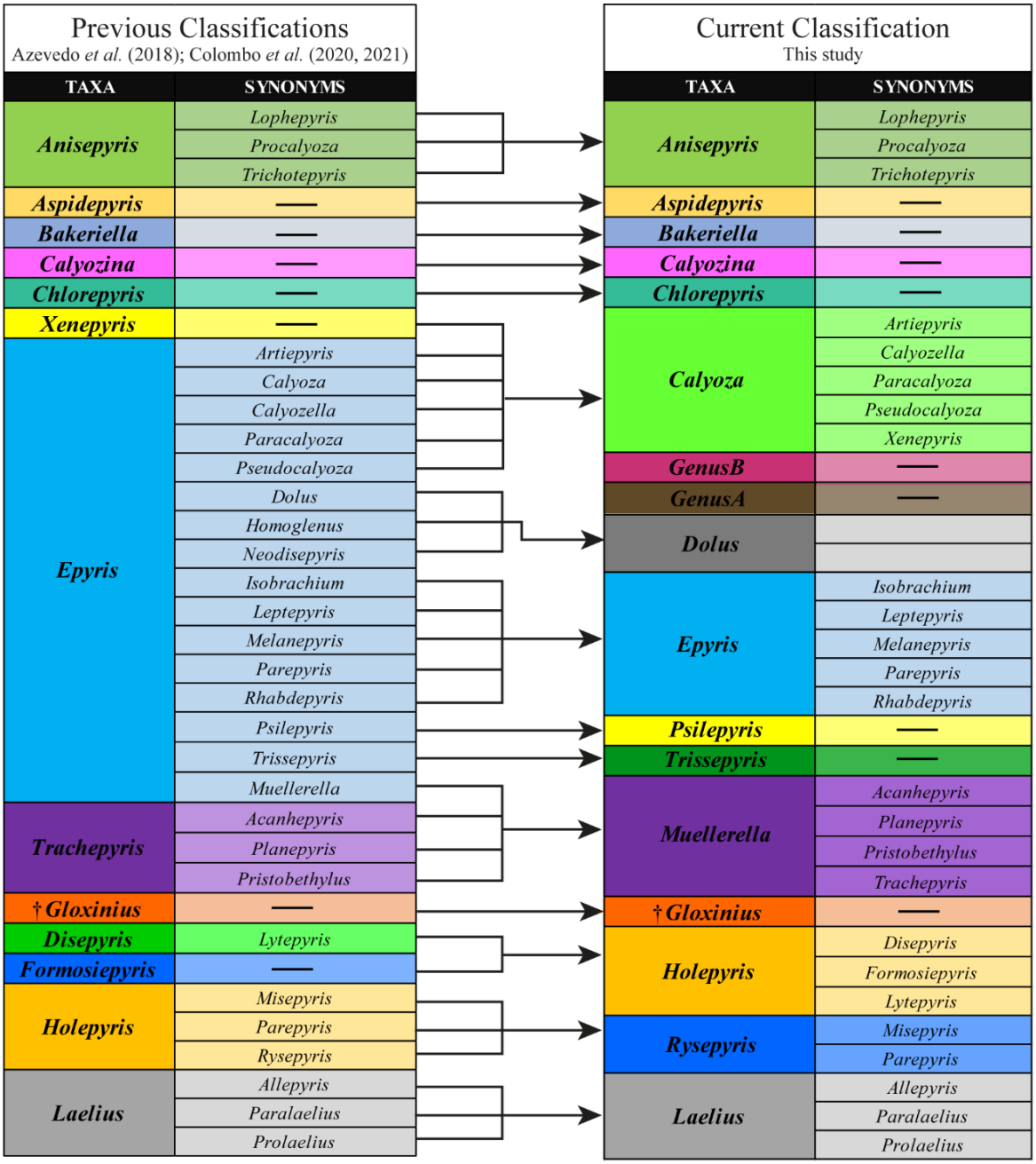

FIGURE 3. Diagram showing taxonomic changes that will be proposed in this study.

DISCUSSION

Unlike other studies, we focused on representing the vast diversity of *Epyris* by sampling from various species groups and numerous geographical regions, while also incorporating other genera of Epyrinae.

The phylogenies presented here support the results found by Alencar & Azevedo (2013) in elevating Sclerodermini and Epyrini to subfamilies; and by Colombo *et al*. (2020) showing that Epyrinae are monophyletic. However, the largest genus of the subfamily, *Epyris*, is non-monophyletic and thus is an unnatural genus. As seen in previous studies, species of *Epyris* had close phylogenetic association with species of *Aspidepyris*, *Calyozina*, *Bakeriella*, and *Muellerella* to be proposed as **stat. rev.** (Alencar & Azevedo, 2013).

Waichert & Azevedo (2009) revised the diagnostic feature of *Laelius* pointing out the presence of 2r-rs&Rs vein short in the forewings, which is also present in *Disepyris* and some *Muellerella* to be proposed as **stat. rev.**, the trapezoidal clypeus with a median apical bump, and the presence of thick black setae on the body surface. As a result, many specimens of *Rhabdepyris* (subgenus *Rhabdepyris*) *sensu* Evans (1965) were transferred to *Laelius*. Barbosa & Azevedo (2011) added another synapomorphy to the genus: three distal hamuli on the hind wing, and established *Prolaelius* as a junior synonym of *Laelius*. These characteristics were present in all *Laelius* specimens in this study, but were not recovered as synapomorphies in the reconstruction with morphological characters.

The genus *Chlorepyris* clustered with *Laelius* and *Anisepyris* in the molecular and TE topologies and showed low support in the morphological topology. Moreover, two lineages were recovered in each analysis. Further morphological study could split *Chlorepyris sensu* Waichert & Azevedo (2009) into two genera with the analyses here as a starting guide. The two clades of *Chlorepyris* comprise (1) all the Australian specimens and a specimen from Peru and (2) the Neotropical specimens (File S2).

Herein, the following morphological characteristics were found that differentiate the Peru + Australia and Neotropical clades of *Chlorepyris*: (1) *Chlorepyris* (Peru + Australia) – the females have a distinct mandible with a large apical tooth, which was often expanded inward, and a denticulate dorsal edge. These features match the description of Evans's *anxius* and *platycephalus* groups of Australian *Chlorepyris* (Evans 1979b, 1982). In males, the mandible always has a large apical tooth, 2–3 intermediary teeth, and a larger dorsal tooth curved upward. In all Australian male specimens, we observed five teeth, three intermediary teeth, but the Peruvian specimen showed a single intermediary tooth. The size of the dorsal tooth varies as well, with extreme size difference between the dorsal and intermediary teeth in *Chlorepyris* sp. 10, which closely resembled the male of *Chlorepyris platycephalus* Westwood, 1874; (2) *Chlorepyris* (Neotropical): the third antennomere is

wider than long in males, such as described for the Neotropical species *Chlorepyris longifoveatus* Azevedo, 1999 and *Chlorepyris vesiculosus* Azevedo, 1999 (Azevedo, 1999b). The mandibles always have five teeth, with a large apical tooth and four smaller dorsal teeth that became progressively larger posteriorly. In Waichert & Azevedo (2009), the expanded *Chlorepyris* was phylogenetically associated with *Trachepyris* (=*Muellerella* to be proposed as **stat. rev.**). Herein, *Muellerella* to be proposed as **stat. rev.** was found within a clade with species of *Epyris*, *Calyozina*, and *Bakeriella*. These specimens shared a thin, slightly elongate 2r-rs&Rs vein of the forewing and thick setae on the scape, with the latter character reconstructed as synapomorphy.

The clade (*Holepyris* + *Rysepyris* to be proposed as **stat. rev.**) was retrieved in all of the analyses. *Holepyris sensu* Azevedo *et al*. (2018) has as junior synonyms *Rysepyris*, *Parepyris* Brèthes and *Mysepyris*. The genera *Formosiepyris* and *Disepyris* were recovered as related to *Holepyris* through the phylogeny of Alencar & Azevedo (2013). According to Alencar & Azevedo (2013), this clade had one synapomorphy, the presence of elongated setae on protarsomere I. This characteristic is considered diagnostic for females of *Disepyris* (Krombein, 1987b; Terayama, 2004), yet the condition is common to all the genera of the clade *Holepyris* + *Formosiepyris* + *Disepyris* (Alencar & Azevedo, 2013). Indeed, they all share the clypeus trilobed and the mesoscutum-mesoscutellar sulcus well impressed deep, and usually trabeculate. Terayama (2004), when describing *Formosiepyris*, indicated its possible phylogenetic proximity to *Disepyris* due to the elongated eyes and medially depressed mesoscutum. The taxonomic analysis of the type species of *Holepyris* and *Disepyris* demonstrate similarities between them (Alencar & Azevedo, 2013). *Disepyris* and *Formosiepyris* have the clypeus with a median lobe wider than usually found in *Holepyris sensu* Azevedo *et al.* (2018). However, African species of *Holepyris*, including its type species *H. africanus* Kieffer, present the same condition. Here, based on the phylogenetic analyses and study of the type species of *Disepyris*, *Formosiepyris* and *Holepyris*, we propose that *Formosiepyris* and *Disepyris* are junior synonyms of *Holepyris*. *Holepyris sensu* Azevedo *et al*. (2018) creates confusion due to the species transferred to this genus when Evans (1964) synonymized *Rysepyris*, *Parepyris* and *Misepyris*. The current morphological concept for *Holepyris sensu* Azevedo *et al*. (2018) comes from *Rysepyris*, whose clypeus is trilobed, which differs from the type species, *H. africanus*. Furthermore, we revalidated *Rysepyris* to be proposed as **stat. rev.**

While previous studies had pointed to a non-monophyletic *Epyris* (Waichert & Azevedo, 2009; Carr *et al*., 2010; Alencar & Azevedo, 2013), none had sampled the wider diversity of the genus. Our study is the first to sample broadly across *Epyris* with an increased number of molecular markers and undoubtedly shows that *Epyris* is non-monophyletic. Several species of *Epyris*, however, formed well-supported clades throughout the analyses. We identified seven lineages of *Epyris* in the total evidence and molecular topologies, named as *Aspidepyris* (*Epyris* group 6), *Calyoza* to be proposed as **stat. rev.** (*Epyris* group 1), *Dolus* to be proposed as **stat. rev.** (*Epyris* group 2), *Epyris* (*sensu stricto*), *GenusB* to be proposed as **gen.n.** (*Epyris* group 5), *GenusA* to be proposed as **gen.n.** (*Epyris* group 4) and *Psilepyris* to be proposed as **stat. rev.** (*Epyris* group 3); another lineage was identified only in the morphological analysis, named as *Trissepyris* to be proposed as **stat. rev.**.

For the first time, the type species of *Epyris*, *E. niger* Westwood, 1832, was recovered in a well-supported clade (PP= 1) that contained both male and female specimens with large mesoscutum-mesoscutellar foveae, referred as large-pitted style by Azevedo *et al.* (2018), as opposed to the well-spaced, small mesoscutellar foveae that are found throughout the rest of *Epyris* species, named as small-pitted style by Azevedo *et al.* (2018). All terminals within this clade have two metapostnotal carina that are at least 2/3 as long as the metapectal-propodeal disc. These specimens are from Europe, Africa, Asia, and Australia.

Another clade recovered within *Epyris sensu* Azevedo *et al*. (2018) is *Calyoza* to be proposed as **stat. rev.** (=*Epyris* group 1) (Fig. 1). Within this clade, all males have the third antennomere reduced to a small, often difficult to detect, ring-shaped antennomere. In some males (*Epyris* (*staphylinoides* group) sp. 6, *E.* (*staphylinoides* group) sp. 7 and *E.* (*staphylinoides* group) sp. 11), the remainder of the antennae is strikingly ramose. The presence of a reduced, ring-shaped third antennomere in males is reported in three different species groups of *Epyris sensu* Azevedo *et al*. (2018) – the *dodecatomus* group, the *staphylinoides* group, and the *subramosus* group (Evans, 1969; Krombein, 1992). The latter two groups contain species that were previously part of *Calyozina* and *Pseudocalyoza* and were synonymized as *Epyris* by Krombein (1992). Only in the *staphylinoides* group do males have ramose antennae (Krombein, 1992). Mandible shape also differs between the *dodecatomus*, *staphylinoides*, and *subramosus* species groups. The *dodecatomus* species group is known exclusively from the New World and was described

in Evans (1969) with four species, two of which have males undescribed. Known males of this species group have slender mandibles with three teeth, while females in the group possess mandibles that are broad, with five teeth. In the *staphylinoides* group, males also possess slender mandibles with 3–4 teeth, with females possessing a broader mandible with 4–5 teeth with a blunt sub-apical tooth on the ventral margin (Krombein, 1992). The single species of the *subramosus* group has the male with a tridentate mandible that is stouter than in either the *dodecatomus* or *staphylinoides* species group and the female has a mandible with five teeth and lacks a subapical tooth.

Alencar & Azevedo (2013) did not find the *Xenepyris* types and therefore did not include this genus in their analysis. *Xenepyris* was described by Kieffer (1913b) and was diagnosed by Azevedo *et al*. (2018) as having glabrous eyes, 12 antennomeres, mesoscutum-mesoscutellar fovea oval and not connected by sulcus, being the unique Epyrinae that has 10 flagellomeres (common for Scleroderminae). Alencar & Azevedo (2013) divided the genera and transferred *Xenepyris* to Epyrinae without explanation. We were unable to locate the two species of *Xenepyris*, and the genus was excluded from the analyses. However, we were able to hypothesize, based on the previous comments, that (1) *Xenepyris* should be transferred to Scleroderminae, due to the presence of the 10 flagellomeres; or (2) it is synonymous of *Epyris* s*ensu* Azevedo *et al*. (2018), as suggested by Alencar & Azevedo (2013); or (3) the third antennomere is reduced to ring-shaped (common among males of *Calyoza*), and was missed by Kieffer (1913b). Kieffer (1913a) described *Artiepyris* with 12 antennomeres, but later Evans (1964) reported that the third antennomere was so reduced and ring-shaped that it was not noticed by Kieffer (1913a). So, Evans (1964) concludes that *Artiepyris* has 13 antennomeres. Argaman (unpublished data) also reported that he studied unknown specimens of *Xenepyris* collected by van Achterberg and stated that the third antennomere was extremely small and ring-shaped. Additionally, information from the description of the type species, *X. compressicornis*, such as large body size, and mesoscutum-mesoscutellar sulcus absent, both diagnostic character of *Calyoza*, corroborate our proposition of *Xenepyris* as a junior synonym of *Calyoza*.

The clade *Epyris* group 2 (=*Dolus* to be proposed as **stat. rev.**) (Fig. 1) contains specimens that are spread throughout North America, South America, Asia, and Africa and are morphologically diverse. While all specimens within this clade have mesoscutum-mesoscutellar suture without sulcus that are well separated, they range in shape from

oblique slits to ovals. The configuration of the metapectal-propodeal disc is similar overall – the median area is distinctly sculptured, but unbounded by strong metapostnotal propodeal carina with distinct inner and outer margins. The male genitalia have harpe wide and cuspis partially divided. *Epyris festivus* is included in this clade and belongs to the *depressigaster* group from Evans (1969) in which males are unknown. The defining feature of the *depressigaster* group is the metasoma strongly depressed apically with sternite V possessing a thin plate overlapping the following sternite (Evans, 1969). However, preservation of specimens in ethanol for long periods causes the metasoma to collapse, making these plates difficult to observe without dissecting the specimens, although the metasoma of most females in this clade was strongly depressed apically. Another feature that Evans (1969) described for the *depressigaster* group is the shape of the mandibles, which are bidentate with a pointed apical tooth and dorsal tooth broad and blunt. All female specimens in this clade have a bidentate mandible with a larger apical tooth, and a dorsal tooth, which was typically blunt, and the clypeus was rounded apically. There was variation in the dorsal tooth – the tooth could be round and symmetrical (*Epyris* sp. 48), receding anteriorly (*Epyris* sp. 57), or receding anteriorly with very slight serrations (*Epyris* sp. 56). In males, the mandible always has a large apical tooth, with 3–4 smaller dorsal teeth, and the shape of the clypeus is either pointed apically (*Epyris* sp. 42, *Epyris* sp. 43, *Epyris* sp. 46, and *Epyris* sp. 47) or rounded apically (remaining male specimens). Because the clade is phylogenetically supported (PP=1) and the species share the morphological diagnostic characteristics abovementioned, we reestablish the taxon *Dolus* to be proposed as **stat. rev.**

Another clade that was recovered within *Epyris sensu* Azevedo *et al.* (2018) is *Psilepyris* to be proposed as **stat. rev.** (*Epyris* group 3), containing eight species from Laos, Borneo, Thailand, Mozambique, Uganda, and the Democratic Republic of Congo. In both sexes, the metapostnotal carinae are usually distinctive; the mesoscutum-mesoscutellar foveae are well separated and droop-shaped and the posterior margin of the mesoscutellum does not touch the transverse anterior carina of the metapectal-propodeal complex. The mandibles were variable and ranged from unidentate, unidentate with a broad cutting edge dorsally, to bidentate. All male specimens have the genitalia subtrapezoidal with harpe wide, cuspis undivided and elongate. This clade is called *Psilepyris* to be proposed as **stat. rev.** because the species share the morphological

characteristics abovementioned with the type-species *Psilepyris indivisus*, so we reestablish the taxon *Psilepyris* to be proposed as **stat. rev.**

GenusA to be proposed as **gen.n.** (*Epyris* group 4) is the sister group to *GenusA* to be proposed as **gen.n.** + *Aspidepyris* in TE topology, but its relationship varies between molecular topologies. *GenusA* was not recovered in the morphological analysis. The clade is composed of three species (PP=1) with shared diagnostic features. All three species share unidentate mandibles, large mesoscutum-mesoscutellar foveae, but separated from each other by at least 1.0× their diameter, and lack strong metapostnotal carinae, with the median area of the metapectal-propodeal disc strongly reticulate. Male genitalia have aedeagus bottle-shaped, harpe elongate and thin and cuspis partially divided.

GenusB to be proposed as **gen.n.** (*Epyris* group 5) contains four Nearctic and one Neotropical species (PP=1) and key out to *Epyris* species group *tricostatus* (Evans, 1969) for *Epyris* sp. 1 and *Epyris* sp. 2, and the *rufipes* species group for *Epyris* sp. 3, *Epyris* sp. 4, and *Epyris rufipes* (Say). All specimens share medium-sized elliptical mesoscutum-mesoscutellar foveae, but separated from each other by at least 2.0× their diameter. In males, the mandibles always have one large apical tooth and three smaller dorsal teeth, with the dorsal tooth larger and curved upward. The clypeus is rounded apically. The genitalia are very short, quadrate aedeagus, harpe bottle-shaped and cuspis undivided. The single female specimen, *Epyris rufipes*, had a large apical tooth and a blunt, receding dorsal tooth and the clypeus is rounded apically.

Epyris group 6 contains specimens from the Nearctic and Neotropical regions. Using Evans (1969), most specimens key out to the *rufipes* species group, but *Epyris* sp. 15 and *Epyris* sp. 16, key to the *subspinosus* group by a short metapectal-propodeal complex with a strong metapostnotal carinae with strong reticulation between and a mandible with a strong apical tooth and blunt 1–2 dorsal teeth. The *subspinosus* group is known only from males and contains four species from Central and South America (Evans, 1969). The other males in this clade key out to the *rufipes* group. The females were all keyed to the *rufipes* species group and possessed simple mandibles as well. *Aspidepyris* is grouped in this clade, being a sister species to *Epyris* sp. 15 on molecular and the TE topologies. However, in the morphological topology, *Aspidepyris* failed to group with other genera and presented two synapomorphies. It is important to highlight that because it is a rare genus, like *Calyozina*, we were able to sequence only one specimen. For this, we will expand the boundaries of *Aspidepyris*. It is possible that *Aspidepyris* are males with a specialized

morphology of species belonging to this clade, because only the two species originally described as *Aspidepyris* (*A. austrinus* Evans and *A. foveolatus* Evans) have the diagnostic features of the genus. Evans (1969) hypothesized that *Aspidepyris* evidently was derived and specialized from the *flavicrus* group of *Epyris*, mainly due to the strong sculpturing of the body. Here, in our analyses, specimens from this group have not been sampled and in future phylogenetic studies may help to clarify the internal relationships of this clade.

We revalidate *Trissepyris* to be proposed as **stat. rev.** based on the morphological uniqueness of the taxon and supported by the morphological topology. *Trissepyris* was synonymized with *Epyris* by Azevedo & Alencar (2010b). However, the authors pointed out that this species has peculiar characters, both in relation to *Epyris*, as well as to Epyrinae. *Trissepyris* is distinguished among the other Epyrinae by having large size (about 15 mm long); the ocellar triangle is very compact, with the distance among the ocelli being less than their individual diameters, whereas in *Epyris* the ocelli are usually distant from one another; the occipital carina is missing at the median part on the ventral side, whereas the pattern of *Epyris* is complete; the posterior half of the notauli is wide, to the extent that one nearly touches the other; the mesoscutum-mesoscutellar foveae are elliptical and parallel, unique in Epyrinae; there is an asymmetry in the number of hamuli of the hind wing: the right wing has four basal hamuli and eight apical hamuli, whereas the left wing has five and nine respectively; but on both sides the basal hamuli are placed at the end of the basal fourth, whereas in Epyrinae, they are usually placed much closer to the base (Azevedo & Alencar, 2010b).

Another junior synonym of *Epyris* that we revalidate here is *Muellerella* to be proposed as **stat. rev.** This genus was described by Saussure (1892) and was synonymized with *Epyris* by Evans (1964) without further information. After analysing the holotype of *M. amabilis*, we concluded that the diagnostic characters match those proposed to *Trachepyris*, and we justify synonymization based on the following shared characteristics: ventral margin of mandible with laminar expansion; scape with spine-shaped pectens; notaulus present; mesoscutum-mesoscutellar suture without sulcus and forewings with 2r-rs&Rs vein short. The name *Muellerella* to be proposed as **stat. rev.** is older than *Trachepyris*, which should be placed as a junior synonym, revalidating *Muellerella* to be proposed as **stat. rev.**

In our analyses, there are three females that were identified as *Muellerella* to be proposed as **stat. rev.** Males within this clade were indistinguishable from male *Epyris*.

Characteristics that were shared amongst all males were a head and metapectal-propodeal suture that was wider than long, notauli that were thin anteriorly but broadening posteriorly, mesoscutum-mesoscutellar foveae small and spaced far apart and genitalia with a long harpe. Males also share a similar mandible with a large apical tooth with 3–4 smaller dorsal teeth, often with the dorsal tooth larger and curved upwards. *Muellerella* to be proposed as **stat. rev.**, despite having been recovered with low statistical support in the morphological analysis, has a synapomorphy (character 209:0 – base of harpe strongly angled, crossing each other). Interestingly, this synapomorphy is exclusive to males, but the three female specimens were included in the cluster. Therefore, more morphological studies need to be carried out in order to investigate characteristics that transcend the sexual dimorphism.

Morphological trait

The genera of Epyrinae have been historically distinguished based on a set of homoplasious characters. The presence of antero-lateral foveae and/or anterior sulcus, as well as the shape, inclination, depth, size and internal sculpturing are taxonomically important for the definition of genera and species (Alencar & Azevedo, 2013). However, there is a spectrum of morphological diversity for the sulcus, which makes its interpretation and coding difficult. Waichert & Azevedo (2009) cited the difficulty in coding this character and their results indicate multiple independently origins of the sulcus and fovea in Epyrinae. Alencar & Azevedo (2013) also recovered this character as homoplastic for Epyrinae.

We mapped those characters in the morphological topology (Fig. 2) and our results do not support previous studies. Unlike all previous studies, we recovered the loss of the sulcus between the mesoscutum-mesoscutellar foveae as a homology. For instance, the very large fovea, like as *Epyris*, *Bakeriella* and *Calyozina* has arisen at least five times independently in Epyrinae (Fig. 2). The small fovea like as *Muellerella* to be proposed as **stat. rev.** has arisen at least four times independently in Epyrinae (Fig. 2). The mesoscutum-mesoscutellar sulcus (87:1) is recovered in †*Gloxinius*, *Holepyris*, *Rysepyris* to be proposed as **stat. rev.**, *Laelius*, *Anisepyris* and *Chlorepyris*.

Although other historically used characters have been misleading, our analyses indicate the mesoscutum-mesoscutellar suture and male genitalia as good characteristics to distinguish the lineages within Epyrinae.

Synapomorphy-less genera and further studies

In the morphological topology, we found that few genera are supported by homologous characters and we present below, possible reasons for the low support found.

First, we treated both sexes as different terminal taxa. We aimed (1) to include all genera in the same topology, as some are known exclusively by males (for example, *Aspidepyris*) or females (for example, *Trissepyris* to be proposed as **stat. rev.**) and (2) to search for homologies that are generic and not related to only one sex. Epyrinae, unlike Pristocerinae, do not have strong sexual dimorphism, but many diagnostic generic characters are only for males and focused on their genitalia. For example, the bottle-shaped aedeagus is diagnostic for *Anisepyris* and the third ring-shaped antennomere of males is diagnostic for *Calyoza*.

Second, our morphological matrix is composed mainly of characters that have already been used in previous studies (see Waichert & Azevedo, 2009 and Alencar & Azevedo, 2013). These characters are exclusive to the external morphology of the Bethylidae and the male genitalia. However, they have proven homoplasious and insufficient to recover clades that were well-supported in molecular analyses. Although still rare, there is precedent for using internal characters to resolve the systematics of other insect families with similarly well-explored external morphological characters. In a study on long-tongued bees (Roig-Alsina & Michener, 1993) and crabonids (Melo, 1999), several external and internal structures were explored, including musculature. Brożek & Bourgoin (2013) described sensory structures on the labium in fifteen fulgoromorphan (Hemiptera) families and provided a range of new characters for phylogenetic studies in the group. Kawada *et al*. (2015) studied the evolution of the metapostnotum in Bethylidae and concluded that, along with other characteristics, metapostnotum characteristics can provide further evidence of potentially erroneously positioned taxa in other subfamilies, such as *Glenosema* Kieffer, which belongs to Scleroderminae but has a similar configuration to genera found in Epyrinae. Barbosa *et al*. (2021) explored the sting apparatus of Chrysidoidea, including the musculature and recovered several

synapomorphies for Bethylidae. Although promising, the internal morphology of Bethylidae has just recently been investigated and it remains poorly explored. Due to the lack of terminology standardization, the inclusion of such characters in phylogenetic analyses has not been implemented. More work with a focus on comparative morphology must be performed, making it possible for phylogenetic studies to include such information.

Third, this is the third phylogenetic study of Bethylidae that encompasses both extinct and extant species. Colombo *et al*. (2020) tested the monophyly of the nine subfamilies of Bethylidae and Vargas *et al*. (2020) revisited the evolutionary history of Scleroderminae and highlighted the difficulty, problems, and advantages of including fossils as terminal taxa. In general, the incompleteness of the data and the difficulty in visualizing the characteristics makes it difficult to establish homologies. Although there are problems, the use of fossil data can make important contributions (Novacek, 1992; Smith, 1998; Kearney & Clark, 2003), and, for that reason, we included these terminals in our analyses.

Fourth, the number of old holotypes, some of which are lost, with descriptions insufficient to extract any information. Well-defined genera are those whose species have been extensively revised. Excluding less speciose genera, like *Aspidepyris* and *Calyozina*, other genera like *Anisepyris*, *Bakeriella*, *Chlorepyris*, *Holepyris sensu strictu* and *Laelius*, had their species studied almost in their entirety. Here, it is these genera that showed monophyly and little variation in the different analyses. Consequently, other genera whose species are lost and poorly preserved are the taxonomic problems, such as *Epyris sensu* Azevedo *et al.* (2018) and its synonyms.

Finally, genera with an unstable taxonomic history, like *Epyris*, might indicate poor taxa delimitation and a prevalence of homoplasious morphological characters. These genera might confound morphological topologies and the search for synapomorphies to define them. *Epyris* is the taxon with the most taxonomic problems within Bethylidae, while also being the second most speciose within the family. This genus is polyphyletic in all previous studies and has largely been considered a taxonomic wastebasket. Here, we were able to show homoplasy in diagnostic characters and split *Epyris sensu* Azevedo *et al*., (2018) into seven genera, including a revised *Epyris* supported by homology, *Calyoza* and *Trissepyris*. Several species that do not fit this new concept have been transferred to

Dolus and *Psilepyris*. These genera urgently need studies based on the world fauna, to redefine and increase the morphological characters.

TAXONOMIC ACCOUNTS

Epyrinae Kieffer, 1914

Type-genus: *Epyris* Westwood, 1832

Epyrini Kieffer 1914, 41: 308; Evans 1964, 132: 90.

Epyrinae Berland 1928, 10: 111; Alencar & Azevedo 2013, 38: 77.

Epyris Westwood, 1832 (Figs 4A, 5A)

Epyris Westwood, 1832, 1: 129. Type-species: *E. niger* Westwood, 1832 by original monotypy.

Isobrachium Förster, 1856. Synonymy by Azevedo *et al.* 2018, 4489: 156.

Leptepyris Kieffer, 1914. Synonymy by Azevedo *et al.* 2018, 4489: 156.

Melanepyris Kieffer, 1913a. Synonymy by Azevedo & Alencar 2010a, 27: 403.

Parepyris Kieffer, 1913a. Synonymy by Evans 1964, 132: 104.

Rhabdepyris Kieffer, 1904. Synonymy by Azevedo *et al.* 2018, 4489: 156.

Diagnosis. **Female**: mandible with one to five apical teeth, without ventral tooth; median clypeal lobe well projected forward; lateral clypeal lobe usually inconspicuous; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; dorsal pronotal area ecarinate; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, very large, subrectangular, distant each other by at least 0.2× total size of fovea; forewing with 2r-rs&Rs vein, long. **Male**: same data of female, except: genitalia with harpe shorter than gonostipes, in dorsal view; aedeagus shorter than basivolsella and subtriangular.

Remarks. We reviewed the types of the type species of the genera *Epyris*, *Melanepyris*, *Parepyris* and *Rhabdepyris*. However, the holotypes of the type species of *Isobrachium* and *Leptepyris* are lost and the synonym was maintained by the same arguments already detailed by Azevedo *et al.* (2018). It represents lineage *Epyris sensu stricto* in our analyses.

Distribution. Old World; 81 species (Appendix 5: Table 8).

***Aspidepyris* Evans, 1964 (Figs 4B–C, 5B–C)**

Aspidepyris Evans, 1964, 132: 115–116. Type-species: *A. foveolatus* Evans, 1954 by original monotypy.

Diagnosis. **Male**: mandible with one to five apical teeth, without ventral tooth; median clypeal lobe well projected forward; lateral clypeal lobe usually conspicuous; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; dorsal pronotal area ecarinate; notaulus present, expanded posteriorly; parapsidal signum usually present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, foveae large to small, circular or elliptical, distant each other by at least 1.0× total size of fovea; forewing with 2r-rs&Rs vein, long; genitalia with aedeagus slender, harpe large apically, cuspis usually elongate. **Female**: same data of male.

Remarks. It represents lineage *Epyris* group 6 in our analyses.

Distribution. New World; 26 species (Appendix 5: Table 2).

***Calyoza* Hope, 1837** to be proposed as **stat. rev. (Figs 4D–G, 5D–E)**

Calyoza Hope, 1837, 2: 56. Type-species: *C. staphylinoides* Hope, 1832 by original monotypy.

Artiepyris Kieffer, 1913a, 7: 108. To be proposed as **syn.n.**

Calyozella Enderlein, 1920, 51: 24. To be proposed as **syn.n.**

Paracalyoza Cameron, 1909, 3: 377. To be proposed as **syn.n.**

Pseudocalyoza Turner, 1915, 16: 298. To be proposed as **syn.n.**

Xenepyris Kieffer, 1913b, 3: 259. To be proposed as **syn.n.**

Diagnosis. **Female**: mandible with one to five apical teeth, with ventral tooth; median clypeal lobe well projected forward; lateral clypeal lobe usually inconspicuous; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; dorsal pronotal area ecarinate; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, foveae large, circular, distant each other by at least 0.5× total size of fovea; forewing with 2r-rs&Rs vein, long. **Male**: same data of female, except: antenna filiform or pectinate; first

flagellomere ring-shaped; genitalia with harpe usually tubular, extremely long; aedeagus shorter than basivolsella and subtriangular.

Remarks. We reviewed the types of the type species of the genera *Calyoza*, *Artiepyris*, *Paracalyoza*, and *Pseudocalyoza*. However, the types of *Calyozella* and *Xenepyris* are lost. It represents lineage *Epyris* group 1 in our analyses.

Distribution. Cosmopolitan, except Nearctic; 25 species (Appendix 5: Table 4).

***Dolus* Motschulsky, 1863** to be proposed as **stat. rev. (Figs 4H, 5F)**

Dolus Motschulsky, 1863, 36: 27. Type-species: *D. politus* Motschulsky, 1863 by subsequent designation.

Homoglenus Kieffer, 1905, 29: 109. To be proposed as **syn.n.**

Neodisepyris Kurian, 1955, 4: 106. To be proposed as **syn.n.**

Diagnosis. **Female**: mandible with one to five apical teeth, without ventral tooth; median clypeal lobe well projected forward; lateral clypeal lobe usually inconspicuous; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; dorsal pronotal area ecarinate; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, foveae medium-sized, subcircular, distant each other by at least 1.0× total size of fovea; forewing with 2r-rs&Rs vein, long; metasoma strongly depressed dorsoventrally, in some species. **Male**: same data of female, except: metasoma not depressed dorsoventrally; genitalia with harpe longer than gonostipes, in dorsal view; aedeagus shorter than basivolsella and subtriangular.

Remarks. Kieffer (1904) described *Homoglenus* with only one originally included species (also described as new), *Homoglenus tripartitus* Kieffer, 1904 (holotype examined here). It is the type of the genus by monotypy and not *Homoglenus punctatus* Kieffer, 1906, described two years later. We reviewed the types of the type species of the genera *Dolus*, *Homoglenus* and *Neodisepyris*. It represents lineage *Epyris* group 2 in our analyses.

Distribution. Cosmopolitan; 84 species (Appendix 5: Table 7).

GenusB to be proposed as **gen.n. (Figs 4I, 5G)**

GenusB Colombo, Tribull & Azevedo. Type species: *Bethylus rufipes* Say, 1824 by original designation.

Diagnosis. **Female**: mandible bidentate; median clypeal lobe well projected forward; lateral clypeal lobe conspicuous, 2× shorter than median lobe; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; eye remarkably large; dorsal pronotal area ecarinate; anteromesoscutum without foveolate transverse groove; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, foveae medium-sized, elliptical, distant each other by at least 2.0× total size of fovea; forewing with 2r-rs&Rs vein, long; protarsus without long spatulate spine-shaped filament. **Male**: unknown.

Remarks. It represents lineage *Epyris* group 5 in our analyses.

Distribution. Nearctic and Neotropical; 01 species (Appendix 5: Table 10).

Etymology. The names derives from *Epyris*, the type-genus of Epyrinae. Gender masculine.

***Holepyris* Kieffer, 1904 (Figs 4J, 5H)**

Holepyris Kieffer, 1906 (in Kieffer & Marshall 1904-1906), 9: 341. Type-species: *Holepyris africanus* Kieffer, 1904 by subsequent designation.

Disepyris Kieffer, 1905, 29: 115-116. To be proposed as **syn.n.**

Formosiepyris Terayama, 2004, 12: 91-92. To be proposed as **syn.n.**

Lytepyris Kieffer, 1913a, 7: 108. To be proposed as **syn.n.**

Diagnosis. **Female**: mandible with three to four apical teeth, without ventral tooth; median clypeal lobe well projected forward; lateral clypeal lobe conspicuous, almost as long as median lobe; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; eye remarkably large; dorsal pronotal area foveolate posteriorly; anteromesoscutum with foveolate transverse groove; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae connected by sulcus, usually trabeculate, not arched posteriorly; forewing with 2r-rs&Rs vein, long or short; protarsus with long spatulate spine-shaped filament. **Male**: same data of female, except: genitalia with harpe longer than gonostipes, in dorsal view; aedeagus shorter than basivolsella and almost bottle-shaped.

Remarks. We reviewed the types of the type species of the genera *Holepyris*, *Disepyris* and *Formosiepyris*. However, the type of genus *Lytepyris* is lost. It represents lineage *Holepyris sensu stricto* in our analyses.

Distribution. Old World; 38 species (Appendix 5: Table 12).

GenusA to be proposed as **gen.n. (Figs 4K, 5I)**

GenusA Colombo, Tribull & Azevedo. Type species: *Epyris idaten* Terayama, 2006 by original designation.

Diagnosis. **Male**: mandible unidentate; median clypeal lobe well projected forward; lateral clypeal lobe conspicuous, 2× shorter than median lobe; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; eye remarkably large; dorsal pronotal area ecarinate; anteromesoscutum without foveolate transverse groove; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, foveae medium-sized, elliptical, distant each other by at least 1.0× total size of fovea; forewing with 2r-rs&Rs vein, long; protarsus without long spatulate spine-shaped filament; genitalia with harpe longer than gonostipes, in dorsal view, bottle-shaped; aedeagus very shorter than basivolsella and almost quadrate; cuspis divided partially. **Female**: unknown.

Remarks. It represents lineage *Epyris* group 4 in our analyses.

Distribution. Oriental; 01 species (Appendix 5: Table 11).

Etymology. The name derives from the specific name of the type-species. Gender masculine.

Muellerella **Saussure, 1892 [1890]** to be proposed as **stat. rev. (Figs 4L, 5J)**

Muellerella Saussure, 1892 [1890], 20. Type-species: *M. amabilis* Saussure, 1892[1890] by original monotypy.

Acanthepyris Kieffer, 1912, 3: 103. To be proposed as **syn.n.**

Planepyris Kieffer, 1905, 29: 108. To be proposed as **syn.n.**

Pristobethylus Kieffer, 1906 (in Kieffer & Marshall 1904-1906), 9: 248. To be proposed as **syn.n.**

Trachepyris Kieffer, 1905, 29: 107. To be proposed as **syn.n.**

Diagnosis. **Female**: mandible with three to four apical teeth, with ventral tooth, ventral margin with laminar expansion and chaetica sensillae; median clypeal lobe well projected forward; lateral clypeal lobe inconspicuous; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped, scape with spine-shaped pectens; occipital carina complete; dorsal pronotal area ecarinate; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, medium-sized, circular, distant each other by at least 1.0× total size of fovea; forewing with 2r-rs&Rs vein short; protarsus strongly spinose. **Male**: same data of female, except: mandible without ventral tooth, ventral margin without laminar expansion and chaetica sensillae; scape with thick setae; genitalia with harpe longer than gonostipes, in dorsal view; cuspis very long, as long as harpe; aedeagus longer than basivolsella and subtrapezoidal.

Remarks. We reviewed the types of the type species of the genera *Muellerella*, *Acanthepyris*, *Planepyris* and *Trachepyris*. However, we did not find the type of the type species of *Pristobethylus* and this is probably deposited in OUMNH (Gordh & Móczár 1990) or is lost.

Distribution. Old World; 21 species (Appendix 5: Table 14).

***Psilepyris* Kieffer, 1913** to be proposed as **stat. rev. (Figs 4M–N, 5K–L)**

Psilepyris Kieffer, 1913a, 7: 108. Type-species: *Epyris indivisus* Kieffer, 1906 by subsequent designation.

Diagnosis. **Female**: mandible with one to five apical teeth, without ventral tooth; median clypeal lobe well projected forward; lateral clypeal lobe usually inconspicuous; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; dorsal pronotal area ecarinate; notaulus present; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, foveae large, droop-shaped, distant each other by at least 1.0× total size of fovea; forewing with 2r-rs&Rs vein, long. **Male**: same data of female, except: genitalia with harpe shorter than gonostipes, in dorsal view; aedeagus shorter than basivolsella and subtrapezoidal; cuspis undivided.

Remarks. We reviewed the type of the type species of the genus *Psilepyris*. It represents lineage *Epyris* group 3 in our analyses.

Distribution. Cosmopolitan; 90 species (Appendix 5: Table 15).

***Rysepyris* Kieffer, 1906** to be proposed as **stat. rev. (Figs 4O, 5M)**

Rysepyris Kieffer, 1906 (in Kieffer & Marshall 1904-1906), 9: 341. Type-species: *Holepyris numicidus* Kieffer, 1906 by subsequent designation.

Misepyris Kieffer, 1913a, 7: 108. To be proposed as **syn.n.**

Parepyris Brèthes, 1913, 24: 87. To be proposed as **syn.n.**

Diagnosis. **Female**: mandible slender with one to two apical teeth, without ventral tooth; median clypeal lobe well projected forward, with dorsal carina; lateral clypeal lobe conspicuous, as long as median lobe; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina complete; dorsal pronotal area with anterior carina and posterior transverse groove; anteromesoscutum short, without foveolate transverse groove; notaulus present, usually impressed on anterior half of anteromesoscutum; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae connected by sulcus, usually trabeculate, not arched posteriorly; forewing with 2r-rs&Rs vein, long or short. **Male**: same data of female, except: genitalia with harpe as long as gonostipes, in dorsal view; cuspis elongate, usually as long as harpe apex; aedeagus shorter than basivolsella and subtriangular.

Remarks. We reviewed the types of the type species of the genera *Misepyris* and *Parepyris*. However, the type of genus *Rysepyris* is lost. It represents lineage *Holepyris* group 1 in our analyses.

Distribution. Cosmopolitan; 133 species (Appendix 5: Table 16).

***Trissepyris* Kieffer, 1905** to be proposed as **stat. rev. (Figs 4P, 5N)**

Trissepyris Kieffer, 1905, 29: 109, 116-117. Type-species: *T. ruficeps* Kieffer, 1905 by original monotypy.

Diagnosis. **Female**: mandible with three apical teeth, without ventral tooth; median clypeal lobe well projected forward; lateral clypeal lobe inconspicuous; antenna filiform with 11 flagellomeres; first flagellomere never ring-shaped; occipital carina incomplete ventrally; ocellar triangle very compact, far from vertex; dorsal pronotal area ecarinate; notaulus present, conspicuously wide posteriorly; parapsidal signum present; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, elliptical, parallel, distant each

other by at least 5.0× total size of fovea; forewing with 2r-rs&Rs vein, long. **Male**: unknown.

Distribution. Afrotropical; 1 species (Appendix 5: Table 17).

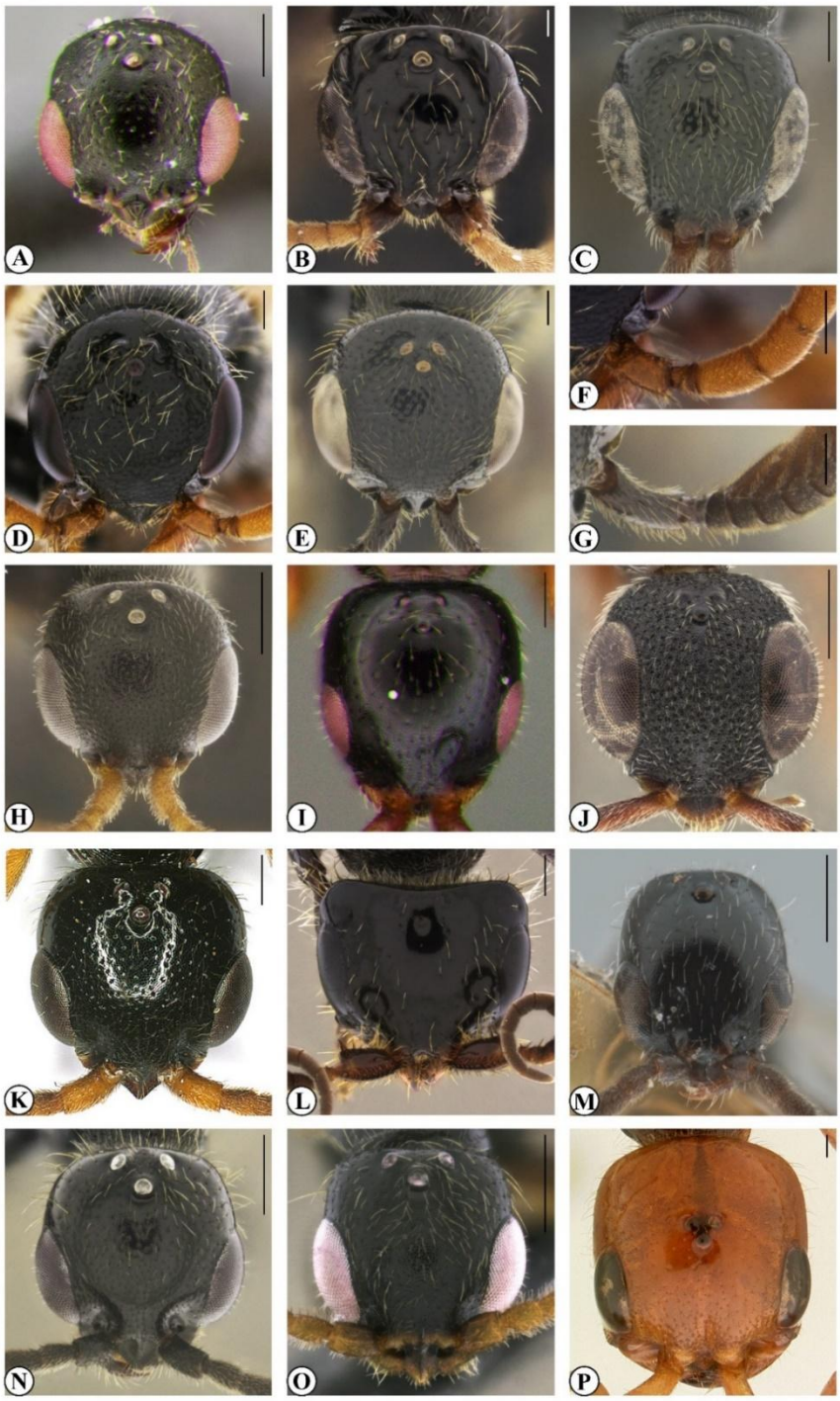

FIGURE 4. Head, dorsal view. (A) *Epyris*; (B) *Aspidepyris* type morphological pattern; (C) *Aspidepyris* non-type morphological pattern; (D-G) *Calyoza* will be proposed as stat. rev.; (F-G) Third antennomere ring-shaped; (H) *Dolus* will be proposed as stat. rev.; (I) *GenusB* gen.n.; (J) *Holepyris*; (K) *GenusA* gen.n. (adapted from Lim *et al*., 2011); (L) *Muellerella* will be proposed as stat. rev.; (M) *Psilepyris* will be proposed as stat. rev., type morphological pattern.; (N) *Psilepyris* will be proposed as stat. rev., non-type morphological pattern; (O) *Rysepyris* will be proposed as stat. rev., (P) *Trissepyris* will be proposed as stat. rev. (adapted from Azevedo & Alencar, 2010b). Scales-bar: 250µm, except 200µm for I and K.

FIGURE 5. Mesosoma, dorsal view. (A) *Epyris*; (B) *Aspidepyris* type morphological pattern; (C) *Aspidepyris* non-type morphological pattern; (D) *Calyoza* will be proposed as stat. rev.; (E) *Calyoza* will be proposed as stat. rev., pectinate form; (F) *Dolus* will be proposed as stat. rev.; (G) *GenusB* gen.n.; (H) *Holepyris*; (I) *GenusA* gen.n. (adapted from Lim *et al*., 2011); (J) *Muellerella* will be proposed as stat. rev.; (K) *Psilepyris* will be proposed as stat. rev., type morphological pattern.; (L) *Psilepyris* will be proposed as stat. rev., non-type morphological pattern; (M) *Rysepyris* will be proposed as stat. rev., (N) *Trissepyris* will be proposed as stat. rev. (adapted from Azevedo & Alencar, 2010b). Scales-bar: 250µm, except 500µm for I and 200µm for G.

CONCLUSIONS

The addition of all extant and extinct genera and the combination of morphological and molecular data in our analyses, have generated a better resolution of the topology of Epyrinae and aided in our understanding of the evolutionary history of this group of wasps. We revalidate six genera of Epyrinae, corresponding to about 40% of the previous number of epyrine genera. Previous studies had pointed to a non-monophyletic *Epyris*, but poorly sampled the genus. Herein, we sample the broad diversity of the genus and conclusively show non-monophyly. Additionally, we included representatives of all extant valid genera, with exception of *Xenepyris*, in the molecular phylogeny. This study did not recover the major species groups within *Epyris* proposed by Evans (1969), like the *rufipes* and *tricostatus* groups. Here, they are invalid and exhibited how historically used characters such as the sculpturing of the metapectal-propodeal complex, clypeus shape, and mandible shape are insufficient to define lineages in Epyrinae and should be used with caution. The type species of *Epyris*, *E. niger*, nests within a clade with shared large, nearly touching mesoscutum-mesoscutellar foveae, and we propose this clade should be retained as *Epyris sensu stricto*. We redefine *Epyris sensu* Azevedo *et al*. (2018) splitting it into eight lineages: *Aspidepyris*, *Calyoza* to be proposed as **stat. rev.**, *Dolus* to be proposed as **stat. rev.**, *Epyris*, *GenusA* to be proposed as **gen.n.**, *GenusB* to be proposed as **gen.n.**, *Psilepyris* to be proposed as **stat. rev.** and *Trissepyris* to be proposed as **stat. rev.** The morphological characters that have been used to classify many of the genera within Epyrinae present problems when analysed phylogenetically. Many diagnostic characteristics are male- or female-specific or are often found in other genera, like a subapical tooth, thick setae on the scape, or spines on the protarsus, and are probably one of the reasons that the molecular topology in this study differs from all morphological phylogenetic analyses. Revising taxonomic descriptions for genera of Epyrinae, and adding new features (for example, internal morphology) to have clear synapomorphies that are not dependent on sex is a necessary step for furthering phylogenetic analyses of these wasps. Alternatively, and perhaps additionally, the amplification of nuclear protein-coding genes could resolve many of the ambiguities in the trees presented here. Although difficult to amplify, nuclear protein-coding genes have been utilized in a variety of Hymenopteran molecular phylogenies (Klopfstein *et al*., 2013; Danforth *et al*., 2013) and could aid future molecular analyses of Epyrinae.

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REFERENCES

Alencar, I.D.C.C. & Azevedo, C.O. (2009) Rediscovery of *Planepyris* Kieffer: a new synomym of *Trachepyris* Kieffer (Hymenoptera, Bethylidae). *Doriana*, **8**, 1–12.

Alencar, I.D.C.C. & Azevedo, C.O. (2011) Review of *Neurepyris* Kieffer, 1905 (Hymenoptera, Bethylidae), a new synonym of *Pristocera* Klug, 1808. *European Journal of Taxonomy*, **4**, 1–12. https://doi.org/10.5852/ejt.2011.4

Alencar, I. D.C.C. & Azevedo, C.O. (2013) Reclassification of Epyrini (Hymenoptera: Bethylidae): a tribal approach with commentary on their genera. *Systematic Entomology*, **38**, 45–80. https://doi.org/10.1111/syen.12295

Alencar, I. D.C.C., Waichert, C. & Azevedo, C.O. (2018) Opening Pandora's box of Pristocerinae: molecular and morphological phylogenies of *Apenesia* (Hymenoptera, Bethylidae) reveal several hidden genera. *Systematic Entomology*, **43**, 481–509. https://doi.org/10.1111/syen.12295

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. (1997) Basic local alignment search tool. *Journal of Molecular Biology*, **215**, 403–410.

Azevedo, C.O. (1999a) Revision of the Neotropical *Dissomphalus* Ashmead, 1893 (Hymenoptera, Bethylidae) with median tergal process. *Arquivos de Zoologia*, **35**, 301–394. https://doi.org/10.11606/issn.2176-7793.v35i4p301-394

Azevedo, C.O. (1999b) On the Neotropical *Rhabdepyris* Kieffer (Hymenoptera, Bethylidae) of the subgenus *Chlorepyris*. *Revista Brasileira de Zoologia*, **16**, 887–897. https://doi.org/10.1590/S0101-81751999000300026

Azevedo, C.O. (2014) Synopsis of *Bakeriella* Kieffer, 1910 (Hymenoptera: Bethylidae). *Zootaxa*, **3878**, 501–535. https://doi.org/10.11646/zootaxa.3878.6.1

Azevedo, C.O. & Alencar, I.D.C.C. (2009) Rediscovery of *Pristepyris* Kieffer (Hymenoptera, Bethylidae), a new synonym of *Acrepyris* Kieffer. *Zootaxa*, **2287**, 45–54. https://doi.org/10.11646/zootaxa.2287.1.2

Azevedo, C.O. & Alencar, I.D.C.C. (2010a) Rediscovery of *Melanepyris* (Hymenoptera: Bethylidae): a new synonym of *Epyris*. *Zoologia* (Curitiba), **27**, 403–407. http://dx.doi.org/10.1590/S1984-46702010000300012

Azevedo, C.O. & Alencar, I.D.C.C. (2010b) Rediscovery of the Afrotropical genus *Trissepyris* Kieffer (Hymenoptera: Bethylidae), a new synonym of *Epyris* Westwood. *Journal of Afrotropical Zoology*, **6**, 3–7.

Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas R., J.M. & Lim, J. Global guide of flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, **4489**, 1–294. https://doi.org/10.11646/zootaxa.4489.1.1

Barbosa, D.N. & Azevedo, C.O. (2011) Phylogeny and reclassification of *Laelius* (Hymenoptera: Bethylidae) and description of four new species. *Insect Systematics & Evolution*, **42**, 237–275. https://doi.org/10.1163/187631211X559777

Barbosa, D.N., Vilhelmsen, L. & Azevedo, C.O. (2021) Morphology of sting apparatus of Chrysidoidea (Hymenoptera, Aculeata). *Arthropod Structure & Development*, **100999**, 1–20. https://doi.org/10.1016/j.asd.2020.100999

Berland, L. (1928) Hyménoptères Vespiformes II. *Faune de France*, **19**, 1–215.

Branstetter, M.G., Danforth, B.N., Pitts, J.P., Faircloth, B.C., Ward, P.S., Buffington, M.L., Gates, M.W., Kula, R.R. & Brady, S.G. Phylogenomic Insights into the Evolution of Stinging Wasps and the Origins of Ants and Bees. *Current Biology*, **27**, 1019–1025. https://doi.org/10.1016/j.cub.2017.03.027

Brożek, J. & Bourgoin, T. (2013) Morphology and distribution of the external labial sensilla in Fulgoromorpha (Insecta: Hemiptera). *Zoomorphology*, **132**, 33–65. https://doi.org/10.1007/s00435-012-0174-z

Carpenter, J.M. (1999) What do we know about chrysidoid (Hymenoptera) relationships? *Zoologica Scripta*, **28**, 215–231. https://doi.org/10.1046/j.1463-6409.1999.00011.x

Carr, M., Young, J.P.W. & Mayhew, P.J. (2010) Phylogeny of bethylid wasps (Hymenoptera: Bethylidae) inferred from 28S and 16S rRNA genes. *Insect Systematics & Evolution*, **41**, 55–73. https://doi.org/10.1163/187631210X486995

Colombo, W.D., Perkovsky, E.E. & Azevedo, C.O. (2020) Phylogenetic overview of flat wasps (Hymenoptera, Bethylidae) reveals Elektroepyrinae, a new fossil subfamily. *Palaeoentomology*, **3**, 269–283. https://doi.org/10.11646/palaeoentomology.3.3.8

Colombo, W.D., Perkovsky, E.E., Waichert, C. & Azevedo, C.O. (2021) Synopsis of the fossil flat wasps Epyrinae (Hymenoptera, Bethylidae), with description of three new genera and 10 new species. *Journal of Systematic Palaeontology*, 1–52. https://doi.org/10.1080/14772019.2021.1882593

Dallwitz, M.J. (1980) A general system for coding taxonomic descriptions. *Taxon*, **29**, 41–46. https://doi.org/10.2307/1219595

Danforth, B.N., Cardinal, S., Praz, C., Almeida, E.A. & Michez, D. (2013) The impact of molecular data on our understanding of bee phylogeny and evolution. *Annual Review of Entomology*, **58**, 57–58. https://doi.org/10.1146/annurev-ento-120811-153633

De Pinna, M.C.C. (1991) Concepts and tests of homology in the cladistic paradigm. *Cladistics*, **7**, 367–394. https://doi.org/10.1111/j.1096-0031.1991.tb00045.x

Dowton, M. & Austin, A.D. (1994) Molecular phylogeny of the insect order Hymenoptera: Apocritan relationships. *Proceedings of the National Academy of Sciences of the United States of America*, **91**, 9911–9915. https://doi.org/10.1073/pnas.91.21.9911

Evans, H.E. (1964) A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology*, **132**, 1–222.

Evans, H.E. (1965) A revision of the genus *Rhabdepyris* in the Americas (Hymenoptera, Bethylidae). *Bulletin of the Museum of Comparative Zoology*, **133**, 67–151.

Evans, H.E. (1969) A revision of the genus *Epyris* in the Americas (Hymenoptera: Bethylidae). *Transactions of the American Entomological Society*, **95**, 181–352.

Evans, H.E. (1979a) A reconsideration of the genus *Bakeriella* (Hymenoptera: Bethylidae). *Journal of the New York Entomological Society*, **87**, 256–266.

Evans, H.E. (1979b) The *Platycephalus* group of the genus *Rhabdepyris* Kieffer (Hymenoptera: Bethylidae: Epyrinae). *Australian Journal of Entomology*, **18**, 377–381.

Evans, H.E. (1982) The *Anxius* group of the genus *Rhabdepyris* Kieffer (Hymenoptera: Bethylidae: Epyrinae). *Australian Journal of Entomology*, **21**, 55–61.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, **3**, 294–299.

Goloboff, P. (1993) Estimating character weights during tree search. *Cladistics*, **9**, 83–91. https://doi.org/10.1006/clad.1993.1003

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelmann, B., Ramírez, M. & Szumik, C. (2003) Improvements to resampling measures of group support. *Cladistics*, **19**, 324–332. https://doi.org/10.1111/j.1096-0031.2003.tb00376.x

Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x.

Gordh, G. & Móczár, L. (1990) A catalog of the world Bethylidae (Hymenoptera: Aculeata). *Memoirs of the American Entomological Institute*, **46**, 1–364.

Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, Cambridge, UK.

Hines, H.M., Hunt, J.H., O'Connor, T.K., Gillespie, J.J. & Cameron, S.A. (2007) Multigene phylogeny reveals eusociality evolved twice in vespid wasps. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3295–3299. https://doi.org/10.1073/pnas.0610140104

Katoh, S. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, **30**, 772–780 (outlines version 7).

Kawada, R. & Buffington, M.L. (2016) A scalable and modular dome illumination system for scientific microphotography on a budget. *PLoS ONE*, **11**, e0153426. https://doi.org/10.1371/journal.pone.0153426

Kawada, R., Lanes, G.O. & Azevedo, C.O. (2015) Evolution of metapostnotum in flat wasps (Hymenoptera, Bethylidae): implications for homology assessments in Chrysidoidea. *PLoS ONE*, **10**, e0140051. https://doi.org/10.1371/journal.pone.0140051

Kearney M. & Clark J.M. (2003) Problems due to missing data in phylogenetic analyses including fossils: a critical review. *Journal of Vertebrate Paleontology*, **23**, 263–274. https://doi.org/10.1671/0272-4634(2003)023[0263:PDTMDI]2.0.CO;2

Kieffer, J.J. (1905) Description de nouveaux Proctotrypides exotiques. *Annales de la Société scientifique de Bruxelles*, **29**, 95–142.

Kieffer, J.J. (1910) Description de nouveaux microhyménoptères du Brésil. *Annales De La Société Entomologique De France*, **78**, 287–348. http://doi.org/10.5281/zenodo.23748

Kieffer, J.J. (1913a) Nouveaux microhyménoptères de l'Afrique équatoriale. *Bollettino del Laboratorio di zoologia generale e agraria della R. Scuola superiore d'agricoltura in Portici*, **7**, 105–112.

Kieffer, J.J. (1913b) Serphides de iles Philippines. *Insecta*, **3**, 253–462. http://doi.org/10.5281/zenodo.23750

Kieffer, J.J. (1914) Bethylidae. *Das Tierreich*, **41**, 1–205.

Klopfstein, S., Vilhelmsen, L., Heraty, J.M., Sharkey, M. & Ronquist, F. (2013) The hymenopteran tree of life: evidence from protein-coding genes and objectively aligned ribosomal data. *PLoS ONE*, **8**, e69344. https://doi.org/10.1371/journal.pone.0069344

Krombein, K.V. (1987a) Synonymic notes on the Bethylidae described by V. de Motschulsky (Hymenoptera: Aculeata). *Proceedings of the Entomological Society of Washington*, **89**, 356–358.

Krombein, K.V. (1987b) Biosystematic studies of Ceylonese wasps. XVIII. The species of *Trachepyris* Kieffer (Hymenoptera: Bethylidae: Epyrinae). *Pan-pacific Entomologist*, **515**, 1–41.

Krombein, K.V. (1992) Systematics of the genera of Epyrinae with ramose male antennae (Hymenoptera: Bethylidae). *Proceedings of the Entomological Society of Washington*, **94**, 345–360.

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, **33**, 1870–1874. https://doi.org/10.1093/molbev/msw054

Kurian, C. (1955) Bethyloidea (Hymenoptera) from India. *Agra University Journal of Research*, **4**, 67–155.

Lanes, G.O. & Azevedo, C.O. (2008) Phylogeny and taxonomy of Sclerodermini (Hymenoptera, Bethylidae, Epyrinae). *Insect Systematic and Evolution*, **39**, 55–86. https://doi.org/10.1163/187631208788784165

Lanes, G.O., Kawada, R., Azevedo, C.O. & Brothers, D.J. (2020) Revisited morphology applied for Systematics of flat wasps (Hymenoptera, Bethylidae). *Zootaxa*, **4752**, 1–127. https://doi.org/10.11646/zootaxa.4752.1.1

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701. https://doi.org/10.1093/molbev/mss020

Lewis, P.O. A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data. *Systematic Biology*, **50**, 913–925. https://doi.org/10.1080/106351501753462876

Lim, J., Lee, J., Koh, S., Lee, B., Azevedo, C.O. & Lee, S. (2011) Taxonomy of *Epyris* Westwood (Hymenoptera: Bethylidae) from Korea, with the descriptions of ten new species. *Zootaxa*, **2866**, 1–38. https://doi.org/10.11646/zootaxa.2866.1.1

Maddison, W.P. & Maddison, D.R. (2019) Mesquite: a modular system for evolutionary analysis. [software]. Available from URL http://www.mesquiteproject.org/

Martinelli, A.B., Waichert, C., Barbosa, D.N., Fagundes, V. Azevedo, C.O. (2017). The use of Proteinase K to access genitalia morphology, vouchering and DNA extraction in minute wasps. *Anais da Academia Brasileira de Ciências*, **89**, 1629–1633. https://doi.org/10.1590/0001-3765201720160825

Melo, G A.R. (1999) Phylogenetic relationships and classification of the major lineages of Apoidea (Hymenoptera) with emphasis on the crabronid wasps. *Scientific Papers*, **14**, 1-55. https://doi.org/10.5962/bhl.title.4053

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November, 2010, pp. 1–8. New Orleans, Louisiana.

Motschulsky, V. (1863) Essai d'un catalogue des Insectes de l'Ile Ceylan. *Bulletin de la Société impériale des naturalistes de Moscou*, **36**, 421–532.

Nixon, K.C. (2002) WinClada ver. 1.0000. Published by the Author, Ithaca, New York. [Software].

Novacek, M. (1992) Fossils as critical data for phylogeny. *In* Novacek M.J., Wheeler Q.D. (eds.). *Extinction and phylogeny*. Columbia University Press, New York, pp. 46 –88.

Paquin, P. & Vink, C.J. Testing compatibility between molecular and morphological techniques for arthropod systematics: a minimally destructive DNA extraction method that preserves morphological integrity, and the effect of lactic acid on DNA

quality. *Journal of Insect Conservation*, **13**, 453–457. https://doi.org/10.1007/s10841-008-9183-0

Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Petersen, M., Lanfear, R., Diez, P.A., Heraty, J., Heraty, K.M., Klopfstein, S., Meier, R., Polidori, C., Schmitt, T., Liu, S., Zhou, X., Wappler, T., Rust, J., Misof, B., Niehuis. (2017) Evolutionary History of the Hymenoptera. *Current Biology*, **27**, 1013–1318. https://doi.org/10.1016/j.cub.2017.01.027

Rambaut, A. (2014) A Graphical Viewer of Phylogenetic Trees. [software]. Available from URL http://tree.bio.ed.ac.uk/software/figtree/

Roig-Alsina, A. & Michener, C. D. (1993) Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). *University of Kansas Science Bulletin* **55**, 123–160. https://doi.org/10.5962/bhl.part.775

Rokas, A., Nylander, J.A.A., Ronquist, F., Stone, G.N. (2002) A maximum-likelihood analysis of eight phylogenetic markers in gallwasps (Hymenoptera: Cynipidae): implications for insect phylogenetic studies. *Molecular Phylogenetics and Evolution*, **22**, 206–219. https://doi.org/10.1006/mpev.2001.1032

Ronquist, F. & Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Sausurre, H.D. de (1892[1890]) Volume XX. Histoire naturallle des Hyménoptères. *In*: Grandidier, A. (Ed.), *Histoire physique, naturelle, et politique de Madagascar*. L'Imprimerie Nationale, Paris pp. i-xxii + 1–590.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. Flook, P., 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, **87**, 651–701. https://doi.org/10.1093/aesa/87.6.651

Smith A.B. (1998) What does Palaeontology contribute to Systematics in a molecular world? *Molecular Phylogeny and Evolution*, **9**: 437 –447. https://doi.org/10.1006/mpev.1998.0488

Sorg, M. (1988) Zur Phylogenie und Systematik der Bethylidae (Insecta: Hymenoptera: Chrysidoidea). *Sonderveröffentlichungen des Geologishcen Instituts der Universität zu Köln*, **63**, 1–146.

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, **30**, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Terayama, M. (2003) Phylogenetic systematics of the family Bethylidae (Insecta: Hymenoptera) Part I. Higher classification. *The Academic Reports of the Faculty of Engineering of Tokyo Polytechnic University*, **26**, 1–15.

Terayama, M. (2004) *Formosiepyris* a new genus of the family Bethylidae (Hymenoptera, Chrysidoidea) from the Oriental Region with a proposal of a new synonym of genus. *Liberal Arts*, **12**, 91–99.

Terayama, M. (2006) *Insects of Japan, Bethylidae (Hymenoptera)*, Vol. **1**. Touka Shobo Co, Fukuoka.

Vargas R., J.M., Colombo, W.D. & Azevedo, C.O. (2020) Revisited phylogeny of Scleroderminae (Hymenoptera: Bethylidae) reveals a plastic evolutionary history. *Arthropod Systematics & Phylogeny*, **78**, 217–243. http://www.doi.org/10.26049/ASP78-2-2020-02

Waichert, C. & Azevedo, C.O. (2009) Phylogenetic analysis of Rhabdepyris (Hymenoptera: Bethylidae) and redefinition of generic limits based on morphological characters. *Zootaxa* **2284**, 1–29. https://doi.org/10.11646/zootaxa.2284.1.1

APPENDIX 1. Terminal taxa of analysis. In bold type species. In green box, terminal taxa included in the analysis; In white box, terminal taxa included in the analysis; In blue box, specimens different.

SPECIES	LOCALITY	DEPOSITED	CODE	MORPHO.	MOLECULAR					TOTAL
Outgroup					16S	18S	28S	COI	CytB	EVIDENCE
Cleptes seoulensis	Genbank	-	-							
Chrysis cembricola	Genbank	-	-							
Chrysis principalis	Genbank	-	-							
Bethylus fuscicornis	Genbank	-	-							
Eupsenella diemenensis	Australia	UFES	-							
Goniozus japonicus	South Korea	-	-							
Apenesia sp. 1	USA	AMNH	-							
Apenesia sp. 2	USA	AMNH	-							
Dissomphalus sp. 1	Genbank	-	-							
Dissomphalus sp. 2	Ghana	CNC	-							
Eleganesia elegans	Genbank	-	-							
Parvoculus sp. 1	South Africa	CNC	-							
Sulcomesitius sp. 1	Saba	BNHM/UMS	-							
Sulcomesitius sp. 2	Saba	BNHM/UMS	-							
Sulcomesitius sp. 3	-	UFES	-							
Allobethylus tomoae	Genbank	-	-							
Cephalonomia sp. 1	USA	AMNH	-							
Cephalonomia sp. 2	USA	AMNH	-							
Plastanoxus sp. 1	Genbank	-	-							
Sclerodermus harmandi	Genbank	-	-							
Ingroup										
Anisepyris sp. 1	Brazil	UFES	-							
Anisepyris sp. 2	Brazil	UFES	-							
Anisepyris sp. 3	Brazil	UFES	-							
Anisepyris sp. 4	Brazil	UFES	-							
Anisepyris sp. 5	USA	AMNH	-							
Anisepyris sp. 6	USA	AMNH	-							
Anisepyris sp. 7	USA	AMNH	-							
Anisepyris sp. 8	USA	AMNH	-							
Anisepyris sp. 9	USA	AMNH	-							
Aspidepyris austrinus	Brazil	UFES	W80							
Bakeriella sp. 1	Venezuela	UFES	-							
Bakeriella sp. 2	Venezuela	UFES	-							
Bakeriella sp. 3	Brazil	UFES	-							
Bakeriella sp. 4	French Guiana	CNC	-							
Bakeriella flavicornis	Brazil	CAS	-							
Calyozina ramicornis	Taiwan	ZMB								
Calyozina nepalensis	Nepal	CNC	W36							
Chlorepyris viridissimus	Brazil	UFES	-							
Chlorepyris sp. 1	French Guiana	CNC	-							
Chlorepyris sp. 2	French Guiana	AMNH	-							
Chlorepyris sp. 3	French Guiana	CNC	-							
Chlorepyris sp. 4	French Guiana	CNC	-							
Chlorepyris sp. 5	French Guiana	AMNH	-							
Chlorepyris sp. 6	Brazil	UFES	-							
Chlorepyris sp. 7	Venezuela	UFES	-							
Chlorepyris sp. 8	Peru	UFES	-							
Chlorepyris sp. 9	Australia	UFES	-							
Chlorepyris sp. 10	Australia	UFES	-							
Chlorepyris sp. 11	Australia	QLD	-							
Chlorepyris sp. 12	Australia	UFES	-							
Chlorepyris sp. 13	Australia	CNC	-							
Chlorepyris sp. 14	Australia	QLD	-							
Chlorepyris sp. 15	Australia	QLD	-							
Chlorepyris sp. 16	Australia	QLD	-							

Chlorepyris sp. 17	Australia	UFES	-							
Chlorepyris sp. 18	Australia	UFES	-							
Chlorepyris sp. 19	Australia	CNC	-							
Chlorepyris sp. 20	Australia	CNC	-							
Disepyris sp. 1	South Africa	ISAM	W44							
Disepyris sp. 2	South Africa	ISAM	W45							
Disepyris sp. 3	South Africa	ISAM	W47							
Epyris afer	Thailand	RMNH	-							
Epyris festivus	Genbank	-	-							
Epyris idaten	South Korea	-	-							
Epyris koreanus	South Korea	-	-							
Epyris niger	Switzerland	CNC	-							
Epyris niwoh	South Korea	-	-							
Epyris ruficeps	Congo DR	MNHN								
Epyris yamatonis	South Korea	-	-							
Epyris sp.1	USA	AMNH	-							
Epyris sp. 2	Nicaragua	CNC	-							
Epyris sp. 3	USA	AMNH	-							
Epyris sp. 4	USA	AMNH	-							
Epyris rufipes	Canada	CNC	-							
Epyris sp. 6	Laos	UFES	-							
Epyris sp. 7	Saba	BNHM/UMS	-							
Epyris sp. 8	Saba	BNHM/UMS	-							
Epyris sp. 9	Thailand	UFES	-							
Epyris sp. 10	Mozambique	MNHM	-							
Epyris sp. 11	Mozambique	CNC	-							
Epyris sp. 12	DR Congo	BNHM	-							
Epyris sp. 13	Uganda	CNC	-							
Epyris sp. 14	USA	AMNH	-							
Epyris sp. 15	Panama	AMNH	-							
Epyris sp. 16	Brazil	UFES	-							
Epyris sp. 17	Venezuela	UFES	-							
Epyris sp. 18	Venezuela	UFES	-							
Epyris sp. 19	French Guiana	CNC	-							
Epyris sp. 20	Brazil	UFES	-							
Epyris sp. 21	Brazil	UFES	-							
Epyris sp. 22	Brazil	UFES	-							
Epyris sp. 23	Brazil	UFES	-							
Epyris sp. 24	Australia	CNC	-							
Epyris sp. 25	Australia	UFES	-							
Epyris sp. 26	Mozambique	CNC	-							
Epyris sp. 27	South Africa	UFES	-							
Epyris sp. 28	Australia	UFES	-							
Epyris sp. 29	Australia	CNC	-							
Epyris sp. 30	Australia	CNC	-							
Epyris sp. 31	Australia	QLD	-							
Epyris sp. 32	Australia	QLD	-							
Epyris sp. 33	Saba	BNHM/UMS	-							
Epyris sp. 34	DR Congo	BNHM	-							
Epyris sp. 35	DR Congo	BNHM	-							
Epyris sp. 36	South Korea	CNC	-							
Epyris sp. 37	Switzerland	CNC	-							
Epyris sp. 38	Kenya	CNC	-							
Epyris sp. 39	Mozambique	CNC	-							
Epyris sp. 40	South Korea	CNC	-							
Epyris sp. 41	South Korea	CNC	-							
Epyris sp. 42	Saba	BNHM/UMS	-							
Epyris sp. 43	USA	CNC	-							
Epyris sp. 44	Kenya	CNC	-							
Epyris sp. 45	South Africa	UFES	-							
Epyris sp. 46	Madagascar	UFES/CAS	-							
Epyris sp. 47	French Guiana	AMNH	-							
Epyris sp. 48	Brazil	UFES	-							

Epyris sp. 49	South Africa	UFES	-							
Epyris sp. 50	South Africa	UFES	-							
Epyris sp. 51	South Africa	UFES	-							
Epyris sp. 52	South Africa	UFES	-							
Epyris sp. 53	South Africa	UFES	-							
Epyris sp. 54	USA	AMNH	-							
Epyris sp. 55	USA	AMNH	-							
Epyris sp. 56	USA	AMNH	-							
Epyris sp. 57	South Africa	UFES	-							
Epyris sp. 58	Central African R.	CNC	-							
Epyris sp. 59	South Africa	UFES	-							
Epyris sp. 60	USA	AMNH	-							
Epyris sp. 61	USA	AMNH	-							
Epyris sp. 62	USA	AMNH	-							
Epyris sp. 63	USA	AMNH	-							
Epyris (*staphyl.*) sp. 1	Saba	BNHM/UMS	-							
Epyris (*staphyl.*) sp. 2	Laos	UFES	-							
Epyris (*staphyl.*) sp. 3	Laos	UFES	-							
Epyris (*staphyl.*) sp. 4	Saba	BNHM/UMS	-							
Epyris (*staphyl.*) sp. 5	Saba	BNHM/UMS	-							
Epyris (*staphyl.*) sp. 6	Saba	BNHM/UMS	-							
Epyris (*staphyl.*) sp. 7	Saba	BNHM/UMS	-							
Epyris (*staphyl.*) sp. 8	Saba	BNHM/UMS	-							
Epyris (*staphyl.*) sp. 9	Thailand	UFES	-							
Epyris (*staphyl.*) sp. 10	Thailand	UFES	-							
Epyris (*staphyl.*) sp. 11	Uganda	CNC	-							
Epyris (*staphyl.*) sp. 12	Uganda	CNC	-							
Epyris (*staphyl.*) sp. 13	DR Congo	BNHM	-							
Epyris (*staphyl.*) sp. 14	Uganda	CNC	-							
Epyris/*Trachepyris* sp. 1	Mozambique	MNHM	-							
Epyris/*Trachepyris* sp. 2	Mozambique	MNHM	-							
Epyris/*Trachepyris* sp. 3	South Africa	UFES	-							
Epyris/*Trachepyris* sp. 4	Thailand	UFES	-							
Epyris/*Trachepyris* sp. 5	Thailand	UFES	-							
Epyris/*Trachepyris* sp. 6	Thailand	UFES	-							
Epyris/*Trachepyris* sp. 7	Thailand	UFES	-							
Epyris/*Trachepyris* sp. 8	Thailand	UFES	-							
Epyris/*Trachepyris* sp. 9	Thailand	UFES	-							
Epyris/*Trachepyris* sp. 10	South Africa	UFES	W65							
Epyris/*Trachepyris* sp. 11	South Africa	UFES	W66							
Formosiepyris marish	Thailand	PMAE	-							
Formosiepyris sp. 1	South Africa	ISAM	W50							
Formosiepyris sp. 2	South Africa	ISAM	W55							
†***Gloxinius bifossatus***	Baltic amber	MCZ	-							
Holepyris africanus	Eritrea	MCSN	-							
Holepyris brevicarinatus	-	-	-							
Holepyris susanowo	-	-	-							
Holepyris sp. 2	South Korea	CNC	-							
Holepyris sp. 3	Saba	BNHM/UMS	-							
Holepyris sp. 4	Madagascar	UFES/CAS	-							
Holepyris sp. 5	Thailand	UFES	-							
Holepyris sp. 6	Papua New Guinea	CNC	-							
Holepyris sp. 7	Australia	CNC	-							
Holepyris sp. 8	Kenya	CNC	-							
Holepyris sp. 9	Mozambique	MNHM	-							
Holepyris sp. 10	Madagascar	UFES/CAS	-							
Holepyris sp. 11	USA	AMNH	-							
Holepyris sp. 12	DR Congo	BNHM	-							
Holepyris sp. 13	Saba	BNHM/UMS	-							
Holepyris sp. 14	Saba	BNHM/UMS	-							
Holepyris sp. 15	Papuan New Guinea	CNC	-							
Holepyris sp. 16	Ghana	CNC	-							
Holepyris sp. 17	Ghana	CNC	-							

Holepyris sp. 18	USA	AMNH	-							
Holepyris sp. 19	USA	AMNH	-							
Holepyris sp. 20	Mexico	CNC	-							
Holepyris sp. 21	Mexico	CNC	-							
Laelius sp. 1	USA	AMNH	-							
Laelius sp. 2	Israel	CNC	-							
Laelius sp. 4	Chile	AMNH	-							
Laelius sp. 5	Brazil	UFES	-							
Laelius sp. 6	USA	AMNH	-							
Laelius sp. 7	USA	AMNH	-							
Laelius sp. 8	USA	AMNH	-							
Laelius sp. 9	USA	AMNH	-							
Trachepyris sp. 1	Mozambique	CNC	-							
Trachepyris sp. 2	South Africa	UFES	-							
Trachepyris sp. 3	Ghana	CNC	-							
TOTAL				**168**	**186**					**194**

APPENDIX 2. List of morphological characters and states. (* = Adapted from Alencar & Azevedo 2013).

1. General body setae thickness*: (0) widely thick; (1) widely very thin.

2. Head in profile: (0) globoid, ventral margin very outcurved; (1) subrectangular, triangular or oval, ventral margin straight or weakly outcurved. Adapted from Vargas *et al.* (2020).

3. Antenna, type*: (0) moniliform; (1) filiform; (2) pectinate or subpectinate.

4. Antennal insertion, position: (0) lateral to clypeus; (1) dorsal to clypeus. Adapted from Lanes & Azevedo (2013).

5. Number of antennomeres: (0) Thirteen; (1) Twelve.

6. Antenna maximum length: (0) not surpassing posterior pronotal margin; (1) not surpassing posterior margin of mesoscutum-mesoscutellar suture; (2) surpassing posterior margin of mesoscutum-mesoscutellar suture; (3) surpassing posterior margin of metapectal-propodeal complex; (4) surpassing posterior margin of tergite II.

7. Antennal rim: (0) not protuberant; (1) protuberant.

8. Antennal rim, distance: (0) more than own diameter; (1) same as or less than own diameter.

9. Scape length*: (0) long, longer than pedicel; (1) short, shorter than pedicel; (2) mid-sized, as long as pedicel.

10. Scape apical width, in dorsal view*: (0) wider than base; (1) as wide as base; (2) narrower than base.

11. Scape spine*: (0) absent; (1) present.

12. Pedicel shape*: (0) rectangular, evenly wide; (1) caliciform, progressively widening.

13. Pedicel length*: (0) long, longer than flagellomere I length; (1) short, shorter than flagellomere I length; (2) mid-sized, as long as flagellomere I length.

14. Pedicel spines*: (0) absent; (1) present.

15. Pedicel pubescence*: (0) apressed; (1) suberect or erect.

16. Relative length of flagellomeres*: (0) uniform; (1) progressively longer; (2) progressively shorter.

17. Ventral sulcus in median flagellomeres: (0) present; (1) absent.

18. Frons: (0) punctate; (1) foveolate.

19. Frons texture: (0) coriaceous; (1) polished.

20. Vertex shape, in dorsal view: (0) outcurved; (1) incurved; (2) straight or nearly so.

21. Mandibular apex, orientation in frontal view*: (0) horizontal or nearly so; (1) vertical or nearly so.

22. Mandibular apex*: (0) as wide as base; (1) wider than base; (2) narrower than base.

23. Laminar expansion on ventral mandibular margin*: (0) present; (1) absent.

24. Number of mandibular distal teeth: (0) one; (1) two; (2) three; (3) four; (4) five; (5) six; (6) eleven.

25. Relative size of ventralmost tooth*: (0) distinctly larger than dorsal ones; (1) as large as dorsal ones.

26. Size of mandible dorsal teeth (all except ventralmost)*: (0) equally sized; (1) differently sized.

27. Dorsal tooth, orientation*: (0) horizontal; (1) vertical.

28. Apex of dorsal tooth, direction*: (0) parallel to ventral ones; (1) strongly curved inward.

29. Mandibular pre-apical tooth: (0) absent; (1) present.

30. Pre-apical tooth, position in ventral view: (0) internal margin, seen behind sensilla; (1) ventral margin, seen in front of sensilla.

31. Ventral depression in ventral margin of mandible: (0) present; (1) absent.

32. Row of long bristles on mandible ventral margin: (0) absent; (1) present.

33. Mandibular sensilla: (0) present; (1) absent.

34. Mandibular sensilla, position*: (0) near inner margin of mandible; (1) near ventral margin of mandible.

35. Shape of mandibular sensilla: (0) cylindrical; (1) spatulate.

36. Exposition of clypeal base, dorsal view*: (0) not covered by frons; (1) covered by frons.

37. Median clypeal lobe, shape: (0) rounded; (1) sharpened; (2) straight; (3) incurved.

38. Median clypeal tooth: (0) ill-defined; (1) defined.

39. Median clypeal carina*: (0) present; (1) absent.

40. Median clypeal carina, in lateral view: (0) mid-high, as long as frons; (1) low, shorter than frons; (2) high, longer than frons.

41. Lateral clypeal lobe: (0) present; (1) absent.

42. Lateral clypeal lobe, size*: (0) reduced; (1) almost as long as median lobe; (2) as long as the median lobe.

43. Lateral clypeal lobe shape: (0) sharpened; (1) rounded; (2) straight.

44. Genal suture, visibility: (0) conspicuous; (1) inconspicuous.

45. Genal projection: (0) evident; (1) not evident.

46. Number of maxillary palpomeres*: (0) three to five; (1) six.

47. Maxillary palpomere III: (0) as long as IV; (1) longer than IV; (2) shorter than IV.

48. Distinct hook-shaped bristles in apex maxillary palpus: (0) present; (1) absent.

49. Number of labial palpomeres*: (0) one; (1) two; (2) three.

50. Hypostomal carina, shape: (0) angled; (1) straight; (2) rounded.

51. Eye outline, frontal view*: (0) protuberant; (1) not protuberant.

52. Eye shape in lateral view*: (0) circular; (1) elongated.

53. Eye setation*: (0) absent or scarse; (1) abundant.

54. Eye, position*: (0) touching base of mandible; (1) not touching base of mandible.

55. Dorsal part of occipital carina*: (0) present; (1) absent.

56. Ventral part of occipital carina*: (0) present; (1) absent.

57. Frontal line*: (0) absent; (1) present.

58. Frontal line*: (0) sulcate; (1) carinate.

59. Frontal line, extension: (0) long, present from posterior margin of clypeus to anterior ocellus; (1) short, present only in anterior third of frons.

60. Frontal line, posterior region: (0) evenly linear; (1) oval-shaped depression; (2) distinctly wider posteriorly.

61. Ocelli outline, dorsal view: (0) protuberant; (1) not protuberant.

62. Intra-ocellar area*: (0) shorter than anterior ocellus size; (1) wider than anterior ocellus size.

63. Anterior ocellus: (0) posterior to supra-ocular line; (1) crossing supra-ocular line; (2) anterior to supra-ocular line.

64. Posterior ocelli: (0) very close to vertex crest, when $\leq 1.0 \times$ ocelli diameter; (1) far from vertex crest, when $>1.0 \times$ and $\leq 2.0 \times$ ocelli diameter; (2) very far from vertex crest, when $>2.0 \times$ ocelli diameter.

65. Sequence of short bristles in vertex: (0) present; (1) absent.

66. Humeral angle*: (0) indistinct; (1) distinct, not projected; (2) distinct, projected.

67. Size of dorsal pronotal area, dorsal view*: (0) short, when distinct wider than long medially; (1) elongate, when distinct longer than wider medially; (2) as long as wide medially.

68. Profile of anterior margin of dorsal pronotal area*: (0) outcurved; (1) straight or nearly so; (2) incurved.

69. Wide anterior pronotal elevation*: (0) present; (1) absent.

70. Pronotal signum, visibility: (0) delimited; (1) not delimited.

71. Transverse pronotal carina: (0) present; (1) absent.

72. Transverse pronotal carina, extension: (0) anterior and laterally; (1) only anterior; (2) only laterally.

73. Transverse pronotal carina, texture: (0) foveolate; (1) sulcate; (2) carinate.

74. Posterior pronotal sulcus on dorsal pronotal area*: (0) present; (1) absent.

75. Posterior pronotal sulcus on dorsal pronotal area, texture*: (0) sequence of foveae; (1) sulcus.

76. Median pronotal line on dorsal pronotal area*: (0) absent; (1) present.

77. Median pronotal line on dorsal pronotal area, texture: (0) sulcate; (1) carinate.

78. Notaulus: (0) absent; (1) present.

79. Posterior extension on notaulus*: (0) reaching posterior margin of mesoscutum; (1) not reaching posterior margin of mesoscutum.

80. Posterior region of notaulus, direction*: (0) convergent; (1) parallel.

81. Notaulus width: (0) narrow; (1) evenly wide; (2) posteriorly wider.

82. Notaulus depth: (0) inconspicuous; (1) shallow; (2) deep.

83. Notaulus, texture: (0) trabeculate; (1) smooth.

84. Parapsidal signum: (0) present; (1) absent.

85. Parapsidal signum width: (0) as long as notauli; (1) shorter than notauli; (2) longer than notauli.

86. Parapsidal signum, texture: (0) carinate; (1) sulcate.

87. Mesoscuto-scutellar suture*: (0) not sulcate medially; (1) sulcate medially.

88. Posterior margin of mesoscuto-scutellar suture: (0) touching anterior margin of mesoscuto-scutellar suture, as suture; (1) not touching anterior margin of mesoscuto-scutellar suture.

89. Mesoscuto-scutellar foveae, dilation*: (0) as dilated as mesoscuto-scutellar sulcus, so that fovea is indistinct; (1) more dilated than mesoscuto-scutellar sulcus, so that fovea is distinct.

90. Posterior margin of mesoscuto-scutellar suture, direction: (0) straight or nearly so; (1) outcurved medially; (2) incurved medially.

91. Mesoscuto-scutellar sulcus, **texture*:** (0) trabeculate; (1) not trabeculate.

92. Median carina-like trabeculate, mesoscuto-scutellar sulcus: (0) without median carina, when as short as lateral trabeculae and lower than level of mesoscutellar surface; (1) with median carina, when higher than lateral trabeculae and at same level of mesoscutellar surface.

93. Mesoscuto-scutellar sulcus, depth: (0) shallow, poorly defined; (1) deep, well-defined.

94. Mesoscuto-scutellar foveae, size*: (0) large, at least 0.80 × maximum size of mesoscutellum; (1) small, ≤0.75 × maximum size of mesoscutellum.

95. Mesoscuto-scutellar foveae, shape: (0) circular; (1) rectangular or nearly so; (2) oval; (3) subtriangular.

96. Distance between inner margins of mesoscuto-scutellar foveae: (0) very distant, longer than 2.0 × size of fovea; (1) very close, smaller than 2.0 × size of fovea.

97. Mesoscuto-scutellar foveae, texture: (0) not trabeculate; (1) trabeculate.

98. Mesoscutellar posterior region, texture*: (0) not foveolate; (1) foveolate.

99. Mesoscutellar posterior region, distance: (0) touching metapostnotal anterior margin; (1) not touching metapostnotal anterior margin.

100. Metascutellum: (0) well developed; (1) ill developed.

101. Metapectal-propodeal disc, width: (0) long, longer than wide; (1) short, wider than long or as long as wide.

102. Transverse anterior carina of metapectal-propodeal disc: (0) present; (1) absent.

103. Transverse anterior carina of metapectal-propodeal disc, visibility: (0) conspicuous; (1) inconspicuous.

104. Metapleural carina, visibility: (0) conspicuous; (1) inconspicuous.

105. Transverse posterior carina of metapectal-propodeal disc*: (0) present; (1) absent.

106. Transverse posterior carina of metapectal-propodeal disc, visibility: (0) conspicuous; (1) inconspicuous.

107. Paraspiracular carina*: (0) present; (1) absent.

108. Paraspiracular carina, visibility: (0) conspicuous; (1) inconspicuous.

109. Paraspiracular sulcus*: (0) present; (1) absent.

110. Paraspicular sulcus, texture: (0) trabeculate; (1) smooth.

111. Metapostnotal median carina*: (0) present; (1) absent.

112. Metapostnotal median carina: (0) complete; (1) incomplete.

113. Metapostnotal carina*: (0) absent; (1) presence.

114. First pair of metapostnotal carina, length: (0) longer than metapostnotal median carina; (1) as long as metapostnotal median carina; shorter than metapostnotal median carina.

115. Posterior region of first pair of metapostnotal carina, orientation: (0) converging posteriorly; (1) parallel; (2) diverging posteriorly.

116. Second pair of metapostnotal carina, length: (0) longer than metapostnotal median carina; (1) as long as metapostnotal median carina; (2) shorter than metapostnotal median carina.

117. Posterior region of second pair of metapostnotal carina, orientation: (0) converging posteriorly; (1) parallel; (2) diverging posteriorly.

118. Third pair of metapostnotal carina, length: (0) longer than metapostnotal median carina; (1) as long as metapostnotal median carina; (2) shorter than metapostnotal median carina.

119. Posterior stretch of third pair of metapostnotal carina, orientation: (0) converging posteriorly; (1) parallel; (2) diverging posteriorly.

120. Metapostnotal-propodeal suture*: (0) present; (1) absent.

121. Metapostnotal-propodeal suture, visibility: (0) conspicuous; (1) inconspicuous.

122. Metapostnotal-propodeal suture, length: (0) shorter than median metapostnotal carina; (1) longer than median metapostnotal carina; (2) as long as median metapostnotal carina.

123. Posterior region of metapostnotal-propodeal suture: (0) divergent; (1) convergent; (2) straight.

124. Median carina of propodeal declivity*: (0) present; (1) absent.

125. Median carina of propodeal declivity, extension: (0) complete; (1) incomplete.

126. Posterior propodeal projection*: (0) presence; (1) absent.

127. First abdominal spiracle, position*: (0) dorsal, on edge of dorsal and lateral surfaces of metapectal-propodeal complex; (1) lateral, on lateral surface of metapectal-propodeal complex; (2) dorso-lateral, on lateral part and dorsal part of metapectal-propodeal complex.

128. First abdominal spiracle, position*: (0) surpassing metapleural carina; (1) not surpassing metapleural carina.

129. First abdominal spiracle, shape*: (0) circular or elliptical and wide, as long as wide; (1) elongate, as a narrow crack, longer than wide.

130. First abdominal spiracle, direction: (0) straight or weakly curved; (1) strongly curved.

131. Propleural epicoxal sulcus, lateral view*: (0) circular or subcircular; (1) elongate.

132. Anterior mesofurcal pit inserted into depression: (0) elongated; (1) drop-shaped; (2) circular or subcircular.

133. Posterior mesofurcal pit, visibility: (0) distinct; (1) indistinct.

134. Posterior mesofurcal pit, shape: (0) circular; (1) elongate; (2) oval.

135. Posterior metafurcal pit inserted into depression: (0) V-shaped; (1) triangle-shaped; (2) crown-shaped; (3) pentagonal-shaped.

136. Lower mesopleural fovea: (0) delimited; (1) not delimited.

137. Lower mesopleural fovea, texture: (0) trabeculate; (1) not trabeculate.

138. Mesopleuron with anterior and lower mesopleural foveae: (0) connected; (1) not connected.

139. Subalar impression: (0) delimited; (1) not delimited.

140. Subalar impression, texture: (0) not trabeculate; (1) trabeculate.

141. Mesopleural suture: (0) delimited; (1) not delimited.

142. Mesopleural suture, texture: (0) trabeculate; (1) smooth.

143. Subalar impression and mesopleural suture: (0) connected; (1) not connected.

144. Mesopleural suture and mesopleural upper fovea: (0) connected; (1) not connected.

145. Position of mesopleural pit*: (0) central; (1) dorsal.

146. Size of mesopleural pit*: (0) broad, occupying almost all of upper fovea area; (1) small, as a puncture.

147. Mesopleural upper elevation*: (0) present; (1) absent.

148. Mesopleural upper elevation, visibility: (0) conspicuous; (1) inconspicuous.

149. Protrochanter, length*: (0) long, at least as long as procoxa; (1) short, when shorter than procoxa.

150. Protrochanter shape, lateral view*: (0) badly wider apicad; (1) distinctly wider apicad.

151. Elongate setae on protarsomere I*: (0) absent; (1) present.

152. Spines on lateral face of protarsomeres I-IV*: (0) absent; (1) present.

153. Spines on lateral face of mesotibia*: (0) absent; (1) present.

154. Spines on apex of mesotibia*: (0) absent; (1) present.

155. Tarsal claw: (0) simple; (1) bifid; (2) trifid.

156. Tarsal claws, direction*: (0) curved; (1) straight or nearly so.

157. Wings, general color: (0) hyaline; (1) subhyaline or yellowish.

158. Costal cell of forewing: (0) absent; (1) present.

159. Radial cell of forewing: (0) absent; (1) present.

160. First cubital cell of forewing: (0) absent; (1) present.

161. Rs+M vein of forewing: (0) absent; (1) present.

162. Cubital vein of forewing: (0) absent; (1) present.

163. Shape of cubital vein at intersection with first medio-cubital cross vein of forewing: (0) rounded; (1) angled; (2) straight or nearly so.

164. Cubital vein of forewing, visibility: (0) widely tubular; (1) widely spectral.

165. Pterostigma, shape: (0) rectangular or subrectangular; (1) circular or subcircular.

166. 2r-rs&Rs vein of forewing*: (0) present; (1) absent.

167. 2r-rs&Rs vein of forewing, size*: (0) short, at most 1.40 × length of Rs&M vein; (1) long, at least 1.60 × length of Rs&M vein.

168. Connection between 2r-rs and 2r-sr&Rs vein of forewing, visibility: (0) angled; (1) curved.

169. Thickness of 2r-rs&Rs vein of forewing, posteriorly: (0) thin; (1) thick.

170. Distal shape of 2r-rs&Rs vein of forewing: (0) straight; (1) slightly arched dorsally; (2) strongly arched dorsally.

171. Forewing distal flexions lines: (0) present; (1) absent.

172. Forewing distal flexions lines, number: (0) one; (1) two; (2) three; (3) four; (5) five.

173. Poststigmal abscissa of R1 vein of forewing: (0) present; (1) absent.

174. Poststigmal abscissa of R1 vein of forewing: (0) without unpigmented anterior spot; (1) with unpigmented anterior spot.

175. Hindwing number of distal hamuli: (0) three; (1) four; (2) five; (3) six; (4) seven; (5) eight.

176. Distance between distal hamuli*: (0) discontinuous, at least one of hamuli distant of others; (1) adjacent, hamuli next one to the others.

177. Jugal lobe*: (0) not distinctly outlined; (1) distinctly outlined.

178. Anterior area of the S2, ventral view: (0) absent; (1) present.

179. Transverse edge of the S2, ventral view*: (0) absent; (1) present.

180. Anterior margin of anterior area of the S2, ventral view*: (0) outcurved with median narrow emargination; (1) slightly concave medially.

181. Differentiation of anterior area of the S2, ventral view*: (0) posterior area of the S2 overlapping anterior area; (1) posterior and anterior area of the S2 fused.

182. Flap on anterior area of the S2: (0) absent; (1) present.

183. Setation on median region of posterior area of the S2, ventral view: (0) absent; (1) present.

184. Size of posterior area of the S2, ventral view: (0) short, as long as wide, or shorter than wide; (1) long, longer than wide.

185. Posterior area of the S2, shape: (0) petiolate; (1) subquadrate.

186. Surface of T2: (0) widely polished; (1) widely coriaceous.

187. Length of T3: (0) long, length/width $\geq 0.7\times$; (1) short, length/width $< 0.7\times$.

188. Texture of T3: (0) widely coriaceous; (1) widely polished.

189. Texture of S3: (0) widely polished; (1) widely coriaceous.

190. Shape of posterior margin of S9*: (0) outcurved; (1) straight; (2) incurved.

191. Lateral margin of S9*: (0) angled; (1) straight.

192. S9 thick setae: (0) absent; (1) with at least one distinctly thick seta.

193. Spiculim of S9: (0) present; (1) absent.

194. Size of spiculum of S9: (0) as long as anterolateral apodeme of the S9; (1) smaller than anterolateral apodeme of the S9; (2) longer than anterolateral apodeme of the S9.

195. Shape of spiculum of S9: (0) evenly narrow; (1) apically narrower; (2) apically wider; (3) evenly wider.

196. Harpe: (0) present; (1) absent.

197. Harpe, insertion: (0) lateral; (1) dorsal.

198. Harpe, extension: (0) evenly wide; (1) wide basally; (2) evenly narrow; (3) very narrow basally; (4) narrow basally.

199. Harpe, shape: (0) laminar or nearly so; (1) tubular or nearly so.

200. Harpe maximum length: (0) shorter than gonostipes maximum length; (1) as long as gonostipes maximum length; (2) longer than gonostipes maximum length.

201. Harpe, when longer: (0) distinctly largest structure of genitalia; (1) distinctly not largest structure of genitalia.

202. Apical invagination of harpe: (0) present; (1) absent.

203. Apical invagination of harpe, size: (0) longer than half of maximum harpe length; (1) shorter than half of maximum harpe length.

204. Apex of harpe: (0) inclined inward; (1) inclined outward; (2) parallel to gonostipes.

205. Basal shape of harpe, lateral view*: (0) inclined ventrad; (1) inclined dorsad; (2) straight.

206. Harpe membranous expansion*: (0) present; (1) absent.

207. Basal projection, inner margin of harpe: (0) present; (1) absent.

208. Base of harpe: (0) strongly angled, crossing each other; (1) not angled, not crossing each other.

209. Harpe with one distinctly very long apical seta: (0) absent; (1) present.

210. Gonostipes, dorsal view: (0) distinctly divided; (1) indistinctly divided or nearly so.

211. Gonostipes shape, ventral view: (0) rectangular; (1) quadrate.

212. Apical projection on basivolsella*: (0) present; (1) absent.

213. Profile of basivolsella*: (0) aligned with gonostipes; (1) anterior to gonostipes; (2) posterior to gonostipes.

214. Emargination between cuspis and digitus*: (0) present; (1) absent.

215. Number of arms of cuspis*: (0) uniramous; (1) biramous, entirely divided; (2) biramous, partially divided.

216. Medial arm of cuspis: (0) as wide as lateral arm; (1) narrow than lateral arm; (2) wider than lateral arm.

217. Cuspis length: (0) very long, at least 7.0 × as long as wide; (1) long, at least 5.0 × as long as wide; (2) medium, at least 4.0 × as long as wide; (3) short, at least 1.5 × as long as wide; (4) very short, at most as long as wide.

218. Cuspis expansion*: (0) absent; (1) present.

219. Setation on cuspis base*: (0) dense; (1) absent or scarce.

220. Digitus apex width: (0) as long as cuspis; (1) anterior to cuspis; (2) posterior to cuspis.

221. Aedeagus shape, dorsal view*: (0) subtrapezoidal, margins of basal half converging apicad; (1) subrectangular, margins of basal half parallel; (2) bottle-shaped, margins of basal half strongly outcurved.

222. Aedeagus apex length: (0) anterior to cuspis; (1) as long as cuspis; (2) posterior to cuspis.

223. Angulation between aedeagal apical lobes: (0) parallel; (1) convergent.

224. Sub-apical cavity of aedeagus, dorsal view*: (0) present; (1) absent.

225. Apical membrane of aedeagus: (0) present; (1) absent.

226. Ventral aedeagal expansion: (0) strongly angled anterad; (1) if present, never angled.

227. Aedeagal apical constriction: (0) apical half abruptly constricted; (1) apical half progressively constricted; (2) apical half not constricted.

228. Base of genital apodeme*: (0) not bifurcated; (1) bifurcated.

229. Base of genital apodeme, orientation: (0) parallel to aedeagus; (1) divergent anteriorly; (2) convergent anteriorly.

230. Extension of genital ring*: (0) complete; (1) incomplete ventrally.

231. Dorsal margin of genital ring, ventral view*: (0) as developed as ventral margin; (1) more developed than ventral margin.

232. General body color*: (0) widely black or castaneous; (1) widely metallic.

APPENDIX 3. Termociclador protocols.

CytB

Primer names:	CB1/CB2
Heated Lid	110 °C
Initial Temp.	95°C for 5 minutes
Start Cycle	40 cycles
Denaturation	95°C for 1 minute
Annealing	42°C for 1 minute
Extension	72°C for 1 minute
End Cycle	
Final Extension	72°C for 10 minutes

COI

Primer names:	HCO2198/LCO1490
Heated Lid	110°C
Initial Temp.	95°C for 5 minutes
Start Cycle	35 cycles
Denaturation	95°C for 1 minute
Annealing	40°C for 1 minute
Extension	72°C for 1.5 minutes
End Cycle	
Final Extension	72°C for 10 minutes

16S

Primer names:	16Saf/16Sar
Heated Lid:	110°C
Initial Temp.	94°C for 5 minutes
Start Cycle	34 cycles
Denaturation	94°C for 1 minute
Annealing	45°C for 1 minute
Extension	72°C for 1 minute
End Cycle	
Final Extension	72°C for 5 minutes

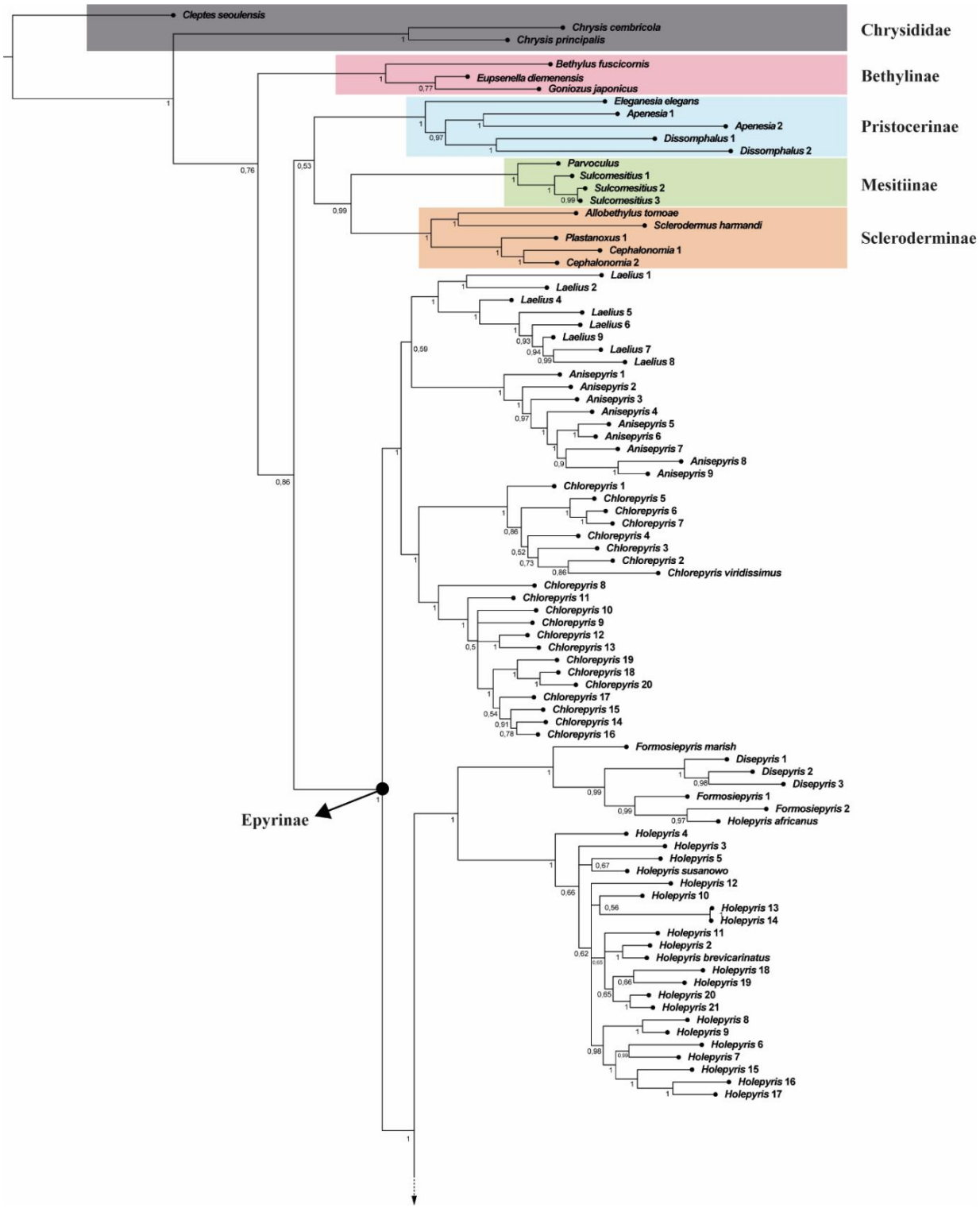
18S

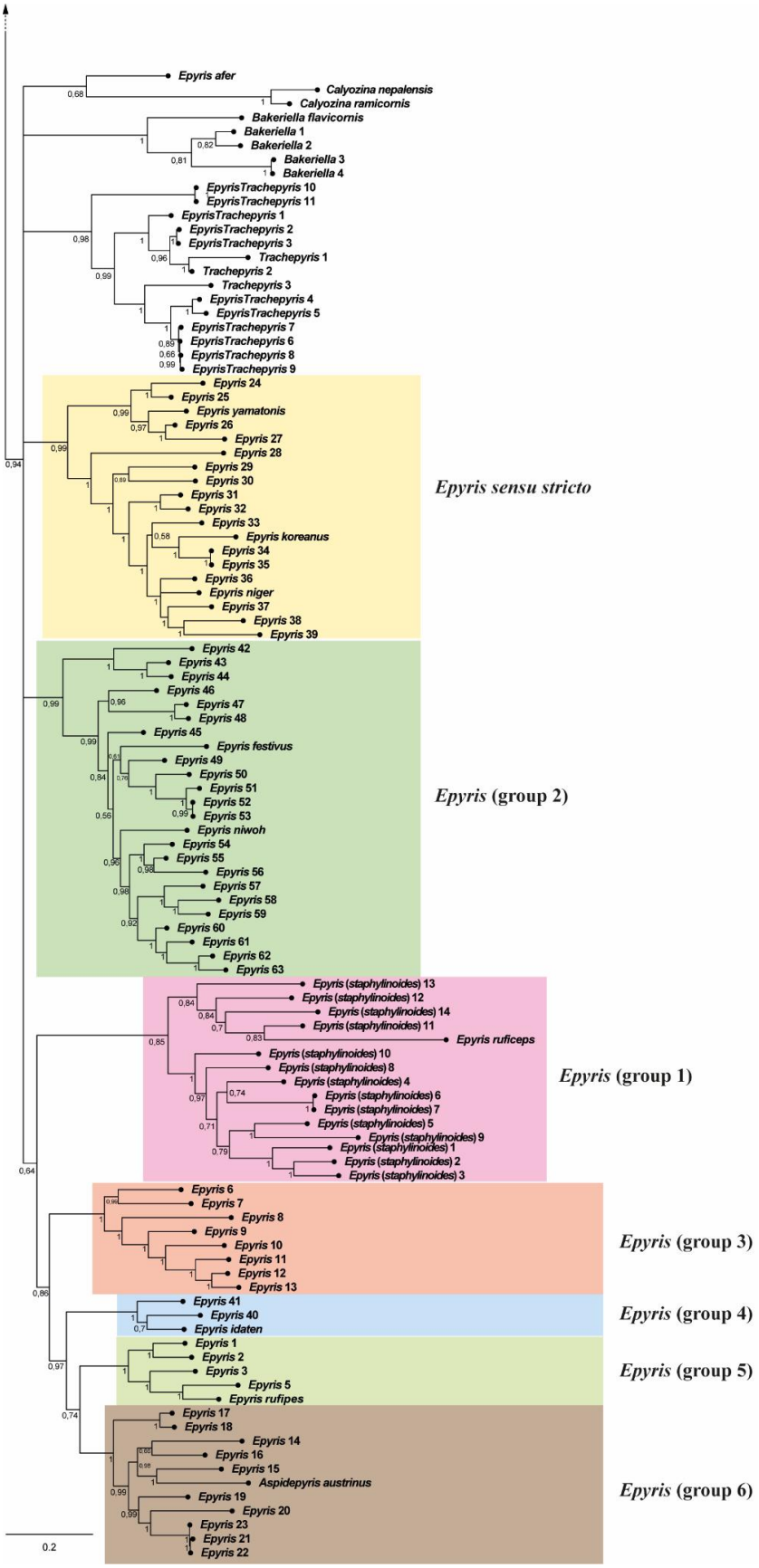
Primer names:	18SF2/18SR2
Heated Lid	110°C
Initial Temp.	95°C for 5 minutes
Start Cycle	34 cycles
Denaturation	95°C for 30 seconds
Annealing	56°C for 40 seconds
Extension	72°C for 40 seconds
End Cycle	
Final Extension	72°C for 10 minutes

28S

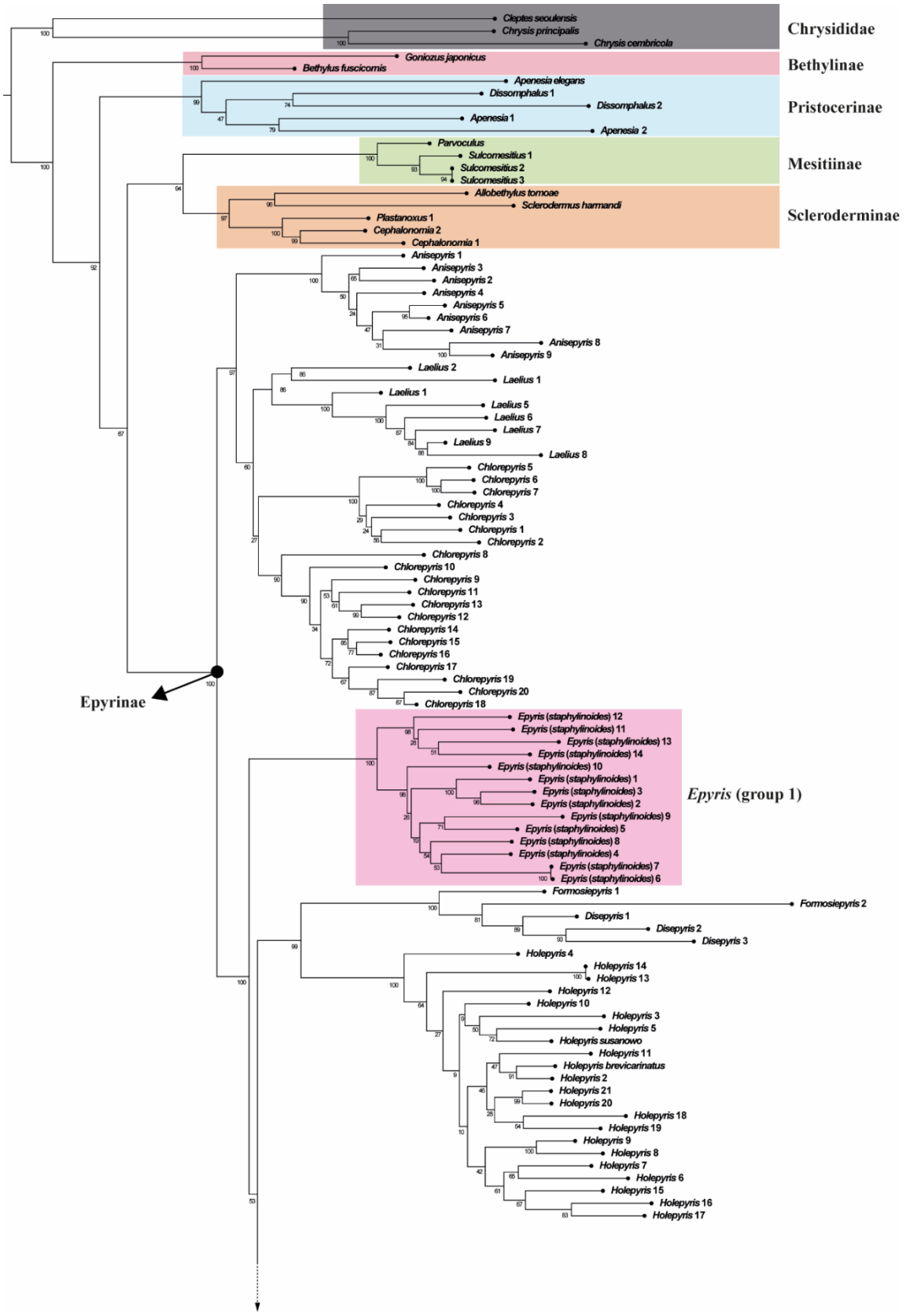
Primer names:	For28SVesp/Rev28SVesp
Heated Lid:	110°C
Initial Temp.	94°C for 5 minutes
Start Cycle	35 cycles
Denaturation	94°C for 1 minute
Annealing	50°C for 1 minute
Extension	72°C for 1 minute
End Cycle	
Final Extension	72°C for 5 minutes

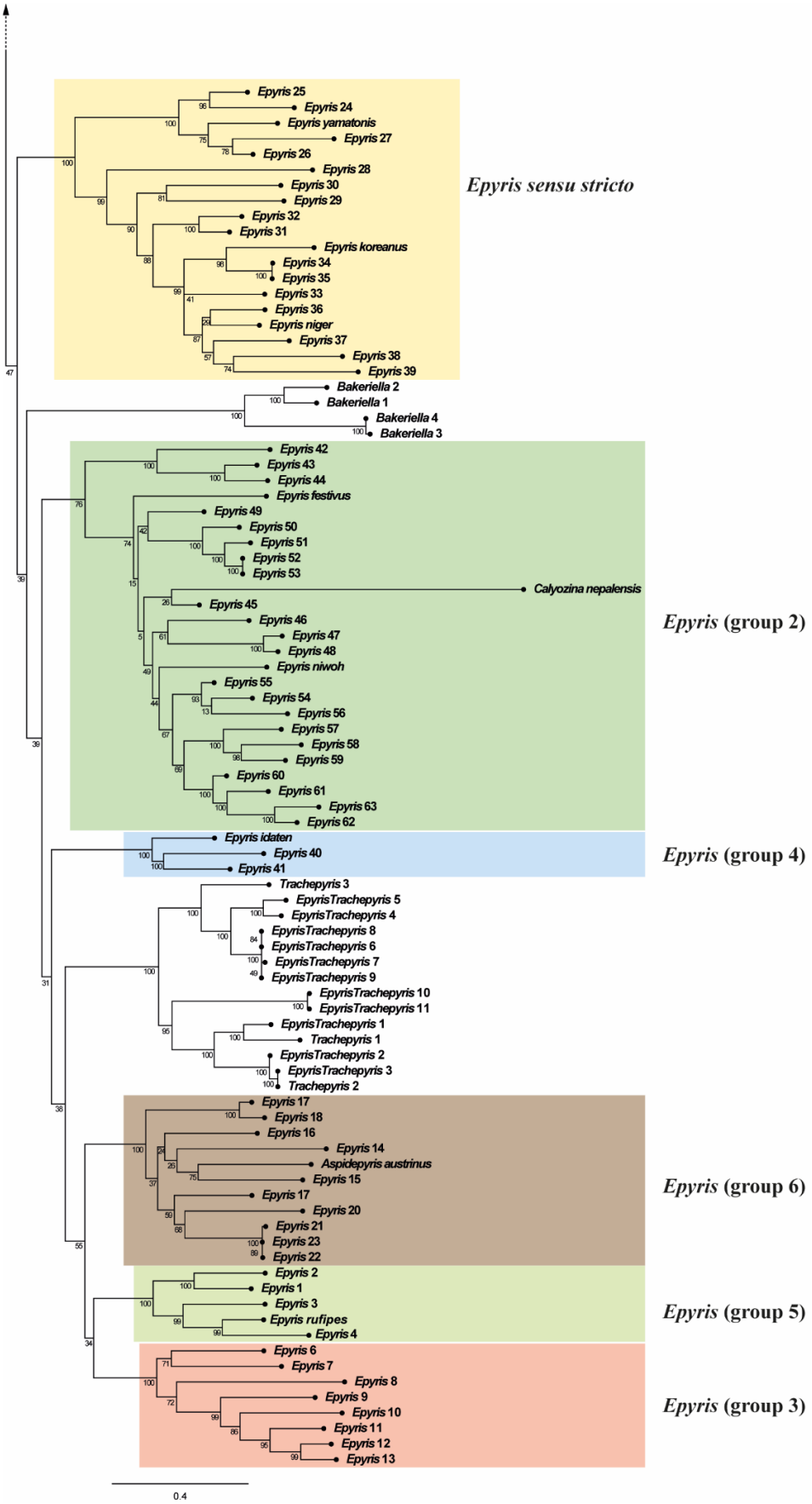
APPENDIX 4. Total evidence topology. PP values are shown above branches.



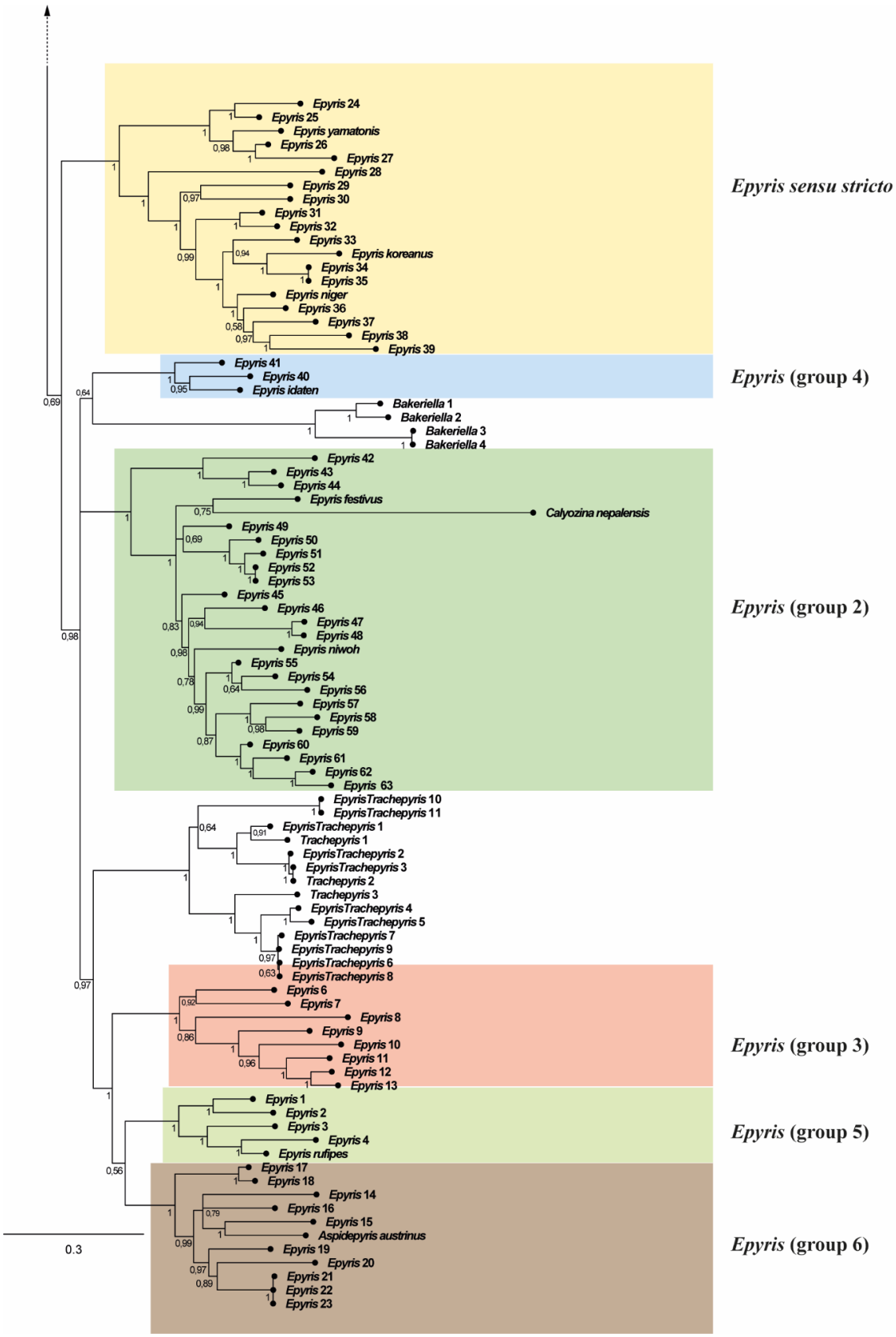

Epyris afer
Calyozina nepalensis
Calyozina ramicornis
Bakeriella flavicornis
Bakeriella 1
Bakeriella 2
Bakeriella 3
Bakeriella 4
EpyrisTrachepyris 10
EpyrisTrachepyris 11
EpyrisTrachepyris 1
EpyrisTrachepyris 2
EpyrisTrachepyris 3
Trachepyris 1
Trachepyris 2
Trachepyris 3
EpyrisTrachepyris 4
EpyrisTrachepyris 5
EpyrisTrachepyris 7
EpyrisTrachepyris 6
EpyrisTrachepyris 8
EpyrisTrachepyris 9
Epyris 24
Epyris 25
Epyris yamatonis
Epyris 26
Epyris 27
Epyris 28
Epyris 29
Epyris 30
Epyris 31
Epyris 32
Epyris 33
Epyris koreanus
Epyris 34
Epyris 35
Epyris 36
Epyris niger
Epyris 37
Epyris 38
Epyris 39
Epyris sensu stricto
Epyris 42
Epyris 43
Epyris 44
Epyris 46
Epyris 47
Epyris 48
Epyris 45
Epyris festivus
Epyris 49
Epyris 50
Epyris 51
Epyris 52
Epyris 53
Epyris niwoh
Epyris 54
Epyris 55
Epyris 56
Epyris 57
Epyris 58
Epyris 59
Epyris 60
Epyris 61
Epyris 62
Epyris 63
Epyris (group 2)
Epyris (staphylinoides) 13
Epyris (staphylinoides) 12
Epyris (staphylinoides) 14
Epyris (staphylinoides) 11
Epyris ruficeps
Epyris (staphylinoides) 10
Epyris (staphylinoides) 8
Epyris (staphylinoides) 4
Epyris (staphylinoides) 6
Epyris (staphylinoides) 7
Epyris (staphylinoides) 5
Epyris (staphylinoides) 9
Epyris (staphylinoides) 1
Epyris (staphylinoides) 2
Epyris (staphylinoides) 3
Epyris (group 1)
Epyris 6
Epyris 7
Epyris 8
Epyris 9
Epyris 10
Epyris 11
Epyris 12
Epyris 13
Epyris (group 3)
Epyris 41
Epyris 40
Epyris idaten
Epyris (group 4)
Epyris 1
Epyris 2
Epyris 3
Epyris 5
Epyris rufipes
Epyris (group 5)
Epyris 17
Epyris 18
Epyris 14
Epyris 16
Epyris 15
Aspidepyris austrinus
Epyris 19
Epyris 20
Epyris 23
Epyris 21
Epyris 22
Epyris (group 6)
0.2

APPENDIX 5. Maximum likelihood topology. Bootstrap values are shown below branches.

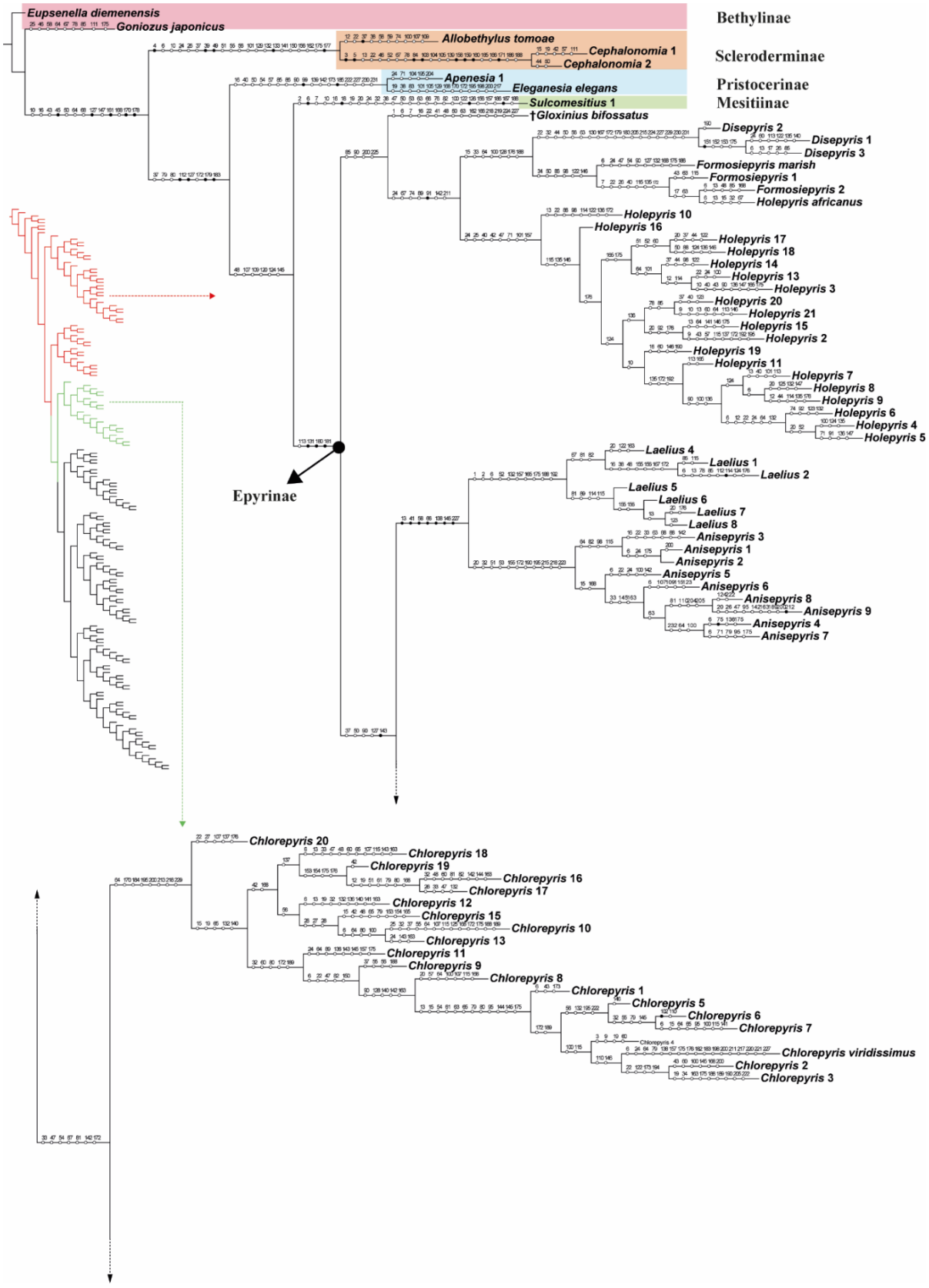


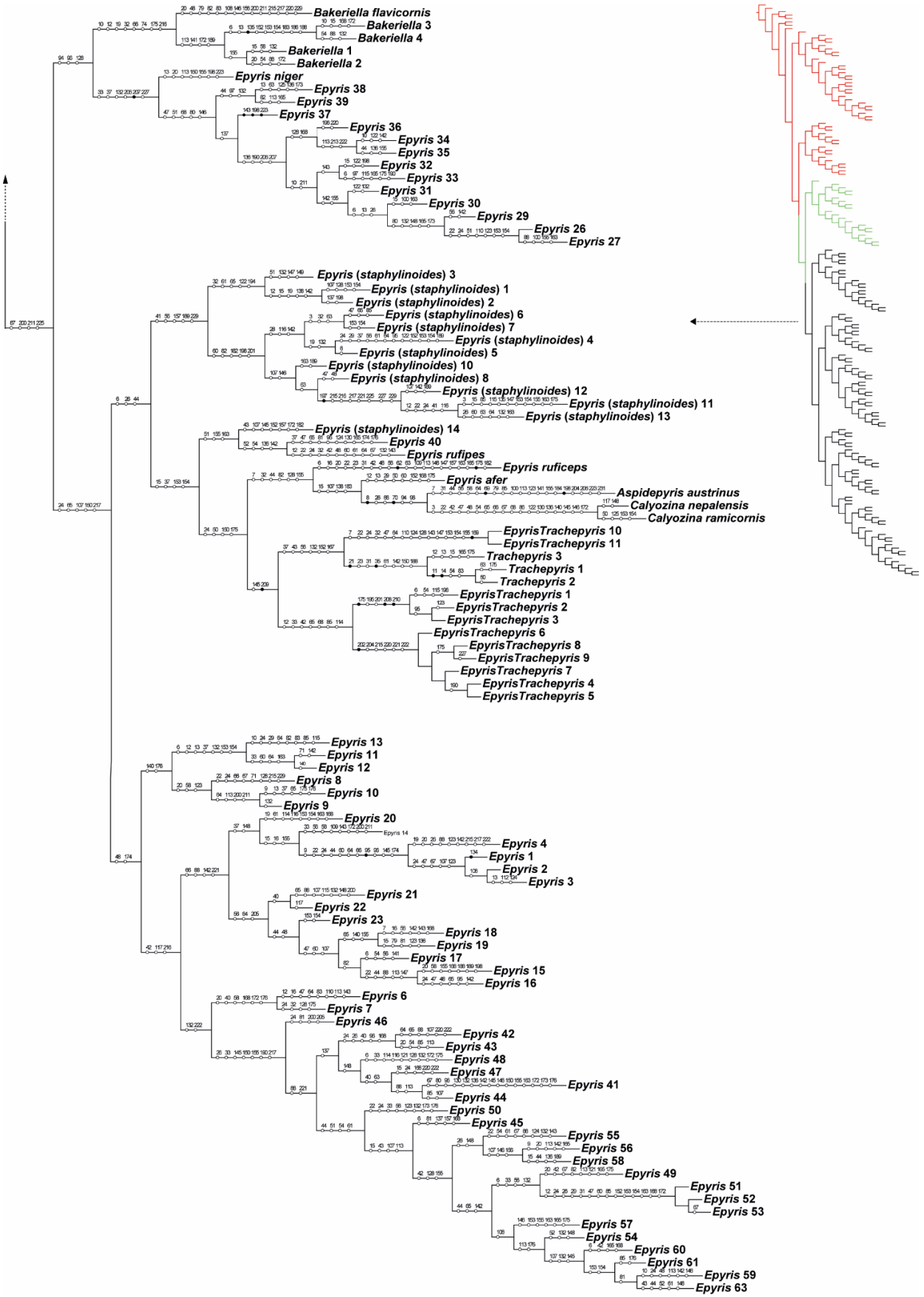

Epyris 25
Epyris 24
Epyris yamatonis
Epyris 27
Epyris 26
Epyris 28
Epyris 30
Epyris 29
Epyris 32
Epyris 31
Epyris koreanus
Epyris 34
Epyris 35
Epyris 33
Epyris 36
Epyris niger
Epyris 37
Epyris 38
Epyris 39
Epyris sensu stricto
Bakeriella 2
Bakeriella 1
Bakeriella 4
Bakeriella 3
Epyris 42
Epyris 43
Epyris 44
Epyris festivus
Epyris 49
Epyris 50
Epyris 51
Epyris 52
Epyris 53
Calyozina nepalensis
Epyris 45
Epyris 46
Epyris 47
Epyris 48
Epyris niwoh
Epyris 55
Epyris 54
Epyris 56
Epyris 57
Epyris 58
Epyris 59
Epyris 60
Epyris 61
Epyris 63
Epyris 62
Epyris (group 2)
Epyris idaten
Epyris 40
Epyris 41
Epyris (group 4)
Trachepyris 3
EpyrisTrachepyris 5
EpyrisTrachepyris 4
EpyrisTrachepyris 8
EpyrisTrachepyris 6
EpyrisTrachepyris 7
EpyrisTrachepyris 9
EpyrisTrachepyris 10
EpyrisTrachepyris 11
EpyrisTrachepyris 1
Trachepyris 1
EpyrisTrachepyris 2
EpyrisTrachepyris 3
Trachepyris 2
Epyris 17
Epyris 18
Epyris 16
Epyris 14
Aspidepyris austrinus
Epyris 15
Epyris 17
Epyris 20
Epyris 21
Epyris 23
Epyris 22
Epyris (group 6)
Epyris 2
Epyris 1
Epyris 3
Epyris rufipes
Epyris 4
Epyris (group 5)
Epyris 6
Epyris 7
Epyris 8
Epyris 9
Epyris 10
Epyris 11
Epyris 12
Epyris 13
Epyris (group 3)
0.4

APPENDIX 6. Bayesian topology. PP values are shown below branches.


Epyris 24
Epyris 25
Epyris yamatonis
Epyris 26
Epyris 27
Epyris 28
Epyris 29
Epyris 30
Epyris 31
Epyris 32
Epyris 33
Epyris koreanus
Epyris 34
Epyris 35
Epyris niger
Epyris 36
Epyris 37
Epyris 38
Epyris 39
Epyris sensu stricto
Epyris 41
Epyris 40
Epyris idaten
Epyris (group 4)
Bakeriella 1
Bakeriella 2
Bakeriella 3
Bakeriella 4
Epyris 42
Epyris 43
Epyris 44
Epyris festivus
Calyozina nepalensis
Epyris 49
Epyris 50
Epyris 51
Epyris 52
Epyris 53
Epyris 45
Epyris 46
Epyris 47
Epyris 48
Epyris niwoh
Epyris 55
Epyris 54
Epyris 56
Epyris 57
Epyris 58
Epyris 59
Epyris 60
Epyris 61
Epyris 62
Epyris 63
Epyris (group 2)
EpyrisTrachepyris 10
EpyrisTrachepyris 11
EpyrisTrachepyris 1
Trachepyris 1
EpyrisTrachepyris 2
EpyrisTrachepyris 3
Trachepyris 2
Trachepyris 3
EpyrisTrachepyris 4
EpyrisTrachepyris 5
EpyrisTrachepyris 7
EpyrisTrachepyris 9
EpyrisTrachepyris 6
EpyrisTrachepyris 8
Epyris 6
Epyris 7
Epyris 8
Epyris 9
Epyris 10
Epyris 11
Epyris 12
Epyris 13
Epyris (group 3)
Epyris 1
Epyris 2
Epyris 3
Epyris 4
Epyris rufipes
Epyris (group 5)
Epyris 17
Epyris 18
Epyris 14
Epyris 16
Epyris 15
Aspidepyris austrinus
Epyris 19
Epyris 20
Epyris 21
Epyris 22
Epyris 23
Epyris (group 6)
0.3

APPENDIX 7. Parsimony topology. Characters are shown above branches.




Bakeriella flavicornis
Bakeriella 3
Bakeriella 4
Bakeriella 1
Bakeriella 2
Epyris niger
Epyris 38
Epyris 39
Epyris 37
Epyris 36
Epyris 34
Epyris 35
Epyris 32
Epyris 33
Epyris 31
Epyris 30
Epyris 29
Epyris 26
Epyris 27
Epyris (staphylinoides) 3
Epyris (staphylinoides) 1
Epyris (staphylinoides) 2
Epyris (staphylinoides) 6
Epyris (staphylinoides) 7
Epyris (staphylinoides) 4
Epyris (staphylinoides) 5
Epyris (staphylinoides) 10
Epyris (staphylinoides) 8
Epyris (staphylinoides) 12
Epyris (staphylinoides) 11
Epyris (staphylinoides) 13
Epyris (staphylinoides) 14
Epyris 40
Epyris rufipes
Epyris ruficeps
Epyris afer
Aspidepyris austrinus
Calyozina nepalensis
Calyozina ramicornis
EpyrisTrachepyris 10
EpyrisTrachepyris 11
Trachepyris 3
Trachepyris 1
Trachepyris 2
EpyrisTrachepyris 1
EpyrisTrachepyris 2
EpyrisTrachepyris 3
EpyrisTrachepyris 6
EpyrisTrachepyris 8
EpyrisTrachepyris 9
EpyrisTrachepyris 7
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Epyris 22
Epyris 23
Epyris 18
Epyris 19
Epyris 17
Epyris 15
Epyris 16
Epyris 6
Epyris 7
Epyris 46
Epyris 42
Epyris 43
Epyris 48
Epyris 47
Epyris 41
Epyris 44
Epyris 50
Epyris 45
Epyris 55
Epyris 56
Epyris 58
Epyris 49
Epyris 51
Epyris 52
Epyris 53
Epyris 57
Epyris 54
Epyris 60
Epyris 61
Epyris 59
Epyris 63

APPENDIX 8. Checklist of all 962 epyrine species, distributed into a new classification that will be proposed in this study.

Table 1. List of *Anisepyris*. Type-species of *Anisepyris*[1]; type-species of *Procalyoza*[2]; type-species of *Trichotepyris*[3]; The type-species of *Lophepyris* is *A. bridwelli* Evans (junior synonym of *A. aeneus* Kieffer).

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*aegnori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
2	*aeneus* Kieffer, 1906	CAS	Neotropical	type
3	*aerini* Barbosa & Azevedo, 2018	UFES	Neotropical	type
4	*aghani* Barbosa & Azevedo, 2018	AMNH	Nearctic	type
5	*albistigmus* Evans, 1966	USNM	Neotropical	type
6	*alienus* Evans, 1966	MCZC	Neotropical	type
7	*amabilis* (Fouts, 1927)	USNM	Nearctic	type
8	*amandili* Barbosa & Azevedo, 2018	UFES	Neotropical	type
9	*amariei* Barbosa & Azevedo, 2018	UFES	Neotropical	type
10	*amazonicus* (Westwood, 1874)[1]	OUMNH	Neotropical	type
11	*amlachi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
12	*amrasis* Barbosa & Azevedo, 2018	UFES	Neotropical	type
13	*amrodi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
14	*analis* (Cresson, 1872)	CNC	Nearctic, Neotropical	type
15	*ancalagoni* Barbosa & Azevedo, 2018	MEL	Neotropical	type
16	*andrethi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
17	*androgi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
18	*anduzei* Evans, 1966	MCZC	Neotropical	type
19	*angrimi* Barbosa & Azevedo, 2018	INPA	Neotropical	type
20	*angrodi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
21	*angulatus* Santos & Azevedo, 2000	UFES	Neotropical	type
22	*angusticeps* (Evans, 1965)	MCZC	Nearctic	type
23	*annaeli* Barbosa & Azevedo, 2018	UFES	Neotropical	type
24	*antiguensis* Evans, 1966	MCZC	Neotropical	type
25	*apache* (Evans, 1965)	MCZC	Nearctic, Neotropical	type
26	*aradunakhori* Barbosa & Azevedo, 2018	INPA	Neotropical	type
27	*aranwei* Barbosa & Azevedo, 2018	CNC	Neotropical	type
28	*arapaho* Evans, 1959	SEMC	Nearctic	type
29	*aratani* Barbosa & Azevedo, 2018	INPA	Neotropical	type
30	*aratari* Barbosa & Azevedo, 2018	UFES	Neotropical	type
31	*arawak* Snelling, 1996	LACM	Neotropical	type
32	*aredheli* Barbosa & Azevedo, 2018	INPA	Neotropical	type
33	*argimilzori* Barbosa & Azevedo, 2018	INPA	Neotropical	type
34	*arieni* Barbosa & Azevedo, 2018	INPA	Neotropical	type
35	*arizonicus* Evans, 1959	USNM	Nearctic	type
36	*arpharazoni* Barbosa & Azevedo, 2018	UFES	Neotropical	type
37	*arsakalthori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
38	*arthadi* Barbosa & Azevedo, 2018	INPA	Neotropical	type
39	*artus* Santos & Azevedo, 2008	UFES	Neotropical	type

40	*arzimrathoni* Barbosa & Azevedo, 2018	UFES	Neotropical	type
41	*asgoni* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
42	*attenuatus* Santos, 2002	UFES	Neotropical	type
43	*aulei* Barbosa & Azevedo, 2018	UFES	Neotropical	type
44	*aureus* Kieffer, 1910	MCZC	Neotropical	type
45	*aurichalceus* (Westwood, 1874)	OUMNH	Nearctic, Neotropical	type
46	*azaghali* Barbosa & Azevedo, 2018	CNC	Neotropical	type
47	*bakeri* Evans, 1966	USNM	Neotropical	type
48	*balrogi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
49	*barachi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
50	*baragundi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
51	*barahiris* Barbosa & Azevedo, 2018	UFES	Neotropical	type
52	*barani* Barbosa & Azevedo, 2018	UFMG	Neotropical	type
53	*basilargus* Santos & Azevedo, 2008	UFES	Neotropical	type
54	*basilongus* Santos & Azevedo, 2008	UFES	Neotropical	type
55	*basipilosus* Santos & Azevedo, 2008	UFES	Neotropical	type
56	*belegi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
57	*belegundi* Barbosa & Azevedo, 2018	IBGE	Neotropical	type
58	*belemiri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
59	*beori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
60	*beregi* Barbosa & Azevedo, 2018	UFMG	Neotropical	type
61	*bereni* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
62	*bifidus* Evans, 1966	USNM	Neotropical	type
63	*bipartitus* Santos & Azevedo, 2000	INPA	Neotropical	type
64	*bogotensis* (Kieffer, 1910)	ZMHB	Neotropical	type
65	*bolivari* Evans, 1966	MCZC	Neotropical	type
66	*bori* Barbosa & Azevedo, 2018	INPA	Neotropical	type
67	*borlachi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
68	*borladi* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
69	*boromiri* Barbosa & Azevedo, 2018	MZPW	Neotropical	type
70	*borthandis* Barbosa & Azevedo, 2018	UFES	Neotropical	type
71	*bradleyi* (Evans, 1959)	CNC	Nearctic, Neotropical	type
72	*brandiri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
73	*brasiliensis* Evans, 1966	USNM	Neotropical	type
74	*bregoi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
75	*bregolasi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
76	*bregori* Barbosa & Azevedo, 2018	INPA	Neotropical	type
77	*breviramus* Santos & Azevedo, 2000	INPA	Neotropical	type
78	*broddai* Barbosa & Azevedo, 2018	CNC	Neotropical	type
79	*calmacili* Barbosa & Azevedo, 2018	UFES	Neotropical	type
80	*caranthiri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
81	*carcharothi* Barbosa & Azevedo, 2018	MZSP	Neotropical	type
82	*carinatus* Santos & Azevedo, 2000	IBGE	Neotropical	type
83	*carineceps* Evans, 1966	MCZC	Neotropical	type
84	*carolinianus* (Evans, 1965)	MCZC	Nearctic	type
85	*celebrimbori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
86	*celegormi* Barbosa & Azevedo, 2018	CNC	Neotropical	type
87	*cepus* Santos & Azevedo, 2008	UFES	Neotropical	type
88	*chupah* Snelling, 1996	LACM	Neotropical	type

89	*cirdani* Barbosa & Azevedo, 2018	UFES	Neotropical	type
90	*ciryoni* Barbosa & Azevedo, 2018	UFES	Neotropical	type
91	*colimae* Evans, 1966	MCZC	Neotropical	type
92	*columbianus* (Ashmead, 1893)	USNM	Nearctic, Neotropical	type
93	*coriaceus* Kieffer, 1908	CAS	Nearctic, Neotropical	type
94	*cubiceps* (Evans, 1967)	CNC	Neotropical	type
95	*cupreolus* (Evans, 1965)	MCZC	Neotropical	type
96	*curufini* Barbosa & Azevedo, 2018	UFES	Neotropical	type
97	*curvicarinatus* (Rosmann & Azevedo, 2005)	UFMG	Neotropical	type
98	*daeroni* Barbosa & Azevedo, 2018	INPA	Neotropical	type
99	*dairuini* Barbosa & Azevedo, 2018	MZSP	Neotropical	type
100	*darlingtoni* Evans, 1959	MCZC	Neotropical	type
101	*delicatus* Evans, 1966	MCZC	Nearctic, Neotropical	type
102	*denethori* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
103	*dentatus* Santos & Azevedo, 2000	MPEG	Neotropical	type
104	*dietrichorum* Evans, 1959	USNM	Nearctic, Neotropical	type
105	*diori* Barbosa & Azevedo, 2018	INPA	Neotropical	type
106	*divisus* Santos, 2002	UFES	Neotropical	type
107	*dominicanus* Evans, 1966	USNM	Neotropical	type
108	*dorlasi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
109	*draugluini* Barbosa & Azevedo, 2018	UFES	Neotropical	type
110	*durini* Barbosa & Azevedo, 2018	UFES	Neotropical	type
111	*earendili* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
112	*earenduri* Barbosa & Azevedo, 2018	MEL	Neotropical	type
113	*earweni* Barbosa & Azevedo, 2018	UFES	Neotropical	type
114	*ecthelion* Barbosa & Azevedo, 2018	CNC	Neotropical	type
115	*ecuadiroanus* Evans, 1966	BPBM	Neotropical	type
116	*eganellus* (Westwood, 1874)	INPA	Neotropical	type
117	*eilineli* Barbosa & Azevedo, 2018	UFES	Neotropical	type
118	*elatani* Barbosa & Azevedo, 2018	UFES	Neotropical	type
119	*elegantulus* Evans, 1966	BPBM	Neotropical	type
120	*elemmirei* Barbosa & Azevedo, 2018	UFES	Neotropical	type
121	*elendili* Barbosa & Azevedo, 2018	MEL	Neotropical	type
122	*elenduri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
123	*elenwei* Barbosa & Azevedo, 2018	UFES	Neotropical	type
124	*elrondi* Barbosa & Azevedo, 2018	CNC	Neotropical	type
125	*elrosi* Barbosa & Azevedo, 2018	MEL	Neotropical	type
126	*eluredi* Barbosa & Azevedo, 2018	CNC	Neotropical	type
127	*elwingi* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
128	*emeldiri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
129	*eoli* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
130	*eonwei* Barbosa & Azevedo, 2018	UFES	Neotropical	type
131	*erellonti* Barbosa & Azevedo, 2018	AMNH	Nearctic	type
132	*estei* Barbosa & Azevedo, 2018	AMNH	Nearctic	type
133	*excisus* Evans, 1959	MCZC	Neotropical	type
134	*falathari* Barbosa & Azevedo, 2018	UFES	Neotropical	type
135	*fasciipennis* Kieffer, 1906	UCDC	Neotropical	type
136	*feanori* Barbosa & Azevedo, 2018	AMNH	Nearctic	type
137	*finarfini* Barbosa & Azevedo, 2018	INPA	Neotropical	type

138	*finduilasi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
139	*fingolfini* Barbosa & Azevedo, 2018	UFES	Neotropical	type
140	*fingoni* Barbosa & Azevedo, 2018	UFES	Nearctic, Neotropical	type
141	*finrodi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
142	*finwei* Barbosa & Azevedo, 2018	MZSP	Neotropical	type
143	*fortunatus* (Evans, 1965)	MCZC	Neotropical	type
144	*foveapertus* Santos & Azevedo, 2008	UFES	Neotropical	type
145	*franciscanus* Evans, 1966	BPBM	Neotropical	type
146	*fuinuri* Barbosa & Azevedo, 2018	MEL	Neotropical	type
147	*fuscicornis* Kieffer, 1908	Lost[?]	Neotropical	literature
148	*galadrieli* Barbosa & Azevedo, 2018	CNC	Neotropical	type
149	*galdori* Barbosa & Azevedo, 2018	MEL	Nearctic, Neotropical	type
150	*gamilziraki* Barbosa & Azevedo, 2018	INPA	Neotropical	type
151	*gelmiri* Barbosa & Azevedo, 2018	DZUP	Neotropical	type
152	*gibbosifrons* Evans, 1959	USNM	Nearctic, Neotropical	type
153	*gildori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
154	*gigaladi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
155	*gimilkhadi* Barbosa & Azevedo, 2018	CNC	Neotropical	type
156	*glaurungi* Barbosa & Azevedo, 2018	CNC	Neotropical	type
157	*glirhuini* Barbosa & Azevedo, 2018	UFMG	Neotropical	type
158	*gloredheli* Barbosa & Azevedo, 2018	CNC	Neotropical	type
159	*glorfindeli* Barbosa & Azevedo, 2018	IBGE	Neotropical	type
160	*gorlimi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
161	*gothmogi* Barbosa & Azevedo, 2018	MEL	Neotropical	type
162	†*gradatus* Sorg, 1988	SMF	Dominican amber	type
163	*grandis* (Ashmead, 1887)	UCDC	Nearctic, Neotropical	type
164	*grisselli* Evans, 1979	FSCA	Neotropical	type
165	*guianae* Evans, 1966	BPBM	Neotropical	type
166	*guilini* Barbosa & Azevedo, 2018	UFES	Neotropical	type
167	*gundori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
168	*gwindori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
169	*hadori* Barbosa & Azevedo, 2018	INPA	Neotropical	type
170	*haldadi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
171	*haldani* Barbosa & Azevedo, 2018	UFES	Neotropical	type
172	*haldari* Barbosa & Azevedo, 2018	INPA	Neotropical	type
173	*haldiri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
174	*halethi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
175	*halmiri* Barbosa & Azevedo, 2018	MZSP	Neotropical	type
176	*harethi* Barbosa & Azevedo, 2018	IBGE	Neotropical	type
177	*hathaldiri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
178	*herumori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
179	*hondurensis* Evans, 1966	AMNH	Neotropical	type
180	*huani* Barbosa & Azevedo, 2018	OSUC	Neotropical	type
181	*hundadi* Barbosa & Azevedo, 2018	INPA	Neotropical	type
182	*hunthori* Barbosa & Azevedo, 2018	UFES	Neotropical	type
183	*huori* Barbosa & Azevedo, 2018	CNC	Neotropical	type
184	*hurini* Barbosa & Azevedo, 2018	MPEG	Neotropical	type
185	*ibuni* Barbosa & Azevedo, 2018	UFES	Neotropical	type
186	*idrili* Barbosa & Azevedo, 2018	UFES	Neotropical	type

187	*ilmarei* Barbosa & Azevedo, 2018	CEPLAC	Neotropical	type
188	*iluvatari* Barbosa & Azevedo, 2018	UFES	Neotropical	type
189	*immarginatus* Evans, 1966	MCZC	Neotropical	type
190	*inca* Evans, 1966	MCZC	Neotropical	type
191	*inconspicuus* Santos, 2002	UFES	Neotropical	type
192	*indisi* Barbosa & Azevedo, 2018	CNC	Neotropical	type
193	*indivisus* Barbosa & Azevedo, 2018	UFES	Neotropical	type
194	*ingwei* Barbosa & Azevedo, 2018	UFES	Neotropical	type
195	*insularis* (Ashmead, 1894)	USNM	Neotropical	type
196	*interruptus* Santos & Azevedo, 2000	INPA	Neotropical	type
197	*inzilbethi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
198	*iorlasi* Barbosa & Azevedo, 2018	INPA	Neotropical	type
199	*iridescens* (Evans, 1965)	MCZC	Neotropical	type
200	*irmoi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
201	*isilduri* Barbosa & Azevedo, 2018	UFES	Neotropical	type
202	*jandirae* Santos & Azevedo, 2000	DZUP	Neotropical	type
203	*jocundus* Evans, 1966	MCZC	Neotropical	type
204	*khimi* Barbosa & Azevedo, 2018	UFES	Neotropical	type
205	*lalaithi* Barbosa & Azevedo, 2018	MZSP	Neotropical	type
206	*laticeps* Evans, 1966	MEL	Neotropical	type
207	*lobatus* Santos & Azevedo, 2000	UFES	Neotropical	type
208	*longimerus* Santos & Azevedo, 2000	UFES	Neotropical	type
209	*lupus* (Evans, 1965)	MCZC	Neotropical	type
210	*megacephalus* (Ashmead, 1893)	USNM	Nearctic	type
211	*metallicus* Kieffer, 1905	HNM	Neotropical	type
212	*mexicanus* (Evans, 1965)	MCZC	Neotropical	type
213	*nigripes* Evans, 1966	MCZC	Neotropical	type
214	*occidentalis* (Ashmead, 1893)	USNM	Nearctic, Neotropical	type
215	*olivaceus* (Evans, 1965)	USNM	Neotropical	type
216	*pallidicornis* Evans, 1966	MCZC	Neotropical	type
217	*pallidipennis* (Kieffer, 1906)[3]	Lost[?]	Palaearctic	literature
218	*papago* Evans, 1966	MCZC	Nearctic	type
219	*penai* Evans, 1966	MCZC	Neotropical	type
220	*peruvianus* (Kieffer, 1910)	ZMHB	Neotropical	type
221	*planiceps* (Fabricius, 1804)	ZMUC	Nearctic, Neotropical	type
222	*plaumanni* (Evans, 1965)	BMNH	Neotropical	type
223	*pollicis* Santos & Azevedo, 2000	IBGE	Neotropical	type
224	*portoricensis* Evans, 1965	USNM	Neotropical	type
225	*proteus* Evans, 1966	MCZC	Neotropical	type
226	*pulchripennis* (Evans, 1965)	USNM	Neotropical	type
227	*punctatus* Santos & Azevedo, 2000	DZUP	Neotropical	type
228	*ramosus* Santos & Azevedo, 2008	MZSP	Neotropical	type
229	*rectus* Santos & Azevedo, 2000	IBGE	Neotropical	type
230	*robustus* Santos & Azevedo, 2000	UFES	Neotropical	type
231	*rotundus* Santos, 2002	UFES	Neotropical	type
232	*rufitarsis* Kieffer, 1908	Lost[?]	Neotropical	literature
233	*rufosigmatus* Kieffer, 1908	MCZC	Neotropical	type
234	*rugosicollis* Brues, 1908	USNM	Nearctic	type
235	*sculptilis* Evans, 1966	MCZC	Nearctic, Neotropical	type

236	*semiviridis* Santos & Azevedo, 2000	INPA	Neotropical	type
237	*similis* Santos & Azevedo, 2000	INPA	Neotropical	type
238	*smithanus* (Westwood, 1874)	BMNH	Neotropical	type
239	*speciosus* Evans, 1967	CAS	Neotropical	type
240	*strictus* Santos & Azevedo, 2000	INPA	Neotropical	type
241	*subaeneus* (Kieffer, 1906)	CAS	Neotropical	type
242	*subviolaceus* Kieffer, 1910	CAS	Nearctic, Neotropical	type
243	*superpilosus* (Azevedo, 1993)	DCBU	Neotropical	type
244	*texanus* (Evans, 1965)	MCZC	Nearctic, Neotropical	type
245	*tlaloc* Evans, 1966	MCZC	Nearctic, Neotropical	type
246	*triangularis* Moreira & Azevedo, 2000	UFES	Neotropical	type
247	*trinitatis* Evans, 1966	MCZC	Neotropical	type
248	*tuberosus* Santos & Azevedo, 2000	UFES	Neotropical	type
249	*venustus* Evans, 1964	MCZC	Neotropical	type
250	*werneri* (Evans, 1965)	USNM	Nearctic, Neotropical	type
251	*westwoodi* (Cameron, 1888)[2]	BMNH	Neotropical	type
252	*williamsi* Evans, 1959	CAS	Nearctic, Neotropical	type
253	*wilsoni* Evans, 1966	MCZC	Neotropical	type
254	*wolcotti* Evans, 1959	USNM	Neotropical	type

Table 2. List of *Aspidepyris*. Type-species[1]. *, to be proposed as **comb. nov.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*angulatus* (Evans, 1969)***** from *Epyris*	BPBM	Neotropical	type
2	*angustatus* (Evans, 1969)* from *Epyris*	MCZ	Neotropical	type
3	*argentinicus* (Evans, 1969)* from *Epyris*	IFML	Neotropical	type
4	*asperatus* (Evans, 1969)* from *Epyris*	HKT	Neotropical	type
5	*austrinus* Evans, 1967	USNM	Neotropical	type
6	*bipunctatus* (Kieffer, 1910)* from *Epyris*	ZMB	Neotropical	type
7	*chilensis* (Azevedo, 1999)* from *Epyris*	MNNC	Neotropical	type
8	*cochise* (Evans, 1969)* from *Epyris*	MCZ	Nearctic, Neotropical	type
9	*cochlear* (Santos & Azevedo, 2003)* from *Epyris*	DZUP	Neotropical	type
10	*distinctus* (Correa & Azevedo, 2002)* from *Epyris*	UFES	Neotropical	type
11	*eriogoni* (Kieffer, 1906)* from *Epyris*	Baker collection[?]	Nearctic, Neotropical	literature
12	*foveolatus* Evans, 1964[1]	AMNH	Neotropical	type
13	*guana* (Snelling, 1906)* from *Epyris*	LACM	Neotropical	type
14	*guatemalensis* (Cameron, 1888)* from *Epyris*	BMNH	Nearctic, Neotropical	type
15	*hirsutus* (Evans, 1969)* from *Epyris*	MCZ	Neotropical	type
16	*hispaniolae* (Evans, 1964)* from *Epyris*	MCZ	Neotropical	type
17	*insolitus* (Evans, 1969)* from *Epyris*	MCZ	Neotropical	type
18	*intermedius* (Evans, 1969)* from *Epyris*	CMNH	Neotropical	type
19	*jareckii* (Snelling, 1996)* from *Epyris*	LACM	Neotropical	type
20	*longus* (Correa & Azevedo, 2002)* from *Epyris*	UFES	Neotropical	type
21	*luteicornis* (Evans, 1969)* from *Epyris*	MCZ	Neotropical	type
22	*manni* (Evans, 1964)* from *Epyris*	MCZ	Neotropical	type
23	*oriplanus* (Kieffer, 1911)* from *Epyris*	BMNH	Neotropical	type
24	*perpolitus* (Evans, 1969)* from *Epyris*	HKT	Neotropical	type
25	*porosus* (Evans, 1969)* from *Epyris*	MCZ	Neotropical	type
26	*tretonotum* (Evans, 1969)* from *Epyris*	HKT	Neotropical	literature

Table 3. List of *Bakeriella*. Type-species[1].

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*absens* Kawada & Azevedo, 2003	CNC	Neotropical	type
2	*aurata* Kawada & Azevedo, 2003	INPA	Neotropical	type
3	*azteca* Evans, 1964	MCZC	Neotropical	type
4	*brasiliana* Evans, 1964	USNM	Neotropical	type
5	*bulbosa* Azevedo & Moreira, 2005	CNC	Neotropical	type
6	*cristata* Evans, 1964	CMNH	Neotropical	type
7	*denteata* Azevedo, 1991	DCBU	Neotropical	type
8	*erythrogaster* Evans, 1979	UCDC	Neotropical	type
9	*flavicornis* Kieffer, 1910[1]	CAS	Neotropical	type
10	*floridana* Evans, 1964	MCZC	Nearctic, Neotropical	type
11	*grandis* Evans, 1979	UCDC	Neotropical	type
12	*grossensis* Azevedo, 1994	MZSP	Neotropical	type
13	*inca* Evans, 1964	CUIC	Neotropical	type
14	*incompleta* Azevedo, 1994	UFES	Neotropical	type
15	*inconspicua* Evans, 1964	USNM	Neotropical	type
16	*lobans* Azevedo & Moreira, 2005	CNC	Neotropical	type
17	*lata* Kawada & Azevedo, 2003	MPEG	Neotropical	type
18	*lindigi* (Kieffer, 1910)	ZMHB	Neotropical	type
19	*mira* Evans, 1997	USNM	Nearctic, Neotropical	type
20	*montivaga* (Kieffer, 1910)	ZMHB	Neotropical	type
21	*nuda* Evans, 1964	CNC	Neotropical	type
22	*olmeca* Evans, 1964	CAS	Neotropical	type
23	*polita* Evans, 1964	CNC	Neotropical	type
24	*quadriceps* Evans, 1979	MCZC	Neotropical	type
25	*quinquepartita* (Kieffer, 1910)	ZMHB	Neotropical	type
26	*reclusa* (Evans, 1969)	MCZC	Neotropical	type
27	*rossi* Evans, 1964	CAS	Neotropical	type
28	*rufocaudata* Evans, 1964	MCZC	Neotropical	type
29	*subcarinata* Evans, 1965	MCZC	Neotropical	type
30	*sulcaticeps* Kawada & Azevedo, 2003	INPA	Neotropical	type

Table 4. List of *Calyoza* species. Type-species of *Calyoza*[1]; [2], type-species of *Artiepyris*; [3], type-species of *Calyozella*; [4], type-species of *Paracalyoza*; [5], type-species of *Pseudocalyoza*; [6], type-species of *Xenepyris*. *, to be proposed as **comb. nov.**; **, to be proposed as **comb. rev.**; ***, to be proposed as **nom. rev. et.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*aequatorialis* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
2	*azurea* (Evans, 1978)**** from *Epyris*	CNC	Neotropical	type
3	*budda* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
4	*camerounensis* (Terayama, 2005)* from *Epyris*	ZMHB	Afrotropical	literature
5	*compressicornis* (Kieffer, 1913)[6]* from *Xenepyris*	Lost[?]	Oriental	literature
6	*dodecatoma* (Kieffer, 1906)[2]* from *Epyris*	MCZC	Neotropical	type
7	*exaratus* (Kieffer, 1922)* from *Xenepyris*	Lost[?]	Oriental	literature
8	*hirtipennis* (Cameron, 1909)[4]* from *Epyris*	BMNH	Oriental	type
9	*indra* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature

10	*leyteana* (Terayama, 2005)* from *Epyris*	PMAE	Oceanian	literature
11	*maya* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
12	*melpa* (Colombo & Azevedo, 2020)* from *Epyris*	MNHN	Oceanian	type
13	*puduma* (Krombein, 1992)* from *Epyris*	USNM	Oriental	type
14	*puncta* (Kieffer, 1906)* from *Epyris*	MHN	Palaearctic	literature
15	*quadripartita* (Benoit, 1957)* from *Epyris*	MRAC	Afrotropical	type
16	*rufiventris* (Kieffer, 1907)* from *Epyris*	BMNH	Australian	type
17	*sabahensis* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
18	*sauteri* (Enderlein, 1920)* from *Epyris*	ZMHB	Palaearctic	type
19	*shakha* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
20	*shiva* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
21	*staphylinoides* Hope, 1837[1]** from *Epyris*	OUMNH	Afrotropical	neotype
22	*subramosua* (Turner, 1915)[5]* from *Epyris*	BMNH	Afrotropical	type
23	*sumatrana* Enderlein, 1917** from *Epyris*	ZMSZ	Oceanian	literature
24	*flavipennis* Enderlein, 1920[3]*** from *Epyris*	ZMSZ	Oceanian	literature
25	*tsunekii* (Terayama, 2008)* from *Epyris*	NIAES	Oceanian	type

Table 5. List of *Calyozina* species examined with emphasis on which types were analysed directly. Type-species[1]. *, to be proposed as **comb. rev.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*dilatata* Azevedo, 1996* from *Epyris*	INPA	Neotropical	type
2	*nepalensis* Terayama, 2005	CNC	Oriental	type
3	*ramicornis* Enderlein, 1912[1]	ZMHB	Oriental	type
4	*thaiana* Terayama, 2005	PMAE	Oriental	type

Table 6. List of *Chlorepyris*. The type-species of *Chlorepyris* is *C. semiviridis* Kieffer, 1913 (junior synonym of *C. viridissimus* Kieffer[1]). *, to be proposed as **comb. nov.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*abjectus* (Evans, 1982)	ANIC	Australian	type
2	*abelam* Colombo & Azevedo, 2020	MNHN	Oceanian	type
3	*ablusus* (Evans, 1982)	ANIC	Australian	type
4	*aethiops* (Turner & Waterson, 1917)* from *Epyris*	BMNH[?]	Afrotropical	literature
5	*aletris* (Evans, 1982)	ANIC	Australian	type
6	*angu* Colombo & Azevedo, 2020	MNHN	Oceanian	type
7	*anxius* (Evans, 1982)	ANIC	Australian	type
8	*arcanellus* (Evans, 1982)	BMNH	Australian	type
9	*arenarius* (Evans, 1982)	ANIC	Australian	type
10	*armatus* (Kieffer, 1904)	MCSN	Oceanian	type
11	*asperulus* (Evans, 1982)	ANIC	Australian	type
12	*atlanticus* (Rosmann & Azevedo, 2005)	DZUP	Neotropical	type
13	*australiae* (Kieffer, 1907)	ZSZM	Australian	literature
14	*avidus* (Evans, 1982)	ANIC	Australian	type
15	*baining* Colombo & Azevedo, 2020	MNHN	Oceanian	type
16	*baruya* Colombo & Azevedo, 2020	MNHN	Oceanian	type
17	*biangai* Colombo & Azevedo, 2020	MNHN	Oceanian	type
18	*biharina* Kurian, 1955	IFRI	Oriental	type
19	*bilibil* Colombo & Azevedo, 2020	MNHN	Oceanian	type

20	*blantoni* (Evans, 1965)	USNM	Neotropical	type
21	*breviventris* (Kieffer, 1906)	BMNH	Australian	type
22	*callosus* (Stein & Azevedo, 2007)	CNC	Neotropical	type
23	*caperatus* (Krombein, 1990)* from *Epyris*	USNM	Sino-Japanese	literature
24	*chambri* Colombo & Azevedo, 2020	MNHN	Oceanian	type
25	*circinnatus* (Rosmann & Azevedo, 2005)	MZSP	Neotropical	type
26	*clavatus* (Rosmann & Azevedo, 2005)	UFMG	Neotropical	type
27	*coeruleus* (Kieffer, 1906)	BMNH	Australian	type
28	†*concaptus* (Brues, 1933)	Konigsberg[?]	Baltic amber	literature
29	*concavus* (Stein & Azevedo, 2007)	CNC	Neotropical	type
30	*cyanosoma* (Evans, 1973)	IFML	Neotropical	type
31	*demissus* (Stein & Azevedo, 2007)	CNC	Neotropical	type
32	†*deploegi* Colombo & Azevedo, 2021	SIZK	Rovno amber	type
33	*duna* Colombo & Azevedo, 2020	MNHN	Oceanian	type
34	*enga* Colombo & Azevedo, 2020	MNHN	Oceanian	type
35	†*engeli* Colombo & Azevedo, 2021	PIN	Baltic amber	type
36	*erythrogaster* (Dodd, 1916)* from *Epyris*	SAM	Australian	literature
37	*etoro* Colombo & Azevedo, 2020	MNHN	Oceanian	type
38	*fasciatus* (Kieffer, 1906)* from *Epyris*	BMNH	Palaearctic	literature
39	*flavipennis* Kieffer, 1914	BMNH	Australian	type
40	*fore* Colombo & Azevedo, 2020	MNHN	Oceanian	type
41	*foveatus* (Cameron, 1905)	Lost[?]	Sri Lanka	literature
42	*fulgens* (Brues, 1907)	USNM	Nearctic, Neotropical	type
43	*fuscinervis* (Cameron, 1899)* from *Epyris*	BMNH[?]	Oriental	literature
44	*gadsup* Colombo & Azevedo, 2020	MNHN	Oceanian	type
45	†*gallicus* (Perrichot & Nel, 2008)	MNHN	Oise amber	type
46	*gogodala* Colombo & Azevedo, 2020	MNHN	Oceanian	type
47	*haroli* Colombo & Azevedo, 2020	MNHN	Oceanian	type
48	*hemipterus* (Kieffer, 1906)* from *Epyris*	Giraud Collection[?]	Palaearctic	literature
49	*hewa* Colombo & Azevedo, 2020	MNHN	Oceanian	type
50	†*hopei* Colombo & Azevedo, 2021	PIN	Baltic amber	type
51	*huli* Colombo & Azevedo, 2020	MNHN	Oceanian	type
52	*humboldti* (Vargas, 2001)	IAVH	Neotropical	type
53	*iatmul* Colombo & Azevedo, 2020	MNHN	Oceanian	type
54	†*invelatus* (Brues, 1933)	Konigsberg[?]	Baltic amber	literature
55	†*jouaulti* Colombo & Azevedo, 2021	SIZK	Rovno amber	type
56	*kaluli* Colombo & Azevedo, 2020	MNHN	Oceanian	type
57	*kongohyasha* (Terayama, 2005)* from *Epyris*	CNC	Oriental	literature
58	*koteka* Colombo & Azevedo, 2020	MNHN	Oceanian	type
59	*kwoma* Colombo & Azevedo, 2020	MNHN	Oceanian	type
60	*latimerus* (Magesky & Azevedo, 2001)	INPA	Neotropical	type
61	*latissimus* (Stein & Azevedo, 2007)	INPA	Neotropical	type
62	*litoralis* (Azevedo, 1992)	DCBU	Neotropical	type
63	*longiceps* (Kieffer, 1913)* from *Epyris*	Lost[?]	Oceanian	literature
64	*longifoveatus* (Azevedo, 1999)	DCBU	Neotropical	type
65	*longimerus* (Magesky & Azevedo, 2001)	INPA	Neotropical	type
66	*luteipennis* (Evans, 1965)	MCZC	Neotropical	type
67	*maisin* Colombo & Azevedo, 2020	MNHN	Oceanian	type
68	*manii* (Kurian, 1955)	IFRI	Oriental	literature

69	†*mckellari* Colombo & Azevedo, 2021	SIZK	Rovno amber	type
70	*metallicus* (Kieffer, 1908)* from *Epyris*	Baker collection[?]	Neotropical	literature
71	†*meunieri* Colombo & Azevedo, 2021	PIN	Baltic amber	type
72	*mexicanus* (Evans, 1965)* from *Epyris*	MCZC	Neotropical	type
73	*mirandus* (Evans, 1969)* from *Epyris*	USNM	Neotropical	type
74	*muscarius* (Westwood, 1874)	HMO	Neotropical	type
75	†*neli* Colombo & Azevedo, 2021	SIZK	Rovno amber	type
76	*nigerrimus* Evans, 1965	SEMC	Neotropical	literature
77	*obliquus* (Kieffer, 1922)* from *Epyris*	Baker collection[?]	Oceanian	literature
78	*obscuripennis* (Kieffer, 1910)* from *Epyris*	Baker collection[?]	Neotropical	literature
79	*ocultatus* (Rosmann & Azevedo, 2005)	DZUP	Neotropical	type
80	*opistolatus* (Magesky & Azevedo, 2001)	INPA	Neotropical	type
81	*origenus* (Kieffer, 1911)	BMNH	Neotropical	type
82	*pectinatus* (Magesky & Azevedo, 2001)	INPA	Neotropical	type
83	*peregrinus* (Evans, 1979)	ANIC	Australian	type
84	*perpulcher* (Evans, 1979)	ANIC	Australian	type
85	†*perrichoti* Colombo & Azevedo, 2021	PIN	Baltic amber	type
86	*platycephalus* (Westwood, 1874)	BMNH	Australian	literature
87	*pleurorrectus* (Magesky & Azevedo, 2001)	INPA	Neotropical	type
88	*puncticeps* (Evans, 1965)	CUIC	Neotropical	type
89	*pusana* Kurian, 1955	IFRI	Oriental	type
90	*quinquelineatus* (Kieffer, 1906)	CAS	Neotropical	type
91	*raripilus* Kieffer, 1922	Baker collection[?]	Oceanian	literature
92	*rufiventris* (Kieffer, 1907)	BMNH	Australian	type
93	*septemlineatus* (Kieffer, 1906)	CAS	Neotropical	type
94	†*setosus* (Brues, 1933)	Konigsberg[?]	Baltic amber	literature
95	*subangulatus* (Rosmann & Azevedo, 2005)	UFES	Neotropical	type
96	*subviridis* (Kieffer, 1911)	BMNH	Neotropical	type
97	*sulcatus* (Rosmann & Azevedo, 2005)	MZSP	Neotropical	type
98	*surinamensis* (Evans, 1969)	RMNH	Neotropical	type
99	*tarapachensis* (Vargas, 2001)	IAVH	Neotropical	type
100	*tricolor* (Evans, 1965)	USNM	Neotropical	type
101	*truncatus* (Kieffer, 1906)	BMNH	Australian	type
102	*unidens* Kieffer, 1922	Baker collection[?]	Oceanian	literature
103	*unifoveatus* (Rosmann & Azevedo, 2005)	MZSP	Neotropical	type
104	*vesculus* (Evans, 1965)	MCZC	Neotropical	type
105	*vesiculosus* (Azevedo, 1999)	KSUC	Neotropical	type
106	*violaceus* (Evans, 1965)	BMNH	Neotropical	type
107	*virescens* (Evans, 1965)	BMNH	Neotropical	type
108	*viridis* (Cameron, 1888)	BMNH	Neotropical	type
109	*viridissimus* (Kieffer, 1911)[1]	BMNH	Neotropical	type

Table 7. List of *Dolus*. *, type-species of *Dolus*; **, type-species of *Homoglenus*; ***, type-species of *Neodisepyris*. *, to be proposed as **comb. nov.**; **, to be proposed as **comb. rev.**; ***, to be proposed as **nom. rev. et.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*acutidens* (Kieffer, 1922)***** from *Epyris*	MNHN	Oceanian	type
2	*alachua* (Evans, 1969)***** from *Epyris*	USNM	Nearctic	type

3	*albipalpis* (Kieffer, 1906)***** from *Epyris*	CAS	Neotropical	type
4	*algoae* (Kieffer, 1911)* from *Epyris*	Brauns collection[?]	Afrotropical	literature
5	*alius* (Gorbatovsky, 1995)***** from *Epyris*	ZIN	Palaearctic	type
6	*amazonicus* (Evans, 1964)***** from *Epyris*	USNM	Neotropical	type
7	*apicalis* Motschulsky, 1863****** from *Epyris*	ZMUM	Saharo-Arabian	literature
8	*bombayensis* (Kurian, 1955)[3]***** from *Epyris*	IFRI	Oriental	type
9	*breviclypeatus* (Lim & Lee, 2011)***** from *Epyris*	SNU	Palaearctic	type
10	*carbunculus* (Nagy, 1970)***** from *Epyris*	Argaman collection[?]	Palaearctic	literature
11	*conjunctus* (Kieffer, 1905)***** from *Epyris*	HNM	Oriental	type
12	*cuprinus* (Evans, 1969)***** from *Epyris*	USNM	Neotropical	type
13	*darani* (Terayama, 2006)***** from *Epyris*	NIAES	Sino-Japanese	type
14	*deficiens* (Krombein, 1956)***** from *Epyris*	USNM	Nearctic	type
15	*depressigaster* (Evans 1966 [1965])***** from *Epyris*	BMNH	Neotropical	type
16	*despectus* (Kieffer, 1922)***** from *Epyris*	Baker collection[?]	Oceanian	literature
17	*duni* (Kurian, 1955)***** from *Epyris*	IFRI	Oriental	type
18	*duttai* (Kurian, 1955)***** from *Epyris*	IFRI	Oriental	type
19	*emiae* (Terayama, 2006)***** from *Epyris*	NIAES	Sino-Japanese	type
20	*enerteros* (Stein & Azevedo, 2011)***** from *Epyris*	MSNG	Oriental	type
21	*erythrocerus* (Kieffer, 1906)***** from *Epyris*	MNHN	Palaearctic	type
22	*exsculptus* (Evans, 1969)***** from *Epyris*	CMNH	Neotropical	type
23	*feai* (Kieffer, 1904)***** from *Epyris*	MSNG	Oriental	literature
24	*festivus* (Evans, 1969)***** from *Epyris*	USNM	Nearctic	literature
25	*finitus* (Lim & Lee, 2011)***** from *Epyris*	SNU	Palaearctic	type
26	*flavicrus* (Kieffer, 1910)***** from *Epyris*	ZMHB	Neotropical	type
27	*geniculatus* (Kieffer, 1904)***** from *Epyris*	MSNG	Afrotropical	literature
28	*gracilipennis* (Kieffer, 1904)***** from *Epyris*	MSNG	Afrotropical	literature
29	*indicus* (Kieffer, 1905)***** from *Epyris*	HNM	Oriental	literature
30	*inermis* (Kieffer, 1906)***** from *Epyris*	HNM	Palaearctic	type
31	*isthmicus* (Evans, 1969)***** from *Epyris*	USNM	Neotropical	type
32	*jugatus* (Evans, 1969)***** from *Epyris*	MCZC	Neotropical	type
33	*konishii* (Terayama, 1999)***** from *Epyris*	NIAES	Sino-Japanese	literature
34	*kuchingensis* (Cameron, 1910)***** from *Epyris*	BMNH	Oriental	type
35	*lienfuaensis* (Terayama, 2005)***** from *Epyris*	NSMT	Oriental	literature
36	*limatulus* (Lim & Lee, 2011)***** from *Epyris*	SNU	Palaearctic	type
37	*liukueiensis* (Terayama, 2005)***** from *Epyris*	NSMT	Oriental	literature
38	*lutescens* (Kieffer, 1905)***** from *Epyris*	MNHN	Australian	type
39	*mackenziei* (Kurian, 1955)***** from *Epyris*	IFRI	Oriental	type
40	*marcapata* (Evans, 1969)***** from *Epyris*	HKT	Neotropical	type
41	*maximus* (Berland, 1928)***** from *Epyris*	MNHN	Palaearctic	literature
42	*meifengensis* (Terayama, 2005)***** from *Epyris*	NSMT	Oriental	literature
43	*mixtecus* (Evans, 1969)***** from *Epyris*	HKT	Neotropical	type
44	*manticolus* (Ashmead, 1890)***** from *Epyris*	USNM	Nearctic, Neotropical	type
45	*mureungensis* (Lim & Lee, 2011)***** from *Epyris*	SNU	Palaearctic	literature
46	*nanshanchiensis* (Terayama, 2005)***** from *Epyris*	NSMT	Oriental	literature
47	*nantohensis* (Terayama, 2005)***** from *Epyris*	PMAE	Oriental	literature
48	*neotropicus* (Evans, 1964)***** from *Epyris*	USNM	Neotropical	type
49	*nigriculus* (Evans, 1969)***** from *Epyris*	MCZC	Neotropical	type
50	*nigrivirens* (Evans, 1973)***** from *Epyris*	AMNH	Neotropical	literature
51	*niwoh* (Terayama, 2006)***** from *Epyris*	HUS	Palaearctic, Sino-Japanese	type

52	*nubatama* (Terayama, 2006)***** from *Epyris*	NIAES	Sino-Japanese	type
53	*osanus* (Evans, 1969)***** from *Epyris*	AMNH	Neotropical	type
54	*otome* (Terayama, 1999)***** from *Epyris*	NIAES	Sino-Japanese	type
55	*pectinatus* (Terayama, 2006)***** from *Epyris*	HUS	Sino-Japanese	literature
56	*philippinensis* (Kieffer, 1913)***** from *Epyris*	Baker collection[?]	Oceanian	literature
57	*piceiventris* (Westwood, 1874)***** from *Epyris*	HMO	Australian	type
58	*pleuralis* (Kieffer, 1922)***** from *Epyris*	MNHN[?]	Oceanian	literature
59	*politus* Motschulsky, 1863[1]****** from *Epyris*	ZMUM	Saharo-Arabian	type
60	*psilommus* (Kieffer, 1922)***** from *Epyris*	Baker collection[?]	Oceanian	literature
61	*pusae* (Kurian, 1955)***** from *Epyris*	IFRI	Oriental	literature
62	*pusillus* (Evans, 1969)***, ***** from *Epyris*	MCZC	Neotropical	literature
63	*quadratus* (Kieffer, 1922)***** from *Epyris*	MNHN	Oceanian	type
64	*reitteri* (Kieffer, 1906)***** from *Epyris*	Reitter collection[?]	Palaearctic	literature
65	*rotundus* (Santos & Azevedo, 2003)***** from *Epyris*	DZUP	Neotropical	type
66	*schingeri* (Evans, 1969)***** from *Epyris*	CAS	Neotropical	type
67	*schwarzi* (Evans, 1969)***** from *Epyris*	USNM	Neotropical	type
68	*sculleni* (Evans, 1969)***** from *Epyris*	MCZC	Nearctic, Neotropical	type
69	*similis* (Bridwell, 1919)***** from *Epyris*	USNM	Oceanian	type
70	*squamosus* (Evans, 1969)***** from *Epyris*	MCZC	Neotropical	type
71	*stangei* (Evans, 1969)***** from *Epyris*	FIFML	Neotropical	type
72	*sublevis* (Kieffer, 1904)***** from *Epyris*	MSNG[?]	Palaearctic	literature
73	*subspinosus* (Kieffer, 1910)***** from *Epyris*	ZMHB	Neotropical	type
74	*tanoi* (Terayama, 2008)***** from *Epyris*	NIAES	Oceanian	type
75	*tenanus* (Evans, 1969)***** from *Epyris*	BPBM	Neotropical	type
76	*texanus* (Ashmead, 1893)***** from *Epyris*	USNM	Nearctic	type
77	*transversarius* (Zu, He & MA, 2003)***** from *Epyris*	Zhejiang University	Oriental	literature
78	*tripartitus* (Kieffer, 1904)[2]***** from *Epyris*	MSNG	Afrotropical	type
79	*unicarina* (Kieffer, 1922)***** from *Epyris*	Baker collection[?]	Oceanian	literature
80	*vierecki* (Krombein, 1962)***** from *Epyris*	USNM	Nearctic	type
81	*vogti* (Evans, 1969)***** from *Epyris*	USNM	Nearctic	type
82	*willinki* (Evans, 1969)***** from *Epyris*	FIFML	Neotropical	type
83	*yakushi* (Terayama, 2006)***** from *Epyris*	KUF	Sino-Japanese	literature
84	*zeteki* (Evans, 1969)***** from *Epyris*	USNM	Neotropical	type

Table 8. List of *Epyris*. [1], type-species of *Epyris*; [2], type-species of *Isobrachium*; [3], type-species of *Leptepyris*; [4], type-species of *Melanepyris*; [5], type-species of *Parepyris* Kieffer; [6], type-species of *Rhabdepyris*. *, to be proposed as **comb. nov.**; **, to be proposed as **comb. rev.**; ***, to be proposed as **nom. rev. et.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*asiaticus* (Kieffer, 1922)	MNHN	Oriental	type
2	*azevedoi* Tribull, 2016	ANIC	Australian	type
3	*bayeri* Hoffer, 1935	Hoffer collection	Palaearctic	literature
4	*bidens* Kieffer, 1922	MNHN	Oceanian	type
5	*bipunctatus* (Kieffer, 1922)	Baker collection[?]	Oceanian	literature
6	*brevipennis* Kieffer, 1906	MNHN	Palaearctic	literature
7	*carpenteri* Tribull, 2016	ANIC	Australian	type
8	*chasanicus* Gorbatovsky, 1995	RAS	Palaearctic	type
9	*claripennis* Kieffer, 1922	MNHN	Oceanian	type

10	*congolensis* Benoit, 1957	MRCB	Afrotropical	literature
11	*crassicornis* Walker, 1874	BMNH	Sino-Japanese	literature
12	*defectus* (Kieffer, 1922)	Baker collection[?]	Oceanian	literature
13	†*deletus* Brues, 1910	AMNH	Florissant Formation	type
14	*dilaticeps* (Benoit, 1957)	MRAC	Afrotropical	literature
15	*erraticus* Smith, 1860	Lost[?]	Oceanian	literature
16	*filiformis* Kieffer, 1914	Baker collection[?]	Oceanian	literature
17	*fulgeocauda* Tribull, 2016	QM	Australian	type
18	*fulvimanus* Kieffer, 1907	BMNH	Australian	type
19	*fuscipalpis* Kieffer, 1906	MNHN[?]	Palaearctic	literature
20	*fuscipes* (Kieffer, 1906)	en aout (Solari)[?]	Palaearctic	type
21	*hagoromonis* Terayama, 1999	NIAES	Sino-Japanese	literature
22	*herschae* Tribull, 2016	CNC	Australian	type
23	*hiten* Terayama, 2006	KUF	Sino-Japanese	literature
24	*imicola* (Kieffer, 1913)[4]	Lost[?]	Oceanian	literature
25	*indicae* (Kurian, 1955)	IFRI	Oriental	type
26	*interruptus* Kieffer, 1904[5]	MSNG	Oceanian	type
27	*jeonbukensis* Lim & Lee, 2011	SNU	Palaearctic	type
28	†*kiefferi* (Brues, 1933)	Königsberg[?]	Baltic amber	literature
29	*kurzenkoi* Gorbatovsky, 1995	RAS	Palaearctic	type
30	*leleji* Gorbatovsky, 1995	RAS	Palaearctic	type
31	*lippensi* Benoit, 1957	RMCB	Afrotropical	literature
32	*loisae* Tribull, 2016	ANIC	Australian	type
33	*longiantennatus* Lim & Lee, 2011	SNU	Palaearctic	type
34	*longicephalus* Terayama, 2005	NSMT	Palaearctic	type
35	*luzonicus* (Kieffer, 1913)	Baker collection[?]	Oceanian	literature
36	*macrocerus* Kieffer, 1906	HNM[?]	Palaearctic	literature
37	*macromma* Kieffer, 1906	HNM[?]	Palaearctic	literature
38	*malayanus* Terayama, 2005	PMAE	Oriental	literature
39	*mian* Colombo & Azevedo, 2020	MNHN	Oceanian	type
40	*min* Colombo & Azevedo, 2020	MNHN	Oceanian	type
41	*miroku* Terayama, 2006	NIAES	Sino-Japanese	type
42	*montanus* Kieffer, 1905	HNM	Oriental	literature
43	*motu* Colombo & Azevedo, 2020	MNHN	Oceanian	type
44	†*moulyi* Falières & Nel, 2018	MNHN	Oise amber	type
45	*mundugumor* Colombo & Azevedo, 2020	MNHN	Oceanian	type
46	*myrmecophilus* Kieffer, 1904[6]***	NHME	Palaearctic	literature
47	*neofiliformis* Azevedo, 2018[3]	Baker collection[?]	Oceanian	literature
48	*neoluzonicus* Azevedo, 2018	MNHN	Oceanian	literature
49	*niger* Westwood, 1832[1]	OUMNH	Palaearctic, Saharo-Arabian	type
50	*nigricornis* (Nees ab Esenbeck, 1834)[2]	Lost[?]	Palaearctic	literature
51	*ogea* Colombo & Azevedo, 2020	MNHN	Oceanian	type
52	*ovatus* Xu, He & Ma, 2003	Zhejiang University	Oriental	literature
53	*pallidinervis* (Kieffer, 1904)	Wasmann Collection [?]	Palaearctic	literature
54	*patnae* Kurian, 1955	IFRI	Oriental	type
55	*politiceps* Muesebeck, 1934	USNM	Oriental	literature
56	*pusillus* Kieffer, 1922	MNHN	Oceanian	type
57	*quaesitor* Kieffer, 1922	MNHN	Oceanian	type
58	†*rectinervis* (Cockerell, 1921)	BMNH	Bouldnor Formation	type

59	*rectinervis* (Cockerell, 1921)	BMNH	Bouldnor Formation	type
60	*ruficollis* Ashmead, 1903	USNM[?]	Oriental	literature
61	*rejectus* Kieffer, 1922	MNHN	Oceanian	type
62	*shohki* Terayama, 2006	NIAES	Sino-Japanese	literature
63	*striatus* Kieffer, 1904	MSNG[?]	Oriental	literature
64	*subramosus* Kieffer, 1922***	Baker collection[?]	Oceanian	literature
65	*tardus* Kieffer, 1906	HNM	Palaearctic	literature
66	*thaianus* Terayama, 2005	PMAE	Oriental	literature
67	†*tenellus* Statz, 1938	LACM	Rott Formation	type
68	*tibialis* Kieffer, 1906	MNHN[?]	Afrotropical	literature
69	*transversus* Kieffer, 1906	HNM[?]	Palaearctic	literature
70	*tricolor* Cameron, 1888	Lost[?]	Palaearctic	literature
71	*tridens* Kieffer, 1922	MNHN	Oceanian	type
72	*tridentatus* Kieffer, 1904	MSNG[?]	Afrotropical	literature
73	*troglodytes* Kieffer, 1922	MNHN	Oceanian	type
74	*truncatidens* (Kieffer, 1922)	MNHN	Oceanian	type
75	*viduatus* (Turner, 1928)	BMNH	Afrotropical	type
76	*voeltzkowii* (Kieffer, 1910)	ZMHB	Madagascan	literature
77	*wanei* Risbec, 1956	Lost[?]	Afrotropical	literature
78	*yakushimanus* Terayama, 1999	NIAES	Sino-Japanese	literature
79	*yamatonis* Terayama, 1999	NIAES	Sino-Japanese	type
80	*yasha* Terayama, 1999	NIAES	Sino-Japanese	type
81	*yetus* Lim & Lee, 2011	SNU	Palaearctic	type

Table 9. List of †*Gloxinius* species examined with emphasis on which types were analysed directly. [1], type-species.

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	†*bifossatus* (Brues, 1939)[1]	MCZC	Baltic amber	type

Table 10. List of *GenusB* to be proposed as **gen.n.** species examined with emphasis on which types were analysed directly. [1], type-species. *, to be proposed as **comb. nov.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*rufipes* (Say, 1824)[1]*	Lost[?]	Nearctic, Neotropical	literature

Table 11. List of *GenusA* to be proposed as **gen.n.** species examined with emphasis on which types were analysed directly. [1], type-species. *, to be proposed as **comb. nov.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*idaten* (Terayama, 2006)[1]*	NIAES	Sino-Japanese	type

Table 12. List of *Holepyris*. [1], type-species of *Holepyris*; [2], type-species of *Disepyris*; [3], type-species of *Formosiepyris*; [4], type-species of *Lytepyris*. *, to be proposed as **comb. nov.**; **, to be proposed as **comb. rev.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*abacinus* (Benoit, 1952)***** from *Disepyris*	MCSN	Saharo-Arabian	type
2	*africanus* Kieffer, 1904[1]	MCSN	Afrotropical	type

3	*agraensis* (Kurian, 1955)* from *Formosiepyris*	IFRI	Oriental	type
4	*algoaensis* Kieffer, 1911	Brauns collection[?]	Afrotropical	literature
5	*angusticollis* Kieffer, 1906	MNHN	Sino-Japanese	literature
6	*arabicus* (Barbosa & Azevedo, 2014)***** from *Disepyris*	UFES	Saharo-Arabian	type
7	*bergevini* Duchaussoy, 1916[1914]	Lost[?]	Saharo-Arabian	literature
8	*berlandi* (Benoit, 1963)***** from *Disepyris*	MNHN	Saharo-Arabian	literature
9	*bidentatus* Kieffer, 1904	MCSN	Palaearctic	literature
10	*biscrensis* (Kieffer, 1906)[4]* from *Disepyris*	HNM	Afrotropical	type
11	*crenulatus* Kieffer, 1906	HNM	Palaearctic	literature
12	*decipulus* (Benoit, 1952)***** from *Disepyris*	MCSN	Saharo-Arabian	type
13	*fasciipennis* Kieffer, 1906	MNHN	Palaearctic	literature
14	*fessus* (Lim & Azevedo, 2014)***** from *Disepyris*	UFES	Palaearctic	type
15	*fuscipennis* Kieffer, 1906	MNHN	Saharo-Arabian	literature
16	*guigliae* (Benoit, 1952)***** from *Disepyris*	MCSN	Saharo-Arabian	type
17	*hyacintho* (Barbosa & Azevedo, 2014)***** from *Disepyris*	UFES	Saharo-Arabian	type
18	*kenyaensis* (Lim & Azevedo, 2014)***** from *Disepyris*	NMKE	Afrotropical	type
19	*levicollis* Kieffer, 1906	HNM	Saharo-Arabian	literature
20	*lineatus* Kieffer, 1906	MNCNM[?]	Palaearctic	literature
21	*maculipennis* (Marshall, 1874)	BMNH[?]	Palaearctic	literature
22	*marishi* (Terayama, 2004)[3]***** from *Formosiepyris*	PMAE	Oriental	type
23	*mongoliaensis* (Lim & Azevedo, 2014)***** from *Disepyris*	UFES	Palaearctic	type
24	*natalensis* Kieffer, 1913	SAFM	Afrotropical	literature
25	*niveus* (Lim & Azevedo, 2014)***** from *Disepyris*	UFES	Saharo-Arabian	type
26	*orientalis* Kieffer, 1906	Lost[?]	Palaearctic	literature
27	*pallidinervis* (Cameron, 1907)***** from *Disepyris*	BMNH	Oriental	type
28	*prolatatus* (Lim & Azevedo, 2014)***** from *Disepyris*	UFES	Saharo-Arabian	type
29	*punctaticollis* Kieffer, 1906	MNHN	Palaearctic	literature
30	*rufipes* (Kieffer, 1905)[2]* from *Disepyris*	MNHN	Oriental	type
31	*rufitarsis* Kieffer, 1906	Lost[?]	Palaearctic	literature
32	*rugulosus* (Xu & He, 2005)***** from *Formosiepyris*	Zhejiang University	Oriental	literature
33	*semiruber* Kieffer, 1911** from *Disepyris*	Brauns collection[?]	Afrotropical	literature
34	*shiva* (Terayama, 2004)***** from *Formosiepyris*	RBCM	Oriental	type
35	*takasago* (Terayama, 2004)***** from *Formosiepyris*	NSMT	Oriental	type
36	*tibialis* Kieffer, 1906	MNHN	Palaearctic	literature
37	*vietnamensis* (Tsujii *et al.*, 2015)***** from *Formosiepyris*	ITLJ	Oriental	type
38	*vittatus* Turner, 1928	BMNH	Afrotropical	literature

Table 13. List of *Laelius*. The type-species of *Laelius* is *L. trogodermatis* Ashmead, 1893 (junior synonym of *L. centratus* Say). [1], type-species of *Allepyris*; [2], type-species of *Paralaelius*; [3], type-species of *Prolaelius*.

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*agraensis* Kurian, 1955	IFRI	Oriental	type
2	*akares* Barbosa & Azevedo, 2009	CAS	Madagascan	type
3	*anfractuosus* Benoit, 1952	MCSN	Saharo-Arabian	type

4	*anthrenivorus* Trani, 1909	IZUN	Palaearctic	literature
5	*antropovi* Gorbatovsky, 1995	Lost[?]	Palaearctic	literature
6	*arryni* Barbosa & Azevedo, 2014	MPEG	Neotropical	type
7	*baratheoni* Barbosa & Azevedo, 2014	UFES	Neotropical	type
8	*billi* Barbosa & Azevedo, 2014	CAS	Neotropical	type
9	*bipartitus* Kieffer, 1906	Perris collection [?]	Palaearctic	literature
10	*borealis* Vikberg, 2005	DABH	Palaearctic	literature
11	*brachistos* Barbosa & Azevedo, 2010	UFES	Saharo-Arabian	type
12	*canchinensis* (Azevedo, 1992)	DCBU	Neotropical	type
13	*centratus* (Say, 1836)	Lost [?]	Nearctic, Neotropical	literature
14	*elisae* Russo, 1938	IZUN [?]	Palaearctic	literature
15	*femoralis* (Förster, 1860)	DBAH	Palaearctic	literature
16	*firmipennis* (Cameron, 1905)[3]	Lost [?]	Afrotropical	literature
17	*foveaticeps* (Rosmann & Azevedo, 2005)	DZUP	Neotropical	type
18	*fulvipes* Kieffer, 1906	MCSN	Palaearctic	type
19	*fumimarginalis* Vikberg, 2005	NHRS	Palaearctic	literature
20	*glossinae* (Turner & Waterson, 1916)	BMNH	Afrotropical	type
21	*gracilis* (Evans, 1965)	CAS	Nearctic, Neotropical	type
22	*haplos* Barbosa & Azevedo, 2011	ANIC	Australian	type
23	*hirticulus* (Evans, 1965)	MCZC	Neotropical	type
24	*huachucae* (Evans, 1965)	MCZC	Nearctic	type
25	*jilinensis* Lim & Lee, 2010	SNU	Sino-Japanese	type
26	*lannisteri* Barbosa & Azevedo, 2014	INPA	Neotropical	type
27	*maboya* (Snelling, 1996)	LACM	Neotropical	type
28	*macfarlanei* Ward, 2013	NZAC	Australian	type
29	*martelli* Barbosa & Azevedo, 2014	UFES	Neotropical	type
30	*mekes* Barbosa & Azevedo, 2009	CASENT	Madagascan	type
31	*mellipes* (Evans, 1965)	USNM	Nearctic	literature
32	*mesitioides* (Duchaussoy, 1916[1914])	Lost [?]	Saharo-Arabian	literature
33	*microneurus* (Kieffer, 1906)[1]	MNHN	Palaearctic, Sino-Japanese	literature
34	*minutulus* (Evans, 1965)	USNM	Neotropical	type
35	*muesebecki* (Evans, 1965)	UNSM	Nearctic, Neotropical	type
36	*multilineatus* (Evans, 1965)	BPBM	Neotropical	type
37	*naniwaensis* Terayama, 2006	NIAES	Sino-Japanese	literature
38	*nigriscapus* (Evans, 1965)	CAS	Neotropical	literature
39	*nigrofemoratus* Terayama, 2006	NIAES	Sino-Japanese	type
40	*ogmos* Barbosa & Azevedo, 2011	QSBG	Oriental	type
41	†*pallidus* Brues, 1933	Lost [?]	Baltic amber	literature
42	*parcepilosus* Vikberg, 2005	DABH	Palaearctic	literature
43	*pedatus* (Say, 1836)[2]	Lost [?]	Nearctic, Neotropical	type
44	*perrisi* Kieffer, 1906	Perris collection [?]	Palaearctic	literature
45	†*preteritus* Barbosa & Azevedo, 2013	SIZK	Rovno amber	type
46	*quadrangulus* Barbosa & Azevedo, 2011	ANIC	Australian	type
47	†*rovnensis* Barbosa & Azevedo, 2013	SIZK	Rovno amber	type
48	*ruficrus* (Kieffer, 1906)	MCSN	Palaearctic	type
49	*rufipes* (Förster, 1860)	DBAH	Palaearctic	type
50	*seticornis* (Duchaussoy, 1916[1914])	Lost [?]	Saharo-Arabian	literature
51	*simplex* Evans, 1978	CAS	Nearctic	literature
52	*sinicus* Xu, He & Terayama, 2003	Zhejiang University	Sino-Japanese	literature

53	*starki* Barbosa & Azevedo, 2014	UFES	Neotropical	type
54	*targaryeni* Barbosa & Azevedo, 2014	UFES	Neotropical	type
55	*tibialis* Kieffer, 1906	Perris collection [?]	Palaearctic	literature
56	*titanokkos* Barbosa & Azevedo, 2011	QSBG	Oriental	type
57	*tullyi* Barbosa & Azevedo, 2014	UFES	Neotropical	type
58	*utilis* Cockerell, 1920	USNM	Nearctic	type
59	*versicolor* (Evans, 1970)	MCZC	Neotropical	type
60	*virilis* Vikberg, 2005	DABH	Palaearctic	literature
61	*voracis* Muesebeck, 1939	USNM	Nearctic, Oriental	type
62	*yamatonis* Terayama, 2006	NIAES	Sino-Japanese	type
63	*yokohamensis* Terayama, 2006	NIAES	Sino-Japanese	type

Table 14. List of *Muellerella*. [1], type-species of *Muellerella*; [2], type-species of *Acanthepyris*; [3], type-species of *Planepyris*; [4], type-species of *Pristobethylus*; [5], type-species of *Trachepyris*. *, to be proposed as **comb. nov.**; **, to be proposed as **comb. rev.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*amabilis* Saussure, 1892 [1890][1]** from *Epyris*	MHNG	Afrotropical	type
2	*appendiculatus* (Kieffer, 1913)[3]* from *Trachepyris*	MCSN	Afrotropical	type
3	*armatitarsis* (Kieffer, 1904)* from *Trachepyris*	MCSN	Saharo-Arabian	type
4	*breviscapus* (Kieffer, 1904)* from *Trachepyris*	MCSN	Afrotropical	type
5	*ceresensis* (Turner, 1928)* from *Trachepyris*	BMNH	Afrotropical	type
6	*crenaticollis* (Kieffer, 1912)* from *Trachepyris*	Fullerborn collection [?]	Afrotropical	literature
7	*flavipennis* (Kieffer, 1907)* from *Trachepyris*	BMNH	Australian	literature
8	*haemorrhoidalis* (Kieffer, 1911)* from *Trachepyris*	BMNH	Oriental	type
9	*hildebrandti* (Kieffer, 1912)[2]* from *Trachepyris*	ZMHB[?]	Afrotropical	type
10	*indicus* (Muesebeck, 1934)* from *Trachepyris*	USNM	Oriental	type
11	*levissimis* (Turner, 1928)* from *Trachepyris*	BMNH	Afrotropical	literature
12	*microphthalmus* (Turner, 1928) * from *Trachepyris*	BMNH	Afrotropical	literature
13	*sanctipauli* (Kurian, 1955)* from *Epyris*	IFRI	Oriental	type
14	*sarawakensis* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
15	*semiserratus* (Kieffer, 1911)* from *Trachepyris*	Brauns collection[?]	Afrotropical	literature
16	*serricolis* (Westwood, 1874)[4]* from *Trachepyris*	HMO	Afrotropical	literature
17	*spiniscapus* (Kieffer, 1904)* from *Trachepyris*	MCSN	Afrotropical	type
18	*spinosipes* (Kieffer, 1905)[5]* from *Trachepyris*	MNHN	Saharo-Arabian	type
19	*superbus* (Terayama, 2005)* from *Epyris*	PMAE	Oceanian, Oriental	literature
20	*torridus* (Kieffer, 1912)* from *Epyris*	ZMHB	Afrotropical	literature
21	*valens* (Kieffer, 1911)* from *Epyris*	BMNH	Oriental	type

Table 15. List of *Psilepyris*. The type-species of *Psilepyris* is *Epyris indivisus* Kieffer, 1906 (junior synonym of *E. clarimontis* Kieffer). *, to be proposed as **comb. nov.**; **, to be proposed as **comb. rev.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*aegyptius* (Kieffer, 1921)* from *Epyris*	NMW[?]	Afrotropical	literature
2	*aequalis* (Lim & Lee, 2011)* from *Epyris*	SNU	Palaearctic	type
3	*afer* (Magretti, 1884)* from *Epyris*	MSNG	Afrotropical	type
4	*agrensis* (Kurian, 1955)* from *Epyris*	IFRI	Oriental	literature

5	*alluaudi* (Kieffer, 1905)* from *Epyris*	MNHN	Afrotropical, Madagascan	literature
6	*apertus* (Kieffer, 1914)* from *Epyris*	Baker collection[?]	Oceanian	literature
7	*arcuatus* (Kieffer, 1906)* from *Epyris*	Marshall collection[?]	Palaearctic	literature
8	*asura* (Terayama, 2006)* from *Epyris*	NIAES	Sino-Japanese	type
9	*atayal* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
10	*berlandi* (Gordh & Móczár, 1990)* from *Epyris*	MNHN	Saharo-Arabian	literature
11	*bicolor* (Fouts, 1934)* from *Epyris*	USNM	Afrotropical	literature
12	*bilineatus* (Thomson, 1862[1861])* from *Epyris*	NRS	Palaearctic	type
13	*biroi* (Móczár, 1966)* from *Epyris*	HNM	Palaearctic	literature
14	*blandus* (Terayama, 2006)* from *Epyris*	NIAES	Sino-Japanese	type
15	*brachypterous* (Ashmead, 1893)* from *Epyris*	ZMB	Nearctic	literature
16	*caffrarius* (Kieffer, 1911)* from *Epyris*	Brauns collection[?]	Afrotropical	literature
17	*californicus* (Ashmead, 1893)* from *Epyris*	USNM	Nearctic, Neotropical	type
18	*cariniceps* (Evans, 1969)* from *Epyris*	CAS	Nearctic, Neotropical	literature
19	*clarimontis* (Kieffer, 1906)* from *Epyris*	CAS	Nearctic, Neotropical	literature
20	*connexus* (Evans, 1967)* from *Epyris*	MCZ	Nearctic	literature
21	*corcyraeus* (Kieffer, 1907)* from *Epyris*	BMNH	Palaearctic	type
22	*coriaceous* (Muesebeck, 1934)* from *Epyris*	USNM	Oriental	type
23	*corticinus* (Evans, 1969)* from *Epyris*	USNM	Nearctic	type
24	*crassifemur* (Evans, 1969)* from *Epyris*	MCZ	Neotropical	type
25	*cubanus* (Evans, 1966)* from *Epyris*	USNM	Neotropical	type
26	*delhiensis* (Kurian, 1955)* from *Epyris*	IFRI	Oriental	type
27	*distans* (Kieffer, 1922)* from *Epyris*	Baker collection[?]	Oceanian	literature
28	*dulicus* (Lim & Lee, 2011)* from *Epyris*	SNU	Palaearctic	type
29	*ebneri* (Kieffer, 1921)* from *Epyris*	NMW[?]	Afrotropical	literature
30	*egestus* (Benoit, 1952)* from *Epyris*	MSNG	Saharo-Arabian	literature
31	*elongatulus* (Turner & Waterson, 1917)* from *Epyris*	BMNH	Afrotropical	type
32	*evanescens* (Kieffer, 1906)* from *Epyris*	HNM	Palaearctic	literature
33	*extraneus* (Bridwell, 1917)* from *Epyris*	BPBM	Neotropical	literature
34	*fallax* (Benoit, 1957)* from *Epyris*	MNCB	Afrotropical	literature
35	*fuelleborni* (Kieffer, 1912)* from *Epyris*	ZMB	Afrotropical	literature
36	*fujianensis* (Xu, He & Ma, 2003)* from *Epyris*	Zhejiang University	Sino-Japanese	literature
37	*gaullei* (Kieffer, 1906)* from *Epyris*	MNHN[?]	Palaearctic	literature
38	*hangunensis* (Terayama, 2005)* from *Epyris*	NSMT	Palaearctic	literature
39	*hispanicus* (Cameron, 1881)* from *Epyris*	BMHN	Palaearctic	literature
40	*hottentottus* (Turner, 1928)* from *Epyris*	BMNH	Afrotropical	type
41	*insulanus* (Kieffer, 1906)* from *Epyris*	Marshall collection[?]	Palaearctic	literature
42	*karli* (Snelling, 1996)* from *Epyris*	LACM	Neotropical	type
43	*karnatakensis* (Terayama, 2005)* from *Epyris*	PMAE	Oriental	literature
44	*kichijo* (Terayama, 2006)* from *Epyris*	NIAES	Sino-Japanese	type
45	*kokuzoh* (Terayama, 2006)* from *Epyris*	NIAES	Sino-Japanese	literature
46	*laticeps* (Kieffer, 1913)* from *Epyris*	MSNG	Afrotropical	type
47	*laticrus* (Kieffer, 1911)* from *Epyris*	BMNH	Oriental	type
48	*longicollis* (Kieffer, 1906)* from *Epyris*	MNHN	Palaearctic	literature
49	*magniceps* (Kieffer, 1922)* from *Epyris*	Baker collection[?]	Oceanian	literature
50	*marshalli* (Kieffer, 1906)* from *Epyris*	Marshall collection[?]	Palearctic	literature
51	*mauritanicus* (Kieffer, 1910)* from *Epyris*	Lost[?]	Palearctic	literature
52	*miaoliensis* (Terayama, 2005)* from *Epyris*	TARI	Oriental	literature
53	*michaelseni* (Kieffer, 1914)* from *Epyris*	Lost[?]	Afrotropical	literature

54	*minoensis* (Terayama, 2006)* from *Epyris*	NIAES	Sino-Japanese	literature
55	*minor* (Kieffer, 1906)* from *Epyris*	HNM[?]	Palaearctic	literature
56	*muiri* (Turner & Waterson, 1917)* from *Epyris*	BMNH	Afrotropical	type
57	*multicarinatus* (Cameron, 1888)* from *Epyris*	BMNH	Neotropical	type
58	*myrmecophilus* (Brues, 1903)* from *Epyris*	MCZ	Nearctic	literature
59	*natalicola* (Kieffer, 1913)* from *Epyris*	SAFM	Afrotropical	literature
60	*neolaticeps* (Azevedo, 2018)* from *Epyris*	MNHN[?]	Afrotropical	literature
61	*nitidiceps* (Cameron, 1888)* from *Epyris*	BMNH	Neotropical	type
62	*oraniensis* (Duchaussoy, 1916[1914])* from *Epyris*	Lost[?]	Afrotropical	literature
63	*paraensis* (Kieffer, 1910)* from *Epyris*	CAS	Neotropical	type
64	*parallelus* (Evans, 1969)* from *Epyris*	IFML	Neotropical	type
65	*paramedius* (Correa & Azevedo, 2002)* from *Epyris*	UFES	Neotropical	type
66	*parvidens* (Kieffer, 1922)* from *Epyris*	Baker collection[?]	Oceanian	literature
67	*penatti* (Stein & Azevedo, 2011)* from *Epyris*	MSNG	Afrotropical	type
68	*perversus* (Benoit, 1957)* from *Epyris*	RMCB	Afrotropical	literature
69	*quinquecarinatus* (Kieffer, 1906)* from *Epyris*	MNHN	Palearctic, Afrotropical, Saharo-Arabian	literature
70	*raptor* (Kieffer, 1922)* from *Epyris*	Baker collection[?]	Oceanian	literature
71	*rhizoperthae* (Menon, Chatterjee & Sarup, 1959)* from *Epyris*	IARI	Oriental	literature
72	*rotundiceps* (Evans, 1969)* from *Epyris*	USNM	Neotropical	type
73	*ruficaudus* (Kieffer, 1913)* from *Epyris*	ISAM[?]	Afrotropical	literature
74	*rufimanus* (Kieffer, 1914)* from *Epyris*	AN collection	Palaearctic	literature
75	*sanctus* (Turner, 1928)* from *Epyris*	BMNH	Afrotropical	type
76	*septemcarinatus* (Evans, 1969)* from *Epyris*	RMNH	Neotropical	type
77	*sepulchralis* (Evans, 1969)* from *Epyris*	MCZ	Nearctic	type
78	*shishami* (Kurian, 1955)* from *Epyris*	IFRI	Oriental	literature
79	*silvestrii* (Kieffer, 1913)* from *Epyris*	Silvestri collection[?]	Afrotropical	literature
80	*sinaloa* (Evans, 1969)* from *Epyris*	CNC	Neotropical	type
81	*spissus* (Evans, 1969)* from *Epyris*	USNM	Nearctic	literature
82	*striatellus* (Evans, 1969)* from *Epyris*	CU	Neotropical	type
83	*subalatus* (Turner, 1928)* from *Epyris*	BMNH	Afrotropical	type
84	*sudosanensis* (Lim & Lee, 2011)* from *Epyris*	SNU	Palaearctic	type
85	*surusumi* (Terayama, 2006)* from *Epyris*	KUF	Sino-Japanese	literature
86	*tennyo* (Terayama, 2006)* from *Epyris*	KUF	Sino-Japanese	literature
87	*tricostatus* (Evans, 1969)* from *Epyris*	USNM	Nearctic	type
88	*variatus* (Correa & Azevedo, 2002)* from *Epyris*	UFES	Neotropical	type
89	*windhukiensis* (Kieffer, 1914)* from *Epyris*	ZMB[?]	Afrotropical	literature
90	*wittei* (Benoit, 1957)* from *Epyris*	RMCB	Afrotropical	literature

Table 16. List of *Rysepyris*. [1], type-species of *Rysepyris*; [2], type-species of *Misepyris*; [3], type-species of *Parepyris* Brèthes. *, to be proposed as **comb. nov.**; **, to be proposed as **comb. rev.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*aeki* (Terayama, 2005)* from *Holepyris*	PMAE	Oriental	literature
2	*aekoh* (Terayama, 2005)* from *Holepyris*	NSMT	Oriental	literature
3	*amamiinsulanus* (Terayama, 1999)* from *Holepyris*	NIAES	Sino-Japanese	type
4	*amplipennis* (Motschulsky, 1863)* from *Holepyris*	ZMUM	Oriental	literature

5	*andrei* (Kieffer, 1905)* from *Holepyris*	André collection[?]	Oriental	literature
6	*angulatus* (Xu, He & Ma, 2003)* from *Holepyris*	Zhejiang University	Oriental	literature
7	*atamensis* (Ashmead, 1904)* from *Holepyris*	USNM	Sino-Japanese	type
8	*atlanticus* (Benoit, 1976)* from *Holepyris*	MRAC	Afrotropical	type
9	*bakeri* (Kieffer, 1906)* from *Holepyris*	CAS	Nearctic	type
10	*benten* (Terayama, 2006)* from *Holepyris*	NIAES	Sino-Japanese	type
11	*bifasciatus* (Kieffer, 1907)* from *Holepyris*	BMNH	Australian	literature
12	*bimini* (Evans, 1977)* from *Holepyris*	AMNH	Neotropical	type
13	*biskranus* (Benoit, 1952)* from *Holepyris*	MCSN	Saharo-Arabian	type
14	*brevicarinatus* (Lim & Lee, 2010)* from *Holepyris*	SNU	Palaearctic	type
15	*breviceps* (Evans, 1977)* from *Holepyris*	USNM	Neotropical	type
16	*cameroni* (Evans, 1964)* from *Holepyris*	BMNH	Neotropical	type
17	*capax* (Evans, 1977)* from *Holepyris*	USNM	Neotropical	type
18	*capensis* (Kieffer, 1911)* from *Epyris*	Brauns collection[?]	Afrotropical	literature
19	*capicola* (Kieffer, 1911)* from *Holepyris*	Brauns collection[?]	Afrotropical	literature
20	*catalinae* (Evans, 1977)* from *Holepyris*	USNM	Nearctic	type
21	*cerostrotoideus* (Benoit, 1957)* from *Holepyris*	MRCB	Afrotropical	type
22	*cerostrototus* (Benoit, 1957)* from *Holepyris*	MRCB	Afrotropical	literature
23	*clytus* (Benoit, 1957)* from *Holepyris*	MRCB	Afrotropical	type
24	*coriaceus* (Evans, 1977)* from *Holepyris*	UCDC	Neotropical	type
25	*coronatus* (Ashmead, 1893)* from *Holepyris*	USNM[?]	Nearctic	literature
26	*crassus* (Evans, 1977)* from *Holepyris*	USNM	Nearctic, Neotropical	type
27	*crinitus* (Lim & Lee, 2010)* from *Holepyris*	SNU	Palaearctic	type
28	*cursor* Kieffer, 1906* from *Holepyris*	Lost[?]	Saharo-Arabian	literature
29	*daiitoku* (Terayama, 2005)* from *Holepyris*	PMAE	Oriental	literature
30	*dimidiatus* (Lim & Lee, 2010)* from *Holepyris*	SNU	Palaearctic	type
31	*dolichocephalus* (Turner, 1928)* from *Holepyris*	BMNH	Afrotropical	literature
32	*dubiosus* (Kieffer, 1922)* from *Holepyris*	Baker collection[?]	Oriental	literature
33	*dubius* (Kieffer, 1904)* from *Holepyris*	MCSN	Palaearctic	literature
34	*eminentus* (Gobbi & Azevedo, 2006)* from *Holepyris*	MPEG	Neotropical	type
35	*erythroderes* (Marshall, 1906)* from *Holepyris*	HNM	Palaearctic, Saharo-Arabian	literature
36	*evansi* (Xu, He & Ma, 2003)* from *Holepyris*	Zhejiang University	Oriental	literature
37	*exaratus* (Kieffer, 1913)* from *Holepyris*	Lost[?]	Oriental	literature
38	*floridanus* (Ashmead, 1887)* from *Holepyris*	USNM	Nearctic	type
39	*fulvus* (Xu, He & Ma, 2003)* from *Holepyris*	Zhejiang University	Oriental	literature
40	*fuscus* (Xu, He & Ma, 2003)* from *Holepyris*	Zhejiang University	Oriental	literature
41	*gaigherae* (Azevedo & van Noort, 2018)* from *Holepyris*	ISAM	Madagascan	type
42	*glabratus* (Fabricius, 1798)* from *Holepyris*	ZMC	Nearctic, Neotropical	type
43	*gouzanze* (Terayama, 2005)* from *Holepyris*	PMAE	Oriental	literature
44	*gracilentus* (Evans, 1977)* from *Holepyris*	CNC	Neotropical	type
45	*gracilis* (Kieffer, 1908)* from *Holepyris*	Lost[?]	Neotropical	literature
46	*graminis* (Evans, 1977)* from *Holepyris*	MCZC	Nearctic, Neotropical	type
47	*grandiceps* (Kieffer, 1921)* from *Holepyris*	Lost[?]	Oriental	literature
48	*gundari* (Terayama, 2005)* from *Holepyris*	PMAE	Oriental	literature
49	*gutianshanensis* (Xu, He & Ma, 2003)* from *Holepyris*	Zhejiang University	Oriental	literature
50	*habilis* (Evans, 1977)* from *Holepyris*	USNM	Nearctic	type
51	*haemorrhoidalis* (Kieffer, 1904)* from *Holepyris*	NRS	Nearctic	literature

52	*hispaniolae* (Evans, 1977)* from *Holepyris*	MCZC	Neotropical	type
53	*hospes* (Perkins, 1910)* from *Holepyris*	BPBM[?]	Neotropical	literature
54	*hotei* (Terayama, 2006)* from *Holepyris*	NIAES	Sino-Japanese	type
55	*hyalinipennis* (Kieffer, 1904)* from *Holepyris*	MCSN	Palearctic	literature
56	*incertus* (Ashmead, 1894)* from *Holepyris*	USNM	Neotropical	type
57	*inermis* (Kieffer, 1906)* from *Holepyris*	Magretti collection[?]	Palearctic	literature
58	*inops* (Evans, 1977)* from *Holepyris*	UCDC	Nearctic	literature
59	*kasparyani* (Gorbatovsky, 1995)* from *Holepyris*	RAS	Palearctic	type
60	*kuchingensis* (Cameron, 1910)* from *Holepyris*	BMNH[?]	Oriental	literature
61	*lautus* (Evans, 1977)* from *Holepyris*	MCZC	Nearctic, Neotropical	type
62	*lavagnei* (Duchaussoy, 1916[1914])* from *Holepyris*	Lost[?]	Palearctic	literature
63	*longicephalus* (Lim & Lee, 2010)* from *Holepyris*	SNU	Palearctic	type
64	*longiceps* (Kieffer, 1913)* from *Holepyris*	Baker collection[?]	Oriental	literature
65	*longicollis* (Cameron, 1888)* from *Holepyris*	BMNH	Neotropical	type
66	*longulus* (Evans, 1977)* from *Holepyris*	MCZC	Neotropical	type
67	*macilentus* (Xu, He & Ma, 2003)* from *Holepyris*	Zhejiang University	Oriental	literature
68	*matsumurai* (Terayama, 1999)* from *Holepyris*	NIAES	Sino-Japanese	literature
69	*mboroi* (Risbec, 1956)* from *Epyris*	MNHN	Afrotropical	type
70	*micidus* (Evans, 1977)* from *Holepyris*	USNM	Nearctic, Neotropical	type
71	*minimus* (Magretti, 1897)* from *Holepyris*	MCSN	Oriental	literature
72	†*minor* (Brues, 1939)* from *Holepyris*	MCZC	Baltic amber	type
73	*montandoni* (Duchaussoy, 1916[1914])* from *Holepyris*	Lost[?]	Palearctic	literature
74	*montivagus* (Evans, 1977)* from *Holepyris*	MCZC	Neotropical	literature
75	*mucro* (Lim & Lee, 2010)* from *Holepyris*	SNU	Palearctic	type
76	*multidentatus* (Kieffer, 1911)* from *Holepyris*	BMNH	Saharo-Arabian	literature
77	*multo* (Lim & Lee, 2010)* from *Holepyris*	SNU	Palearctic	type
78	*napocaensis* (Nagy, 1968)* from *Holepyris*	AN collection	Palearctic	literature
79	*neglectus* (Kieffer, 1906)* from *Holepyris*	HNM	Palearctic	literature
80	†*neodubius* (Azevedo, 2018)* from *Holepyris*	Lost[?]	Baltic amber	literature
81	*nigerrimus* (Kieffer, 1906)* from *Holepyris*	MNHN	Palearctic	literature
82	*numidicus* Kieffer, 1906[1]* from *Holepyris*	Lost[?]	Saharo-Arabian	literature
83	*omotoensis* (Terayama, 1999)* from *Holepyris*	NIAES	Sino-Japanese	type
84	*opacicollis* (Motschulsky, 1863)* from *Holepyris*	ZMUM	Oriental	literature
85	*opacus* (Kieffer, 1906)* from *Holepyris*	MNHN	Saharo-Arabian	literature
86	*orokaiva* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
87	*parvus* (Magretti, 1897)* from *Holepyris*	MCSN	Oriental	literature
88	*pauper* (Evans, 1977)* from *Holepyris*	UCR	Nearctic, Neotropical	type
89	*pauxillus* (Evans, 1977)* from *Holepyris*	CAS	Nearctic	type
90	*pedestris* Kieffer, 1904* from *Holepyris*	MCSN	Palearctic	literature
91	*philippinensis* (Kieffer, 1922)* from *Holepyris*	Baker collection[?]	Oriental	literature
92	†*planiceps* (Brues, 1933)* from *Holepyris*	Lost[?]	Baltic amber	literature
93	*plebejus* (Benoit, 1957)* from *Holepyris*	MRCB	Afrotropical	type
94	*pondo* (Turner, 1928)* from *Holepyris*	BMNH	Afrotropical	literature
95	*precursor* (Brues, 1933)* from *Holepyris*	Lost[?]	Baltic amber	literature
96	*pygmaeus* (Ashmead, 1895)* from *Holepyris*	BMNH	Neotropical	literature
97	†*rasnitsyni* (Colombo & Azevedo, 2021)* from *Holepyris*	PIN	Baltic amber	type
98	*remotus* (Kieffer, 1911)[2]* from *Holepyris*	BMNH	Nearctic, Neotropical	type

99	*robustus* (Brues, 1933)* from *Holepyris*	Lost[?]	Baltic amber	literature
100	*ruficollis* (Kieffer, 1906)* from *Holepyris*	HNM	Saharo-Arabian	literature
101	*ruficornis* Kieffer, 1906* from *Holepyris*	Lost[?]	Saharo-Arabian	literature
102	*rwindius* (Benoit, 1957)* from *Holepyris*	MRCB	Afrotropical	type
103	*sambia* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
104	*scorteus* (Evans, 1977)* from *Holepyris*	USNM	Nearctic, Neotropical	type
105	*seidakka* (Terayama, 2005)* from *Holepyris*	NSMT	Oriental	literature
106	*shamensis* (Terayama, 2005)* from *Holepyris*	NIAES	Oriental	type
107	*sinensis* (Xu, He & Ma, 2003)* from *Holepyris*	Zhejiang University	Oriental	literature
108	*skip* (Snelling, 1996)* from *Holepyris*	LACM	Neotropical	type
109	*strigosus* (Evans, 1977)* from *Holepyris*	UCDC	Neotropical	type
110	*subapterus* (Melander & Brues, 1903)* from *Holepyris*	MCZC	Nearctic	literature
111	*subtilis* (Evans, 1977)* from *Holepyris*	USNM	Nearctic, Neotropical	type
112	*susanowo* (Terayama, 1999)* from *Holepyris*	NIAES	Sino-Japanese	type
113	*swagap* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
114	*sylvanidis* (Brèthes, 1913)[3]* from *Holepyris*	BMNH	Neotropical	type
115	*sylvaticus* Turner, 1928* from *Holepyris*	BMNH[?]	Afrotropical	literature
116	*tairora* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
117	*telefol* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
118	*tenuis* (Evans, 1977)* from *Holepyris*	CNC	Neotropical	type
119	†*terayamai* (Colombo & Azevedo, 2021)* from *Holepyris*	SIZK	Rovno amber	type
120	*thailandensis* (Terayama, 2005)* from *Holepyris*	NIAES	Oriental	type
121	*tricarinatus* (Kieffer, 1906)* from *Holepyris*	MNHN	Palearctic	literature
122	*troglodytes* (Turner & Waterson, 1917)* from *Holepyris*	BMNH[?]	Afrotropical	literature
123	*tsembaga* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
124	*tsugaruensis* (Terayama, 2006)* from *Holepyris*	NIAES	Sino-Japanese	type
125	*turrialbae* (Evans, 1977)* from *Holepyris*	USNM	Neotropical	type
126	*ulmi* (Szabo, 1960)* from *Holepyris*	HNM	Palearctic	literature
127	*vagneri* (Kieffer, 1914)* from *Holepyris*	ZMHB[?]	Afrotropical	literature
128	*vison* (Evans, 1970)* from *Holepyris*	CNC	Neotropical	type
129	*wiru* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
130	*yaifo* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type
131	*yambaru* (Terayama, 1999)* from *Holepyris*	NIAES	Sino-Japanese	type
132	*yebis* (Terayama, 2006)* from *Holepyris*	NIAES	Sino-Japanese	type
133	*zia* (Colombo & Azevedo, 2020)* from *Holepyris*	MNHN	Oceanian	type

Table 17. List of *Trissepyris* species examined with emphasis on which types were analysed directly. [1], type-species. *, to be proposed as **comb. rev.**

#	SPECIES	COLLECTION	OCURRENCE	STUDY
1	*ruficeps* Kieffer, 1905[1]* from *Epyris*	MNHN	Afrotropical	type

Table 18. Species that will be transferred from Epyrinae to other subfamilies of Bethylidae.

#	SPECIES	COLLECTION	OCURRENCE	STUDY
	Pristocerinae			
1	*Pristocera amatorius* (Cameron, 1897)* from *Epyris*	BMNH[?]	Oriental	literature
2	*Propristocera foveatus* (Kieffer, 1904)* from *Epyris*	MSNG	Palaearctic	type
	Scleroderminae			
3	*Plastanoxus tricristatus* (Ward, 2013)* from *Epyris*	NZAC	Australian	literature

Table 19. Species mislisted in *Epyris* by previous studies.

#	SPECIES	COLLECTION	OCURRENCE	REMARKS
1	*Mesitius apterus* (Cameron, 1888)	BMNH	Saharo-Arabian	Transferred by Kieffer (1905)
2	*Cleptidea scutellaris* (Cameron, 1887)	BMNH	Neotropical	Transferred for Chrysididae by Kimsey & Bohart (1991)

SUPPLEMENTARY MATERIAL. Morphological matrix.

TAXA/CHARACTERS	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6
Outgroup																										
Allobethylus tomoae	1	1	1	0	0	0	0	1	0	0	0	1	1	0	1	1	1	0	0	2	1	2	1	2	0	0
Apenesia sp. 1	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	0	1	0	0	2	1	1	1	4	0	1
Cephalonomia sp. 1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	2	1	0	1	2	0	0
Cephalonomia sp. 2	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	2	1	0	1	2	0	0
Eleganesia elegans	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	0	1	0	1	2	1	1	1	3	0	1
Eupsenella diemenensis	1	1	1	1	0	1	0	1	0	2	0	0	1	0	1	2	1	0	0	2	1	1	1	3	0	1
Goniozus japonicus	1	1	1	1	0	1	0	1	0	2	0	0	1	0	1	2	1	0	0	2	1	1	1	3	1	1
Sulcomesitius sp. 1	1	0	1	1	0	4	1	1	0	0	0	0	1	0	1	2	1	1	1	0	1	1	1	1	0	1
Ingroup																										
Anisepyris sp. 1	1	1	1	1	0	2	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	3	0	0
Anisepyris sp. 2	1	1	1	1	0	2	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	3	0	0
Anisepyris sp. 3	1	1	1	1	0	3	0	1	0	1	0	0	0	0	1	0	1	0	0	1	1	0	1	4	0	0
Anisepyris sp. 4	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	1	1	1	1	4	0	0
Anisepyris sp. 5	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	3	0	0
Anisepyris sp. 6	1	1	1	1	0	2	0	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1	1	4	0	0
Anisepyris sp. 7	1	1	1	1	0	2	0	1	0	1	0	0	0	0	0	1	1	0	0	1	1	1	1	4	0	0
Anisepyris sp. 8	1	1	1	1	0	3	0	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1	1	4	0	0
Anisepyris sp. 9	1	1	1	1	0	3	0	1	0	1	0	0	1	0	0	1	1	0	0	2	1	1	1	4	0	1
Aspidepyris austrinus	1	1	1	1	0	3	0	0	0	1	0	0	2	0	1	1	1	0	1	2	1	1	1	2	0	0
Bakeriella flavicornis	1	1	1	1	0	2	0	1	0	0	0	1	1	0	1	1	1	0	1	1	1	1	1	4	0	0
Bakeriella sp. 1	1	1	1	1	0	2	0	1	0	0	0	1	1	0	0	1	1	0	1	2	1	1	1	4	0	0
Bakeriella sp. 2	1	1	1	1	0	2	0	1	0	0	0	1	1	0	1	1	1	0	1	1	1	1	1	4	0	0
Bakeriella sp. 3	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	1	2	1	1	1	4	0	0
Bakeriella sp. 4	1	1	1	1	0	1	0	1	0	0	0	1	0	0	1	1	1	0	1	2	1	1	1	4	0	0
Calyozina nepalensis	1	1	2	1	0	3	1	0	0	1	0	0	2	0	1	1	1	0	0	1	1	0	1	3	0	0
Calyozina ramicornis	1	1	2	1	0	1	1	0	0	1	0	0	2	0	1	1	1	0	0	1	1	0	1	?	?	?
Chlorepyris viridissimus	1	1	1	1	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1	2	1	0	1	3	0	0
Chlorepyris sp. 1	1	1	1	1	0	3	0	1	0	1	0	0	0	0	1	1	1	0	1	2	1	0	1	4	0	0
Chlorepyris sp. 2	1	1	1	1	0	3	0	1	0	0	0	0	1	0	1	1	1	0	1	2	1	1	1	4	0	0
Chlorepyris sp. 3	1	1	1	1	0	2	0	1	0	0	0	0	0	0	1	1	1	0	0	2	1	1	1	4	0	0
Chlorepyris sp. 4	1	1	2	1	0	2	0	1	1	0	0	0	0	0	1	1	1	0	0	2	1	0	1	4	0	0
Chlorepyris sp. 5	1	1	1	1	0	2	0	1	0	0	0	0	0	0	1	1	1	0	1	2	1	0	1	4	0	0
Chlorepyris sp. 6	1	1	1	1	0	2	0	1	0	1	0	0	0	0	1	1	1	0	1	2	1	0	1	4	0	0
Chlorepyris sp. 7	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	1	2	1	0	1	4	0	0
Chlorepyris sp. 8	1	1	1	1	0	2	0	1	0	1	0	0	1	0	0	1	1	0	1	1	1	0	1	4	0	0
Chlorepyris sp. 9	1	1	1	1	0	2	0	1	0	1	0	0	1	0	0	1	1	0	1	2	1	0	1	4	0	0
Chlorepyris sp. 10	1	1	1	1	0	2	0	1	0	1	0	0	1	0	0	1	1	0	1	2	1	1	1	4	1	1
Chlorepyris sp. 11	1	1	1	1	0	3	0	1	0	1	0	0	1	0	0	1	1	0	1	2	1	1	1	3	0	0
Chlorepyris sp. 12	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	1	1	1	1	4	0	0
Chlorepyris sp. 13	1	1	1	1	0	2	0	1	0	1	0	0	1	0	0	1	1	0	1	2	1	1	1	3	0	1
Chlorepyris sp. 15	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	4	0	1
Chlorepyris sp. 16	1	1	1	1	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	2	1	1	1	4	0	0
Chlorepyris sp. 17	1	1	1	1	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	2	1	1	1	4	0	1
Chlorepyris sp. 18	1	1	1	1	0	2	0	1	0	1	0	0	0	0	0	1	1	0	1	2	1	1	1	4	0	0
Chlorepyris sp. 19	1	1	1	1	0	?	0	1	0	1	0	0	1	0	0	1	1	0	1	2	1	1	1	4	0	0
Chlorepyris sp. 20	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	1	1	0	0	2	1	0	1	4	0	0
Disepyris sp. 1	1	1	1	1	0	3	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	2	1	3	0	0
Disepyris sp. 2	1	1	1	1	0	3	0	1	0	0	0	0	1	0	0	0	1	0	0	2	1	2	0	2	0	0
Disepyris sp. 3	1	1	1	1	0	0	0	1	0	0	0	0	2	0	0	1	0	0	0	1	1	2	0	2	0	1
Epyris (*staphyl.*) sp. 1	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	1	2	1	2	1	0	-	-
Epyris (*staphyl.*) sp. 2	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	1	2	1	2	1	0	-	-
Epyris (*staphyl.*) sp. 3	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	2	1	2	1	0	-	-
Epyris (*staphyl.*) sp. 4	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	1	1	1	0	1	4	0	1
Epyris (*staphyl.*) sp. 5	1	1	1	1	0	2	0	1	0	1	0	1	0	0	1	1	1	0	1	1	1	1	1	0	-	-
Epyris (*staphyl.*) sp. 6	1	1	2	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	2	1	0	1	2	0	1
Epyris (*staphyl.*) sp. 7	1	1	2	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	2	1	0	1	2	0	1
Epyris (*staphyl.*) sp. 8	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	1	1	1	2	1	0	-	-
Epyris (*staphyl.*) sp. 10	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	2	1	0	-	-
Epyris (*staphyl.*) sp. 11	1	1	2	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	1	1	0	1	3	0	1
Epyris (*staphyl.*) sp. 12	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	1	1	1	2	1	0	-	-
Epyris (*staphyl* .) sp. 13	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	1	1	0	1	3	0	0
Epyris (*staphyl.*) sp. 14	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	2	1	2	1	0	-	-
Epyris afer	1	1	1	1	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	2	1	1	1	3	0	1
Epyris niger	1	1	1	1	0	3	0	1	0	1	0	0	2	0	1	1	1	0	0	1	1	1	1	4	0	0
Epyris ruficeps	1	1	1	1	0	0	1	1	0	1	0	0	2	0	0	0	1	0	1	0	1	0	0	2	0	1
Epyris sp. 1	1	1	1	1	0	3	0	1	2	1	0	0	2	0	0	0	1	0	0	2	1	0	1	4	0	0
Epyris sp. 2	1	1	1	1	0	3	0	1	2	1	0	0	2	0	0	0	1	0	0	2	1	0	1	4	0	0
Epyris sp. 3	1	1	1	1	0	3	0	1	2	1	0	0	0	0	0	0	1	0	0	2	1	0	1	4	0	0
Epyris sp. 4	1	1	1	1	0	3	0	1	2	1	0	0	2	0	0	0	1	0	1	1	1	0	1	3	0	1
Epyris rufipes	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	2	1	0	1	3	0	1
Epyris sp. 6	1	1	1	1	0	?	0	1	0	1	0	1	1	0	1	0	?	0	0	1	1	2	1	0	-	-
Epyris sp. 7	1	1	1	1	0	3	0	1	0	1	0	0	2	0	1	1	1	0	0	1	1	0	1	3	0	0

	2			3										4										5	
TAXA/CHARACTERS	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**
Outgroup																									
Allobethylus tomoae	1	0	0	-	1	0	1	-	-	0	3	1	1	-	0	0	2	0	1	1	0	1	1	1	1
Apenesia sp. 1	1	0	0	-	1	0	1	-	-	0	0	0	0	0	0	0	2	0	1	1	0	1	2	2	0
Cephalonomia sp. 1	1	0	0	-	1	0	1	-	-	0	2	0	1	-	0	2	2	0	1	0	0	1	1	1	1
Cephalonomia sp. 2	1	0	0	-	1	0	1	-	-	0	2	0	1	-	0	0	2	1	1	0	0	1	1	2	1
Eleganesia elegans	1	0	0	-	1	0	1	-	-	0	0	1	0	0	0	0	2	0	1	1	0	1	2	2	0
Eupsenella diemenensis	1	0	0	-	1	0	1	-	-	1	1	0	0	2	1	0	1	0	0	1	0	1	2	0	0
Goniozus japonicus	1	0	0	-	1	0	1	-	-	1	1	0	0	2	0	0	1	0	0	0	0	1	2	0	0
Sulcomesitius sp. 1	1	0	0	-	1	1	1	-	-	1	0	1	0	2	0	0	2	0	1	1	2	0	2	0	0
Ingroup																									
Anisepyris sp. 1	1	0	0	-	1	1	1	-	-	1	1	0	0	2	1	-	-	0	1	1	0	0	2	2	1
Anisepyris sp. 2	1	0	0	-	1	1	1	-	-	1	1	0	0	2	1	-	-	0	1	1	0	0	2	2	1
Anisepyris sp. 3	1	0	0	-	1	1	0	0	0	1	1	0	0	2	1	-	-	0	1	1	1	0	2	2	1
Anisepyris sp. 4	1	0	0	-	1	1	0	0	0	1	1	0	0	2	1	-	-	0	1	1	1	0	2	2	1
Anisepyris sp. 5	1	0	0	-	1	1	1	-	-	1	1	0	0	2	1	-	-	0	1	1	1	0	2	2	1
Anisepyris sp. 6	1	0	0	-	1	1	0	0	0	1	1	0	0	2	1	-	-	0	1	1	1	0	2	2	1
Anisepyris sp. 7	1	0	0	-	1	1	0	0	0	1	1	0	0	2	1	-	-	0	1	1	1	0	2	2	1
Anisepyris sp. 8	1	0	0	-	1	1	0	0	0	1	1	0	0	2	1	-	-	0	1	1	1	0	2	2	1
Anisepyris sp. 9	1	0	0	-	1	1	0	0	0	1	1	0	0	2	1	-	-	0	1	1	0	0	2	2	1
Aspidepyris austrinus	1	0	0	-	0	1	0	0	0	1	0	0	0	1	0	0	1	1	1	1	2	0	2	0	0
Bakeriella flavicornis	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	2	1	2	2	0
Bakeriella sp. 1	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Bakeriella sp. 2	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Bakeriella sp. 3	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Bakeriella sp. 4	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Calyozina nepalensis	1	0	0	-	1	0	1	-	-	1	0	0	0	2	0	1	1	0	1	1	0	1	2	0	0
Calyozina ramicornis	?	?	0	-	1	?	1	-	-	1	0	0	0	2	0	1	1	0	1	1	0	1	2	2	0
Chlorepyris viridissimus	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 1	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	2	2	0
Chlorepyris sp. 2	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	2	2	0
Chlorepyris sp. 3	1	0	0	-	1	1	0	1	0	1	1	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 4	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 5	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 6	1	0	0	-	1	0	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 7	1	0	0	-	1	0	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 8	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 9	1	0	0	-	1	1	0	0	0	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 10	0	1	0	-	1	1	0	0	0	1	2	0	0	1	0	1	2	0	1	1	2	0	2	2	0
Chlorepyris sp. 11	1	0	0	-	1	1	?	?	?	1	1	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Chlorepyris sp. 12	1	0	0	-	1	1	0	0	0	1	0	0	0	1	0	1	2	0	1	1	2	0	2	2	0
Chlorepyris sp. 13	0	1	0	-	1	0	0	0	0	1	0	0	0	1	0	1	2	0	1	1	0	0	2	2	0
Chlorepyris sp. 15	0	1	0	-	1	0	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	1	?	?	0
Chlorepyris sp. 16	1	0	0	-	1	1	0	0	0	1	0	0	0	1	0	1	2	0	1	1	2	1	2	2	1
Chlorepyris sp. 17	1	0	0	-	1	0	1	-	-	1	0	0	0	1	0	1	2	0	1	1	1	0	2	2	1
Chlorepyris sp. 18	1	0	0	-	1	0	1	-	-	1	0	0	0	1	0	1	2	0	1	1	1	1	2	2	0
Chlorepyris sp. 19	1	0	0	-	1	0	0	0	0	1	0	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Chlorepyris sp. 20	0	0	0	-	1	0	0	0	0	1	1	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Disepyris sp. 1	1	0	0	-	1	1	0	0	0	1	0	0	0	2	0	1	1	1	1	1	1	0	2	2	0
Disepyris sp. 2	1	0	0	-	1	1	0	0	0	1	0	0	0	2	0	1	1	1	1	1	0	0	2	2	0
Disepyris sp. 3	1	0	0	-	1	1	0	0	0	1	0	0	0	2	0	1	1	1	1	1	0	0	2	2	0
Epyris (*staphyl.*) sp. 1	-	-	0	-	1	1	0	0	0	1	1	0	0	1	1	-	-	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 2	-	-	0	-	1	1	0	0	0	1	1	0	0	1	1	-	-	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 3	-	-	0	-	1	1	0	0	0	1	1	0	0	1	1	-	-	1	1	1	2	0	2	2	1
Epyris (*staphyl.*) sp. 4	0	1	1	1	1	0	?	?	?	1	2	0	0	1	1	-	-	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 5	-	-	0	-	1	0	?	?	?	1	1	0	0	1	1	-	-	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 6	1	1	0	-	1	1	0	0	0	1	1	0	0	1	1	-	-	1	1	1	0	0	2	2	0
Epyris (*staphyl.*) sp. 7	1	1	0	-	1	1	0	0	0	1	1	0	0	1	1	-	-	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 8	-	-	0	-	1	0	0	0	0	1	1	0	0	1	1	-	-	1	1	1	0	1	2	2	0
Epyris (*staphyl.*) sp. 10	-	-	0	-	1	0	0	0	0	1	1	0	0	1	1	-	-	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 11	1	0	0	-	1	1	0	0	0	1	1	0	0	1	0	0	1	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 12	-	-	0	-	1	1	0	0	0	1	1	0	0	1	1	-	-	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 13	1	0	0	-	1	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	2	0	2	2	0
Epyris (*staphyl.*) sp. 14	-	-	0	-	1	0	0	0	0	1	0	0	0	1	0	0	2	1	1	1	2	0	2	2	1
Epyris afer	1	0	1	1	1	1	1	-	-	1	0	0	0	2	0	0	1	0	1	1	1	0	2	2	0
Epyris niger	1	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	2	0	2	2	0
Epyris ruficeps	1	0	0	-	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	1	2	1	2	0	0
Epyris sp. 1	1	0	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	1	2	2	0
Epyris sp. 2	1	0	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	1	2	2	0
Epyris sp. 3	1	0	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	1	2	2	0
Epyris sp. 4	1	0	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	2	1	2	2	0
Epyris rufipes	1	0	0	-	1	1	0	0	0	1	0	0	0	1	0	1	1	1	1	1	2	1	2	2	1
Epyris sp. 6	-	-	0	-	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	2	2	0
Epyris sp. 7	1	0	0	-	1	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	2	1	2	2	0

TAXA/CHARACTERS	52	3	4	5	6	7	8	9	60	1	2	3	4	5	6	7	8	9	70	1	2	3	4	5	6
Outgroup																									
Allobethylus tomoae	1	0	1	1	1	1	1	0	0	0	1	0	2	1	0	0	2	1	1	1	-	-	0	0	0
Apenesia sp. 1	1	0	0	0	0	0	-	-	-	0	1	0	2	1	0	0	2	1	1	0	1	1	1	-	0
Cephalonomia sp. 1	0	0	1	1	1	0	-	-	-	0	1	0	2	1	0	1	2	1	1	1	-	-	1	-	0
Cephalonomia sp. 2	0	0	1	1	1	1	0	1	0	0	1	0	2	1	0	1	2	1	1	1	-	-	1	-	0
Eleganesia elegans	1	0	0	0	0	0	-	-	-	0	1	0	2	1	0	0	2	1	1	1	-	-	1	-	0
Eupsenella diemenensis	1	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	1	1	1	1	-	-	1	-	0
Goniozus japonicus	1	0	1	0	0	1	1	1	0	0	1	0	0	1	0	2	1	1	1	1	-	-	1	-	0
Sulcomesitius sp. 1	1	1	1	0	0	1	0	1	0	0	1	2	2	1	2	0	2	1	1	1	-	-	1	-	1
Ingroup																									
Anisepyris sp. 1	1	1	1	0	0	1	1	1	0	0	1	0	1	1	1	0	2	1	1	0	0	1	0	0	0
Anisepyris sp. 2	1	1	1	0	0	1	1	1	0	0	1	0	1	1	1	0	2	1	1	0	0	1	0	0	0
Anisepyris sp. 3	1	1	1	0	0	1	1	1	0	0	1	2	1	1	1	0	1	1	1	1	-	-	0	0	0
Anisepyris sp. 4	1	1	1	0	0	1	0	1	0	0	1	2	1	1	1	0	2	1	1	0	0	1	0	1	0
Anisepyris sp. 5	1	1	1	0	0	1	1	1	0	0	1	1	2	1	1	0	2	1	1	0	0	1	0	0	0
Anisepyris sp. 6	1	1	1	0	0	1	1	1	0	0	1	1	2	1	1	0	2	1	1	0	0	1	0	0	0
Anisepyris sp. 7	1	1	1	0	0	1	1	1	0	0	1	2	1	1	1	0	2	1	1	1	-	-	0	0	0
Anisepyris sp. 8	1	1	1	0	0	1	0	1	0	0	1	2	2	1	1	0	2	1	1	0	0	1	0	0	0
Anisepyris sp. 9	1	1	1	0	0	1	0	1	0	0	1	2	2	1	1	0	2	1	1	0	0	1	0	0	0
Aspidepyris austrinus	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1	2	1	0	0	1	-	-	1	-	0
Bakeriella flavicornis	1	0	0	0	0	1	0	1	0	0	1	0	1	1	1	2	1	1	1	0	0	1	0	0	1
Bakeriella sp. 1	1	0	0	0	0	1	1	1	0	0	1	0	2	1	1	2	1	1	1	1	-	-	0	0	0
Bakeriella sp. 2	1	0	1	0	0	1	0	1	0	0	1	0	1	1	1	2	1	1	1	1	-	-	0	0	0
Bakeriella sp. 3	1	0	0	0	0	1	0	1	0	0	1	0	2	1	1	2	1	1	1	0	0	0	0	0	1
Bakeriella sp. 4	1	0	1	0	0	1	0	1	0	0	1	0	2	1	1	2	1	1	1	0	0	0	0	0	1
Calyozina nepalensis	1	0	1	0	0	1	0	1	0	0	1	0	2	1	2	0	2	1	0	1	-	-	1	-	0
Calyozina ramicornis	1	0	1	0	0	1	0	1	0	0	1	0	2	1	2	0	2	1	0	1	-	-	1	-	0
Chlorepyris viridissimus	1	0	1	0	0	1	0	1	2	1	1	1	1	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 1	1	0	1	0	0	1	0	1	2	1	1	1	0	1	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 2	1	0	1	0	0	1	0	1	0	1	1	1	0	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 3	1	0	1	0	0	1	0	1	1	1	1	1	0	1	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 4	1	0	1	0	0	1	0	1	0	1	1	1	0	1	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 5	1	0	1	0	1	1	0	1	2	1	1	1	0	1	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 6	1	0	1	1	1	1	0	1	2	1	1	1	0	1	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 7	1	0	1	1	1	1	0	1	2	1	1	1	1	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 8	1	0	0	0	0	0	-	-	-	0	1	0	1	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 9	1	0	0	1	1	1	0	1	2	0	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 10	1	0	0	1	1	1	0	1	0	0	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 11	1	0	0	0	0	1	0	1	2	0	1	0	1	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 12	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 13	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 15	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 16	1	0	0	0	0	1	0	1	2	1	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 17	1	0	0	0	0	1	0	1	0	1	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 18	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 19	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0
Chlorepyris sp. 20	1	0	0	0	0	1	0	1	0	0	1	0	0	1	0	2	1	1	1	1	-	-	1	-	0
Disepyris sp. 1	1	0	1	0	1	1	0	1	2	0	1	2	1	1	0	2	2	1	1	1	-	-	0	0	0
Disepyris sp. 2	1	0	1	0	1	1	0	1	0	0	1	2	1	1	0	2	2	1	1	1	-	-	0	0	0
Disepyris sp. 3	1	0	1	0	1	1	0	1	0	0	1	2	1	1	0	2	2	1	1	1	-	-	0	0	0
Epyris (*staphyl.*) sp. 1	1	0	0	0	1	1	0	1	0	1	1	0	1	1	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 2	1	0	0	0	1	1	0	1	0	1	1	0	1	1	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 3	1	0	0	0	1	1	0	1	0	1	1	0	1	1	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 4	1	0	0	0	0	1	0	1	2	1	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 5	1	0	0	0	1	1	0	1	2	0	1	0	1	0	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 6	1	0	0	0	1	1	0	1	2	0	1	1	2	1	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 7	1	0	0	0	1	1	0	1	2	0	1	1	2	0	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 8	1	0	0	0	1	1	0	1	2	0	1	1	2	1	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 10	1	0	0	0	1	1	0	1	2	0	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 11	1	0	0	0	1	1	0	1	2	0	1	1	2	1	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 12	1	0	0	0	1	1	0	1	2	0	1	1	2	0	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 13	1	0	0	0	1	1	0	1	0	0	1	0	1	1	0	2	1	1	1	1	-	-	1	-	0
Epyris (*staphyl.*) sp. 14	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	2	1	1	1	1	-	-	1	-	0
Epyris afer	1	0	0	0	0	1	0	1	2	0	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0
Epyris niger	1	0	0	0	0	1	0	1	0	0	1	0	2	1	0	2	1	1	1	1	-	-	1	-	0
Epyris ruficeps	1	0	0	0	1	1	0	1	0	0	0	1	2	0	0	2	?	1	1	1	-	-	1	-	0
Epyris sp. 1	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	1	1	1	1	1	-	-	1	-	0
Epyris sp. 2	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	1	1	1	1	1	-	-	1	-	0
Epyris sp. 3	1	0	0	0	0	1	0	1	2	0	1	0	0	1	0	1	1	1	1	1	-	-	1	-	0
Epyris sp. 4	1	0	0	0	0	1	0	1	2	0	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0
Epyris rufipes	0	0	1	0	0	1	0	1	2	1	1	0	0	0	0	1	1	1	1	1	-	-	1	-	0
Epyris sp. 6	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	1	1	1	1	-	-	1	-	0
Epyris sp. 7	1	0	0	0	0	1	1	1	0	0	1	0	1	1	0	2	1	1	1	1	-	-	1	-	0

TAXA/CHARACTERS	7 7	8	9	8 0	1	2	3	4	5	6	7	8	9	9 0	1	2	3	4	5	6	7	8	9	1 0 0	1
Outgroup																									
Allobethylus tomoae	-	1	0	1	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	0	1	0
Apenesia sp. 1	-	1	1	0	2	1	1	0	0	0	1	0	1	0	1	-	1	-	0	0	0	0	1	0	1
Cephalonomia sp. 1	-	0	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	0
Cephalonomia sp. 2	-	0	-	-	-	-	-	1	-	-	0	0	-	-	-	-	-	1	2	0	0	0	1	1	0
Eleganesia elegans	-	1	1	0	2	1	0	0	0	0	1	0	1	0	1	-	1	-	0	0	0	0	1	0	0
Eupsenella diemenensis	-	1	0	1	0	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	0	1	1
Goniozus japonicus	-	0	-	-	-	-	-	0	2	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1
Sulcomesitius sp. 1	0	1	1	0	1	2	1	0	1	1	1	0	1	1	1	-	1	1	0	0	0	0	0	1	1
Ingroup																									
Anisepyris sp. 1	-	1	0	0	1	2	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	1	1	1	1
Anisepyris sp. 2	-	1	0	0	1	2	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	1	1	1	1
Anisepyris sp. 3	-	1	0	0	1	2	1	0	1	1	1	1	1	2	1	-	1	-	2	0	0	1	1	1	1
Anisepyris sp. 4	-	1	0	0	1	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	0	1	1
Anisepyris sp. 5	-	1	1	0	1	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	0	1	1
Anisepyris sp. 6	-	1	0	0	1	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Anisepyris sp. 7	-	1	1	0	1	1	1	0	1	1	1	0	1	2	1	-	1	-	0	0	0	0	0	1	1
Anisepyris sp. 8	-	1	0	0	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Anisepyris sp. 9	-	1	0	0	2	1	1	0	1	1	1	0	1	2	1	-	1	-	0	0	0	0	1	1	1
Aspidepyris austrinus	-	1	0	0	2	2	1	0	1	1	0	0	-	-	-	-	-	0	0	1	0	0	0	1	1
Bakeriella flavicornis	1	1	0	0	2	2	0	0	0	1	0	0	-	-	-	-	-	0	1	1	0	0	1	1	1
Bakeriella sp. 1	-	1	1	0	2	1	1	0	0	1	0	0	-	-	-	-	-	0	1	1	0	0	1	1	1
Bakeriella sp. 2	-	1	1	0	2	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	1	1	1
Bakeriella sp. 3	1	1	1	0	2	1	1	0	0	1	0	0	-	-	-	-	-	0	1	1	0	0	1	1	1
Bakeriella sp. 4	1	1	1	0	2	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	1	1	1
Calyozina nepalensis	-	1	1	0	2	2	1	0	0	0	0	0	-	-	-	-	-	0	0	1	0	0	1	1	1
Calyozina ramicornis	-	1	1	0	2	2	0	0	0	0	0	0	-	-	-	-	-	0	0	1	0	0	1	1	1
Chlorepyris viridissimus	-	1	1	0	2	2	1	0	1	1	1	0	1	0	1	-	1	-	0	0	0	0	0	1	1
Chlorepyris sp. 1	-	1	0	0	2	2	1	0	0	1	1	0	1	0	1	-	1	-	0	0	0	0	1	1	1
Chlorepyris sp. 2	-	1	0	0	2	2	1	0	1	1	1	0	1	0	1	-	1	-	0	0	0	0	1	1	1
Chlorepyris sp. 3	-	1	0	0	2	2	1	0	0	1	1	0	1	0	1	-	1	-	0	0	0	0	0	1	1
Chlorepyris sp. 4	-	1	0	0	2	2	1	0	0	1	1	0	1	0	1	-	1	-	0	0	0	0	0	1	1
Chlorepyris sp. 5	-	1	0	0	2	2	1	0	0	1	1	0	1	0	1	-	1	-	0	0	0	0	1	1	1
Chlorepyris sp. 6	-	1	1	0	2	2	1	0	1	1	1	0	1	0	1	-	1	-	0	0	0	0	1	1	1
Chlorepyris sp. 7	-	1	1	0	2	2	1	0	1	1	1	0	1	0	1	-	1	-	2	0	0	0	0	1	1
Chlorepyris sp. 8	-	1	1	1	2	2	1	0	1	1	1	0	1	0	1	-	1	-	2	0	0	0	0	1	1
Chlorepyris sp. 9	-	1	1	1	2	2	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 10	-	1	1	1	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	0	1	1
Chlorepyris sp. 11	-	1	1	1	2	1	1	0	1	1	1	0	0	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 12	-	1	1	0	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 13	-	1	1	1	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	0	1	1
Chlorepyris sp. 15	-	1	0	0	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 16	-	1	0	1	0	0	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 17	-	1	0	1	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 18	-	1	1	0	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 19	-	1	1	0	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Chlorepyris sp. 20	-	1	1	0	2	1	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1
Disepyris sp. 1	-	1	1	1	0	0	-	0	2	1	1	0	0	0	0	0	1	-	-	-	0	0	0	1	1
Disepyris sp. 2	-	1	1	1	0	0	-	0	2	1	1	0	0	0	0	1	1	-	-	-	0	0	0	1	1
Disepyris sp. 3	-	1	1	1	0	0	-	0	0	1	1	0	0	0	0	1	1	-	-	-	0	0	0	1	1
Epyris (*staphyl.*) sp. 1	-	1	1	0	2	1	1	0	1	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 2	-	1	1	0	2	1	1	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 3	-	1	1	0	2	1	1	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 4	-	1	1	0	2	2	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 5	-	1	1	0	2	2	1	0	1	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 6	-	1	1	0	2	2	1	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 7	-	1	1	0	2	2	1	0	1	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 8	-	1	1	0	2	2	1	0	1	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 10	-	1	1	0	2	2	1	0	1	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 11	-	1	1	0	2	2	1	0	0	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 12	-	1	1	0	2	2	1	0	1	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 13	-	1	1	0	2	2	1	0	1	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris (*staphyl.*) sp. 14	-	1	1	1	2	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1
Epyris afer	-	1	1	0	2	2	0	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1
Epyris niger	-	1	1	0	2	1	1	0	1	1	0	0	-	-	-	-	-	0	1	1	0	0	1	1	1
Epyris ruficeps	-	1	1	0	2	2	0	0	0	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1
Epyris sp. 1	-	1	1	1	2	1	1	0	1	1	0	1	-	-	-	-	-	1	3	1	0	0	1	1	1
Epyris sp. 2	-	1	1	1	2	1	1	0	1	1	0	1	-	-	-	-	-	1	3	1	0	0	1	1	1
Epyris sp. 3	-	1	1	1	2	1	1	0	1	1	0	1	-	-	-	-	-	1	3	1	0	0	1	1	1
Epyris sp. 4	-	1	1	0	2	1	1	0	1	1	0	0	-	-	-	-	-	1	3	1	0	0	1	1	1
Epyris rufipes	-	1	1	0	2	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1
Epyris sp. 6	-	1	1	0	2	1	0	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1
Epyris sp. 7	-	1	1	0	2	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1

TAXA/CHARACTERS	10 2	3	4	5	6	7	8	9	11 0	1	2	3	4	5	6	7	8	9	12 0	1	2	3	4	5	6
Outgroup																									
Allobethylus tomoae	0	0	0	0	0	0	0	0	0	0	1	0	-	-	-	-	-	-	1	-	-	-	1	-	1
Apenesia sp. 1	0	0	1	0	0	1	-	1	-	0	0	0	-	-	-	-	-	-	1	-	-	-	1	-	1
Cephalonomia sp. 1	0	1	1	1	-	1	-	1	-	1	-	0	-	-	-	-	-	-	1	-	-	-	1	-	1
Cephalonomia sp. 2	0	1	1	1	-	1	-	1	-	0	1	0	-	-	-	-	-	-	1	-	-	-	1	-	1
Eleganesia elegans	0	0	0	1	-	1	-	1	-	0	0	0	-	-	-	-	-	-	1	-	-	-	1	-	1
Eupsenella diemenensis	0	0	1	1	-	1	-	1	-	0	1	0	-	-	-	-	-	-	0	0	0	1	1	-	1
Goniozus japonicus	0	0	0	0	0	1	-	1	-	1	-	0	-	-	-	-	-	-	1	-	-	-	1	-	1
Sulcomesitius sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	2	1	0	0	0
Ingroup																									
Anisepyris sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2	0	-	-	0	0	0	1	0	0	1
Anisepyris sp. 2	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2	0	-	-	0	0	0	1	0	0	1
Anisepyris sp. 3	0	0	0	0	0	0	0	0	0	0	0	1	2	2	-	-	-	-	0	0	0	1	0	0	1
Anisepyris sp. 4	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	0	-	-	0	0	0	1	0	0	1
Anisepyris sp. 5	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	0	2	1	0	0	0	1	0	0	1
Anisepyris sp. 6	0	0	0	0	0	1	-	1	-	0	0	1	2	1	-	-	-	-	0	0	0	2	0	0	1
Anisepyris sp. 7	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Anisepyris sp. 8	0	0	0	0	0	0	0	0	1	0	0	1	2	0	-	-	-	-	0	0	0	1	1	-	1
Anisepyris sp. 9	0	0	0	0	0	0	0	0	1	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Aspidepyris austrinus	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	2	2	0	0	1
Bakeriella flavicornis	0	0	0	0	0	0	1	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Bakeriella sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1
Bakeriella sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1
Bakeriella sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1
Bakeriella sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1
Calyozina nepalensis	0	0	0	0	0	0	0	0	0	0	0	1	2	1	2	1	2	1	0	0	0	1	0	0	1
Calyozina ramicornis	0	0	0	0	0	0	0	0	0	0	0	1	2	1	2	0	-	-	0	0	0	1	0	1	1
Chlorepyris viridissimus	0	0	0	0	0	0	0	0	1	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 2	0	0	0	0	0	0	0	0	1	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1
Chlorepyris sp. 3	0	0	0	0	0	0	0	0	1	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1
Chlorepyris sp. 4	0	0	0	0	0	0	0	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 5	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 6	1	-	0	0	0	0	0	0	1	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 7	0	0	0	0	0	0	0	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 8	0	0	0	0	0	1	-	0	0	0	0	1	1	1	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 9	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 10	0	0	0	0	0	1	-	0	0	0	0	1	2	2	-	-	-	-	0	0	0	1	0	1	1
Chlorepyris sp. 11	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	0	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 12	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 13	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 15	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 16	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 17	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 18	0	0	0	0	0	1	-	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 19	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Chlorepyris sp. 20	0	0	0	0	0	1	-	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Disepyris sp. 1	0	0	0	0	0	0	0	1	-	0	0	0	-	-	-	-	-	-	0	0	2	1	0	0	1
Disepyris sp. 2	0	0	0	0	0	0	0	1	-	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Disepyris sp. 3	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	-	-	-	-	0	0	2	1	0	0	1
Epyris (*staphyl.*) sp. 2	0	0	0	0	0	1	-	0	0	0	0	1	2	0	-	-	-	-	0	0	2	1	0	0	1
Epyris (*staphyl.*) sp. 3	0	0	0	0	0	1	-	0	0	0	0	1	2	0	-	-	-	-	0	0	2	1	0	0	1
Epyris (*staphyl.*) sp. 4	0	0	0	0	0	1	-	0	0	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1
Epyris (*staphyl.*) sp. 5	0	0	0	0	0	1	-	0	0	0	0	1	2	1	1	0	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 6	0	0	0	0	0	1	-	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 7	0	0	0	0	0	1	-	0	0	0	0	1	2	1	1	0	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 8	0	0	0	0	0	0	1	0	0	0	0	1	2	0	-	-	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 10	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	0	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 11	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	0	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 12	0	0	0	0	0	1	-	0	0	0	0	1	2	0	2	0	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 13	0	0	0	0	0	0	1	0	0	0	0	1	2	0	1	0	-	-	0	0	0	1	0	0	1
Epyris (*staphyl.*) sp. 14	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	2	0	0	1
Epyris afer	0	0	0	0	0	0	0	0	0	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1
Epyris niger	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1
Epyris ruficeps	0	0	0	0	0	1	-	1	-	0	0	0	-	-	-	-	-	-	0	0	2	1	0	0	1
Epyris sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	2	0	0	1
Epyris sp. 2	0	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	-	0	0	0	2	0	0	1
Epyris sp. 3	0	0	0	0	0	0	1	0	0	0	0	1	0	-	-	-	-	-	0	0	0	2	1	-	1
Epyris sp. 4	0	0	0	0	0	1	-	0	0	0	0	1	2	2	2	2	2	2	0	0	0	0	0	0	1
Epyris rufipes	0	0	0	0	0	1	-	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	0	0	1
Epyris sp. 6	0	0	0	0	0	1	-	0	1	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1
Epyris sp. 7	0	0	0	0	0	1	-	0	0	0	0	1	2	2	2	2	-	-	0	0	0	1	0	0	1

TAXA/CHARACTERS	127	8	9	130	1	2	3	4	5	6	7	8	9	140	1	2	3	4	5	6	7	8	9	150	1	2
Outgroup																										
Allobethylus tomoae	1	1	0	-	1	0	1	-	-	1	-	-	0	0	1	-	-	-	0	1	1	-	0	1	0	0
Apenesia sp. 1	2	0	1	0	1	2	0	0	1	1	-	-	1	-	0	0	-	1	0	1	1	-	0	0	0	0
Cephalonomia sp. 1	1	1	0	-	1	0	1	-	-	1	-	-	1	-	1	-	-	-	0	1	1	-	0	1	0	0
Cephalonomia sp. 2	1	1	0	-	1	0	1	-	-	1	-	-	1	-	1	-	-	-	0	1	1	-	0	1	0	0
Eleganesia elegans	2	0	0	0	1	2	0	0	1	1	-	-	1	-	0	0	-	1	0	1	1	-	0	0	0	0
Eupsenella diemenensis	0	0	1	0	1	1	0	0	1	1	-	-	0	0	0	1	0	1	0	0	0	1	1	0	0	0
Goniozus japonicus	0	1	1	0	1	1	0	0	1	1	-	-	0	0	0	1	0	1	0	0	0	1	1	0	0	0
Sulcomesitius sp. 1	2	0	1	0	1	1	0	0	1	1	-	-	0	0	0	1	0	1	1	0	1	-	1	0	0	0
Ingroup																										
Anisepyris sp. 1	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	1	1	1	0	0	1	-	1	0	0	0
Anisepyris sp. 2	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	1	1	1	0	0	1	-	1	0	0	0
Anisepyris sp. 3	0	0	1	0	0	2	0	0	1	1	-	-	0	0	0	0	1	1	0	0	1	-	1	0	0	0
Anisepyris sp. 4	0	0	1	0	0	2	0	0	1	1	-	-	0	0	0	1	1	1	1	0	1	-	1	0	0	0
Anisepyris sp. 5	0	0	1	0	0	2	0	0	1	1	-	-	0	0	0	0	1	1	0	0	1	-	1	0	0	0
Anisepyris sp. 6	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	1	1	1	1	0	1	-	1	0	0	0
Anisepyris sp. 7	0	0	1	0	0	2	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	-	1	0	0	0
Anisepyris sp. 8	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	1	1	1	1	0	1	-	1	0	0	0
Anisepyris sp. 9	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	0	1	1	1	0	1	-	1	0	0	0
Aspidepyris austrinus	0	1	1	0	0	1	0	0	1	0	1	1	0	0	1	-	-	-	1	0	0	0	1	0	0	0
Bakeriella flavicornis	0	1	1	0	0	2	0	0	2	0	1	1	0	0	0	0	1	1	0	1	1	-	1	0	0	0
Bakeriella sp. 1	0	1	1	0	0	1	0	0	1	0	1	1	0	0	1	-	1	-	0	0	1	-	1	0	0	0
Bakeriella sp. 2	0	1	1	0	0	2	0	0	1	0	1	1	0	0	1	-	1	-	0	0	1	-	1	0	0	0
Bakeriella sp. 3	0	1	1	0	0	2	0	0	3	0	1	1	0	0	1	-	-	-	1	0	1	-	1	0	0	1
Bakeriella sp. 4	0	1	1	0	0	1	0	0	3	0	1	1	0	0	1	-	-	-	1	0	1	-	1	0	0	1
Calyozina nepalensis	0	1	1	1	0	2	0	0	2	1	-	-	0	1	0	0	1	1	0	1	0	1	1	0	0	0
Calyozina ramicornis	0	1	1	1	0	?	?	?	?	1	-	-	0	1	0	0	1	1	0	1	0	0	?	?	0	0
Chlorepyris viridissimus	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	1	1	-	1	1	0	0
Chlorepyris sp. 1	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	-	?	?	0	0
Chlorepyris sp. 2	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	1	1	-	1	1	0	0
Chlorepyris sp. 3	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	1	-	1	1	0	0
Chlorepyris sp. 4	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	-	1	1	0	0
Chlorepyris sp. 5	0	1	1	0	0	2	0	0	1	0	1	0	0	0	0	1	1	0	0	1	1	-	1	1	0	0
Chlorepyris sp. 6	0	1	1	0	0	2	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	-	1	1	0	0
Chlorepyris sp. 7	0	1	1	0	0	2	0	0	1	0	1	0	0	0	1	-	-	-	1	0	1	-	1	1	0	0
Chlorepyris sp. 8	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	-	1	1	0	0
Chlorepyris sp. 9	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	1	-	1	1	0	0
Chlorepyris sp. 10	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	1	-	1	0	0	0
Chlorepyris sp. 11	0	0	1	0	0	0	0	0	1	1	-	-	0	1	0	0	0	1	0	0	1	-	1	0	0	0
Chlorepyris sp. 12	0	0	1	0	0	0	0	0	1	1	-	-	0	0	1	-	-	-	1	0	1	-	1	0	0	0
Chlorepyris sp. 13	0	0	1	0	0	2	0	0	1	0	1	0	0	1	0	0	0	1	1	0	1	-	1	0	0	0
Chlorepyris sp. 15	0	0	1	0	0	2	0	0	1	?	?	?	0	1	?	?	?	?	?	?	?	?	1	0	0	0
Chlorepyris sp. 16	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1	-	1	0	0	0
Chlorepyris sp. 17	0	0	1	0	0	2	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	-	1	0	0	0
Chlorepyris sp. 18	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	-	1	0	0	0
Chlorepyris sp. 19	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	-	1	0	0	0
Chlorepyris sp. 20	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	-	?	?	?	?
Disepyris sp. 1	2	1	1	1	0	2	0	0	2	1	-	-	0	1	0	0	0	1	1	0	1	-	1	0	1	1
Disepyris sp. 2	2	1	1	1	0	2	0	0	1	1	-	-	0	0	0	0	0	1	1	0	1	-	1	0	0	0
Disepyris sp. 3	2	1	1	1	0	2	0	0	1	1	-	-	0	0	0	0	0	1	1	0	1	-	1	0	1	1
Epyris (*staphyl.*) sp. 1	0	1	1	0	0	2	0	0	1	0	1	1	0	0	0	1	1	1	1	0	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 2	0	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 3	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	-	0	1	0	0
Epyris (*staphyl.*) sp. 4	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1
Epyris (*staphyl.*) sp. 5	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 6	0	1	1	0	0	2	0	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 7	0	1	1	0	0	2	0	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 8	0	1	1	0	0	2	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 10	0	1	1	0	0	2	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 11	0	1	1	0	0	2	0	0	2	0	1	0	0	0	0	0	1	1	1	1	1	-	1	1	0	0
Epyris (*staphyl.*) sp. 12	0	1	1	0	0	2	0	0	1	0	1	0	0	0	0	1	1	1	1	1	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 13	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0
Epyris (*staphyl.*) sp. 14	0	0	1	0	0	2	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1
Epyris afer	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1
Epyris niger	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0
Epyris ruficeps	0	1	1	0	0	2	0	0	?	0	1	0	0	0	0	0	0	1	1	1	1	-	1	0	0	0
Epyris sp. 1	0	0	1	0	0	2	0	2	1	1	-	-	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0
Epyris sp. 2	0	0	1	0	0	2	0	0	1	1	-	-	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0
Epyris sp. 3	0	0	1	0	0	2	0	0	1	1	-	-	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0
Epyris sp. 4	0	0	1	0	0	2	0	0	1	1	-	-	0	0	0	0	0	1	1	0	0	1	-	1	1	0	0
Epyris rufipes	0	0	1	0	0	0	0	0	1	1	-	-	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0
Epyris sp. 6	0	0	1	0	0	1	0	0	1	1	-	-	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0
Epyris sp. 7	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0

TAXA/CHARACTERS	153	4	5	6	7	8	9	160	1	2	3	4	5	6	7	8	9	170	1	2	3	4	5	6	7
Outgroup																									
Allobethylus tomoae	0	0	0	1	0	1	1	1	0	0	-	-	0	0	1	1	1	0	0	1	1	-	0	1	0
Apenesia sp. 1	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	2	0	0	?	?	1
Cephalonomia sp. 1	0	0	0	1	0	0	0	0	0	0	-	-	1	1	-	-	-	-	1	-	1	-	0	1	0
Cephalonomia sp. 2	0	0	0	1	0	0	0	0	0	0	-	-	1	1	-	-	-	-	1	-	1	-	0	1	0
Eleganesia elegans	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	0	1	0	0	3	0	0	3	0	1
Eupsenella diemenensis	0	0	1	0	0	1	1	1	1	1	-	0	0	0	1	0	1	2	0	0	0	0	1	1	1
Goniozus japonicus	0	0	1	0	0	1	1	1	1	1	-	0	0	0	1	0	1	2	0	1	1	-	2	1	1
Sulcomesitius sp. 1	0	0	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	2	1	-	1	1	1
Ingroup																									
Anisepyris sp. 1	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	-	0	1	1
Anisepyris sp. 2	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	-	0	1	1
Anisepyris sp. 3	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	-	1	1	1
Anisepyris sp. 4	0	0	2	0	0	1	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	-	2	1	1
Anisepyris sp. 5	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	1	1	-	?	?	?
Anisepyris sp. 6	0	0	2	0	0	1	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	-	1	1	1
Anisepyris sp. 7	0	0	2	0	0	1	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	-	0	1	1
Anisepyris sp. 8	0	0	2	0	0	1	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	-	1	1	1
Anisepyris sp. 9	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	1	1	-	1	1	1
Aspidepyris austrinus	1	1	0	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	3	1	-	2	1	1
Bakeriella flavicornis	0	0	1	1	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	1	-	2	1	1
Bakeriella sp. 1	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	2	1	-	2	1	1
Bakeriella sp. 2	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	-	2	1	1
Bakeriella sp. 3	1	1	1	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	1	1	-	2	1	1
Bakeriella sp. 4	1	1	1	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	2	1	-	2	1	1
Calyozina nepalensis	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	2	1	-	2	1	1
Calyozina ramicornis	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	2	1	-	?	?	1
Chlorepyris viridissimus	1	1	2	0	1	1	1	1	0	1	0	1	0	0	1	1	1	0	0	3	1	-	1	0	1
Chlorepyris sp. 1	0	0	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	2	0	0	2	1	1
Chlorepyris sp. 2	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	3	0	0	2	1	1
Chlorepyris sp. 3	1	1	2	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	0	3	0	0	3	1	1
Chlorepyris sp. 4	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	3	1	-	2	1	1
Chlorepyris sp. 5	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	3	1	-	2	1	1
Chlorepyris sp. 6	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	3	1	-	2	1	1
Chlorepyris sp. 7	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	3	1	-	2	1	1
Chlorepyris sp. 8	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	2	1	-	1	1	1
Chlorepyris sp. 9	0	0	2	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	0	2	1	-	1	1	1
Chlorepyris sp. 10	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	0	2	1	-	2	1	1
Chlorepyris sp. 11	0	0	2	0	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	2	1	-	2	1	1
Chlorepyris sp. 12	0	0	1	0	0	1	1	1	0	1	2	1	0	0	1	0	1	0	0	3	1	-	1	1	1
Chlorepyris sp. 13	0	0	1	0	0	1	1	1	0	1	2	1	0	0	1	0	1	0	0	3	1	-	1	1	1
Chlorepyris sp. 15	1	1	1	0	0	1	1	1	0	1	1	1	1	0	1	0	1	0	0	3	1	-	?	?	?
Chlorepyris sp. 16	1	1	1	0	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	3	1	-	2	0	1
Chlorepyris sp. 17	1	1	2	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	0	3	1	-	2	0	1
Chlorepyris sp. 18	0	0	2	0	0	1	1	1	0	1	2	1	0	0	1	0	1	0	0	3	1	-	1	1	1
Chlorepyris sp. 19	1	1	1	0	0	1	1	1	0	1	1	1	0	0	1	0	1	0	0	3	1	-	2	0	1
Chlorepyris sp. 20	0	0	2	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	0	3	1	-	1	0	1
Disepyris sp. 1	1	1	1	1	0	1	1	1	0	1	1	1	0	0	0	-	1	-	0	1	1	-	2	0	1
Disepyris sp. 2	0	?	1	1	0	1	1	1	0	1	1	1	0	0	0	-	1	-	0	1	1	-	1	0	1
Disepyris sp. 3	1	1	1	1	0	1	1	1	0	1	1	1	0	0	0	-	1	-	0	1	1	-	2	0	1
Epyris (*staphyl.*) sp. 1	1	1	1	0	1	1	1	1	0	1	0	1	0	0	1	0	1	1	0	2	0	0	1	1	1
Epyris (*staphyl.*) sp. 2	0	0	1	0	1	1	1	1	0	1	0	1	0	0	1	0	1	1	0	3	0	0	1	1	1
Epyris (*staphyl.*) sp. 3	0	0	1	0	1	1	1	1	0	1	0	1	0	0	1	1	1	1	0	2	0	0	1	1	1
Epyris (*staphyl.*) sp. 4	1	1	1	0	1	1	1	1	0	1	0	1	0	0	1	0	1	1	0	3	0	0	1	1	1
Epyris (*staphyl.*) sp. 5	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	0	1	1	0	3	0	0	2	1	1
Epyris (*staphyl.*) sp. 6	0	0	1	0	1	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	2	1	1
Epyris (*staphyl.*) sp. 7	1	1	1	0	1	1	1	1	0	1	1	1	0	0	1	0	1	1	0	3	0	0	2	1	1
Epyris (*staphyl.*) sp. 8	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris (*staphyl.*) sp. 10	0	0	1	0	1	1	1	1	0	1	2	1	0	0	1	0	1	1	0	3	0	0	1	1	1
Epyris (*staphyl.*) sp. 11	1	1	2	0	1	1	1	1	0	1	2	1	0	0	1	1	1	1	0	3	0	0	2	1	1
Epyris (*staphyl.*) sp. 12	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris (*staphyl.*) sp. 13	0	0	1	0	1	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris (*staphyl.*) sp. 14	1	1	0	0	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	2	0	0	1	1	1
Epyris afer	1	1	2	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris niger	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris ruficeps	1	1	2	0	1	1	1	1	0	1	1	1	1	0	1	0	1	1	0	3	1	-	5	1	1
Epyris sp. 1	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	?	?	1
Epyris sp. 2	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris sp. 3	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	?	?	?
Epyris sp. 4	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris rufipes	1	1	0	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1	0	3	0	0	1	1	1
Epyris sp. 6	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	4	0	1	1	0	1
Epyris sp. 7	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	4	0	1	2	0	1

TAXA/CHARACTERS	17 8	9	18 0	1	2	3	4	5	6	7	8	9	19 0	1	2	3	4	5	6	7	8	9	20 0	1	2	3
Outgroup																										
Allobethylus tomoae	1	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apenesia sp. 1	1	1	1	0	0	1	1	1	0	1	1	1	1	0	1	0	2	3	0	0	0	0	1	-	1	-
Cephalonomia sp. 1	1	0	1	0	0	0	0	0	1	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cephalonomia sp. 2	1	0	1	0	0	0	0	0	1	1	0	1	2	0	0	0	2	1	0	0	0	0	0	-	1	-
Eleganesia elegans	1	1	1	0	0	1	1	1	0	1	1	1	2	0	1	0	2	0	0	0	2	0	2	1	1	-
Eupsenella diemenensis	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniozus japonicus	0	0	1	0	0	0	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sulcomesitius sp. 1	1	1	1	0	0	1	0	0	1	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ingroup																										
Anisepyris sp. 1	1	1	0	1	0	1	1	0	0	1	1	1	2	0	1	0	2	0	0	0	0	0	2	1	1	-
Anisepyris sp. 2	1	1	0	1	0	1	1	0	0	1	1	1	2	0	1	0	2	0	0	0	0	0	1	-	1	-
Anisepyris sp. 3	1	1	0	1	0	1	1	0	0	1	1	1	2	0	1	0	2	0	0	0	0	0	1	-	1	-
Anisepyris sp. 4	1	1	0	1	0	1	1	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anisepyris sp. 5	1	1	0	1	0	1	1	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anisepyris sp. 6	1	1	0	1	0	1	1	0	0	1	1	1	2	0	1	0	2	0	0	0	0	0	1	-	1	-
Anisepyris sp. 7	1	1	0	1	0	1	1	0	0	1	1	1	1	0	1	0	2	0	0	0	0	0	2	1	1	-
Anisepyris sp. 8	1	1	0	1	0	1	1	0	0	1	1	1	2	0	1	0	2	0	0	0	0	0	2	1	1	-
Anisepyris sp. 9	1	1	0	1	0	1	1	0	0	1	1	0	2	0	1	0	2	0	0	0	0	0	0	-	1	-
Aspidepyris austrinus	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	2	0	0	0	4	0	2	1	1	-
Bakeriella flavicornis	1	1	0	1	0	1	1	0	0	1	1	0	0	0	1	0	2	1	0	0	0	0	1	-	1	-
Bakeriella sp. 1	1	1	0	1	0	1	1	0	0	1	1	1	0	0	0	0	2	1	0	0	0	0	2	1	1	-
Bakeriella sp. 2	1	1	0	1	0	1	1	0	0	1	1	1	0	0	0	0	2	1	0	0	0	0	2	1	1	-
Bakeriella sp. 3	1	1	0	1	0	0	1	0	1	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bakeriella sp. 4	1	1	0	1	0	0	1	0	1	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calyozina nepalensis	1	1	0	1	0	0	1	0	0	1	1	0	2	0	1	0	2	0	0	0	0	0	0	-	1	-
Calyozina ramicornis	?	?	?	?	?	?	?	?	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chlorepyris viridissimus	1	1	0	1	1	0	0	0	0	1	1	0	0	0	1	0	2	0	0	0	2	0	2	1	1	-
Chlorepyris sp. 1	1	1	0	1	0	1	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chlorepyris sp. 2	1	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	-	1	-
Chlorepyris sp. 3	1	1	0	1	0	1	0	0	0	1	0	1	2	0	1	0	0	0	0	0	1	0	1	-	1	-
Chlorepyris sp. 4	1	1	0	1	0	1	0	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chlorepyris sp. 5	1	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	2	1	0	0	0	0	1	-	1	-
Chlorepyris sp. 6	1	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	2	1	0	0	0	0	1	-	1	-
Chlorepyris sp. 7	1	1	0	1	0	1	0	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chlorepyris sp. 8	1	1	0	1	0	1	0	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chlorepyris sp. 9	1	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	2	0	0	0	0	0	0	-	1	-
Chlorepyris sp. 10	1	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	2	0	0	0	0	0	0	-	1	-
Chlorepyris sp. 11	1	1	0	1	0	1	0	0	0	1	1	1	1	0	1	0	2	0	0	0	0	0	0	-	1	-
Chlorepyris sp. 12	1	1	0	1	0	1	0	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chlorepyris sp. 13	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	2	0	0	0	0	0	0	-	1	-
Chlorepyris sp. 15	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	2	0	0	0	0	0	0	-	1	-
Chlorepyris sp. 16	1	1	0	1	0	1	0	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chlorepyris sp. 17	1	1	0	1	0	1	0	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chlorepyris sp. 18	1	1	0	1	0	1	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chlorepyris sp. 19	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	2	0	0	0	0	0	0	-	1	-
Chlorepyris sp. 20	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	2	0	0	0	0	0	0	-	1	-
Disepyris sp. 1	1	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	2	0	0	0	0	0	2	1	1	-
Disepyris sp. 2	1	0	0	1	0	0	1	0	0	1	0	1	2	0	1	0	2	1	0	0	0	0	2	1	1	-
Disepyris sp. 3	1	0	0	1	0	0	1	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris (*staphyl.*) sp. 1	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	2	1	1	-
Epyris (*staphyl.*) sp. 2	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	0	0	1	0	0	2	0	2	1	1	-
Epyris (*staphyl.*) sp. 3	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	2	1	1	-
Epyris (*staphyl.*) sp. 4	1	1	0	1	1	1	1	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris (*staphyl.*) sp. 5	1	1	0	1	?	1	1	0	0	1	1	1	0	0	1	0	0	1	0	0	2	0	2	0	1	-
Epyris (*staphyl.*) sp. 6	1	1	0	1	1	1	1	0	0	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris (*staphyl.*) sp. 7	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	0	2	1	0	0	2	0	2	0	1	-
Epyris (*staphyl.*) sp. 8	1	1	0	1	?	1	1	0	0	1	1	1	0	0	1	0	2	1	0	0	2	0	2	0	1	-
Epyris (*staphyl.*) sp. 10	1	1	0	1	1	1	1	0	0	1	1	0	0	0	1	0	2	1	0	0	2	0	2	0	1	-
Epyris (*staphyl.*) sp. 11	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	0	2	1	0	1	2	0	2	0	1	-
Epyris (*staphyl.*) sp. 12	1	1	0	1	1	1	1	0	0	1	1	0	0	0	1	0	2	1	0	1	2	0	2	0	1	-
Epyris (*staphyl.*) sp. 13	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	0	2	1	0	1	2	0	2	0	1	-
Epyris (*staphyl.*) sp. 14	1	1	0	1	1	1	1	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris afer	1	1	0	1	0	0	1	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris niger	1	1	0	1	0	1	1	0	0	1	1	0	0	0	1	0	2	1	0	0	3	0	2	1	1	-
Epyris ruficeps	1	1	0	1	1	1	1	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 1	1	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	2	1	0	0	1	0	1	-	1	-
Epyris sp. 2	1	1	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 3	1	1	0	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 4	1	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	2	1	0	0	0	0	1	-	1	-
Epyris rufipes	1	1	0	1	0	1	1	0	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 6	1	1	0	1	0	1	1	0	0	1	1	0	0	0	1	0	2	1	1	-	-	-	-	-	-	-
Epyris sp. 7	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

TAXA/CHARACTERS	204	5	6	7	8	9	2101	1	2	3	4	5	6	7	8	9	2200	1	2	3	4	5	6	7	8	9	2300	1	2
Outgroup																													
Allobethylus tomoae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Apenesia sp. 1	0	2	1	1	1	0	0	0	1	0	0	0	-	4	0	1	0	1	2	0	1	1	1	2	0	0	1	1	0
Cephalonomia sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Cephalonomia sp. 2	2	2	1	1	1	0	0	0	1	0	0	0	-	4	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0
Eleganesia elegans	2	2	1	1	1	0	0	0	1	0	0	0	-	2	0	1	0	1	2	0	1	1	1	2	0	0	1	1	0
Eupsenella diemenensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Goniozus japonicus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Sulcomesitius sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Ingroup																													
Anisepyris sp. 1	2	2	1	1	1	0	0	0	1	0	0	2	0	4	1	1	0	2	1	1	0	1	1	0	0	0	0	0	0
Anisepyris sp. 2	2	2	1	1	1	0	0	0	1	0	0	2	0	4	1	1	0	2	0	1	0	1	1	0	0	0	0	0	0
Anisepyris sp. 3	2	2	1	1	1	0	0	0	1	0	0	2	0	4	1	1	0	2	0	1	0	1	1	0	0	0	0	0	0
Anisepyris sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Anisepyris sp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Anisepyris sp. 6	2	2	1	1	1	0	0	0	1	0	0	2	0	4	1	1	0	2	1	1	0	1	1	0	0	0	0	0	0
Anisepyris sp. 7	2	2	1	1	1	0	0	0	1	0	0	2	0	4	1	1	0	2	1	1	0	1	1	0	0	0	0	0	1
Anisepyris sp. 8	1	1	1	1	1	0	0	0	1	0	0	2	0	4	1	1	0	2	2	1	0	1	1	0	0	0	0	0	0
Anisepyris sp. 9	1	1	1	1	1	0	0	0	0	0	0	2	0	4	1	1	0	2	1	1	0	1	1	0	0	0	0	0	0
Aspidepyris austrinus	0	2	0	1	1	0	0	1	1	0	0	0	-	0	0	1	1	0	0	1	1	0	1	2	0	0	0	1	0
Bakeriella flavicornis	2	2	1	1	1	0	0	0	1	0	0	2	1	2	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0
Bakeriella sp. 1	2	2	1	1	1	0	0	1	1	0	0	1	1	4	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Bakeriella sp. 2	2	2	1	1	1	0	0	1	1	0	0	1	1	4	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
Bakeriella sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Bakeriella sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Calyozina nepalensis	2	1	1	1	1	0	0	0	1	2	0	0	-	3	0	1	0	0	0	0	1	1	1	2	0	2	0	0	0
Calyozina ramicornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Chlorepyris viridissimus	2	2	1	1	1	0	0	1	1	2	0	0	-	0	0	1	1	0	0	0	1	1	1	2	0	1	0	0	1
Chlorepyris sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Chlorepyris sp. 2	2	2	1	1	1	0	0	0	1	2	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	1	0	0	1
Chlorepyris sp. 3	2	1	1	1	1	0	0	0	1	2	0	0	-	4	0	1	0	2	1	0	1	1	1	1	0	1	0	0	0
Chlorepyris sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Chlorepyris sp. 5	2	2	1	1	1	0	0	0	1	2	0	0	-	3	1	1	0	2	1	0	1	1	1	1	0	1	0	0	0
Chlorepyris sp. 6	2	2	1	1	1	0	0	0	1	2	0	0	-	3	1	1	0	2	1	0	1	1	1	1	0	1	0	0	0
Chlorepyris sp. 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Chlorepyris sp. 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Chlorepyris sp. 9	2	0	1	1	1	0	0	0	1	1	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	2	0	0	0
Chlorepyris sp. 10	2	0	1	1	1	0	0	0	1	1	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	2	0	0	0
Chlorepyris sp. 11	2	2	1	1	1	0	0	0	1	1	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	2	0	0	0
Chlorepyris sp. 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Chlorepyris sp. 13	2	0	1	1	1	0	0	0	1	1	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	2	0	0	0
Chlorepyris sp. 15	2	0	1	1	1	0	0	0	1	1	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	2	0	0	0
Chlorepyris sp. 16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Chlorepyris sp. 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Chlorepyris sp. 18	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Chlorepyris sp. 19	2	0	1	1	1	0	0	0	1	1	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	2	0	0	0
Chlorepyris sp. 20	2	0	1	1	1	0	0	0	1	1	0	0	-	4	1	1	0	2	0	0	1	1	1	1	0	2	0	0	0
Disepyris sp. 1	2	1	0	1	1	0	0	0	1	1	2	0	1	0	3	0	1	0	1	1	0	0	0	1	2	0	2	1	1	0
Disepyris sp. 2	2	1	1	1	1	0	0	0	1	1	2	0	1	0	3	0	1	0	1	1	0	0	0	1	2	0	2	1	1	0
Disepyris sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris (*staphyl.*) sp. 1	2	2	1	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris (*staphyl.*) sp. 2	2	0	1	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris (*staphyl.*) sp. 3	2	0	1	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris (*staphyl.*) sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris (*staphyl.*) sp. 5	2	0	1	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris (*staphyl.*) sp. 6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris (*staphyl.*) sp. 7	2	2	1	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris (*staphyl.*) sp. 8	2	2	1	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris (*staphyl.*) sp. 10	2	2	1	1	1	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris (*staphyl.*) sp. 11	2	2	1	1	1	0	0	0	1	1	0	0	2	2	0	0	1	1	1	0	0	1	1	1	2	0	0	0	0	0
Epyris (*staphyl.*) sp. 12	2	2	1	1	1	0	0	0	1	1	2	0	2	2	0	0	1	1	1	0	0	1	1	1	2	0	0	0	0	0
Epyris (*staphyl.*) sp. 13	2	2	1	1	1	0	0	0	1	1	2	0	2	2	0	0	1	1	1	0	0	1	1	1	2	0	0	0	0	0
Epyris (*staphyl.*) sp. 14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris afer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris niger	2	1	0	0	1	0	0	0	1	1	0	0	1	0	4	0	1	0	1	0	1	1	0	1	2	0	0	0	0	0
Epyris ruficeps	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 1	0	0	1	1	1	0	0	0	1	1	0	0	0	-	1	0	1	1	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Epyris sp. 3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Epyris sp. 4	2	2	0	1	1	0	0	1	1	0	0	1	1	4	0	1	0	1	1	0	1	0	1	2	0	0	0	0	0	0
Epyris rufipes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 6	-	-	-	-	-	-	0	0	1	0	0	1	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0
Epyris sp. 7	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0

TAXA/CHARACTERS	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6	7
										1										2							

Epyris sp. 8	1	1	1	1	0	2	0	1	0	1	0	0	1	0	1	1	1	0	0	1	1	0	1	3	0	0	1
Epyris sp. 9	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Epyris sp. 10	1	1	1	1	0	2	0	1	2	1	0	0	0	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Epyris sp. 11	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 12	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 13	1	1	1	1	0	1	0	1	0	0	0	1	0	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 14	1	1	1	1	0	3	0	1	0	1	0	0	2	0	0	0	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 15	1	1	1	1	0	3	0	1	0	1	0	0	2	0	1	1	1	0	0	1	1	0	1	0	-	-	-
Epyris sp. 16	1	1	1	1	0	3	0	1	0	1	0	0	2	0	1	1	1	0	0	2	1	0	1	2	0	0	1
Epyris sp. 17	1	1	1	1	0	1	0	1	0	1	0	0	2	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 18	1	1	1	1	0	3	1	1	0	1	0	0	1	0	1	0	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 19	1	1	1	1	0	3	0	1	0	1	0	0	2	0	0	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 20	1	1	1	1	0	2	0	1	0	1	0	0	2	0	1	1	1	0	1	2	1	2	1	0	-	-	-
Epyris sp. 21	1	1	1	1	0	2	0	1	0	1	0	0	2	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 22	1	1	1	1	0	2	0	1	0	1	0	0	1	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 23	1	1	1	1	0	2	0	1	0	1	0	0	1	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 26	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	2	1	0	1	2	0	1	1
Epyris sp. 27	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	2	1	0	1	2	0	1	1
Epyris sp. 29	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	2	1	1	1	4	0	1	1
Epyris sp. 30	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	2	1	1	1	4	0	1	1
Epyris sp. 31	1	1	1	1	0	3	0	1	0	0	0	0	1	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 32	1	1	1	1	0	3	0	1	0	0	0	0	1	0	0	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 33	1	1	1	1	0	2	0	1	0	0	0	0	1	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 34	1	1	1	1	0	3	0	1	0	0	0	0	1	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 35	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 36	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 37	1	1	1	1	0	3	0	1	0	1	0	0	1	0	0	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 38	1	1	1	1	0	2	0	1	0	1	0	0	0	0	0	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 39	1	1	1	1	?	?	0	1	0	1	0	0	1	0	0	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 40	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 41	1	1	1	1	0	?	0	1	0	1	0	1	1	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Epyris sp. 42	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Epyris sp. 43	1	1	1	1	0	3	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	4	0	0	1
Epyris sp. 44	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 45	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	2	1	0	1	1	0	1	1
Epyris sp. 46	1	1	1	1	0	3	0	1	0	1	0	0	2	0	1	1	1	0	0	2	1	0	1	4	0	1	1
Epyris sp. 47	1	1	1	1	0	3	0	1	0	1	0	0	1	0	0	1	1	0	0	2	1	0	1	3	0	1	1
Epyris sp. 48	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	2	1	0	1	1	0	1	1
Epyris sp. 49	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1
Epyris sp. 50	1	1	1	1	0	2	0	1	0	1	0	0	0	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Epyris sp. 51	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	2	1	0	1	3	0	0	1
Epyris sp. 52	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	2	1	0	1	3	0	0	1
Epyris sp. 53	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	2	1	0	1	3	0	0	1
Epyris sp. 54	1	1	1	1	0	2	0	1	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1
Epyris sp. 55	1	1	1	1	0	2	0	1	0	1	0	0	2	0	0	1	1	0	0	2	1	2	1	3	0	0	1
Epyris sp. 56	1	1	1	1	0	2	0	1	1	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	1
Epyris sp. 57	1	1	1	1	0	2	0	1	0	1	0	0	0	0	0	1	1	0	0	2	1	0	1	1	0	1	1
Epyris sp. 58	1	1	1	1	0	3	0	1	0	1	0	0	2	0	1	1	1	0	0	2	1	0	1	3	0	0	1
Epyris sp. 59	1	1	1	1	0	2	0	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1	4	0	1	1
Epyris sp. 60	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	2	1	0	1	3	0	1	1
Epyris sp. 61	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 63	1	1	1	1	0	2	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	1	0	1	1
Epyris/Trachepyris sp. 1	1	1	1	1	0	2	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 2	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 3	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 4	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 5	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 6	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 7	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 8	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 9	1	1	1	1	0	3	0	1	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	4	0	1	1
Epyris/Trachepyris sp. 10	1	1	1	1	0	3	1	1	0	1	0	0	1	0	0	1	1	0	1	2	1	2	1	0	-	-	-
Epyris/Trachepyris sp. 11	1	1	1	1	0	3	1	1	0	1	0	0	1	0	0	1	1	0	1	2	1	2	1	0	-	-	-
Formosiepyris marish	1	1	1	1	0	2	0	1	0	1	0	0	1	0	0	2	1	0	0	2	1	1	1	3	0	0	1
Formosiepyris sp. 1	1	1	1	1	0	3	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	0	0	2	0	1	1
Formosiepyris sp. 2	1	1	1	1	0	2	1	1	0	1	0	0	2	0	0	2	0	0	0	1	1	0	0	2	0	1	1
†*Gloxinius bifossatus*	0	1	1	1	0	2	1	1	0	1	0	0	1	0	1	2	1	0	0	2	1	0	1	4	0	1	1
Holepyris africanus	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	2	0	0	0	1	1	0	1	2	0	1	1
Holepyris sp. 2	1	1	1	1	0	3	0	1	2	0	0	0	1	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Holepyris sp. 3	1	1	1	1	0	1	0	1	0	1	0	1	1	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Holepyris sp. 4	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	2	1	0	1	1	1	0	1
Holepyris sp. 5	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	2	1	0	1	1	1	0	1
Holepyris sp. 6	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	1	1	0	1	1	1	0	1
Holepyris sp. 7	1	1	1	1	0	3	0	1	0	1	0	0	2	0	1	1	1	0	0	1	1	2	1	0	-	-	-

	2		**3**										**4**										**5**				
TAXA/CHARACTERS	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**
Epyris sp. 8	0	0	-	1	1	0	0	0	1	1	0	0	0	0	0	2	0	1	1	2	1	2	2	0	1	0	0

Epyris sp. 9	-	0	-	1	1	0	0	0	1	1	0	0	0	0	0	2	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 10	-	0	-	1	1	0	0	0	1	0	0	0	1	0	0	2	0	1	?	?	?	?	?	0	1	0	0
Epyris sp. 11	-	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 12	-	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 13	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	2	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 14	-	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 15	-	0	-	1	0	0	0	0	1	1	0	0	1	0	1	1	0	1	1	0	0	2	2	0	1	0	0
Epyris sp. 16	0	0	-	1	0	0	0	0	1	1	0	0	1	0	1	1	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 17	-	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	2	2	0	1	0	1
Epyris sp. 18	-	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	2	2	0	1	0	0
Epyris sp. 19	-	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	2	2	0	1	0	0
Epyris sp. 20	-	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 21	-	0	-	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 22	-	0	-	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	2	1	2	2	0	1	0	0
Epyris sp. 23	-	0	-	1	0	0	0	0	1	1	0	0	1	0	1	1	1	1	1	2	0	2	2	0	1	0	0
Epyris sp. 26	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	0	1	0	1
Epyris sp. 27	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	0	1	0	1
Epyris sp. 29	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	0
Epyris sp. 30	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	1
Epyris sp. 31	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	0
Epyris sp. 32	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	1
Epyris sp. 33	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	0
Epyris sp. 34	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	0
Epyris sp. 35	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	1	1	1	0	0	2	2	1	1	0	1
Epyris sp. 36	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	1
Epyris sp. 37	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	0	1	1	0	0	2	2	1	1	0	0
Epyris sp. 38	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	1	1	1	0	0	2	2	1	1	0	1
Epyris sp. 39	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	2	1	1	1	0	0	2	2	1	1	0	1
Epyris sp. 40	-	0	-	1	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0	2	2	1	0	0	1
Epyris sp. 41	-	0	-	1	0	1	-	-	1	1	0	0	0	0	1	2	0	1	1	0	0	2	2	0	1	0	0
Epyris sp. 42	0	0	-	1	0	1	-	-	1	1	0	0	2	0	1	2	0	1	1	2	0	2	2	0	1	0	0
Epyris sp. 43	0	0	-	1	0	1	-	-	1	1	0	0	2	0	1	2	0	1	1	2	0	2	2	0	1	0	1
Epyris sp. 44	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 45	0	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	2	1	1	0	1
Epyris sp. 46	0	0	-	1	0	1	-	-	1	0	0	0	1	0	1	2	0	1	1	2	0	2	2	0	1	0	0
Epyris sp. 47	0	0	-	1	0	1	-	-	1	1	0	0	0	0	1	2	0	1	1	2	0	2	2	0	1	0	0
Epyris sp. 48	0	0	-	1	0	0	0	0	1	1	0	0	1	0	1	2	0	1	1	2	0	2	2	0	1	0	0
Epyris sp. 49	0	0	-	1	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	2	0	2	2	1	1	0	1
Epyris sp. 50	-	0	-	1	0	0	0	0	1	0	0	0	1	0	1	2	1	1	1	2	1	2	2	1	1	0	1
Epyris sp. 51	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	2	2	1	1	0	1
Epyris sp. 52	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	2	2	1	1	0	1
Epyris sp. 53	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	2	2	1	1	0	1
Epyris sp. 54	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	1	0	1	1	2	1	2	2	1	0	0	1
Epyris sp. 55	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	1	1	1	1	2	1	2	2	1	1	0	0
Epyris sp. 56	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	1	1	1	1	2	1	2	2	1	1	0	1
Epyris sp. 57	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	1	0	1	1	2	1	2	2	1	1	0	1
Epyris sp. 58	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	1	0	1	1	2	0	2	2	1	1	0	1
Epyris sp. 59	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	1	0	1	1	2	0	2	2	1	1	0	1
Epyris sp. 60	0	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	0	1	1	2	1	2	2	1	1	0	1
Epyris sp. 61	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Epyris sp. 63	0	0	-	1	0	1	-	-	1	0	0	0	1	0	0	0	1	1	1	2	1	2	2	1	0	0	1
Epyris/Trachepyris sp. 1	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	?	?	0	2	0	0	1	0	1
Epyris/Trachepyris sp. 2	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 3	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 4	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 5	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 6	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 7	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 8	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 9	1	0	-	1	0	1	-	-	1	0	0	0	1	0	1	1	1	1	1	2	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 10	-	0	-	1	1	0	1	0	1	2	0	0	1	0	0	2	1	1	1	0	0	2	0	0	1	0	0
Epyris/Trachepyris sp. 11	-	0	-	1	1	0	1	0	1	2	0	0	1	0	0	2	1	1	1	0	0	2	0	0	1	0	0
Formosiepyris marish	0	0	-	1	0	0	1	0	1	0	0	0	2	0	1	1	0	1	1	2	0	2	0	0	1	0	0
Formosiepyris sp. 1	0	0	-	1	0	0	1	0	1	0	0	0	0	0	1	2	0	1	1	0	0	2	0	0	1	0	1
Formosiepyris sp. 2	0	0	-	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0	1	2	0	0	1	0	1
†*Gloxinius bifossatus*	0	0	-	1	0	?	?	?	1	0	0	0	2	1	-	-	0	1	1	0	1	2	0	0	1	0	1
Holepyris africanus	0	0	-	1	1	0	1	0	1	0	0	0	1	0	1	1	0	1	1	0	0	2	0	0	1	0	1
Holepyris sp. 2	-	0	-	1	0	1	-	-	1	0	0	0	0	0	2	2	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 3	-	0	-	1	0	1	-	-	1	0	0	0	0	0	2	2	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 4	0	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	1	0	0	0	1
Holepyris sp. 5	0	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	1	0	0	0	1
Holepyris sp. 6	0	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 7	-	0	-	1	0	1	-	-	1	0	0	0	0	0	2	1	0	1	1	2	0	2	1	0	1	0	1

TAXA/CHARACTERS	**5 5**	**6**	**7**	**8**	**9**	**6 0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**7 0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**8 0**	**1**

Epyris sp. 8	0	0	1	1	1	0	0	1	0	1	0	1	1	1	1	1	0	1	2	1	-	0	-	1	1	0	2
Epyris sp. 9	0	0	1	1	1	0	0	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 10	0	0	1	1	1	0	0	1	0	0	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 11	0	0	1	0	1	2	0	1	0	0	0	0	2	1	1	1	0	1	2	1	-	0	-	1	1	0	2
Epyris sp. 12	0	0	1	0	1	2	0	1	0	0	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 13	0	0	1	0	1	0	0	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 14	0	1	1	1	1	0	0	1	0	1	1	1	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 15	0	1	1	1	1	2	0	1	0	0	0	1	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 16	0	1	1	0	1	2	0	1	0	1	1	1	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 17	0	0	1	0	1	2	0	1	0	1	0	1	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 18	0	0	1	0	1	2	0	1	0	0	1	1	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 19	0	1	1	0	1	2	0	1	0	0	1	1	2	1	1	1	1	-	-	1	-	0	-	1	0	1	1
Epyris sp. 20	0	0	1	0	1	0	1	1	0	1	0	1	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 21	0	1	1	0	1	0	0	1	0	0	1	1	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 22	0	1	1	0	1	0	0	1	0	0	0	1	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 23	0	1	1	0	1	0	0	1	0	0	0	1	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 26	0	0	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 27	0	0	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 29	0	1	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 30	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 31	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 32	0	0	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 33	0	0	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 34	0	0	1	0	1	2	0	1	0	2	1	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	2
Epyris sp. 35	0	0	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 36	0	0	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 37	0	0	1	0	1	2	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 38	0	0	1	0	1	2	0	1	1	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 39	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 40	0	0	1	0	1	0	0	1	?	1	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	1	0
Epyris sp. 41	0	0	1	0	1	0	0	1	2	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 42	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 43	0	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 44	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 45	0	0	1	0	1	0	1	1	0	1	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	0
Epyris sp. 46	0	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	1	-	-	1	-	0	-	1	1	0	0
Epyris sp. 47	0	0	1	0	1	0	0	1	1	1	1	0	0	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 48	0	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 49	0	1	1	0	1	0	1	1	0	1	0	0	1	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 50	0	1	1	0	1	0	1	1	0	2	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 51	0	1	1	0	1	2	1	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Epyris sp. 52	0	1	1	0	1	2	1	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Epyris sp. 53	0	1	1	0	1	2	1	1	0	2	0	0	1	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Epyris sp. 54	0	0	1	0	1	0	1	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Epyris sp. 55	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 56	0	0	1	0	1	0	1	1	0	2	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris sp. 57	0	0	1	0	1	0	1	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Epyris sp. 58	0	0	1	0	1	0	1	1	0	2	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 59	0	0	1	0	1	0	1	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris sp. 60	0	0	1	0	1	0	1	1	0	2	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Epyris sp. 61	?	?	?	?	?	?	?	?	?	?	?	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Epyris sp. 63	0	0	1	0	1	0	0	1	0	2	1	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	2
Epyris/Trachepyris sp. 1	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 2	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 3	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 4	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 5	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 6	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 7	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 8	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 9	0	0	1	0	1	0	0	1	0	2	1	0	2	2	1	1	1	-	-	1	-	0	-	1	1	1	1
Epyris/Trachepyris sp. 10	0	1	1	0	1	0	0	1	0	1	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Epyris/Trachepyris sp. 11	0	1	1	0	1	0	0	1	0	1	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	1	2
Formosiepyris marish	0	0	1	0	1	0	0	1	1	1	1	0	2	2	1	1	1	-	-	0	0	0	-	1	1	1	0
Formosiepyris sp. 1	0	0	1	0	1	0	0	1	0	1	1	0	2	2	1	1	1	-	-	0	0	0	-	0	-	-	-
Formosiepyris sp. 2	0	0	1	0	1	0	0	1	2	1	1	0	2	2	1	1	1	-	-	0	0	0	-	1	1	1	0
†*Gloxinius bifossatus*	0	0	?	?	?	?	0	?	2	2	1	0	0	1	1	1	1	-	-	1	-	0	-	0	-	-	-
Holepyris africanus	0	0	1	0	1	0	0	1	2	1	1	0	1	2	1	1	1	-	-	0	0	0	-	0	-	-	-
Holepyris sp. 2	0	0	0	-	-	-	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 3	0	0	1	0	1	0	0	1	0	0	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 4	0	0	1	0	1	0	0	1	0	1	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 5	0	0	1	0	1	0	0	1	0	1	1	0	2	1	1	1	1	-	-	0	0	0	-	0	-	-	-
Holepyris sp. 6	0	0	1	0	1	0	0	1	0	1	1	0	2	1	1	1	0	1	1	1	-	0	-	0	-	-	-
Holepyris sp. 7	0	0	1	0	1	0	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-

	8								9										0								
TAXA/CHARACTERS	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Epyris sp. 8	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 9	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 10	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 11	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 12	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 13	2	0	0	0	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 14	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 15	2	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 16	2	1	0	1	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 17	2	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 18	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 19	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 20	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 21	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	1
Epyris sp. 22	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 23	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	?
Epyris sp. 26	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 27	1	1	0	0	1	0	0	-	-	-	-	-	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Epyris sp. 29	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 30	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Epyris sp. 31	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 32	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 33	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 34	1	1	0	0	1	0	0	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 35	1	1	0	0	1	0	0	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 36	1	1	0	0	1	0	1	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 37	1	1	0	0	1	0	0	-	-	-	-	-	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 38	1	1	0	0	1	0	0	-	-	-	-	-	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 39	2	1	0	0	1	0	0	-	-	-	-	-	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 40	1	1	0	1	1	0	1	-	-	-	-	-	1	2	1	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 41	1	1	0	1	1	0	0	-	-	-	-	-	1	2	1	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 42	1	1	0	1	1	0	0	-	-	-	-	-	1	2	1	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 43	1	1	0	0	1	0	1	-	-	-	-	-	1	2	1	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 44	1	1	0	0	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 45	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 46	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 47	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 48	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 49	0	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 50	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 51	1	1	0	2	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 52	1	1	0	2	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 53	1	1	0	2	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 54	1	1	0	2	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	1
Epyris sp. 55	1	1	0	1	1	0	0	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Epyris sp. 56	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 57	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	0	1
Epyris sp. 58	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 59	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 60	1	1	0	2	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 61	1	1	0	0	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris sp. 63	1	1	0	1	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 1	1	1	0	2	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 2	1	1	0	2	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 3	1	1	0	2	1	0	1	-	-	-	-	-	1	2	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 4	1	1	0	2	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 5	1	1	0	2	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 6	1	1	0	2	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 7	1	1	0	2	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 8	1	1	0	2	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 9	1	1	0	2	1	0	1	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 10	1	1	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Epyris/Trachepyris sp. 11	1	1	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Formosiepyris marish	0	-	0	2	0	1	0	0	2	0	0	1	-	-	-	-	1	0	1	1	0	0	0	0	0	0	0
Formosiepyris sp. 1	-	-	0	2	0	1	0	0	0	0	0	1	-	-	-	-	1	0	1	1	0	0	0	0	0	0	0
Formosiepyris sp. 2	0	-	0	0	0	1	0	0	0	0	0	1	-	-	-	-	1	0	1	1	0	0	0	0	0	0	0
†*Gloxinius bifossatus*	-	-	0	2	1	1	0	1	0	1	-	1	-	-	-	-	0	1	1	1	0	0	0	?	?	0	0
Holepyris africanus	-	-	0	2	0	1	0	0	0	0	0	1	-	-	-	-	1	0	1	1	0	0	0	0	0	0	0
Holepyris sp. 2	-	-	0	2	1	1	0	0	0	0	1	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 3	-	-	0	2	1	1	0	0	2	0	1	1	-	-	-	-	0	1	1	1	0	0	0	0	0	0	0
Holepyris sp. 4	-	-	0	2	1	1	0	0	2	0	0	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 5	-	-	0	2	1	1	0	0	2	1	-	1	-	-	-	-	0	0	1	0	0	0	0	0	0	0	0
Holepyris sp. 6	-	-	0	2	1	1	0	0	2	0	1	1	-	-	-	-	0	0	1	0	0	0	0	0	0	0	0
Holepyris sp. 7	-	-	0	2	1	1	0	0	2	0	0	1	-	-	-	-	0	0	1	1	0	0	0	0	0	0	0

	1	1							1										1								
	0	**1**							**2**										**3**								

TAXA/CHARACTERS	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Epyris sp. 8	0	0	0	0	1	2	2	-	-	-	-	0	0	0	2	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 9	0	0	0	0	0	-	-	-	-	-	-	0	0	0	2	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 10	0	0	0	0	0	-	-	-	-	-	-	0	0	0	2	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 11	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 12	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 13	0	0	0	0	1	2	0	2	0	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 14	1	-	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 15	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 16	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 17	0	0	0	0	1	2	0	2	1	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 18	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 19	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 20	0	0	0	0	1	1	2	1	2	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 21	0	0	0	0	1	2	0	2	1	-	-	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1
Epyris sp. 22	0	0	0	0	1	2	1	2	0	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 23	0	0	0	0	1	2	1	2	1	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 26	0	1	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1	0	1	1	0	0	0	0	0	1
Epyris sp. 27	0	1	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1	0	1	1	0	0	0	0	0	1
Epyris sp. 29	0	0	0	0	1	2	1	-	-	-	-	0	0	2	2	0	0	1	0	1	1	0	0	0	0	0	1
Epyris sp. 30	0	0	0	0	1	2	1	-	-	-	-	0	0	2	2	0	0	1	0	1	1	0	0	1	0	0	1
Epyris sp. 31	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 32	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1
Epyris sp. 33	0	0	0	0	1	2	0	-	-	-	-	0	0	2	2	0	0	1	0	1	1	0	0	1	0	0	1
Epyris sp. 34	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 35	0	0	0	0	0	-	-	-	-	-	-	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 36	0	0	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 37	0	0	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1	0	1	1	0	0	1	0	0	1
Epyris sp. 38	0	0	0	0	1	2	1	-	-	-	-	0	0	2	1	0	1	1	0	1	1	0	0	0	0	0	1
Epyris sp. 39	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
Epyris sp. 40	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	1	-	1	0	0	1	1	0	2	0	0	1
Epyris sp. 41	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	1	0	2	0	0	1
Epyris sp. 42	0	0	0	0	1	2	2	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 43	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 44	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 45	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 46	0	0	0	0	1	2	2	2	2	2	2	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 47	0	0	0	0	1	2	1	2	1	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Epyris sp. 48	0	0	0	0	1	1	1	1	1	2	1	0	1	0	1	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 49	0	0	0	0	1	2	1	2	1	-	-	0	1	0	1	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 50	0	0	0	0	1	2	1	2	1	-	-	0	0	0	2	0	0	1	0	0	1	0	0	2	0	0	1
Epyris sp. 51	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 52	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 53	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 54	0	0	0	0	1	2	1	2	1	-	-	0	0	0	1	0	0	1	0	1	1	0	0	2	0	0	1
Epyris sp. 55	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	1	-	1	0	1	1	0	0	2	0	0	1
Epyris sp. 56	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1
Epyris sp. 57	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1
Epyris sp. 58	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1
Epyris sp. 59	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
Epyris sp. 60	0	0	0	0	1	2	1	2	1	-	-	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
Epyris sp. 61	0	0	0	0	1	2	1	2	1	-	-	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
Epyris sp. 63	0	0	0	0	1	2	1	2	1	2	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
Epyris/Trachepyris sp. 1	0	0	0	0	1	1	2	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 2	0	0	0	0	1	1	0	-	-	-	-	0	0	0	0	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 3	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 4	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 5	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 6	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 7	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 8	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 9	0	0	0	0	1	1	0	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	1
Epyris/Trachepyris sp. 10	0	1	0	0	1	2	0	-	-	-	-	0	0	2	1	1	-	1	0	1	1	0	0	1	0	0	1
Epyris/Trachepyris sp. 11	0	1	0	0	1	2	0	-	-	-	-	0	0	2	1	1	-	1	0	1	1	0	0	1	0	0	1
Formosiepyris marish	0	0	0	0	1	2	0	-	-	-	-	0	0	2	1	0	0	1	0	1	1	0	0	1	0	0	1
Formosiepyris sp. 1	0	0	0	0	1	2	2	2	0	-	-	0	0	2	1	0	0	1	2	1	1	0	0	2	0	0	2
Formosiepyris sp. 2	0	0	0	0	1	2	1	2	0	-	-	0	0	2	1	0	0	1	2	1	1	0	0	2	0	0	2
†*Gloxinius bifossatus*	0	0	0	0	1	?	?	?	?	?	?	0	0	0	1	?	?	1	?	?	?	?	0	?	?	?	?
Holepyris africanus	0	0	0	0	1	2	1	2	0	-	-	0	0	2	1	0	0	1	2	1	1	0	0	2	0	0	2
Holepyris sp. 2	0	0	0	0	1	2	2	-	-	-	-	0	0	0	1	1	?	1	2	0	1	0	0	1	0	0	2
Holepyris sp. 3	0	0	0	0	1	1	1	-	-	-	-	0	0	0	1	0	0	1	2	0	1	0	0	1	0	0	2
Holepyris sp. 4	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	0	0	1	2	0	1	0	0	1	0	0	2
Holepyris sp. 5	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	1	-	1	2	0	1	0	0	1	0	0	1
Holepyris sp. 6	0	0	0	0	1	2	1	2	1	-	-	0	0	0	0	1	-	1	2	0	1	0	0	0	0	0	1
Holepyris sp. 7	0	0	0	0	0	-	-	-	-	-	-	0	0	0	2	0	0	1	2	0	1	0	0	2	0	0	1

	13				14										15										16		
TAXA/CHARACTERS	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**
Epyris sp. 8	1	-	-	0	1	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 9	1	-	-	0	1	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 10	1	-	-	0	1	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 11	1	-	-	0	1	0	1	1	1	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1
Epyris sp. 12	1	-	-	0	0	0	0	1	1	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1
Epyris sp. 13	1	-	-	0	1	0	0	1	1	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1
Epyris sp. 14	1	-	-	0	0	0	1	0	1	1	0	1	-	1	1	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 15	1	-	-	0	0	0	1	1	1	1	0	1	-	1	1	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 16	1	-	-	0	0	0	0	1	1	0	0	1	-	1	1	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 17	1	-	-	0	0	1	-	-	-	1	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 18	1	-	-	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 19	0	1	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 20	0	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1	0	1
Epyris sp. 21	1	-	-	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 22	1	-	-	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 23	1	-	-	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1
Epyris sp. 26	1	-	-	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	1	0	0	0	1	1	1	0	1
Epyris sp. 27	1	-	-	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	1	2	0	0	1	1	1	0	1
Epyris sp. 29	1	-	-	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 30	1	-	-	0	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 31	1	-	-	0	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 32	1	-	-	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 33	1	-	-	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 34	1	-	-	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 35	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 36	1	-	-	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 37	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 38	1	-	-	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 39	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Epyris sp. 40	1	-	-	0	0	0	1	1	1	1	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	0	1
Epyris sp. 41	1	-	-	0	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 42	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	2	0	0	1	1	1	0	1
Epyris sp. 43	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	2	0	0	1	1	1	0	1
Epyris sp. 44	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	2	0	0	1	1	1	0	1
Epyris sp. 45	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	0	1
Epyris sp. 46	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	2	0	0	1	1	1	0	1
Epyris sp. 47	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	2	0	0	1	1	1	0	1
Epyris sp. 48	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	2	0	0	1	1	1	0	1
Epyris sp. 49	0	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 50	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	2	0	0	1	1	1	0	1
Epyris sp. 51	0	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1	1	1	0	1
Epyris sp. 52	0	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1	1	1	0	1
Epyris sp. 53	0	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1	1	1	0	1
Epyris sp. 54	0	1	0	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 55	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 56	0	1	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1
Epyris sp. 57	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	1
Epyris sp. 58	1	-	-	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1
Epyris sp. 59	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1	0	1
Epyris sp. 60	0	1	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1
Epyris sp. 61	0	1	0	0	0	0	1	1	1	1	1	0	0	?	?	?	?	1	1	0	0	0	1	1	1	0	1
Epyris sp. 63	0	1	0	0	0	0	1	1	1	1	1	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 2	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 3	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 4	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 5	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 6	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 7	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 8	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 9	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 10	0	1	0	0	0	0	0	0	1	0	0	1	-	1	0	0	1	0	0	0	0	0	1	1	1	0	1
Epyris/Trachepyris sp. 11	0	1	0	0	0	0	0	0	1	0	0	1	-	1	0	0	1	0	0	0	0	0	1	1	1	0	1
Formosiepyris marish	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	0	0	1	1	1	0	1
Formosiepyris sp. 1	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	1	0	1	1	1	0	1
Formosiepyris sp. 2	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	1	0	1	1	1	0	1
†*Gloxinius bifossatus*	1	-	-	0	0	0	1	0	1	1	0	1	-	1	0	0	0	0	0	?	?	0	1	1	1	0	0
Holepyris africanus	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	1	0	1	1	1	0	1
Holepyris sp. 2	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 3	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 4	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 5	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 6	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 7	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1

1 **1** **1**

	6							7										8									
TAXA/CHARACTERS	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Epyris sp. 8	0	1	0	0	1	1	1	1	0	4	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 9	0	1	0	0	1	1	1	1	0	3	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 10	0	1	0	0	1	1	1	1	0	3	0	1	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 11	1	1	0	0	1	1	1	1	0	4	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 12	1	1	0	0	1	1	1	1	0	4	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 13	0	1	0	0	1	1	1	1	0	4	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 14	0	1	0	0	1	1	1	1	0	2	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 15	0	1	0	0	1	0	1	1	0	2	0	1	3	1	1	1	1	0	1	0	1	1	0	0	1	0	1
Epyris sp. 16	1	1	0	0	1	1	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 17	1	1	0	0	1	1	1	1	0	2	0	1	3	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 18	1	1	0	0	1	0	1	1	0	2	0	1	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 19	0	1	0	0	1	1	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 20	1	1	0	0	1	0	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 21	0	1	0	0	1	1	1	1	0	3	0	1	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 22	0	1	0	0	1	1	1	1	0	3	0	1	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 23	0	1	0	0	1	1	1	1	0	3	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 26	0	1	1	0	1	1	1	1	0	3	1	-	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 27	1	1	1	0	1	1	1	1	0	3	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 29	0	1	1	0	1	1	1	1	0	3	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 30	1	1	0	0	1	1	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 31	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 32	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 33	0	1	1	0	1	1	1	1	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 34	0	1	0	0	1	0	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 35	0	1	0	0	1	0	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 36	0	1	0	0	1	0	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 37	0	1	0	0	1	1	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 38	0	1	0	0	1	1	1	1	0	3	1	-	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 39	0	1	1	0	1	1	1	1	0	3	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 40	1	1	1	0	1	1	1	1	0	3	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 41	1	1	0	0	1	1	1	1	0	4	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 42	0	1	0	0	1	0	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 43	0	1	0	0	1	0	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 44	0	1	0	0	1	1	1	1	0	3	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 45	0	1	0	0	1	0	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 46	0	1	0	0	1	1	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 47	0	1	0	0	1	0	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 48	0	1	0	0	1	1	1	1	0	4	0	1	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 49	0	1	1	0	1	1	1	1	0	3	0	1	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 50	0	1	0	0	1	1	1	1	0	3	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 51	1	1	0	0	1	0	1	1	0	2	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 52	1	1	0	0	1	0	1	1	0	2	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 53	1	1	0	0	1	0	1	1	0	2	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 54	0	1	0	0	1	1	1	1	0	3	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 55	0	1	0	0	1	1	1	1	0	3	0	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 56	0	1	1	0	1	1	1	1	0	3	0	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 57	1	1	1	0	1	1	1	1	0	3	0	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 58	0	1	0	0	1	1	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris sp. 59	0	1	0	0	1	1	1	1	0	3	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 60	0	1	1	0	1	0	1	1	0	3	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 61	0	1	0	0	1	1	1	1	0	3	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris sp. 63	0	1	0	0	1	1	1	1	0	3	0	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris/Trachepyris sp. 1	0	1	0	0	1	0	1	0	0	3	0	0	4	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris/Trachepyris sp. 2	0	1	0	0	1	0	1	0	0	3	0	0	4	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 3	0	1	0	0	1	0	1	0	0	3	0	0	4	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 4	0	1	0	0	1	0	1	0	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 5	0	1	0	0	1	0	1	0	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 6	0	1	0	0	1	0	1	0	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 7	0	1	0	0	1	0	1	0	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 8	0	1	0	0	1	0	1	0	0	3	0	0	3	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 9	0	1	0	0	1	0	1	0	0	3	0	0	3	1	1	1	1	0	1	0	1	1	0	0	1	1	1
Epyris/Trachepyris sp. 10	0	1	0	0	0	-	0	-	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Epyris/Trachepyris sp. 11	0	1	0	0	0	-	0	-	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Formosiepyris marish	0	1	0	0	1	0	1	0	0	2	1	-	0	0	1	1	1	0	1	0	1	1	0	1	1	0	1
Formosiepyris sp. 1	1	1	0	0	1	1	1	0	0	3	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	0	1
Formosiepyris sp. 2	1	1	0	0	1	0	1	0	0	3	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	0	1
†*Gloxinius bifossatus*	-	-	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Holepyris africanus	1	1	0	0	1	1	1	0	0	3	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	0	1
Holepyris sp. 2	0	1	0	0	1	1	1	1	0	3	1	-	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 3	0	1	0	0	1	1	1	1	0	1	1	-	0	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 4	0	1	0	0	1	1	1	1	0	1	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 5	0	1	0	0	1	1	1	1	0	1	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 6	1	1	0	0	1	1	1	1	0	1	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 7	0	1	0	0	1	1	1	1	0	1	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0

	9										0										1						
TAXA/CHARACTERS	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**
Epyris sp. 8	0	0	1	0	2	1	0	0	0	0	2	1	1	-	0	2	1	1	1	0	0	1	1	0	0	2	0
Epyris sp. 9	0	0	1	0	2	1	0	0	0	0	0	-	1	-	2	2	1	1	1	0	0	0	1	0	0	0	-
Epyris sp. 10	0	0	1	0	2	1	0	0	0	0	0	-	1	-	2	2	1	1	1	0	0	0	1	0	0	0	-
Epyris sp. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 14	0	0	0	0	2	1	0	0	0	0	0	-	1	-	2	2	0	1	1	0	0	0	1	0	0	0	-
Epyris sp. 15	0	0	1	0	2	1	0	0	2	0	2	1	1	-	0	0	1	1	1	0	0	1	1	0	0	0	-
Epyris sp. 16	0	0	1	0	2	1	0	0	0	0	2	1	1	-	0	0	1	1	1	0	0	1	1	0	0	0	-
Epyris sp. 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 18	0	0	1	0	2	1	0	0	0	0	2	1	1	-	0	0	1	1	1	0	0	1	1	0	0	0	-
Epyris sp. 19	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 21	0	0	1	0	2	1	0	0	0	0	1	-	1	-	0	0	1	1	1	0	0	1	1	0	0	0	-
Epyris sp. 22	0	0	1	0	2	1	0	0	0	0	2	1	1	-	0	0	1	1	1	0	0	1	1	0	0	0	-
Epyris sp. 23	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epyris sp. 26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 31	1	0	1	0	2	1	0	0	0	0	1	1	1	-	2	1	1	1	1	0	0	0	1	0	0	1	0
Epyris sp. 32	1	0	1	0	2	1	0	0	3	0	1	1	1	-	2	1	1	1	1	0	0	0	1	0	0	1	0
Epyris sp. 33	0	0	1	0	2	1	0	0	0	0	2	1	1	-	2	1	1	1	1	0	0	0	1	0	0	1	0
Epyris sp. 34	1	0	1	0	2	1	0	0	0	0	2	1	1	-	0	1	1	1	1	0	0	1	1	2	0	1	0
Epyris sp. 35	1	0	1	0	2	1	0	0	0	0	2	1	1	-	0	1	1	1	1	0	0	1	1	2	0	1	0
Epyris sp. 36	1	0	1	0	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	0	0	1	0
Epyris sp. 37	0	0	1	0	2	1	0	0	3	0	2	1	1	-	2	1	0	0	1	0	0	1	1	0	0	1	0
Epyris sp. 38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 39	0	0	1	0	2	1	0	0	0	0	2	1	1	-	2	2	0	0	1	0	0	1	1	0	0	1	0
Epyris sp. 40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 41	1	0	0	0	2	3	0	0	2	0	2	1	1	-	0	0	0	1	1	0	0	0	1	0	0	1	1
Epyris sp. 42	1	0	1	0	2	1	0	0	0	0	2	1	1	-	0	2	1	1	1	0	0	1	1	0	0	1	1
Epyris sp. 43	1	0	1	0	2	1	0	0	0	0	2	1	1	-	0	2	1	1	1	0	0	1	1	0	0	1	1
Epyris sp. 44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 46	1	0	1	0	2	1	0	0	0	0	1	?	1	-	0	1	1	1	1	0	0	1	1	0	0	1	1
Epyris sp. 47	1	0	0	0	2	3	0	0	2	0	2	1	1	-	0	0	0	1	1	0	0	0	1	0	0	1	1
Epyris sp. 48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 54	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 55	2	0	1	0	2	1	0	0	0	0	2	1	1	-	0	2	1	1	1	0	0	1	1	0	0	1	1
Epyris sp. 56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 58	2	0	1	0	2	1	0	0	0	0	2	1	1	-	0	2	1	1	1	0	0	1	1	0	0	1	1
Epyris sp. 59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris sp. 63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epyris/Trachepyris sp. 1	0	0	1	0	2	1	0	0	2	0	2	0	1	-	2	2	1	1	0	1	1	1	1	0	0	0	-
Epyris/Trachepyris sp. 2	0	0	1	0	2	1	0	0	1	0	2	0	1	-	2	2	1	1	0	1	1	1	1	0	0	0	-
Epyris/Trachepyris sp. 3	0	0	1	0	2	1	0	0	1	0	2	0	1	-	2	2	1	1	0	1	1	1	1	0	0	0	-
Epyris/Trachepyris sp. 4	1	0	1	0	2	0	0	0	1	0	2	1	0	0	0	2	1	1	1	1	0	1	1	0	0	1	2
Epyris/Trachepyris sp. 5	1	0	1	0	2	0	0	0	1	0	2	1	0	0	0	2	1	1	1	1	0	1	1	0	0	1	2
Epyris/Trachepyris sp. 6	0	0	1	0	2	0	0	0	1	0	2	1	0	0	0	2	1	1	1	1	0	1	1	0	0	1	2
Epyris/Trachepyris sp. 7	0	0	1	0	2	0	0	0	1	0	2	1	0	0	0	2	1	1	1	1	0	1	1	0	0	1	2
Epyris/Trachepyris sp. 8	0	0	1	0	2	0	0	0	1	0	2	1	0	0	0	2	1	1	1	1	0	1	1	0	0	1	2
Epyris/Trachepyris sp. 9	0	0	1	0	2	0	0	0	1	0	2	1	0	0	0	2	1	1	1	1	0	1	1	0	0	1	2
Epyris/Trachepyris sp. 10	0	1	1	0	2	0	0	0	1	0	2	1	1	-	2	0	1	1	1	1	0	0	1	2	0	0	-
Epyris/Trachepyris sp. 11	0	1	1	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Formosiepyris marish	0	1	1	0	2	0	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	2	0	0	-
Formosiepyris sp. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Formosiepyris sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
†*Gloxinius bifossatus*	?	?	?	?	?	?	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	0	1	2	0	?	?
Holepyris africanus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 2	0	0	0	0	2	3	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-
Holepyris sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 7	0	0	0	0	2	3	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-

	2			2										2		
	1			2										3		
TAXA/CHARACTERS	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**
Epyris sp. 8	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0
Epyris sp. 9	1	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0
Epyris sp. 10	1	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0
Epyris sp. 11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 14	1	0	1	0	1	0	-	-	-	1	1	0	0	0	0	0
Epyris sp. 15	1	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 16	1	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 18	1	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 19	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Epyris sp. 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 21	1	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 22	1	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 23	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Epyris sp. 26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 31	4	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 32	4	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 33	4	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 34	4	0	1	0	1	1	0	1	0	1	2	0	0	0	0	0
Epyris sp. 35	4	0	1	0	1	1	0	1	0	1	2	0	0	0	0	0
Epyris sp. 36	4	0	1	1	1	0	0	1	0	1	2	0	0	0	0	0
Epyris sp. 37	4	0	1	0	1	0	1	1	0	1	2	0	0	0	0	0
Epyris sp. 38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 39	4	0	1	1	1	1	0	1	0	1	2	0	0	0	0	0
Epyris sp. 40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 41	4	0	1	0	2	2	0	1	0	1	1	0	1	0	0	0
Epyris sp. 42	2	0	1	1	1	0	0	1	0	1	1	0	0	0	0	0
Epyris sp. 43	2	0	1	0	2	2	0	1	0	1	1	0	0	0	0	0
Epyris sp. 44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?
Epyris sp. 45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 46	2	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0
Epyris sp. 47	2	0	1	1	1	0	0	1	0	1	1	0	0	0	0	0
Epyris sp. 48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 54	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 55	2	0	1	0	2	2	0	1	0	1	1	0	0	0	0	0
Epyris sp. 56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 58	2	0	1	0	2	2	0	1	0	1	1	0	0	0	0	0
Epyris sp. 59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris sp. 63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Epyris/*Trachepyris* sp. 1	0	0	1	1	0	0	0	1	0	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 2	0	0	1	1	0	0	0	1	0	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 3	0	0	1	1	0	0	0	1	0	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 4	1	0	1	0	1	1	0	1	1	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 5	1	0	1	0	1	1	0	1	1	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 6	1	0	1	0	1	1	0	1	1	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 7	1	0	1	0	1	1	0	1	1	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 8	1	0	1	0	1	1	0	1	1	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 9	1	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0
Epyris/*Trachepyris* sp. 10	0	0	1	1	0	0	0	1	1	1	2	0	0	0	0	0
Epyris/*Trachepyris* sp. 11	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Formosiepyris marish	3	0	0	1	2	2	0	1	1	1	0	0	0	0	0	0
Formosiepyris sp. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Formosiepyris sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
†*Gloxinius bifossatus*	?	1	0	0	2	1	0	0	0	?	2	?	?	?	?	0
Holepyris africanus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 2	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Holepyris sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 7	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0

										1										2							
TAXA/CHARACTERS	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Holepyris sp. 8	1	1	1	1	0	2	0	1	0	1	0	0	0	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Holepyris sp. 9	1	1	1	1	0	2	0	1	0	1	0	1	0	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Holepyris sp. 10	1	1	1	1	0	1	0	1	0	0	0	0	2	0	1	1	1	0	0	1	1	0	1	1	1	0	1
Holepyris sp. 11	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Holepyris sp. 13	1	1	1	1	0	1	0	1	0	0	0	1	2	0	1	1	1	0	0	1	1	0	1	1	1	0	1
Holepyris sp. 14	1	1	1	1	0	3	0	1	0	0	0	0	2	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Holepyris sp. 15	1	1	1	1	0	3	0	1	0	0	0	0	2	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Holepyris sp. 16	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Holepyris sp. 17	1	1	1	1	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0	2	1	2	1	0	-	-	-
Holepyris sp. 18	1	1	1	1	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Holepyris sp. 19	1	1	1	1	0	3	0	1	0	1	0	0	1	0	1	2	1	0	0	1	1	2	1	0	-	-	-
Holepyris sp. 20	1	1	1	1	0	3	0	1	0	0	0	0	1	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Holepyris sp. 21	1	1	1	1	0	3	0	1	2	1	0	0	2	0	1	1	1	0	0	1	1	2	1	0	-	-	-
Laelius sp. 1	0	0	1	1	0	2	0	1	0	1	0	0	0	0	1	2	1	0	0	2	1	1	1	4	0	0	1
Laelius sp. 2	0	0	1	1	0	3	0	1	0	1	0	0	2	0	1	2	1	0	0	2	1	1	1	4	0	0	1
Laelius sp. 4	0	0	1	1	0	2	0	1	0	1	0	1	0	0	1	1	1	0	0	1	1	1	1	4	0	0	1
Laelius sp. 5	0	0	1	1	0	2	0	1	0	1	0	1	0	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Laelius sp. 6	0	0	1	1	0	2	0	1	0	1	0	1	0	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Laelius sp. 7	0	0	1	1	0	?	0	1	0	1	0	1	1	0	1	1	1	0	0	1	1	1	1	4	0	0	1
Laelius sp. 8	0	0	1	1	0	1	0	1	0	1	0	1	1	0	1	1	1	0	0	2	1	1	1	4	0	0	1
Trachepyris sp. 1	1	1	1	1	0	1	0	1	0	0	1	0	1	1	0	1	1	0	0	1	0	1	0	4	1	0	1
Trachepyris sp. 2	1	1	1	1	0	1	0	1	0	0	1	0	1	1	0	1	1	0	0	1	0	1	0	4	1	0	1
Trachepyris sp. 3	1	1	1	1	0	1	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	0	4	1	0	1

	2		**3**										**4**										**5**				
TAXA/CHARACTERS	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**
Holepyris sp. 8	-	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 9	-	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	1	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 10	0	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 11	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Holepyris sp. 13	0	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 14	-	0	-	1	0	1	-	-	1	1	0	0	1	0	2	1	1	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 15	-	0	-	1	0	1	-	-	1	0	0	0	0	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 16	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Holepyris sp. 17	-	0	-	1	0	1	-	-	1	1	0	0	1	0	2	1	1	1	1	2	0	2	1	1	0	0	1
Holepyris sp. 18	-	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	2	1	0	0	1
Holepyris sp. 19	-	0	-	1	0	1	-	-	1	0	0	0	1	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 20	-	0	-	1	0	1	-	-	1	1	0	0	2	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Holepyris sp. 21	-	0	-	1	0	1	-	-	1	0	0	0	0	0	2	1	0	1	1	2	0	2	1	0	1	0	1
Laelius sp. 1	0	0	-	1	0	1	-	-	1	1	1	0	1	1	-	-	0	1	1	0	1	2	2	0	0	0	1
Laelius sp. 2	0	0	-	1	0	1	-	-	1	1	1	0	1	1	-	-	0	1	1	0	1	2	2	0	0	0	1
Laelius sp. 4	0	0	-	1	0	1	-	-	1	1	0	0	1	1	-	-	0	1	1	0	0	2	2	0	0	0	1
Laelius sp. 5	0	0	-	1	0	1	-	-	1	1	0	0	1	1	-	-	0	1	1	0	0	2	2	0	0	0	1
Laelius sp. 6	0	0	-	1	0	1	-	-	1	1	0	0	1	1	-	-	0	1	1	0	0	2	2	0	0	0	1
Laelius sp. 7	0	0	-	1	0	1	-	-	1	1	0	0	1	1	-	-	0	1	1	0	0	2	2	0	0	0	1
Laelius sp. 8	0	0	-	1	0	1	-	-	1	1	0	0	1	1	-	-	0	1	1	0	0	2	2	0	0	0	1
Trachepyris sp. 1	1	0	-	0	0	0	1	1	1	2	0	0	1	0	0	2	1	1	1	2	0	2	0	0	1	0	1
Trachepyris sp. 2	1	0	-	0	0	0	1	1	1	2	0	0	1	0	0	2	1	1	1	2	0	2	1	0	1	0	1
Trachepyris sp. 3	0	0	-	0	0	0	1	1	1	2	0	0	1	0	0	2	1	1	1	2	0	2	0	0	1	0	0

	5					**6**										**7**									**8**		
TAXA/CHARACTERS	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**
Holepyris sp. 8	0	0	1	0	1	0	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 9	0	0	1	0	1	0	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 10	0	0	1	0	1	0	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 11	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	-	-	-
Holepyris sp. 13	0	0	1	0	1	0	0	1	0	0	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 14	0	0	1	0	1	0	0	1	0	0	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 15	0	0	1	0	1	0	0	1	0	0	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 16	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	-	-	-
Holepyris sp. 17	0	0	1	0	1	2	0	1	0	1	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 18	0	0	1	0	1	2	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 19	0	0	1	0	1	2	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	0	-	-	-
Holepyris sp. 20	0	0	1	0	1	0	0	1	0	2	1	0	2	1	1	1	0	1	1	0	0	0	-	1	1	1	0
Holepyris sp. 21	0	0	1	0	1	2	0	1	0	1	1	0	2	1	1	1	0	1	1	0	0	0	-	1	1	1	0
Laelius sp. 1	0	0	1	1	1	0	1	1	0	2	1	1	2	2	1	1	1	-	-	1	-	0	-	1	1	1	0
Laelius sp. 2	0	0	1	1	1	0	0	1	0	2	1	1	2	2	1	1	1	-	-	1	-	0	-	0	-	-	-
Laelius sp. 4	0	0	1	1	1	0	1	1	0	2	1	1	2	2	1	1	1	-	-	1	-	0	-	1	0	0	0
Laelius sp. 5	0	0	1	1	1	0	0	1	0	2	1	1	0	2	1	1	1	-	-	0	0	0	-	1	0	0	2
Laelius sp. 6	0	0	1	1	1	0	0	1	0	2	1	1	0	2	1	1	1	-	-	0	0	0	-	1	1	0	2
Laelius sp. 7	0	0	1	1	1	0	0	1	0	2	1	1	0	2	1	1	1	-	-	0	0	0	-	1	1	0	2
Laelius sp. 8	0	0	1	1	1	0	0	1	0	2	1	1	0	2	1	1	1	-	-	0	0	0	-	1	1	0	2
Trachepyris sp. 1	0	1	1	0	1	0	1	1	1	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Trachepyris sp. 2	0	1	1	0	1	0	1	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1
Trachepyris sp. 3	0	1	1	0	1	0	1	1	0	2	0	0	2	1	1	1	1	-	-	1	-	0	-	1	1	0	1

TAXA/CHARACTERS	8 2	3	4	5	6	7	8	9	9 0	1	2	3	4	5	6	7	8	9	10 0	1	2	3	4	5	6	7	8
Holepyris sp. 8	-	-	0	2	1	1	0	0	2	0	0	1	-	-	-	-	0	0	1	0	0	0	0	0	0	0	0
Holepyris sp. 9	-	-	0	2	1	1	0	0	2	0	0	1	-	-	-	-	0	0	1	0	0	0	0	0	0	0	0
Holepyris sp. 10	-	-	0	2	1	1	1	0	0	0	0	1	-	-	-	-	1	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 11	-	-	0	2	1	1	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 13	-	-	0	2	1	1	0	0	0	0	1	1	-	-	-	-	0	0	1	1	0	0	0	0	0	0	0
Holepyris sp. 14	-	-	0	2	1	1	0	0	0	0	1	1	-	-	-	-	1	1	1	1	0	0	0	0	0	0	0
Holepyris sp. 15	-	-	0	2	1	1	0	0	0	0	1	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 16	-	-	0	2	1	1	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 17	-	-	0	2	1	1	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 18	-	-	0	2	1	1	1	0	0	0	1	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 19	-	-	0	2	1	1	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 20	0	1	0	1	1	1	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Holepyris sp. 21	0	1	0	1	1	1	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0
Laelius sp. 1	0	1	0	0	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Laelius sp. 2	-	-	0	2	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Laelius sp. 4	0	1	0	1	1	1	0	1	2	1	-	1	-	2	0	0	0	1	1	1	0	0	0	0	0	0	0
Laelius sp. 5	1	1	0	1	1	1	0	0	2	1	-	1	-	-	-	-	0	1	1	1	0	0	0	0	0	0	0
Laelius sp. 6	1	1	0	1	1	1	0	0	2	1	-	1	-	-	-	-	0	1	1	1	0	0	0	0	0	0	0
Laelius sp. 7	1	1	0	1	1	1	0	0	2	1	-	1	-	-	-	-	0	1	1	1	0	0	0	0	0	0	0
Laelius sp. 8	1	1	0	1	1	1	0	0	2	1	-	1	-	-	-	-	0	1	1	1	0	0	0	0	0	0	0
Trachepyris sp. 1	1	0	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Trachepyris sp. 2	1	0	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-
Trachepyris sp. 3	1	1	0	0	1	0	0	-	-	-	-	-	1	0	0	0	0	1	1	1	0	0	0	0	0	1	-

TAXA/CHARACTERS	10 11 9	0	1	2	3	4	5	6	7	8	9	12 0	1	2	3	4	5	6	7	8	9	13 0	1	2	3	4	5
Holepyris sp. 8	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	0	1	1	2	0	1	0	0	0	0	0	1
Holepyris sp. 9	0	0	0	0	1	1	1	2	0	-	-	0	0	0	2	0	0	1	2	0	1	0	0	2	0	0	2
Holepyris sp. 10	0	0	0	0	1	1	0	-	-	-	-	0	0	2	1	0	0	1	2	0	1	0	0	2	0	0	1
Holepyris sp. 11	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	1	-	1	2	0	1	0	0	2	0	0	1
Holepyris sp. 13	0	0	0	0	1	1	1	-	-	-	-	0	0	0	1	0	0	1	2	0	1	0	0	2	0	0	2
Holepyris sp. 14	0	0	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1	2	0	1	0	0	2	0	0	2
Holepyris sp. 15	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	1	-	1	2	0	1	0	0	2	0	0	2
Holepyris sp. 16	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1	2	0	1	0	0	1	0	0	2
Holepyris sp. 17	0	0	0	0	1	2	1	-	-	-	-	0	0	2	1	0	0	1	2	0	1	0	0	1	0	0	2
Holepyris sp. 18	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	1	-	1	2	0	1	0	0	1	0	0	2
Holepyris sp. 19	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	1	-	1	2	0	1	0	0	2	0	0	2
Holepyris sp. 20	0	0	0	0	1	2	1	-	-	-	-	0	0	0	2	1	-	1	2	0	1	0	0	1	0	0	2
Holepyris sp. 21	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	1	-	1	2	0	1	0	0	1	0	0	2
Laelius sp. 1	0	0	0	0	1	2	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Laelius sp. 2	0	0	0	1	1	0	0	-	-	-	-	0	0	1	1	1	-	1	0	0	1	0	0	1	0	0	1
Laelius sp. 4	0	0	0	0	1	2	0	-	-	-	-	0	0	2	2	0	0	1	0	0	1	0	0	1	0	0	1
Laelius sp. 5	0	0	0	0	1	1	1	-	-	-	-	0	0	0	2	0	0	1	0	0	1	0	0	1	0	0	1
Laelius sp. 6	0	0	0	0	1	1	1	-	-	-	-	0	0	0	2	0	0	1	0	0	1	0	0	1	0	0	1
Laelius sp. 7	0	0	0	0	1	1	1	-	-	-	-	0	0	0	2	0	0	1	0	0	1	0	0	1	0	0	1
Laelius sp. 8	0	0	0	0	1	1	1	-	-	-	-	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1
Trachepyris sp. 1	0	0	0	0	1	2	0	-	-	-	-	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0	1
Trachepyris sp. 2	0	0	0	0	1	2	0	-	-	-	-	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0	1
Trachepyris sp. 3	0	0	0	0	1	2	0	-	-	-	-	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0	1

TAXA/CHARACTERS	13 14 6	7	8	9	0	1	2	3	4	5	6	7	8	9	15 0	1	2	3	4	5	6	7	8	9	16 0	1	2
Holepyris sp. 8	0	1	0	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 9	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 10	0	1	0	0	0	0	0	0	1	1	0	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 11	1	-	-	0	0	0	0	0	1	1	1	0	1	?	?	?	?	?	?	?	?	1	1	1	1	0	1
Holepyris sp. 13	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 14	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 15	0	1	0	0	0	1	-	-	-	1	0	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 16	1	-	-	0	0	0	0	0	1	1	1	1	-	?	?	?	?	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 17	1	-	-	0	0	0	0	0	1	1	1	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 18	0	1	0	0	0	0	0	0	1	1	0	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 19	1	-	-	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 20	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Holepyris sp. 21	0	1	0	0	0	0	0	0	1	1	0	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Laelius sp. 1	1	-	-	0	0	0	0	1	1	1	0	1	-	1	0	0	0	0	0	0	0	1	1	1	1	0	1
Laelius sp. 2	1	-	-	0	0	0	1	1	1	0	1	1	-	1	0	0	0	0	0	0	0	1	1	1	1	0	1
Laelius sp. 4	1	-	-	0	0	0	1	1	1	0	0	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Laelius sp. 5	0	1	1	0	0	0	1	1	1	0	1	1	-	1	0	0	0	0	0	1	0	1	1	1	1	0	1
Laelius sp. 6	0	1	1	0	0	0	1	1	1	0	1	1	-	1	0	0	0	0	0	0	0	1	1	1	1	0	1
Laelius sp. 7	0	1	1	0	0	0	1	1	1	0	1	1	-	1	0	0	0	0	0	0	0	1	1	1	1	0	1
Laelius sp. 8	0	1	1	0	0	0	1	1	1	0	1	1	-	1	0	0	0	0	0	0	0	1	1	1	1	0	1
Trachepyris sp. 1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	1	1	0	1
Trachepyris sp. 2	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	1	1	0	1
Trachepyris sp. 3	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	1	1	0	1

TAXA/CHARACTERS	16 3	4	5	6	7	8	9	17 0	1	2	3	4	5	6	7	8	9	18 0	1	2	3	4	5	6	7	8	9
Holepyris sp. 8	1	1	0	0	1	1	1	1	0	1	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 9	1	1	0	0	1	1	1	1	0	1	1	-	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 10	0	1	0	0	1	1	1	1	0	1	1	-	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 11	1	1	1	0	1	1	1	1	0	1	1	-	?	?	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 13	0	1	1	0	1	1	1	1	0	1	1	-	2	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 14	0	1	1	0	1	1	1	1	0	1	1	-	2	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 15	0	1	0	0	1	1	1	1	0	2	1	-	2	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 16	0	1	0	0	1	1	1	1	0	2	1	-	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 17	0	1	1	0	1	1	1	1	0	1	1	-	2	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 18	0	1	1	0	1	1	1	1	0	2	1	-	2	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 19	0	1	0	0	1	1	1	1	0	2	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 20	0	1	0	0	1	1	1	1	0	2	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Holepyris sp. 21	0	1	0	0	1	1	1	1	0	2	1	-	1	0	1	1	1	0	1	0	1	1	0	0	1	1	0
Laelius sp. 1	0	1	1	0	0	-	1	-	0	0	1	-	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0
Laelius sp. 2	0	1	1	0	0	-	1	-	0	0	1	-	0	0	1	1	1	0	1	0	1	1	0	0	1	0	0
Laelius sp. 4	1	1	1	0	1	0	1	1	0	2	1	-	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0
Laelius sp. 5	0	1	1	0	1	1	1	1	0	2	1	-	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0
Laelius sp. 6	0	1	1	0	1	1	1	1	0	2	1	-	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0
Laelius sp. 7	0	1	1	0	1	1	1	1	0	2	1	-	0	0	1	1	1	0	1	0	1	1	0	0	1	0	0
Laelius sp. 8	0	1	1	0	1	1	1	1	0	2	1	-	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0
Trachepyris sp. 1	0	1	0	0	0	-	1	-	0	3	0	0	3	1	1	1	1	0	1	0	1	1	0	0	1	0	0
Trachepyris sp. 2	1	1	0	0	0	-	1	-	0	3	0	0	2	1	1	1	1	0	1	0	1	1	0	0	1	0	0
Trachepyris sp. 3	1	1	1	0	0	-	1	-	0	3	0	0	0	1	1	1	1	0	1	0	1	1	0	0	1	0	0

TAXA/CHARACTERS	19 0	1	2	3	4	5	6	7	8	9	20 0	1	2	3	4	5	6	7	8	9	21 0	1	2	3	4	5	6
Holepyris sp. 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 11	0	0	0	0	2	1	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-
Holepyris sp. 13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 14	0	0	1	0	2	1	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-
Holepyris sp. 15	0	0	1	0	2	1	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-
Holepyris sp. 16	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Holepyris sp. 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holepyris sp. 19	1	0	1	0	2	1	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-
Holepyris sp. 20	0	0	1	0	2	1	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-
Holepyris sp. 21	0	0	1	0	2	1	0	0	0	0	2	1	1	-	2	2	1	1	1	0	0	1	1	0	0	0	-
Laelius sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laelius sp. 2	0	0	0	0	2	1	0	0	0	0	0	-	1	-	2	2	1	1	1	0	0	0	1	0	0	1	0
Laelius sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laelius sp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laelius sp. 6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laelius sp. 7	0	0	0	0	2	1	0	0	0	0	2	1	1	-	2	1	1	1	1	0	0	1	1	0	0	0	-
Laelius sp. 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachepyris sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachepyris sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachepyris sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TAXA/CHARACTERS	21 7	8	9	22 0	1	2	3	4	5	6	7	8	9	23 0	1	2
Holepyris sp. 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 11	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Holepyris sp. 13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 14	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Holepyris sp. 15	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Holepyris sp. 16	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Holepyris sp. 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Holepyris sp. 19	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Holepyris sp. 20	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Holepyris sp. 21	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Laelius sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Laelius sp. 2	4	0	1	0	2	2	0	0	1	1	0	0	0	0	0	0
Laelius sp. 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Laelius sp. 5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Laelius sp. 6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Laelius sp. 7	3	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0
Laelius sp. 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Trachepyris sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Trachepyris sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Trachepyris sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0