

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

**Revisitando a filogenia dos Scleroderminae (Hymenoptera, Bethyidae),
com ênfase nos gêneros com 10 flagelomos antenais**

Juan Manuel Vargas Rojas

**Vitória, ES
Julho, 2017**

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Juan Manuel Vargas Rojas

Orientador: Celso Oliveira Azevedo

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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Dedicatória

*À Sarah, minha filha adorada, pelo carinho e a alegria de viver,
pelo presente cotidiano de confiar a sua vida nos meus braços.*

*À Alexandra, minha companheira, pela vontade de caminhar lado a
lado comigo, pela consideração e a compreensão.*

*A Dora e Jorge, meus pais, pelo presente da vida, o cuidado
permanente, as palavras de amor e sua imensa capacidade de
compromisso.*

*Aos meus irmãos, Claudia Marcela e Jorge Enrique, pela mais
longa e verdadeira amizade que eu já conheci.*

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longe, este caminho do conhecimento e uma estreita amizade.*

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*A meus sobrinhos Juan Felipe e Jose Alejandro, pela saudade e por
nos esperar sempre com os braços abertos cheios de
positividade.*

*Ao tio Adolfo, pelo amor e bênçãos que sempre teve para com a
Sarah e nós, pelos ensinamentos de vida e o calor do seu eterno
sorriso.*

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Eu agradeço fundamentalmente o aprendizado que esta experiência me deu sobre a minha própria vida e identidade, sobre o grande compromisso que a academia tem com a sociedade e a responsabilidade que qualquer profissional tem de dar sentido aos títulos, como o título de doutor, os quais não fazem maior significado no isolamento, mesmo que aparentemente produtivo. É como o professor Alexandre Pires tem me ensinado durante este período acadêmico, sobre o bem pensar, o bom raciocínio não é facilmente atingível, tão só o questionamento constante das certezas aparentes consegue iluminar o caminho da consciência.

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Apresentação

Nasci na cidade de Bogotá, capital da Colômbia, em 1969, minha vida profissional se compõe de duas experiências fundamentais, meu ingresso no ano 1986, aos meus 16 anos, na *Escuela de Cadetes de Policia General Santander* e a minha decisão de estudar biologia, inicialmente no ano 1991 na *Pontificia Universidad Javeriana* e depois na *Universidad Nacional de Colombia*, onde me formei em 2001.

Ao longo da minha graduação os meus interesses científicos se focaram nos insetos e, dentro desse universo, eu fui convidado pelo professor Fernando Fernández para trabalhar com vespas, foi assim que eu deparei com um grupo que ninguém trabalhava na Colômbia e que talvez desse muito trabalho a fazer, a família Bethylidae. Visto que ninguém na Colômbia poderia me ajudar com meus anseios de conhecimento sobre estes organismos, tive a necessidade de procurar esta ajuda e foi na *International Society of Hymenopterists* que eu achei o contato do professor Celso Azevedo, quem naquela época me co-orientou no meu trabalho de graduação com o gênero *Dissomphalus*. Depois da minha graduação, eu fiz trabalho prático e teórico na área da taxonomia entomológica que deu como resultado a publicação de alguns artigos descrevendo duas espécies novas dos gêneros *Rhabdepyris* (Vargas 2001) e cinco espécies novas da subfamília Pristocerinae (Vargas & Terayama 2002).

Entre 2001 e 2008, eu trabalhei em diferentes áreas de atuação, seja como comandante da polícia ambiental de Bogotá, como avaliador de projetos para o Ministério de Agricultura e o Serviço Nacional de Aprendizagem (SENA), ou como professor, sempre tentando exercer dentro do âmbito da minha profissão. Nesta ocasião, senti necessidade de continuar procurando explicações para as limitações que disciplinas como a biologia apresentavam no mundo laboral. Foi assim que cheguei à idéia de mudar o meu perfil retornando à academia na *Universidad Nacional de Colombia*, achei que fazendo um mestrado em Ciências Agrárias, eu poderia criar um nexos mais consistente com a realidade laboral, compreender melhor quais são as competências do Profissional em biologia e, talvez, perceber claramente a abrangência social da ciência.

Durante o período de mestrado, desenvolvi trabalho taxonômico e algumas publicações como um capítulo de livro sobre a família Bethylidae na região neotropical (Vargas & Terayama 2006), o primeiro registro de cópula forética para *Dissomphalus xanthopus* (Vargas 2007) e a revisão do gênero *Alongatepyris* (Vargas & Azevedo 2008). Alguns trabalhos posteriores com a família Cicadellidae (Hemiptera, Auchenorrhyncha) foram produto da interação com o meu co-orientador de mestrado, o professor Paul Freytag da University of Kentucky, com quem eu publiquei duas espécies do gênero *Palingonalia* (Freytag & Vargas 2007) e uma espécie nova do gênero *Paracatua* (Beltran et al. 2011), estes trabalhos ampliaram a minha visão sobre a diversidade morfológica e o campo de aplicação da taxonomia.

Formei-me como mestre no ano 2007 e entrei para o serviço público em 2009 no *Instituto Colombiano Agropecuario* (ICA), no cargo de profissional especializado com funções de analista em diagnóstico de pragas. O trabalho no ICA exigiu de mim um importante esforço de aprofundamento técnico-científico em outras ordens de artrópodes como Thysanoptera, Hemiptera (especialmente Heteroptera e Sternorrhyncha), Diptera, Coleoptera, Lepidoptera e Acari (especialmente Eriophyidae, Tarsonemidae, Tenuipalpidae e Tetranychidae entre outras), aprendi a valorizar importantes realidades socioeconômicas e a interagir de maneira transdisciplinar com outras áreas técnicas, científicas e administrativas. No ano 2012, após três anos de serviço, fui nomeado como Coordenador da Rede de Laboratórios de Diagnóstico Fitossanitário do ICA, compreendendo nove laboratórios em diferentes partes do país.

Em 2013, foi-me dada a oportunidade de continuar a minha carreira acadêmica

mediante licença de estudos, que eu decidi aproveitar viajando ao Brasil para continuar com meus estudos sobre biologia animal através do primeiro objeto de estudo que tinha me acompanhado durante meus estudos de graduação, os Bethylidae. Assim, eu fiz as minhas malas e cheguei ao Brasil no mês de agosto de 2013, com apenas um ano de ter casado e com a minha filha Sarah de nove meses de idade.

Este é um tempo em que minha vida tem mudado vertiginosamente, incorporando experiências e desafios inesperados, com certeza a minha mente tem mudado no seu jeito de raciocinar e minha vida tem deixado para trás o foco individual para abrir passo a uma consciência coletiva.

Trabalhos preliminares

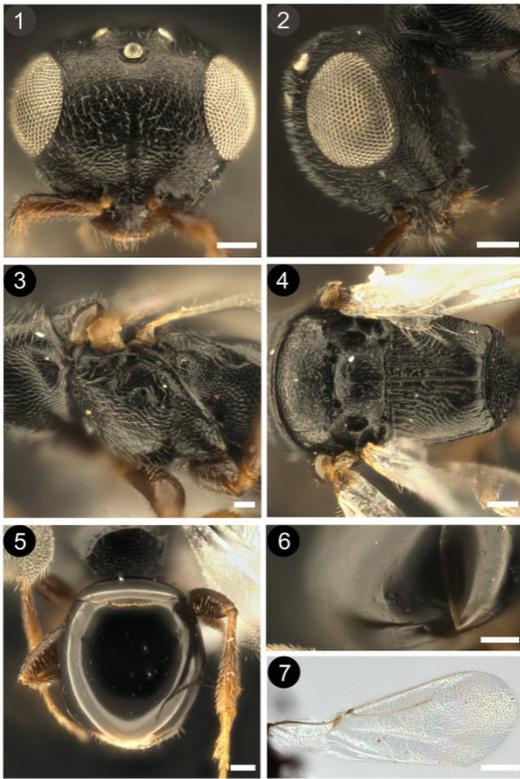
Como parte do processo acadêmico do doutorado e com o objetivo de melhorar a prática da leitura, a escrita e a formalização da produção científica, foram desenvolvidos dois trabalhos taxonômicos que serviram para me introduzir no âmbito da subfamília Scleroderminae, e entender melhor a taxonomia e o seu estado geral de conhecimento.

Neste sentido, foi publicado na revista *Zootaxa* (Vargas & Azevedo 2016a) um estudo do gênero *Pararhabdepyris* Gorbatovsky, 1995, táxon que é facilmente reconhecido, entre os gêneros de Scleroderminae, dado a forma subtriangular incomum da cabeça. Até 2016, eram reconhecidas só três espécies válidas, *P. paradoxus* do extremo leste da Rússia (Gorbatovsky 1995) e da Coreia do Sul (Lim & Lee 2014), *P. lophos* da Tailândia e *P. balios* da Austrália (Azevedo & Barbosa 2010). Estas espécies sugeriam que a distribuição era restrita à latitude leste superior (101° to 146° E). No entanto, outras amostragens providenciaram material novo. Em 2015, foram analisadas quatro fêmeas coletadas durante os inventários de insetos feitos no Iêmen (2005) e nos Emirados Árabes Unidos (2009), coordenados pelo Dr. Anthony van Harten, e na República Centro Africana (2001), coordenadas pelo Dr. Simon van Noort.

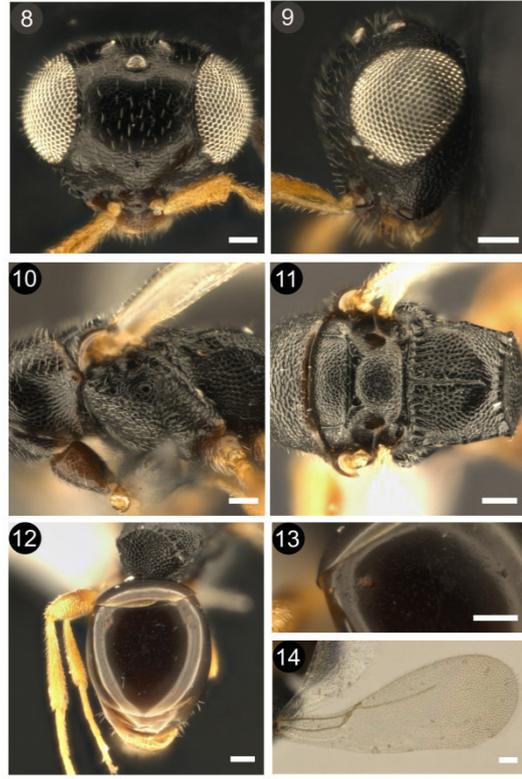
Os impactos deste trabalho podem ser resumidos dizendo-se que este gênero, apesar de extremamente raro, duplicou-se seu tamanho em número de espécies e que a sua distribuição, que tinha sido ampliada para o Oeste por Azevedo *et al.* (2015) em um estudo de nível genérico, foi confirmada com a descrição das espécies *P. arabo*, *P. wafrika* e *P. ngangu*, táxons que apresentaram desafio para a caracterização específica; pois este gênero como muito outros dentro desta subfamília, apresenta nível alto de variação gradual na expressão das suas características (Fig. 1).

O segundo trabalho durante o meu doutorado foi publicado como capítulo de livro nas *Mémoires du Muséum national d'Histoire naturelle* (Vargas & Azevedo 2016b), este estudo abordou o gênero oriental *Galodoxa* e a sua única espécie *G. torquata*, somente conhecida a partir de fêmeas achadas nas Filipinas e Indonésia (Sulawesi). Neste trabalho, foi revisado o holótipo depositado no *Zoologisk Museum Statens Naturhistoriske Museum*, Copenhague (ZMUC, L. Vilhelmsen) e três fêmeas adicionais da Malásia e da Papua Nova Guiné, depositadas nas coleções do *Museum of Comparative Zoology*, Cambridge (MCZH, P. Perkins), *Muséum national d'Histoire naturelle* (MNHN, C. Villemant), e *American Entomological Institute* (AEIC, D. Wahl), mais três inestimáveis espécimes macho do Laos e da Papua Nova Guiné, achado pelo Dr. Azevedo durante uma visita à coleção do *Bernice Pauahi Bishop Museum* (BPBM, J. Boone).

I



II



III

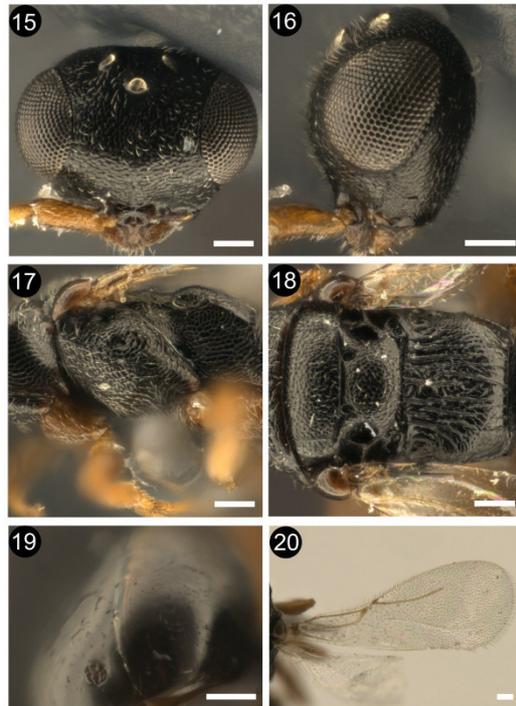


Figura 1. Pranchas I-III. Espécies novas de *Pararhabdepyris* publicadas por Vargas & Azevedo (2016a), exibindo os principais caracteres diagnósticos e descritivos.

Galodoxa foi proposto por Nagy (1974) a partir da observação de uma fêmea coletada nas Filipinas, um espécime aberrante que ele considerou uma subfamília nova e que posteriormente Azevedo & Lanes (2009), com base em uma avaliação cladística, realocaram em Scleroderminae. A grande novidade deste segundo trabalho foi a descrição do macho, desconhecido até então, e a associação dos sexos, mais o registro de variações intra-específicas, a atualização da diagnose genérica mediante a inclusão dos caracteres do macho e a atualização da distribuição geográfica, que até 2009 ficava restrita às Filipinas e Indonésia.

Lanes & Azevedo (2009) propuseram que a distribuição do gênero poderia superar os 1000 km², isto foi confirmando por dos registros novos na Malásia e Laos, a 1900 km do registro antigo mais noroeste nas Filipinas, e dos registros novos na Papua Nova Guiné, a 2000 km do registro antigo mais sudeste na Indonésia, de modo que atualmente a distribuição abrange ao redor de 3600 km² (Fig. 2); concomitantemente o rango de elevação foi ampliado de 580 m para 1480 m.

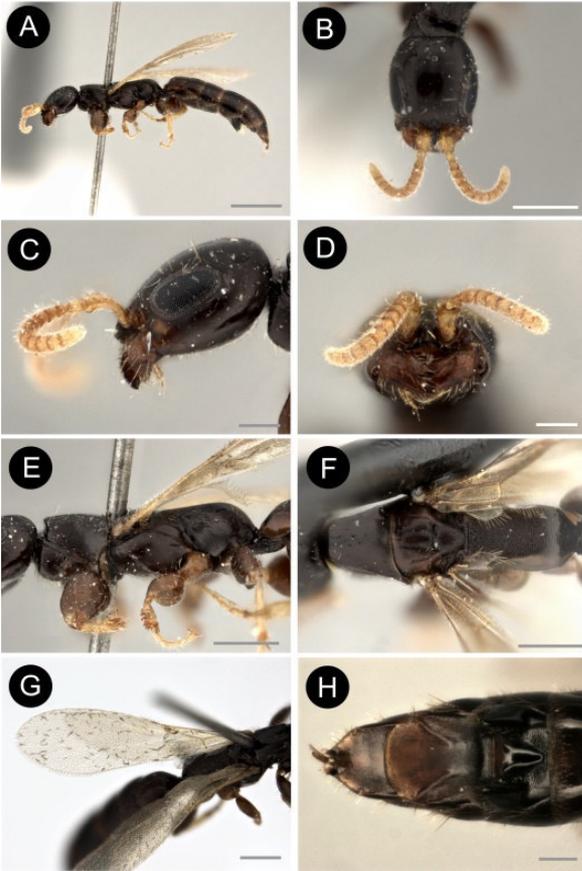


Figura 2. Distribuição de *Galodoxa torquata* (■Dados antigos; ●Dados novos) apresentada por Vargas & Azevedo (2016b)

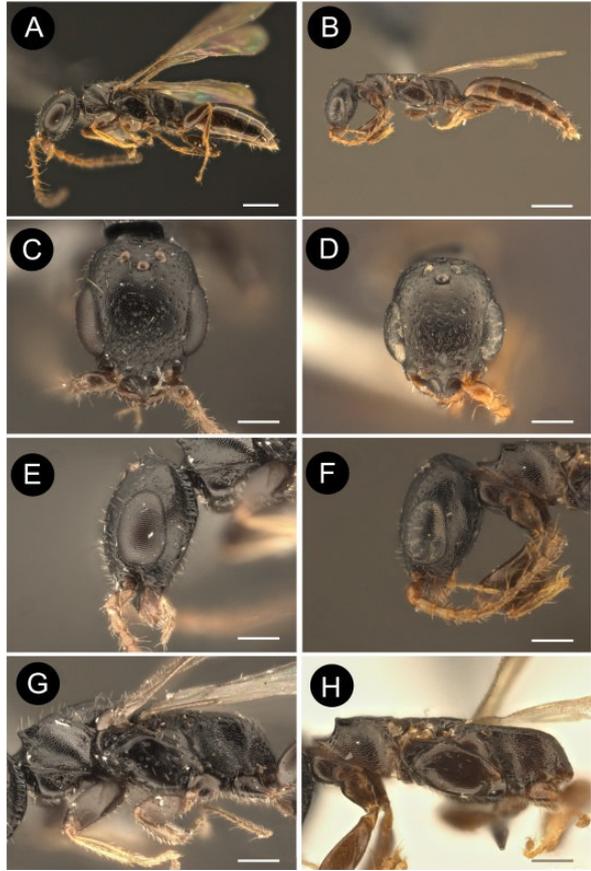
A associação dos sexos foi baseada na descrição e ilustração de 15 caracteres (Figura 3) e foi discutida a associação de *Galodoxa* com Mesitiinae com base em alguns caracteres, como a linha pronotal longitudinal e a modificação do esternito metasomal V; também foram feitas considerações ao respeito da possível função de algumas variações estruturais próprias do macho (antenas com setas compridas e áreas glandulares no tergito metasomal II) e da fêmea (mandíbulas fortes, pernas engrossadas com espinhos e expansões metassomais).

Estes dois trabalhos preliminares foram fundamentais no desenvolvimento e amadurecimento de competências necessárias na análise científica, e para assumir o nível de raciocínio próprio da pesquisa.

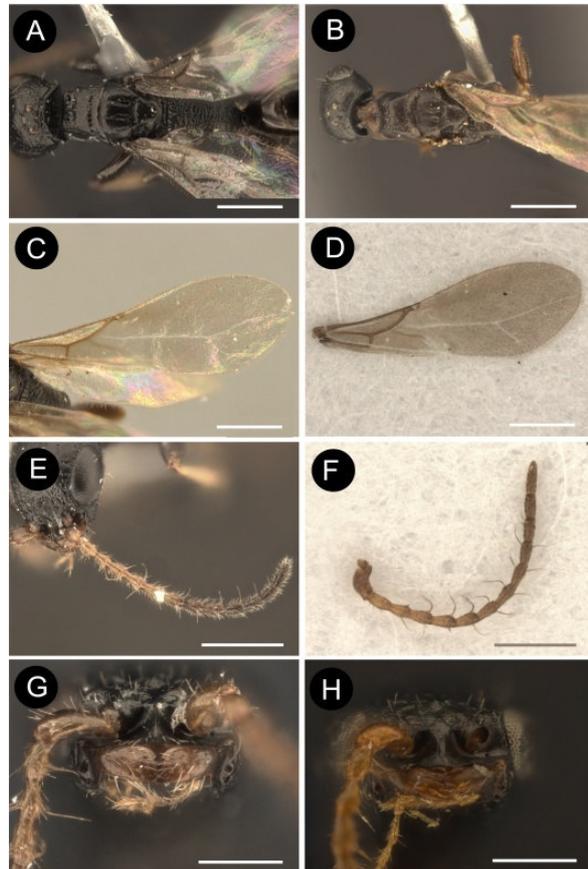
I



II



III



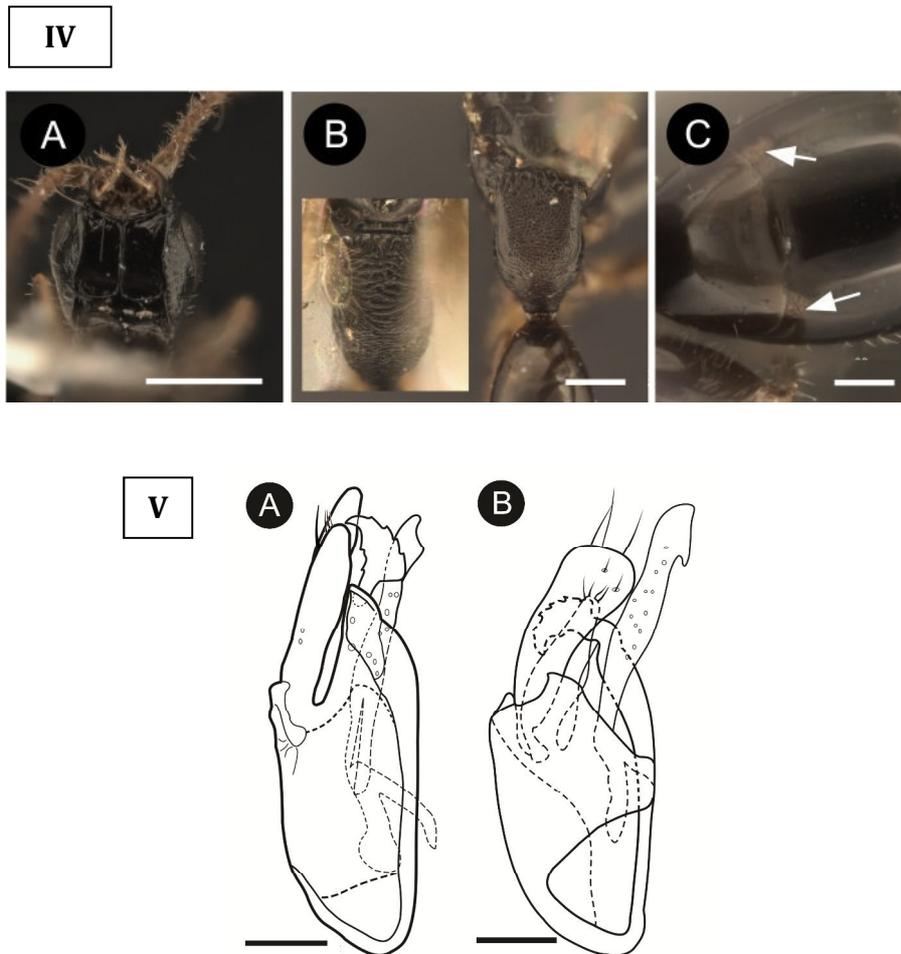


Figura 3. Pranchas I-V. Caracteres mais relevantes de *Galodoxa torquata*. I. Fêmea; II, e III. Características externas do macho, Laos (esquerda), Papua (direita); IV. Detalhe da cabeça, disco propodeal e metassomo; V. Genitália do macho, Laos (esquerda), Papua (direita). (Tomado de Vargas & Azevedo 2016b)

Sobre o projeto desta tese

A presente tese é composta de um único capítulo, uma vez que os outros capítulos já foram publicados. O projeto nasceu enquanto eu era analista de diagnóstico e retomando meu interesse em investigações passadas com a família Bethyliidae então, baseado no interesse que tem o setor agrícola no controle biológico, eu pensei que seria importante fazer uma análise filogenética do gênero *Cephalonomia*, o segundo gênero com mais espécies dentro da subfamília Scleroderminae, onde pertence *C. stephanoderis* um dos controladores biológicos mais estudados e importantes no cultivo do café. Posteriormente, depois da minha chegada em Vitória (ES), o projeto foi modificado por sugestão do meu orientador e reajustado com base na extensa bibliografia existente no laboratório.

Revisitando a literatura e o material abundante disponível, ao redor de 250.000 espécimes, por conta de empréstimo proveniente de diversos projetos mundiais sob parceria do meu orientador, ficou evidente a necessidade ampliar o escopo e fazer a atualização do conhecimento da subfamília Scleroderminae, dado as novidades acrescentadas à tribo desde a análise feita por Lanes & Azevedo (2008) e a recente revisão do seu status taxonômico (Alencar & Azevedo 2013).

Em 2013, já o Dr. Azevedo tinha claro que os Scleroderminae mereciam ser revisados, pois os gêneros descritos depois de 2008, ou não analisados até 2013 (Lanes

& Azevedo 2008), correspondiam a uma terça parte da quantidade de gêneros incluídos nesta última análise filogenética; além do exposto, gêneros como *Pararhabdepyris*, *Galodoxa*, *Alloplastanoxus*, *Proplastanoxus*, *Prorops* e *Israelius*, apresentavam, segundo a literatura, padrões morfológicos pouco estudados taxonomicamente e filogeneticamente, particularmente no contexto da antiga tribo Cephalonomiini *sensu* Evans (1964) e em general da subfamília. Portanto, a proposta foi fazer uma análise filogenética da recentemente redefinida subfamília Scleroderminae, incluindo a maior quantidade possível de informação morfológica sobre os gêneros recentemente descritos, e incluindo as novidades que a amostragem conseguisse prover.

Finalmente, a partir dos resultados e conclusões da presente tese, é extremamente recomendável empreender as análises filogenéticas dos gêneros *Sclerodermus*, *Cephalonomia* e *Plastanoxus*, três dos gêneros com maior quantidade de espécies dentro de Scleroderminae, e cujo conhecimento é fundamental para resolver e compreender as relações evolutivas entre os táxons com extrema redução estrutural.

Referências

- 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.
- Azevedo, C.O. & Barbosa, D.N. (2010) Two new species *Pararhabdepyris* Gorbатовskii (Hymenoptera, Bethylidae) from Australia and Thailand. *Zootaxa* **2668**: 55–62.
- Azevedo, C.O., Garcia, R., Gobbi, F.T. & van Noort, S. (2015) Insecta, Hymenoptera, Bethylidae: range extension and filling gaps in Central African Republic. *Check List* **11**: 1–4. <http://dx.doi.org/10.15560/11.2.1606>
- 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 Leiden* **83**: 841–851.
- Beltran, C.E. et al. (2011) A New Species of *Paracatua* Melichar (Cicadellidae: Cicadellinae) from Colombia. The American Entomological Society. *Entomological News* **122**: 214–222. DOI: <http://dx.doi.org/10.3157/021.122.0302>
- Evans, H.E. (1964) A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology* **132**: 1–222.
- Freytag, P.H. & Vargas, J.M. (2007) Two new species of *Palingonalia* (Hemiptera: Cicadellidae: Cicadellinae) from Colombia. *Entomological News* **118**: 223–226. DOI: [http://dx.doi.org/10.3157/0013-872X\(2007\)118\[223:TNSOPH\]2.0.CO;2](http://dx.doi.org/10.3157/0013-872X(2007)118[223:TNSOPH]2.0.CO;2)
- Gorbатовsky, V.V. (1995) Family Bethylidae – bethylids. In: Lehr, P.A. (Ed.), Key To The Insects Of Russian Far East. Vol. 4. Neuropteroidea, Mecoptera, Hymenoptera. Part 1. Nauka, Saint Petersburg: pp.179–190.
- Lanes, G.O. & Azevedo, C.O. (2008) Phylogeny and Taxonomy of Sclerodermini (Hymenoptera, Bethylidae, Epyrinae). *Insect Systematic and Evolution* **39**: 55–86.
- Lim, J & Lee, S. (2015) *Pararhabdepyris* Gorbатовskii (Hymenoptera: Bethylidae), new to Korea and the first record of *Allobethylus* Kieffer. *Journal of Asia-Pacific Biodiversity* **7**: 457–461.
- Nagy, C.G. (1974) A new bethylid subfamily allied to Protopristocerinae. *Bolletino de Societa Entomologica Italiana* **106**: 126–129.
- Vargas, J.M. (2001) Dos espécies nuevas de *Rhabdepyris* (Hymenoptera, Bethylidae) de Colombia. *Iheringia, Série Zoológica* **90**: 133–139.
- Vargas, J.M. (2007) First record of phoretic copulation in *Dissomphalus xanthopus* Ashmead (Hymenoptera: Bethylidae). *Entomological News* **118**: 470–474.
- Vargas, J.M. & Azevedo, C.O. (2008) Revision of *Alongatepyris* (Hymenoptera:

- Bethylidae) with description of a new species from Colombia. *Revista Brasileira de Zoologia* **25**: 843–846.
- Vargas, J.M. & Terayama, M. (2002) Five new species of the subfamily Pristocerinae (Insecta, Hymenoptera, Bethylidae) from Colombia. *Biogeography* **4**: 25–31.
- Vargas, J.M. & Terayama, M. (2006) Familia Bethylidae. In: Fernández, F. & Sharkey, M.J. (Eds), *Introducción a los Hymenoptera de la Región Neotropical*. Sociedad Colombiana de Entomología y Universidad Nacional de Colombia, Bogotá, pp.427–442.
- Vargas, J.M. & Azevedo, C. O. (2016a) Three new species of *Pararhabdepyris* Gorbатовsky (Hymenoptera, Bethylidae) from Central Africa and the Arabian Peninsula. *Zootaxa* **4117**: 429–439. <http://doi.org/10.11646/zootaxa.4117.3.10>
- Vargas, J.M. & Azevedo, C. O. (2016b) Discovery of the male of *Galodoxa* Nagy (Hymenoptera: Bethylidae), with emended generic diagnosis, 393–406, in ROBILLARD T., LEGENDRE F., VILLEMANT C. & LEPONCE M. (Eds), *Insects of Mount Wilhelm, Papua New Guinea*. Muséum national d'Histoire naturelle, Paris, 573 p. (Mémoires du Muséum national d'Histoire naturelle; 209).

Resumo

Scleroderminae tem atualmente 22 gêneros, sete deles com 10 flagelômeros antenais. Todos os estudos filogenéticos prévios jamais acessaram estes gêneros. Desta forma, o objetivo principal do presente trabalho é revisitar as filogenias propostas para esta subfamília dando ênfase nos gêneros com 10 flagelômeros antenais, os quais se correspondem com antigo sentido dos Cephalonomiini. Para isto, analisamos 83 terminais de 21 gêneros de Scleroderminae e codificamos 118 caracteres informativos. Seis gêneros novos são propostos, descritos e ilustrados como se segue: gêneros novos A, B, C, D, E e F. Vinte e seis espécies novas são descritas e ilustradas assim: A **sp. nov.** 01 da Tailândia, B **sp. nov.** 02 de Madagascar, B **sp. nov.** 03 de Madagascar, B **sp. nov.** 04 de Madagascar, C **sp. nov.** 05 de Madagascar, D **sp. nov.** 06 de Madagascar, E **sp. nov.** 07 de Madagascar, F **sp. nov.** 08 de Madagascar, *Allobethylus sp. nov.* 09 de Vanuatu, *Alloplastanoxus sp. nov.* 10 de Madagascar, *Alloplastanoxus sp. nov.* 11 do Brasil, *Discleroderma sp. nov.* 12 da Indonésia, *Discleroderma sp. nov.* 13 da Tailândia, *Discleroderma sp. nov.* 14 da Tailândia, *Glenosema sp. nov.* 15 da França, *Israelius sp. nov.* 16 dos Emirados Árabes Unidos, *Israelius sp. nov.* 17 da África do Sul, *Israelius sp. nov.* 18 de Madagascar, *Megaprosternum sp. nov.* 19 das Ilhas Marianas, *Megaprosternum sp. nov.* 20 do Laos, *Nothepyris sp. nov.* 21 do Brasil, *Nothepyris sp. nov.* 22 da Republica Dominicana, *Prorops sp. nov.* 23 da Tailândia, *Prorops sp. nov.* 24 do Vietnam, *Prorops sp. nov.* 25 dos Emirados Árabes Unidos e *Tuberepyris sp. nov.* 26 da África do Sul. Além disso, descrevemos aqui pela primeira vez o macho de *Nothepyris brasiliensis* Evans, a fêmea de *Megaprosternum longiceps* Azevedo e o primeiro macho áptero de *Glenosema*. O status de *Sierola depressa marquisensis* é elevado e a espécie será transferida para *Thlastepyris*. Será proposta a transferência de *Israelius amputatus* dentro do novo gênero B. Os Scleroderminae são recuperados como clado com baixo suporte de reamostragem simétrica e o caráter notauli reto foi achado como sinapomorfia putativa para Scleroderminae. A extensa homoplasia através da topologia é considerada como evidência da elevada diversidade morfológica na subfamília. A monofilia de Cephalonomiini não é recuperada. Os clados recuperados por ponderação implícita incluem clados com 11 flagelômeros como (*Nothepyris* + *Discleroderma*), (*Chilepyris* + *Glenosema*), (*Solepyris* + (*Tuberepyris* + (*Alongatepyris* + *Thlastepyris*))) os quais nos chamamos de “clado de corpo achatado”, o clado D composto principalmente por gêneros com 10 flagelômeros, e dois subclados D1 e D2, recuperados pela pesagem implícita, que parecem representar duas grandes linhagens diferentes. A reamostragem simétrica suporta como clados os gêneros *Discleroderma*, *Glenosema*, *Alloplastanoxus*, *Pararhabdepyris* e *Prorops*. O reconhecimento de *Nothepyris*, *Allobethylus*, *Plastanoxus*, *Cephalonomia* e *Israelius* como grupos parafiléticos, reflete sua incipiente taxonomia. *Israelius* torna-se um clado a partir da modificação taxonômica proposta. *Chilepyris* é reconhecido como grupo irmão de *Glenosema*. A associação macho-fêmea de *Galodoxa* proposta por Vargas & Azevedo (2016) é recuperada e apoiada. *Megaprosternum* é achado como polifilético em relação com *Platepyris* é recuperado como o grupo irmão de *Cephalonomia* com base na descrição de uma nova espécie com 10 flagelômeros e prosterno pentagonal grande. O suporte para outras linhagens e seu impacto na classificação de Scleroderminae é discutido. Vários estados de caráter são mapeados para a nova filogenia, especialmente o número de flagelômeros que foi encontrado homoplástico, e são apresentadas considerações sobre a evolução dos caracteres.

Palavras-chave. Chrysoidea, evolução de caracteres, gêneros novos, homoplasia.

Abstract

The Scleroderminae have currently 22 genera, seven of them have antennae with 10 flagellomeres. All the previous phylogenetic studies never accessed these genera in their whole range. Thus the main aim of this study is to revisit the phylogenies proposed for Scleroderminae emphasizing these genera, which correspond to the old sense of Cephalonomiini. For that, we analyzed 83 terminals of 21 genera of Scleroderminae and scored 118 codified informative characters. Six new genera are proposed, described and illustrated as follows: new genera A, B, C, D, E and F. Twenty-six new species are described and illustrated as follows: A **sp. nov.** 01 from Thailand, B **sp. nov.** 02 from Madagascar, B **sp. nov.** 03 from Madagascar, B **sp. nov.** 04 from Madagascar, C **sp. nov.** 05 from Madagascar, D **sp. nov.** 06 from Madagascar, E **sp. nov.** 07 from Madagascar, F **sp. nov.** 08 from Madagascar, *Allobethylus* **sp. nov.** 09 from Vanuatu, *Alloplastanoxus* **sp. nov.** 10 from Madagascar, *Alloplastanoxus* **sp. nov.** 11 from Brazil, *Discleroderma* **sp. nov.** 12 from Indonesia, *Discleroderma* **sp. nov.** 13 from Thailand, *Discleroderma* **sp. nov.** 14 from Thailand, *Glenosema* **sp. nov.** 15 from France, *Israelius* **sp. nov.** 16 from United Arab Emirates, *Israelius* **sp. nov.** 17 from South Africa, *Israelius* **sp. nov.** 18 from Madagascar, *Megaprosternum* **sp. nov.** 19 from Mariana Islands, *Megaprosternum* **sp. nov.** 20 from Laos, *Nothepyris* **sp. nov.** 21 from Brazil, *Nothepyris* **sp. nov.** 22 from Dominican Republic, *Prorops* **sp. nov.** 23 from Thailand, *Prorops* **sp. nov.** 24 from Vietnam, *Prorops* **sp. nov.** 25 from United Arab Emirates and *Tuberepyris* **sp. nov.** 26 from South Africa. Additionally we describe by the first time the male of *Nothepyris brasiliensis* Evans, the female of *Megaprosternum longiceps* Azevedo and the first apterous male of *Glenosema*. *Sierola depressa marquisensis* had its status elevated and it will be transferred to *Thlastepyris* and the transference of *Israelius amputatus* into the genus B will be proposed. Scleroderminae are recovered as a clade with low but positive symmetrical resampling support and the character notauli straight was found as putative synapomorphy for Scleroderminae. The extensive homoplasy across the topology is regarded as evidence of the high morphological diversity in the subfamily. The monophyly of Cephalonomiini is not recovered. The clades recovered by implied weighting include the 11-flagellomered clades (*Nothepyris* + *Discleroderma*), (*Chilepyris* + *Glenosema*), (*Solepyris* + (*Tuberepyris* + (*Alongatepyris* + *Thlastepyris*))) that we call flat-bodied clade, a clade D composed mainly by 10-flagellomered genera, and two subclades D1 and D2, recovered by implied weighting, that appears to represent two different lineages. The symmetrical resampling supports as a clade the genera *Discleroderma*, *Glenosema*, *Alloplastanoxus*, *Pararhabdepyris* and *Prorops*. The recognition of *Nothepyris*, *Allobethylus*, *Plastanoxus*, *Cephalonomia* and *Israelius* as paraphyletic groups, reflecting their poor taxonomy. *Israelius* becomes a clade from the taxonomic modification proposed. *Chilepyris* is recognized as sister-group of *Glenosema*. The male-female association of *Galodoxa* proposed by Vargas & Azevedo (2016) is recovered and supported. *Megaprosternum* was found to be polyphyletic in relation to *Platepyris* and based on the description of a new species with 10 flagellomeres and large pentagonal prosternum is recovered as sister-group of *Cephalonomia*. Support for other lineages and their impact on the classification of Scleroderminae is discussed. Several character states are mapped onto the new phylogeny, especially the number of flagellomeres that was found homoplastic, and several considerations about the evolution of the characters are presented.

Key words. Chrysoidea, character evolution, new genera, homoplasy.

Revisiting the phylogeny of Scleroderminae (Hymenoptera, Bethylidae), with emphasis on the 10-flagellomered genera

Introduction

Bethylidae belong to Chrysidoidea (Hymenoptera) and have shown to be a monophyletic taxon and sister-group of Chrysididae (Brothers & Carpenter 1993; Ronquist et al. 1999; Ronquist 1999; Carr et al. 2010). Bethylidae are external gregarious parasitoid of larval stage of Coleoptera and Lepidoptera (Evans 1964). The family has about 2481 species (Alencar & Azevedo 2013), arranged in 102 genera, which are currently divided into five extant subfamilies: Bethylinae, Epyrinae, Mesitiinae, Pristocerinae and Scleroderminae, the last being according to Evans (1964) a result of the individualization of the more specialized stock of species inside the old Epyrinae and grouped in the tribes Sclerodermini and Cephalonomiini.

After a cladistic treatment, these latter tribes became a single one (Lanes & Azevedo 2008) and later it was restated to the status of subfamily by Alencar & Azevedo (2013). Scleroderminae comprise 193 species in 22 genera of wasps, one of them fossil, characterized by having the body length between 0.7 and 6 mm, the forewing venation reduced and the cuticle widely polished, with the parasitoid behavior, mainly on larvae of Coleoptera in protected or cryptic conditions. Several groups exhibit strong sexual dimorphism. Some have the body very flattened.

Classification development

During the XIX century, an important stock of betilids was considered as a subfamily of Proctotrupidae, only in the beginning of the XX century Bethylidae were formally recognized as family (Ashmead 1900). In the Kieffer's (1914) comprehension this group had the subfamily status with the tribes Mesitiini, Epyrini, Pristocerini, Sclerodermini and Bethylini. Berland (1928) changed the subfamily status of Kieffer's classification to the family level and the tribes to the subfamily level (Bethylinae, Pristocerinae, Mesitiinae, Epyrinae and Scleroderminae).

Fifty years later, Evans (1964) reorganized the classification of Epyrinae in tribes Epyrini, Sclerodermini and created the new tribe Cephalonomiini, based on an appearing connection of the more generalized *Epyris* and *Rhabdepyris* with *Sclerodermus* through *Chilepyris* and *Nesepyrus* (= *Allobethylus*) and with *Cephalonomia* through *Laelius* and *Plastanoxus*.

Phylogenetic knowledge

Terayama (1995) made the first phylogenetic analysis of Sclerodermini *sensu* Evans (1964) based on nine genera and 27 characters. He concluded that the reduced venation in addition to the body sculpture simplification support the specialization tendency. However, he found several homoplasies and suggested that more characters were necessary. Later, Terayama (2006) proposed a hypothetical arrangement of relationships between Sclerodermini and five genera of Cephalonomiini, from an unknown data matrix. That proposal recovered as monophyletic the tribes defined by Evans (1964), and proposed (Sclerodermini + Cephalonomiini) as sister-group of Epyrini.

Lanes & Azevedo (2008), taking into account the scarcity of apomorphic characters and the low resolution of anterior analyses to distinguish the two tribes, suggested that they would configure a single clade and that one of them would be a paraphyletic group. The analysis was based in 72 morphological characters from 124 specimens of 35 species

in 13 genera. As a result, several genera were reorganized and two genera of Cephalonomiini were consistently found subordinated inside Sclerodermini. In this work they have synonymized the two tribes and pointed out the Kieffer's (1914) proposal the most adjusted to the current knowledge; besides it was found a high level of incongruence among characters, low resolution inside several clades and groups defined by autapomorphies. The genera of Cephalonomiini were only represented by two of the seven genera described until that time.

Carr *et al.* (2010) using molecular tools and based on seven genera (three from Cephalonomiini and two from Sclerodermini), found association of Sclerodermini as a sister group of Cephalonomiini and closely related with Mesitiinae, suggesting the polyphyly of Epyrinae and the monophyly of Cephalonomiini.

Alencar & Azevedo (2013) studied the phylogeny of Epyrini through 391 characters, representing Sclerodermini *sensu* Lanes & Azevedo (2008) with four genera. The definitions of the limits of Epyrini respect Epyrinae were analyzed; in addition, they confirmed several suggestions made by Carr *et al.* (2010), eliminated all tribal definition inside Epyrinae and gave to Sclerodermini *sensu* Lanes & Azevedo (2008) and Epyrini *sensu* Evans (1964) the subfamily status.

Between 2005 and 2014, six genera and 21 species have been added to Scleroderminae, reducing the number of monotypic genera. As a consequence of these novelties, several questions have been raised regarding about the character congruence, the internal relationship resolution, and the group definition in light of several terminals that were never phylogenetically accessed. Therefore, the present work seeks to introduce a more update phylogenetic hypothesis to the subfamily with emphasis on the 10-flagellomered genera, based on parsimony and using morphological characters.

Materials and methods

Taxonomic sampling

The examined material came from all the zoogeographic regions. For most taxa, we coded females, the gender that has been used more frequently to characterize the Scleroderminae; however the male was coded in case of *Nothepyrus brasiliensis* and *Glenosema* sp. nov. 15, depending on the importance of the terminal. The specimens came from several collections, as follows:

AEIC – American Entomological Institute, Gainesville, USA
BMNH – The Natural History Museum, London, United Kingdom
BPBM – Bernice Pauahi Bishop Museum, Honolulu, USA
CASC – California Academy of Sciences, San Francisco, USA
CNCI – Canadian National Collection of Insects, Ottawa, Canada
CZMA – Coleção Zoológica da Universidade Estadual do Maranhão, Caxias, Brazil
IAVH – Instituto Alexander von Humboldt, Villa de Leyva, Colombia
IBGE – Instituto Brasileiro de Geografia e Estatística, Brasília, Brazil
ISAM – Iziko South African Museum, Cape Town, South Africa
MCSN – Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy
MPEG – Museu Paraense Emílio Goeldi, Belém, Brazil
MNHN – Muséum National d'Histoire Naturelle, Paris, France
NHRS – Naturhistoriska Riksmuseet, Stockholm, Sweden
QSBG – Queen Sirikit Botanical Garden, Chaing Mai, Thailand
PMAE – Royal Alberta Museum, Edmonton, Canada
RMNH – Nationaal Natuurhistorisch Museum, Leiden, The Netherlands

Terminology

Morphological terms generally follow Evans (1964), additional terminology is based on Azevedo (1999); the sculpture nomenclature follows Eady (1969) and Azevedo (2003), several clarifications were made through the ontological query of morphological terms in the Hymenoptera Glossary (HAO) (Yoder et al. 2010), with additional terms for metapostnotal structures (Kawada et al. 2015) and wing venation codification (Ramos & Azevedo 2012). Taxonomic abbreviations include LH (length of head in dorsal view); WH (maximum width of head including eyes in dorsal view); WF (minimum width of front in dorsal view); HE (height of eye in dorsal view); WOT (width of ocellar triangle in dorsal view); VOL (vertex-ocular line in dorsal view), LFW (length of forewing after tegula).

Outgroups selection

In order to evaluate the presumed homologous hypotheses that indicate cladistic relationships, we take *Sulcomesitius nepalensis* Móczár, 1986, *Heterocoelia finus* Barbosa & Azevedo, 2011 and *Mesitius absentis* Barbosa & Azevedo, 2011, as representatives of Mesitiinae, hypothesized as specific sister group of Scleroderminae by Carr et al. (2010) and Jiang *et al.* (2015), and the species *Anisepyris proteus* Evans, 1966, as closer additional outgroup. Even more, assuming that this analysis is critical due to the subjectivity and high incongruence among characters on previous investigations, we follow here the reasons on outgroup selection exposed by Wiley & Lieberman (2011) (Appendix 1).

Ingroup selection

In the present work we studied Scleroderminae, recovered as monophyletic by Lanes & Azevedo (2008), with focus on the old tribe Cephalonomiini *sensu* Evans (1964) recovered as monophyletic by (Carr et al. 2010). For this purpose we included 20 genera from 22 described, and several terminals with 10-flagellomered antennae were taken into account to represent the old Cephalonomiini. In total, we observed 31 terminals with 11-flagellomered antennae, 48 terminals with 10-flagellomered antennae and eight terminals representing new taxonomical patterns (see UGs on Appendix 1), which we describe here as new genera.

Character codification

Several characters were excluded because of overlapping ranges of intraspecific variation, the difficulty in guaranteeing character independence, like in the head capsule characters, especially relative to cuticle areas not well defined by sclerites. The characters were treated as hypotheses of primary homology following De Pinna (1991). We worked on improving character-coding system, avoiding as much as possible the continuous quantitative characters and the intraspecific polymorphisms (see Appendix 3).

Several important characters have been proposed from the codification of new features of the forewing (especially associated with venation); several characters are used again or modified mostly from Terayama (1995), Lanes & Azevedo (2008) and Alencar & Azevedo (2013).

Phylogenetic analyses

The morphological dataset was analyzed using parsimony, taking into account the coherence with several groups generally accepted by previous researches. The characters were treated as unordered. Characters coded as inapplicable were treated as missing data (see Appendix 4).

The searches for the most parsimonious trees were carried out with the software TNT ver. 1.1 (Goloboff et al. 2008). Characters were treated under two weighting schemes: equal and implied weights (Goloboff 1993; Goloboff et al. 2008). We used Traditional Search algorithms with parameter sets as follows: space for 20,000 trees in memory; Wagner trees random seed 0; 1,000 replications; TBR algorithm; 10 trees saved per replication; other parameter as in default mode; the tree was rooted with *Anisepyrus* Kieffer. This procedure was repeated with trees from RAM. Branch support was investigated using symmetric resampling (Goloboff et al. 2003).

Also, heuristic searches (Goloboff et al. 2003, 2008) were performed under New Technology methods using a sectorial search, ratchet weighting probability of 5% with 2,000 iterations, tree-drifting of 50 cycles, tree-fusing of five rounds, and a best score hit of 5 times. 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; the script returned a value of $k = 16.220703$ for our data set, which was tested and employed. The k values were tested inversely from 17 to 1. Most parsimonious trees and the best score (as indicator of tree length) were calculated for each k value using a Traditional Search in TNT; $k = 16$ was the largest value that provided a lowest best score (Figs 5 and 12) and consistent monophyly of certain groups i.e. *Glenosema*, (*Nothepyrus* + *Discleroderma*) and (*Alongatepyrus* + *Thlastepyrus*). Smaller values of k did not provide increased resolution even if converge on a single solution. We chose the k produced by the setk script for a subsequent implied weighting New Technology search as outlined for the equal weighting analysis.

The cladogram recovered with the software TNT was manipulated and edited with Winclada ver. 1.00.08 (Nixon 1999–2002). Relative-support values were calculated using symmetric resampling (Goloboff et al. 2003), this support was calculated in TNT with 2,000 iterations on the equal weighting data employing New Technology searches, and the branches were regarded as supported with GC values above 0. One implied weighting tree was taken, with lower values weighting more strongly against homoplastic characters (Figs 5 and 12). For the results, characters were mapped onto the implied weighting tree using Winclada. Unambiguous character state changes were preferably optimized; sometimes the ACCTRAN or DELTRAN optimizations were used according to the coherence in the argumentation (Agnarsson & Miller 2008).

[suggested place for Fig. 1]

Illustrations

The specimens were photographed under a Leica Z16 APO stereomicroscope with a camera adaptor coupled to a Leica DFC 295 video camera (Leica Microsystems, Switzerland). The software Leica Application Suite V3.version 6.0 and Microsystems by Leica (Switzerland) Limited (LAS) were used to capture individual focal planes. Helicon Focus (HeliconSoft version 4.2.9) software was responsible for stacking the layers into a single combined-focus image using the following parameters: method C pyramid and full

resolution. All illustrations and plates were edited in software for images edition and vectorization.

[suggested place for Figs 2-4 = Morphology, here]

Results

Morphological data

A total of 266 states on 118 characters were selected from an initial list of 141 characters compiled mainly from Terayama (1995), Lanes & Azevedo (2008) and Alencar & Azevedo (2013). The final characters list was deemed potentially phylogenetically informative and visible especially in winged Scleroderminae.

Analyses of the matrix produce a poorly resolved consensus tree (Fig. 7). The symmetric-resampling tree (Fig. 6) show a much more resolution indicating a significant phylogenetic signal. The results of the implied weighting analysis provided support and monophyly for the subfamily, for most of genera (*Discleroderma*, *Glenosema*, *Alloplastanoxus*, *Pararhabdepyris*, *Thlastepyris*, *Tuberepyris*, *Israelius* and *Prorops*) and for the clade (clade C + clade D). The implied weighting tree-building method showed general congruence for genus level. The following discussion of relationships is based on the implied weighting (k value: 16.220703) parsimony of a tree with L=1095, Ci=13 and Ri=60. Scleroderminae were monophyletic consistently with the studies of Lanes & Azevedo (2008), Alencar & Azevedo (2013), Carr et al. (2010) and Jiang et al. (2015).

We were able to recognize seven additional morphological patterns, six of them that deserve genus status. It is important to point out that, at least taxonomically, all the new patterns match with the old Cephalonomiini *sensu* Evans (1964), especially by the presence of 10 flagellomeres or less, condition that according to Evans (1964) characterizes the tribe along with other features like the presence of prostigma, the presence of closed submedian cell and the forewing angled on the anterior margin opposite the prostigma, this although synonymized with Sclerodermini (Lanes & Azevedo 2008) even nowadays remains considered as monophyletic (Carr *et al.* 2010). One special case associated with this character is represented by *Bethyloopsis fullawayi*, a species with 10 flagellomeres as described by Fouts (1935) and included into Sclerodermini by Terayama (1995); this is the single species that exhibits brachypterous condition within Scleroderminae. In addition, based on New genus F sp. nov. 08 and *Cephalonomia cisidophaga*, two additional character states (seven and eight flagellomeres) were analyzed here. For purposes of phylogenetic analysis, *B. fullawayi* is also considered here as one additional morphological pattern, which increase the possibility of studying the structure of relationships within the 10-flagellomered genera and with the remaining genera within the subfamily. It should be noted here that the association made by Terayama (1995) left this genus within Sclerodermini based on the general similarity of this species with *Allobethylus*, which in the present analysis appears as sister-group of *Bethyloopsis*.

Monophyly

The tribe Cephalonomiini *sensu* Evans (1964) is not recovered as a clade because the presence of *Megaprosternum* inside the clade D and because, at least, one species with 10 flagellomeres (*Bethyloopsis fullawayi*) is recovered out of this clade. However it is important to note that in the symmetrical resampling tree this species appears inside the clade D.

Although the subfamily is weakly supported in symmetrical resampling, the positive value of the support indicates that the best alternative is to maintain the group as it has been defined taxonomically and recovered by Lanes & Azevedo (2008), most of the genera and their morphological characters are in an incipient state of study; the high intergeneric variability and the frequent appearance of new species and genera suggest that it is important to be prudent in the face of any nomenclatural decision, at least until the most unstable genera (e.g. *Nothepyrus*, *Allobethylus*, *Glenosema*, *Plastanoxus*, *Cephalonomia* and *Israelius*) or diverse genera (*Cephalonomia* and *Sclerodermus*) have been taxonomically and phylogenetically reviewed.

In the most parsimonious tree under implied weighting, several clades are listed and discussed as follows: clade A (*Nothepyrus* + *Discleroderma*); clade B (*Chilepyris* + *Glenosema*); clade C (*Solepyris* + (*Tuberepyris* + *Thlastepyrus*)), that we call “flat-bodied clade” due to its flattened body habitus and clade D (Figs 5 and 12), subdivided in clade D1, in which its 19 terminal are strongly sculptured, fully winged and with 10-flagellomered antennae. and clade D2, in which its 31 terminals have reduction of sculpture and tendency of wing reduction (aptery or microptery), and the number of flagellomeres varying from seven to eleven. Our character coding seems to have been consistent with taxa historically considered as closely related always grouping together, if not in a monophyletic assemblage then in a paraphyletic group.

The genera that were recovered as monophyletic include *Discleroderma*, *Glenosema*, *Galodoxa*, *Sclerodermus*, *Solepyris*, *Tuberepyris*, *Alongatepyris*, *Alloplastanoxus*, *Pararhabdepyris*, *Israelius* and *Prorops*. *Megaprosternum* was considered paraphyletic because of the presence of *Platepyris sepalus*. However this relation is considered an artifact and a consequence of the information scarcity resulting of the extreme morphological reduction present on apterous and micropterous forms and because the characters of *P. sepalus* were documented from literature.

The clade C has several flat-bodied taxa, except *Megaprosternum* and is supported by the following character states: the malar space absent (1:0), the hypostomal carina not emarginated medially (20:0), the pronotum collar inconspicuous (35:0), the propleural neck and the anterior angles visible in dorsal view (39:1) and the upper mesopleural fovea present (108:0). *Solepyris*, *Tuberepyris*, *Alongatepyris* and *Thlastepyrus* are characterized by having the body flattened and an uncommon wing venation interpreted as derived among the 11-flagellomered genera.

After the alpha-taxonomical analysis we consider *Sierola depressa marquisensis* as a new combination of *Thlastepyrus* based on the M+Cu vein incomplete (81:1); therefore the clade (*Alongatepyris ingens* + *Sierola depressa marquisensis*) is consistent with the proposals made by Terayama (1995) and Lanes & Azevedo (2008). Thus, taking into account the extreme similarity between *Alongatepyris* and *Thlastepyrus* specially supported by DELTRAN optimization of character states: the Rsc segment absent on the area distal to stigma (89:1), the 1Cu cell extremely shorter than the R cell on the forewing (98:1), the mesopleural prepectal groove present (104:0) and by unambiguous optimization of characters: the metapostnotal-propodeal carina present on the metapectal-propodeal complex (71:1), the metasomal tergite I with the lateral margins ventrally in contact (115:0). A further revision of the holotype of *T. pertenuis* is required in order to verify the potential synonymy of *Alongatepyris* with *Thlastepyrus* suggested by Lanes & Azevedo (2008).

Cephalonomia was rendered as polyphyletic by excluding among its species *C. hypobori* and including *Plastanoxus chittendenii* and *P. westwoodi*, two species without closed cells on forewing. Two groups inside *Cephalonomia* were well separated, the micropterous and apterous forms from fully winged forms. An apterous male that we consider taxonomically belonging to *Glenosema* was recovered inside the apterous

Cephalonomia; this situation has been considered as an artifact due to the extreme scarcity of characters typical of the aptery phenomenon.

Cephalonomia shows several fragmentary arrangements weakly supported by symmetric resampling, situation that appears consistent with its wide morphological range of variation; this is a huge genera with poorly known taxonomy. Notwithstanding, it is important to note that in the most parsimonious tree obtained by implied weighting all the terminals of *Cephalonomia* appear grouped in a clade including apterous, micropterous and fully-winged forms (Figs 5 and 12). *Cephalonomia hypobori* is the only terminal that falls outside of *Cephalonomia* clade on the most parsimonious tree under implied weighting, this situation could be associated with the reduced sculpture and the unusual forewing venation of *C. hypobori* that exhibit the R cell closed by tubular and well defined veins.

[suggested place for Figs 5-7]

Discussion

We focus our discussion on the characters that might be regarded as important for defining the relationships among genera of Scleroderminae, especially because of their taxonomic meaning. There are extensive homoplasies across the tree, as noted by Lanes & Azevedo (2008), even discarding those characters with dubious or undefined homology.

The single putative synapomorphy that supported Scleroderminae is the notauli straight (46:2); the terminals share this feature when the notauli is present. However there are homoplasies that could help to define the subfamily as follows: the eye contour not protruding (25:0), the mesoscutum median length as long as the mesoscutellum (44:1), the forewing with fusion of the Sc&R1a vein (84:1) and the mesopleuron with the subtegular fovea not subdivided (114:0), when optimizing with DELTRAN the forewing with fusion of the Sc&R1a vein (84:1), what Evans (1964) referred as prostigma, is revealed as a second synapomorphy, it probably means that this fusion could be a secondary gain associated with convergent patterns of reduction in the forewing venation. These attributes are not shared by all the terminals but all together represent a general scenario that groups, in any way, the morphological possibilities of this subfamily.

The support found here is higher than that found by Lanes & Azevedo (2008), in terms of number of informative characters, because the three characters addressed by them to support the clade (Sclerodermini + Cephalonomiini) were discarded here due to its ambiguous codification, the antennal insertion lateral to the clypeus (char 16:1 on Lanes & Azevedo 2008) depends on the very variable shape of the clypeal lobe, including the presence of the clypeal carina; the antennal scape thin (char 18:1 in Lanes & Azevedo 2008) is a continuous quantitative character imprecisely defined and, the metacarpus vein present (char 67:0 in Lanes & Azevedo 2008) is a plesiomorphy that does not occur in Scleroderminae.

Given the high homoplastic behavior of most characters, we consider valuable to explore the DELTRAN optimization, this situation agrees well with the characters variability showed in the subfamily diagnosis made by Alencar & Azevedo (2013).

Clade A: Nothepyris + Discleroderma

Lanes & Azevedo (2008) reinstated the genus *Nothepyris* Evans, 1973, and recovered the clade (*Discleroderma* + *Nothepyris*) suggesting the monophyly of this clade as shown

in the implied weighting tree. Here *Nothepyris* + *Discleroderma* is found as a sister-group of the remaining genera including the old Cephalonomiini, a similar position of *Nothepyris* as originally proposed by Terayama (1995), where this genus appears as a sister-group of the remaining genera, including *Bethylopsis* as the only one 10-flagellomered genera.

The monophyly of (*Nothepyris* + *Discleroderma*) is supported by the following character states: the anterior margin of the clypeus angulated (6:0), the anterior margin of torulus reaching the anterior margin of clypeus (10:1), the head globoid (12:0), the mandible with two teeth (15:1), the ocellar triangle far from the vertex crest (29:1), the occipital carina absent (33:1), the pronotal collar conspicuous (35:1), the pronotal surface depressed (36:1) and the C vein absent (79:1). The clade could be diagnosed by the forewing with the 1Cu cell and the R cell subequal with the r-rs&Rsc vein developed, reduced or absent, the body robust, sculptured and the head globoid alike with Mesitiinae.

However, *Nothepyris* is recovered as paraphyletic group in respect to *Discleroderma* due to characters like: the clypeus lobes relative length (3), the presence of two parallel carinae along the anterior margin of clypeus in anterior view (8), the gena visibility behind the eye in dorsal view (14), the r-rs presence/absence (87), the forewing 1cu-a vein angulation (97) and the subtegular fovea shape (112). Thus the genus appears separated of *Discleroderma* mainly because of the autapomorphies, e.g. the metasomal tergites with dorsal modifications (116:2). In a primary hypothesis we consider as homologous feature the metasomal modifications type (116), with the ventral calli in *Nothepyris* and the dorsal processes in *Discleroderma*, but the reciprocal illumination allows us to identify this as homoplasy, maybe due to a violation of the independence criterion; then this character should to be divided in different hypotheses for types of metasomal modifications, in order to guarantee the character independence; currently, the separation of these types of modifications only produces non informative autapomorphies for *Galodoxa* (ventral expansions), *Discleroderma* (dorsal calli), *Nothepyris* (ventral calli) and New genus B sp. nov. 4.

Discleroderma is recovered as monophyletic based on three synapomorphies, the pronotal surface depressed forward (36:1), the metasomal modifications in dorsal position (116:1) and the metasomal apex orientation upward (118:0). The presence of metasomal sternal modifications (116), mainly calli, in *Nothepyris* and New genus B sp. nov. 04, is a novelty for Scleroderminae that deserves further studies. The paraphyletic condition of *Nothepyris* in respect to *Discleroderma*, points out that this two genera deserve an alpha taxonomic revision in order to include new specific character states and to define more clearly the identity of the groups, from this revisionary work new characters should be coded to resolve the phylogenetic status of *Nothepyris*. Because of that, it is premature to propose a synonym of these two genera.

Clade B: Chilepyris + *Glenosema*

Chilepyris appears as sister-group of *Glenosema*, this clade is supported by the following character states: the malar space absent (1:0), the notauli absent (45:0), the scutellar apex widely rounded (50:0) the forewing stigma long (86:0), and several homoplasies like the malar sulcus absent (2:1), the median clypeal lobe as long as the lateral lobes (3:1), the hind wing with 4 hamuli (102:3), the mesopleural pit central (107:1), the subtegular fovea short and isolated (111:0). The association of these genera is supported mainly by homoplasies but the clade is recovered in the symmetric resampling (Fig. 6). On the other hand, *Glenosema* appears as a clade, as recovered by Lanes & Azevedo (2008), and supported by character states: the mandible with seven teeth (15:6) as synapomorphy, and additionally by the mandibular teeth large (16:1), the

upper margin of mandible denticulate (17:0), the metapectal-propodeal complex without a pleural anterior transverse uniform concavity (69:1) and the anterior margin of the forewing angulate (78:1). Due to the general extreme reduction on the apterous male of *Glenosema* described here as a new species, the diagnostic characters became obscured and the terminal could not be recovered within the clade.

Galodoxa

This genus is represented by the two sexes bearing out the sex association proposed by Vargas & Azevedo (2016) and supported by the median clypeal lobe delimitation distinct (5:1), the hypostomal carina not emarginate (20:0), the pronotal disc median line present (37:0), the metanotal inter-flap space narrow (56:1), the transverse posterior carina of the metapectal-propodeal complex absent (57:0), the propodeal spiracle below metapleural carina (64:1), the Sc&R1a vein short (85:1), the r-rs segment absent (87:1), the Rsc segment absent (89:1) and the upper mesopleural fovea absent (108:1). The observations above agree with the comments made by Azevedo & Lanes (2009) specifically about the median clypeal lobe projected. The association of *Galodoxa* with *Alongatepyris* and *Thlastepyris* through the length comparison between R cell and 1Cu cell is clearly homoplastic and is not recovered by the present analysis, even under implied weighting analyses; the absence of r-rs&Rsc vein is homoplastic; Azevedo & Lanes (2009) found in *Galodoxa* the C vein present and this character shared with *Alongatepyris*, *Bethylopsis*, and *Allobethylus*. However for us this character state is absent in the last two genera.

Allobethylus

This was not recovered as monophyletic genus, an important intrageneric variation is evidenced by characters like: the head shape in lateral view (12), the gena visibility behind eye (14), the pleural anterior dorsoventral cavity of the metapectal-propodeal complex (69), the Cua vein presence (92), the number of mandibular teeth (15), the occipital carina presence (33), the forewing color (101), the propleural epicoxal sulcus presence (38), the notauli presence (45), the presence of transverse posterior carina on metapectal-propodeal complex (57) and the upper mesopleural fovea presence (108). The genus has few species and generic revision at global scale is required in order to come up new characters and states to better understand its phylogenetic status. Because of that, it is premature to take any alpha taxonomic decision of *Allobethylus*.

Clade C: (Solepyris + (Tuberepyris + (Alongatepyris + Thlastepyris)))

This interesting clade is supported by symmetrical resampling and groups four genera with flattened body as main shared feature. Here *Solepyris*, *Tuberepyris*, *Alongatepyris* and *Thlastepyris* are joined through the character states: the malar space size absent (1:0), the hypostomal carina not emarginate (20:0), the pronotum collar inconspicuous (35:1), the propleural neck and anterior angles visible in dorsal view (39:1), and the upper mesopleural fovea present (108:0). Additionally, it is interesting to note that the character state the M+Cu vein incomplete (81:1) is present in at least one species of the three genera, although not totally represented by the present data. The clade (*Alongatepyris* + *Thlastepyris*) is diagnosed by the forewing with the 1Cu cell extremely reduced compared with the R cell, the r-rs&Rsc vein extremely reduced or absent and the body extremely flattened with polished surface. The clade C corresponds with three genera that bear the forewing vein reduced, the C vein absent, the M+Cu vein incomplete or absent, in which

Tuberepyris appears as sister-group of (*Alongatepyris* + *Thlastepyris*) as proposed by Lanes & Azevedo (2008).

The very wide distribution of the rare species on the clade (*Alongatepyris* + *Thlastepyris*), including Hawaii, Colombia and Brazil, and the very long distances among collecting localities suggest the possibility of species dispersion from an unknown origin through human transport of materials; one possible hypotheses could be deduced from the label information of the holotype of *Sierola depressa marquisensis*, that was taken in Marquesas Islands on *Paspalum conjugatum*, this spreading perennial grass is probably originated from the American tropics and is naturalized in almost every tropical and subtropical regions (Heuzé 2016), this information lead us to think that this genera could make up an American lineage introduced in Marquesas Island together with its host inside material of *P. conjugatum*, weed cataloged on the risk status as invasive introduced in several Pacific Islands (Florence et al. 2013).

Clade D: “10-flagellomered genera” + Megaprosternum

Cephalonomiini *sensu* Evans (1964) are found as a polyphyletic group and recovered as a part of a clade together with a big cluster of other groups, many of them new. This clade appears subdivided into two monophyletic clades referred here as D1 and D2. The clade D is defined by three unambiguous character states: the antenna with 10 flagellomeres (22:1) with three derivate states, eleven, eight and seven flagellomeres (22:0, 2, 3), the length of the 1cu-a vein inconspicuous (95:1) and the subtegular foveae subdivided (114:1). The character state the 1cu-a vein inconspicuous (95:1) is the single synapomorphy that supports the clade. However, using the slow optimization the character state the 1Cu cell shorter than R cell (98:1) allows to study the reduction of the Cua vein in the forewing, in which the plesiomorphic state is the 1cu-a vein subequal in length than the radial cell. This character is complex and seems to be polymorphic, bearing out the idea that the pattern present in the clade D is other than that in *Galodoxa*, *Tuberepyris* or *Alongatepyris* (Azevedo & Lanes 2009), in which the R cell shows different shape or proportion, this hypothesis deserves a further analysis.

Clade D1

Although the clade D is not supported by the symmetrical resampling, it is recovered under the implied weighting analyses and defined by the head lateral margins convex (13:1), the eye contour slightly protruding (25:1), the basal triangle present on the metapectal-propodeal disc (59:0) and the mesopleural pit with a posterior elevation (106:1). Within this clade the genera *Alloplastanoxus* and *Pararhabdepyris* are recovered monophyletic with support (Fig. 6); *Pararhabdepyris* is diagnosed by having the forewing with the 1Cu cell shorter than the R cell, the body robust, sculptured, and the head subgloboid, whereas *Alloplastanoxus* is diagnosed by having the 1Cu cell shorter than the R cell, the body flattened, sculptured, and the head flattened and subrounded. The remaining terminals appear in the symmetrical resampling in a polytomy associated with the *Plastanoxus-Cephalonomia* complex. Based on the clade (sp. nov. 02 + sp. nov. 03), we suggest (sp. nov. 04 + (*Israelius amputatus* + (sp. nov. 02 + sp. nov. 03))) as a new genus B with four species, therefore we propose *I. amputatus* as a new combination into this new genus. The terminals sp. nov. 01, sp. nov. 05, sp. nov. 06 and sp. nov. 07 and sp. nov. 08 are four clearly differentiated monotypic genera, identified by autapomorphies or morphological incompatibilities with other groups. Mapping the character 66 into the clade D1 is possible to infer a secondary transformation from circular to ovoid propodeal spiracle shape that characterizes this clade.

Proplastanoxus is not clearly defined by any synapomorphic or autapomorphic characters; it is a sort of intermediary steps among several terminals, including some forms of *Plastanoxus*. In fact, the character states (23:1) and (106:0) suggest a possible association between *Proplastanoxus* and *Plastanoxus incompletus*, another example of instability of the latter genus.

Clade D2

Although the clade D2 is not supported by the symmetrical resampling, it is recovered under the implied weighting analyses and defined by the clypeal lobes subequal (3), the mandible robust (19), the frontal line absent (23), the scutellar process inconspicuous (51), the subtegular fovea evenly linear (112) and the subtegular fovea anterior segment U-shaped present (113). *Israelius*, *Prorops* and *Megaprosternum* are recovered as supported clades. However neither *Plastanoxus* nor *Cephalonomia* are recovered as a consistent clade, appearing scattered along the clade D. The ACCTRAN optimization includes for clade D2 the character states: the eye elliptical in full lateral view (24:0) and the Rs+M vein present (91:0). The DELTRAN optimization includes the mesoscutum as long as the scutellum (44:1) and the metapectal-propodeal disc polished (76:3). The most external terminal of this clade is New genus F sp. nov. 08, supported as sister-group of *Israelius*, is mainly characterized by the autapomorphic characters state 7-flagellomered antenna segments (22:3) and the Rs+M vein present (91:0) not as a dilated vein, like in *Israelius*, but as a defined stub.

Megaprosternum

This genus is recovered inside the clade D2 contrary to the proposal of Lanes & Azevedo (2008) in which *Megaprosternum* appears as a sister-group of *Solepyris*, due to the large prosternum. The evidence of this hypothesis is the discovery of a new species from Tinian Island (Mariana Islands), included as a terminal, and exhibiting the antennae with 10 flagellomeres (22:1), the pronotal collar inconspicuous (35:0), the pronotal surface depressed forward (36:1), the neck and the anterior angles visible in dorsal view (39:1), the prosternum size large (40:1) and the sternal inner margins extending posteriorly beyond half the length of the prosternum (42:0). In such way, *Megaprosternum* is diagnosed by having the prosternum large and pentagonal, the forewing without closed cells, the Sc+R vein present, the Sc&R1a vein present, the r-rs&Rsc vein absent, the body extremely depressed, the cuticular surface polished and the antennae with 10 or 11 flagellomeres.

Plastanoxus

The *Plastanoxus* terminals appear scattered throughout the clade D; this is coherent with the taxonomical state of the art of this genus. The literature of this genus is extremely weak when referring to characters like the number of closed cells on forewing, there is no revisionary research published and the intrageneric variation is considerable large, that is a good example of a paraphyly that reflect a bad taxonomy (Ebach et al. 2006). *Plastanoxus ahusiensis*, *P. laevis* and *P. incompletus* share the character states: the lateral margins of the head straight (13:0), the eye contour slightly protruding (25:1), the presence of distinct basal triangle on metapectal-propodeal disc (59:0), the anal vein present (93:0), the mesopleural pit with the posterior tubercle (106:1), whereas characters like the mandible intercondylar lobe (18), the r-rs segment (87), the anal vein (93) and the1cu-a vein (94) are absent in *P. chittendenii* and *P. westwoodi*.

Evans (1964) commented that *Plastanoxus* and *Cephalonomia* are two closely related and widely distributed genera, mainly differentiated by the variety of extreme dimorphism in *Cephalonomia* and the presence of the r-rs&Rsc vein in *Plastanoxus*. In fact, there are intermediate states of these features that difficult the genera individualization. The male genitalia with divided parameres could differentiate *Plastanoxus* from *Cephalonomia* but the knowledge about this character and its distribution in both genera is still very poorly understood, limited to *P. chittendenii* (Evans 1964) and *P. anamiensis* (Terayama 1987). The better known species of *Plastanoxus* are *P. chittendenii*, *P. laevis*, *P. westwoodi* and *P. incompletus*, which are insufficient to establish a morphological ground plan for the entire genus.

The remaining species have not been studied in detail, at least taxonomically. *Plastanoxus ahusiensis* was originally described in the monotypic genus *Snappania* (Hedqvist 1975) and later transferred to *Plastanoxus* by Evans (1978), its species bears two closed cell in the forewing; further studies about this species are inexistent. *Plastanoxus incompletus* was described by Evans (1964) and considered by the author of special interest only due to the nearly absence of the r-rs&Rsc vein, detail that is used as a base to suppose a close relationship with *Cephalonomia*, a relationship that had already been questioned by Gahan (1931) who observed a difference in the antennae of several specimens identified as *C. westwoodi*; this observation led him to transfer it to *Plastanoxus*. Evans (1964) found several males of *P. chittendenii* as remarkably similar to *C. tarsalis*. Several authors described the notauli as absent in *Plastanoxus*, but Terayama (2006) found this character partially present, for instance, in *P. anamiensis*.

Some species of *Plastanoxus*, such as *P. atrescens* (fossil), *P. laevis* and *P. incompletus*, have the forewing with the 1Cu cell but, although the presence of this character state has been registered by Evans (1964, 1978) it has been neglected in later studies, including the most recent diagnosis made by Terayama (2006); from our point of view the distribution of this character is certainly widely represented throughout the Scleroderminae, specially within the clade D.

Israelius

Israelius was supported by unambiguous optimization of following character states: the scutellar process absent (51:2) and the Rsa&M vein abruptly widened at the Rsa segment (83:1), additionally the DELTRAN optimization favor the transformation of the forewing r-rs segment from a plesiomorphic tubular vein (88:0) to a derivate nebulous vein (88:1) in two species, to spectral vein (88:2) in one species and the absence in the fourth species; this is a new condition that updates the diagnosis made by Richards (1952), showing this vein as a polymorphic character.

The clade (sp. nov. 08 + *Israelius*) is found associated as sister-group of the remaining genera within clade D2, including *Cephalonomia hypobori*, *Prorops*, *Megaprosternum* and *Cephalonomia*, generally sharing the most derived character states, specially referred to the circular and lateral propodeal spiracle, the extreme modifications in the head shape and the wing and sculpture reduction. It is important to note that the Rs+M in the sp. nov. 08 have not appeared as an angulation on Rsa&M but as a conspicuous short stub, this confirms our interpretation of this angulations as a remnant of Rs+M. However the state has not been codified because it is an autapomorphy of sp. nov. 08.

Cephalonomia

Cephalonomia was recovered as a polyphyletic group supported by the homoplastic character state the gena visible behind the eye in dorsal view (14:1) favoring a

transformation from the hidden to visible genes and a posterior reversion to the hidden condition. The ACCTRAN optimization recovers the following character states: the metapleural carina of the metapectal-propodeal complex present (62:1) as a secondary origin, at least in the fully winged forms, and the hamuli irregularly spaced (103:1) as a secondary origin. The DELTRAN optimization recovers the state of character malar sulcus present (2:0) as a single origin with a secondary loss in some species, including the apterous ones. It is important to note that apterous and micropterous terminals of *Cephalonomia* were recovered by the most parsimonious tree under implied weighting inside the genus group, indicating that the characters on the matrix are enough informative to identify the sexual dimorphism.

The terminals

The position of several terminals is debatable due to scarcity of information associated with the state of material preservation, the inaccessibility or extreme morphological reduction. The characters used were insufficient to locate terminals like *Platepyris sepalus* and the apterous male of *Glenosema*, the extreme reduction of the features or the absence of the main structures in several groups make difficult to solve the placement of several terminals. This male is taxonomically identified as the first strictly apterous male in *Glenosema*, and therefore the position of this terminal into *Cephalonomia* has to be understood as an artifact due to the lack of data.

Bethylopsis fullawayi, even bearing antennae with 10 flagellomeres, appears in the most parsimonious tree under the implied weighting analyses as sister-group of *Sclerodermus*; this arrangement is consistent with the structure of relationships showed in the strict consensus tree and the equal weighting tree in Lanes & Azevedo (2008). The placement of terminals with 11-flagellomered antennae inside the clade D, and closely related with 10-flagellomered antennae groups, lead us to reconsider the weight that traditionally has been assigned to the number of flagellomeres. Although there seems to be a general tendency to loss or reduction of flagellomeres, the plasticity of this character shows that there may be other types of secondary losses or gains, as is the case for the intrageneric variation exhibited by *Megaprosternum*.

The unambiguous optimization favors a single origin of each type of reduction in sp. nov. 08 and *Cephalonomia cisidophaga* and a reversal to the plesiomorphic state in *Megaprosternum*, but we cannot solve the homoplastic condition represented by *Bethylopsis*. The association between the clade D with *Megaprosternum* is supported by the record of, at least, one species of *Megaprosternum* with 10 flagellomeres, discovered on specimens from Mariana Islands, Fiji and Australia.

As a taxonomical observation we suggest the median clypeal lobe strongly projected, deeply emarginated and separated from lateral ones, as an autapomorphy of *Sclerodermus*, the largest genus within Scleroderminae (more than 80 described species); although the character state median clypeal lobe delimitation (5:1) was coded to evaluate this hypothesis, the depth emargination among lobes and the inversely trapezoidal median lobe in *Sclerodermus* are features not present in other genera, then considered autapomorphic for this genus.

Character mapping

Some characters discussed here were selected based on their traditional use in taxonomic or phylogenetic analyses of Scleroderminae. Then, the aim of this abridged discussion is to avoid the ambiguity and allow us to interpret the informative characters and their fraction of apparent synapomorphy, for this we use the (Rc) Rescaled

Consistency Index (Farris 1989). Some characters have complex transformation patterns as pointed out below.

Head shape (12, Rc: 0): this character is somewhat stable only when dealing with the clades *Nothepeyris* + *Discleroderma*, *Chilepeyris* + *Glenosema*, *Pararhabdepyris*, clade C and *Prorops*, but showed an important inter- and intrageneric variation. The codification of cuticular areas seems to be complicated due to the scarcity of landmarks as support to define homology between sclerites. The codification of the head shape even hides simpler degrees of homology that were unreachable, e.g., it is quite probable that, what we considered globose in *Nothepeyris* + *Discleroderma*, may not be homologous of the same state in Mesitiinae, *Prorops* and/or *Pararhabdepyris*, given the particular and complex modifications of the cephalic capsule of the latter genus. In the same way, what was considered here as depressed head, present in many groups, may correspond to several different transformation series. In fact, the most widely distributed state is the oval head, a concept encompassing several types of undifferentiated head forms, which fit more or less to an oval geometric pattern.

The cephalic capsule of bethylids is very different in comparison to the other families of Chrysidoidea (Carpenter 1986). The same scenario is found in Scleroderminae when compared to other bethylids due to their widely distributed prognathism. However, certain groups such as *Pararhabdepyris*, *Discleroderma*, *Nothepeyris* and New genus A exhibit an apparent hypognathism (Vargas & Azevedo 2016a), which may have a convergent secondary origin.

Another example of homoplastic feature on the head is the eye contour projection (25, Rc: 0), in most non-aculeates, and even in most aculeate Hymenoptera, the non-protuberant eye is considered primitive (Brothers 1975); in this context, the protuberant eye in Mesitiinae suggests a secondary and convergent origin of the protuberant eye in Scleroderminae. However, the eyes of Mesitiinae are much more protruding than in Scleroderminae or any other bethylid subfamilies. Thus the condition of the protuberant eye in these both subfamilies could be interpreted as a multistated transformation series.

Number of antennal flagellomeres (22, Rc: 0.3) (Fig. 8A): this character has been traditionally used to support the classification of the tribes Sclerodermini and Cephalonomiini (*sensu* Evans 1964); however with the discovery of several additional states, the interpretation becomes more complex. The topology shows (Fig. 8A), in general, a transformation of states, but with the presence of *Bethylopsis* with 10 flagellomeres among the clades with 11 flagellomeres. Finally, immersed within the clades with 10-flagellomered antennae, there are sp. nov. 08 with the antennae 7-flagellomered, the genus *Megaprosternum* with 11- and 10-flagellomered antennae and, inside *Cephalonomia* the species *C. cisidophaga* with 8-flagellomered antennae.

This scenario shows us a homoplastic condition at suprageneric level that matches with the point of view of Rasnitsyn (1980) who considered the number of flagellomeres to be convergent; an old proposal, if we consider that, according to Carpenter (1986), to all appearances, the variation on the number of flagellomeres within Aculeata is a long history of reductions, in which the ground plan of the antennae with 11 flagellomeres is only a step in a sequence of transformations, from the multi-segmented antennae passing through 13, 11 and 10 flagellomeres. Notwithstanding, particularly in Chrysidoidea, the antennae with 10 flagellomeres in the female is considered a reduction from the antennae with 11 flagellomeres found in males; a plasticity that has been observed between sexes of the same species, instability considered as support for the interpretation of the possibility of a secondary increase, as in *Megaprosternum*.

Pronotal collar presence (35, Rc: 0.4): Brothers (1975) considered the presence of pronotal collar plesiomorphic in Aculeata and the absence apomorphic in scolebythid and

plumariid females. In the present topology this character is generally present, but it is absent in the clade C and *Megaprosternum*. Thus we consider the absence of the pronotal collar an apomorphic state in the flat Scleroderminae and convergent respect *Megaprosternum* possibly related with different series of complex transformation from a robust to depressed body.

Prosternum size (40, Rc: 0.1): according to Brothers (1975) the large prosternum (propleura diverging at an angle and thus exposing the prosternum anterior to the procoxae) could be understood as a parallel secondary origin. In Scleroderminae the genera that exhibit this enlarged prosternum are *Solepyris* and *Megaprosternum*, but bearing a different shape that is elongate triangular and widened pentagonal, respectively (Azevedo 2006); thus the large prosternum in *Megaprosternum* and *Solepyris* is consistent with this view.

Presence of the notauli (45, Rc: 0.1) (Fig. 8B): this character appears to be closely associated with the robustness and the presence of carinae on the metapectal-propodeal disc and the mesopleural foveae on the fully winged species. In fact, several groups that exhibit any level of reduction or loss on the wing structure typically lack the notauli as well. The topology shows several taxa on clade D with minute body size, in which the notauli is present maybe in addition to relatively conspicuous metapleural, transverse anterior and posterior carinae in the metapectal-propodeal disc and the robust body, here the unambiguous optimization and the Rc suggest a homoplastic condition explainable by the convergence on complex expressions of the sculpture, independent from the general body size.

Although, inside the 11-flagellomered group seems to exist a tendency to lose the notauli, specially when the general reduction of the characters is extreme as in *Glenosema* and *Sclerodermus*, it is important to note that in the 10-flagellomered genera, *Alloplastanoxus*, *Pararhabdepyris*, sp. nov. 01, sp. nov. 02 + sp. nov. 03, sp. nov. 05, sp. nov. 06 and sp. nov. 07, in which the notauli are present, there are conspicuous carinae or rugulous sculpture and faint reduction of structures and there is no register of aptery, any type of sexual dimorfism nor an extreme loss of forewing veins.

Shape of the notauli (46, Rc: 0.1): the notauli are present in the clade (*Nothepyris* + *Discleroderma*), but *Discleroderma* sp. nov. 12 (Thailand) lost it, the character is conserved in *Galodoxa* and, at least, two species of *Allobethylus*.

The straight notauli was a character state recovered as a potential synapomorphy for Scleroderminae. This is an inconsistent conclusion because the character was inapplicable for many terminals, due to the absence of the notauli, main in the non-macropterous forms. However this hypothesis could be explained by the association between the absence of notauli and the reduction or absence of other structures in many terminals, associated with secondary losses. The remaining characters associated with the notauli are ambiguous.

Propodeal spiracle position (65, Rc: 0.3) (Fig. 9A): the propodeal spiracle shows a tendency to relocate from the dorsal position in 11-flagellomered genera to the lateral position in the 10-flagellomered genera. This character seems to be a potential synapomorphy of the clade D2, that could inform about the evolutionary relationships inside more restricted levels.

Propodeal spiracle shape (66, Rc: 0.2) (Fig. 9B): the elliptical spiracle appears to be the plesiomorphic state. The apomorphic state (circular spiracle) seems to be widely distributed throughout the clade (*Bethylopsis* + (clade C + clade D)) except by a more or less defined group of terminals closely associated with *Pararhabdepyris*. The elliptical spiracle inside the clade D1 is interpreted as a secondary acquisition.

Angulation of the anterior margin of the forewing (78, Rc: 0.2): the outgroup terminals do not bear such angulation, so it should be regarded as a derivate feature associated with

several patterns of vein reduction. The brachyptery, microptery and aptery phenomena obscured the definition of this character. However from the topology we consider it as a convergence in *Glenosema* respect the major clade formed by *Bethyloopsis* and *Sclerodermus* (11-flagellomered genera with reduced wing or venation) plus the clade C (flat-bodied clade) and the clade D (homoplastic flagellomere segmentation).

Presence C vein (79, Rc: 0.5) (Fig. 10A): the transformation begins in the outgroup, with the presence of the C vein, and continues to *Allobethylus*, with the single exception of the clade *Nothepyris* + *Discleroderma* where C vein is absent. The absence of the C vein is evident in the node of *Bethyloopsis* and all of its relatives, including the clades C and D. This kind of situation lead us to think in the possibility that (*Nothepyris* + *Discleroderma*) would have a more internal position inside topology.

Presence of r-rs&Rsc veins (87, Rc: 0.1; 89, Rc: 0.1) (Fig. 10B): these characters showed intrageneric variation in *Nothepyris*, *Alongatepyris*, *Israelius*, *Plastanoxus* and *Prorops*. The unambiguous optimization shows the presence of these veins as a plesiomorphy within Scleroderminae, except the more specialized genera *Cephalonomia* and *Prorops*; over these general hypotheses appear several secondary gains and losses that made the characters to be homoplastic at suprageneric level.

M+Cu vein (80, Rc: 0.4): this vein is generally present in the groups with two closed cells. However could be absent or interrupted in some genera like *Solepyris*, *Thlastepyris* and the new genus D. This condition is considered here as a convergence.

Presence of Sc+R1a (84, Rc: 0.1): the so called prostigma (Evans 1964) is interpreted here as a fusion between the distal end of Sc+R vein and the anterior end of Rsa&M, the Sc+R of Brothers (1975), R1 of Goulet & Huber (1993) or R1a of Ramos & Azevedo (2012), the unambiguous optimization shows the character as an apomorphy throughout the Scleroderminae, then we infer that its absence should be regarded as a secondary loss convergent in *Megaprosternum* and some species of new genus B, associated with two different kinds of venation reduction. Due to the optical limitations we cannot discard some coding artifact.

Presence of Cua vein (92, Rc: 0.5) (Fig. 11A): when present, it is plesiomorphic and appears in the genera *Nothepyris*, *Discleroderma*, *Chilepyris*, *Glenosema* and *Galodoxa*. Its absence is considered apomorphic and characterize the groups *Allobethylus*, *Bethyloopsis*, *Sclerodermus*, the clade C and the clade D.

Presence of A vein (93, Rc: 0.3): the presence of this vein appears to be plesiomorphic. Its absence in several clades or groups should be considered as a convergence, so its absence is not enough to define genera as *Cephalonomia* and *Megaprosternum*, in addition to the ontological weakness of the character.

Presence of 1cu-a vein (94, Rc: 0.3; 95, Rc: 0.3): this transverse vein is generally present and long in the other subfamilies of bethylids and in the fully-winged 11-flagellomered genera; conversely in the clade D, when present, is almost always short. Therefore the character 95 is a potential synapomorphy to the clade D.

1Cu cell length compared with R cell length (98, Rc: 0.1) (Fig. 11B): the plesiomorphic state (cells subequal) are present in almost all the 11-flagellomered genera except *Galodoxa* and one species of *Allobethylus* (Table. 1). The apomorphic character state first appears in the clade C, especially in the genera *Tuberepyris*, *Alongatepyris* and *Thlastepyris*. Several 10-flagellomered genera share this character state, condition that was designed for the first time by Richards (1952) for *Israelius carthami* and later by Hedqvist (1975) for *Plastanoxus ahusiensis*. Evans (1964) described the presence of the 1Cu cell for *P. laevis* and *P. incompletus* without including illustrations or any further analysis of the character. However, Terayama (2005, 2006) suggested that the presence of A vein is associated to the presence of two closed cells in 10-flagellomered genera (see the descriptions of *Proplastanoxus* and *Alloplastanoxus*, respectively). The character

state is absent in several taxa inside the clade D as *Cephalonomia*, *Israelius amputatus*, sp. nov. 05 and sp. nov. 01.

The 1Cu cell shorter than the R cell has been considered unusual in Scleroderminae, but several terminals has this character state; it seems that several features like this, poorly known until now, actually are common throughout the Scleroderminae. The derivate state appears especially in the 10-flagellomered terminals, *Galodoxa* and, at least, one species of *Allobethylus*. However out of the clade D the pattern seems to be independent when the 1cu-a vein is taken into account. In the genera *Galodoxa* and *Allobethylus* the Cua vein is triangular and wider than in the 10-flagellomered terminals. The apparently plesiomorphic condition of subequal length in sp. nov. 05 and *Israelius amputatus* could be an independent evolution that deserves a further analysis and an improved coding. Finally, the character transformation becomes ambiguous due to the inapplicability or absence of the character.

There are three patterns of length of the 1Cu cell. One includes *Galodoxa* and *Allobethylus* sp. nov. 9, in which the 1Cu cell is, at most, half as long as the length of R cell; the second including (*Tuberepyris* + (*Alongatepyris* + *Thlastepyris*)), in which the 1Cu cell is extremely short and sometimes fused with R cell and the third pattern includes the 10-, and 7-flagellomered genera, having as an exception two terminals (new genus A and new genus C), in which the 1Cu cell is not clearly shorter than R cell but with a transverse 1cu-a vein extremely short or inconspicuous.

Although there is no clear synapomorphies to define the clades like *Chilepyris* + *Glenosema*, (*Tuberepyris* + (*Alongatepyris* + *Thlastepyris*)), clade D1 and clade D2, values between 0.1 and 0.3 of rescaled consistency index indicate that there are enough characters with synapomorphic fractions to inform on relationships inside Scleroderminae.

In groups where the tegula is present, eg. microptery (*Glenosema* and *Cephalonomia cisidophaga*) and brachyptery (*Bethylopsis fullawayi*), the tiny or small wing could have a secondary origin, without this necessarily implying a specific association with the wing venation transformation. The more plesiotypical groups share different combinations of kinds of cell or vein reduction, especially in respect to the r-rs&Rsc vein (*Nothepyris*, *Discleroderma*, *Galodoxa*, *Allobethylus* and *Chilepyris*). In general, the r-rs&Rsc vein disappears early in the evolution of the subfamily and reappears secondarily in different clades with accentuated intrageneric venation variability, so the wing appears to be composed by several homoplastic characters as showed especially by the presence/absence (+/-) in the eight patterns defined below (Table 1). However, the wing characters exploration demonstrated to be useful and informative. The genera *Bethylopsis*, *Sclerodermus*, *Megaprosternum* and *Cephalonomia* are defined widely by absence of veins, which implies an important ontological weakness in the definition of these groups because of its inapplicability. The existence of different patterns of forewing venation and shape, in several groups and clades of Scleroderminae, confirm what Carpenter (1986) established for Chrysidoidea when said that the pathways of reduction have been different in most of the groups and the resultant patterns differ in detail.

The wing and venation reduction associated with the simplification of the sculpture on the body surface do not support Scleroderminae as a more specialized subfamily of Bethyridae compared with Epyrinae, as argued by Evans (1964). Thus, it should be reinterpreted following that Kukalová-Peck (2008) referred as post-Paleozoic adaptations (generally diverse reductions and fusions).

Another important way to improve this analysis, taking into account the gradual transformation of the Scleroderminae morphology, is by coding quantitative continuous morphological characters as suggested by Wiens (2001), evaluating the character state definition from the character distribution along series of conspecific individuals.

Table 1. Patterns of forewing venation. Each colored block corresponds with a single pattern, defined strictly by vein presence (+) or absence (-) [i: incomplete, c: complete, ?: inapplicable].

Pattern	Taxon	C	Sc+R	M+Cu	Rsa&M	ICu cell<R	Icu-a	Icu-ashor	r-rs	Rsc	A
1	<i>Chilepyris</i>	+	+	+	+	-	+	-	+/-	+/-	+
	<i>Glenosema</i>	+	+	+	+	-	+	-	+	+	+
	<i>Nothepyris</i>	-	+	+	+	-	+	-	+/-	+/-	+
	<i>Discleroderma</i>	-	+	+	+	-	+	-	-	-	+
2	<i>Galodoxa</i>	+	+	+	+	+	+	+	-	-	+
	<i>Allobethylus</i>	+	+	+	+	+	+	+	+	+	+
3	<i>Bethylopsis</i>	-	+	+	?	?	?	?	?	?	+
4	<i>Sclerodermus</i>	-	+	+	+	-	+/-	-	-	-	+/-
5	<i>Solepyris</i>	-	+	i+	+	-	+	-	+/-	+/-	+
	<i>Thlastepyris</i>	-	+	i/c+	+	+	+	+	+/-	-	+
6	<i>Alloplastanoxus</i>	-	+	+	+	+	+	+	+	+/-	+/-
	<i>Israelius</i>	-	+	+	+	+	+	+	+	+/-	+/-
	<i>Proplastanoxus</i>	-	+	+	+	+	+	+	+	+/-	+/-
	New genus B	-	+	+	+	+	+	+	+	+/-	+/-
	New genus D	-	+	+	+	+	+	+	+	+/-	+/-
	New genus E	-	+	+	+	+	+	+	+	+/-	+/-
	New genus F	-	+	+	+	+	+	+	+	+/-	+/-
	New genus A	-	+	+	+	+	+	+	+	+/-	+/-
	New genus C	-	+	+	+	+	+	-	+	+/-	+/-
<i>Plastanoxus</i>	-	+	+	+	+	+/-	-	+/-	+/-	+/-	
7	<i>Prorops</i>	-	+	+	+	-	-	?	+	+/-	-
8	<i>Megaprosternum</i>	-	+	-	-	?	-	?	-	-	-
	<i>Cephalonomia</i>	-	+/-	-	+/-	?	-	?	-	-	-

The extensive morphological homoplasy seen in our analyses of several characters is consistent with the plasticity registered by several authors for many characters in Hymenoptera (Ronquist et al. 1999, Sharkey et al. 2011 and Heraty et al. 2013), this could have as a possible reason a given selective pressure that might influence the whole character system such that the evolution of many individual characters occurs in a “concerted” manner (Blanke et al. 2013). This phenomenon includes character complexes as the head capsule, the antennae, the wings, the metapectal-propodeal complex, and the thoracic structures associated with the flight, among others. Thus Scleroderminae could be an example of concerted evolution because of their complex patterns of state change.

The character analysis indicates that the options on the morphological space of Scleroderminae could vary among the following independent processes: i) loss of structures (aptery), ii) reduction (brachyptery, microptery, vein reduction, antennal segment reduction, pronotal collar reduction), iii) shape transformation (propodeal spiracle shape, eyes shape, mandibular shape, head shape, legs shape, general flattening) and iv) change in scale (general miniaturization, allometry, secondary loss of texture on the integument).

Based on the disparity concept proposed by Oyston et al. (2015), Scleroderminae and more specifically the clade D could be recognized as a recently evolved, complex and widely unknown lineage that is currently defined by a big bunch of homoplasies, implying a possible earlier high morphological diversification.

The codification

The character coding experience in this work was, like said by several authors (cited by Hawkins *et al.* 1997) quite subjective, so we agree with Heraty et al. (2013) about compiling morphological data, across any group of study, necessarily requires a collaborative approach among specialists, because the comparison of alternative approaches to character construction, although important, is still in its infancy (Harris 2003). Besides, we suggest the following options to improve the character codification in

posterior phylogenetic approaches of Scleroderminae:

- i) Evaluation of the phylogenetic relationships at generic level in order to discriminate possible intraspecific fixed characters from the large number of apparently variable characters, or artifacts produced by small samples (Wiens 2001), example of this are *Nothepyris*, *Discleroderma*, *Allobethylus*, *Sclerodermus*, *Cephalonomia* and *Plastanoxus*, in which the variation of characters within the forewing venation as the r-rs&Rsc vein or the variation of general sculpture have not been defined and for which there is no precedent for taxonomic revision or phylogenetic analysis at generic level.
- ii) Phylogenetic analyses of *Cephalonomia*, *Sclerodermus* and *Plastanoxus*, three genera that together sum up about 72% of total species in Scleroderminae.
- iii) Observation of large series of specimens by species in order to coding characters as quantitative continuous variables (Wiens 2001) could supply more objectivity to the coding process, valuable series of specimens could be obtained for conspicuous genera like *Sclerodermus*, *Cephalonomia*, New genus B (from Madagascar) or *Plastanoxus*.
- iv) In the framework of the Hymenoptera Anatomy Ontology project (Yoder et al. 2010), it is evident that Scleroderminae lacks a stable morphological ontology, especially for those groups that bear some kind of structure reduction or cryptic morphology, like the apterous or subapterous forms of *Sclerodermus* and/or *Cephalonomia* or the extremely depressed genera like *Megaprosternum*, *Alongatepyris*, *Thlastepyris* or *Solepyris*, in which structures of the head and the thoracic sclerites suffer important transformations like the pronotal collar reduction, the increase of the prosternal size, the structure displacement or atypical vein reduction. Therefore it is important to clarify many ambiguous anatomical terms through comprehensive morphological studies, before the beginning of the coding process. Example of this situation is the ambiguous definition of terms for the cephalic areas, the mesopleural foveae, the metathoracic areas, the general sculpture and the wing venation.
- v) Finally, the proposition of a robust molecular analyses in order to interpose the morphological tree.

[suggested place for Figs 8-12 here]

Conclusions

The addition of a high percentage of genera and the parsimony analysis under implied weighting analyses have generated an increased resolution on the topology of Scleroderminae, compared with previous phylogenies. The morphological data provided informative evidence for the monophyly of *Discleroderma*, *Glenosema*, *Allobethylus*, *Pararhabdepyris*, *Megaprosternum*, *Prorops* and *Israelius*, and for clades (*Nothepyris* + *Discleroderma*), (*Chilepyris* + *Glenosema*), (*Solepyris* + (*Tuberepyris* + (*Alongatepyris* + *Thlastepyris*))), additionally the analysis was useful to confirm the sex association of *Galodoxa* proposed by Vargas & Azevedo (2016a).

Scleroderminae have increased in 6 new genera, amount corresponding to about 28% of the previous number and duplicating the number of genera in the 10-flagellomered group, becoming a considerably bigger clade exhibiting new and complex relationships. Even though, our results closely mirror some of the earlier intuitive concepts proposed by Evans (1964), Terayama (1995), Lanes & Azevedo (2008) and Alencar & Azevedo (2013) and in some aspects the molecular results of Carr et al. (2010), the monophyly of Cephalonomiini *sensu* Evans (1964) is not recovered, contrary to the hypotheses exposed

by Terayama (2006), Lanes & Azevedo (2008), Carr (2010), Alencar & Azevedo (2013) and Jiang et al. (2015), due to the polyphyly respect *Megaprosternum* and *Bethylopsis fullawayi*.

In relation with the hypotheses by Evans (1964) about a linear tendency of morphological reduction from taxa more generalized in Epyrini to more specialized taxa in Cephalonomiini, in the present analysis many characters and clades suggest the presence in Scleroderminae of a set of complex patterns of reduction; a complex history, which is fragmentarily told by the terminals and their morphological plasticity, when conceptualized and codified in characters.

Although the ground plan of the antenna metamerism appears to have 11 flagellomeres, certain groups had this number modified. The plasticity is registered for this character throughout the entire Aculeata and particularly evident as a faint sexual dimorphism. In particular, the clade D2 appears to be a group characterized by a secondary flagellomere number variation with the intrageneric variation between 10 and 11 flagellomeres on *Megaprosternum*, in addition to the extreme reduction or the disappearance of the forewing veins, the secondary extreme reduction or the loss of the wing membrane (microptery and aptery), the extreme reduction of the sculpture and the general body miniaturization.

The presence of the notauli in *Nothepyris*, *Discleroderma*, *Allobethylus* and some terminals within the clade D1 as *Alloplastanoxus*, *Pararhabdepyris*, new genus A, new genus B and new genus C and its absence in *Glenosema*, *Bethylopsis*, *Sclerodermus* and most of the genera on the clade D, suggest that the absence is not necessarily related with the reduction on the body size (Evans 1964), but a result of some kind of fossorial adaptation of the flight system. In addition, there is a pattern of relocation of the propodeal spiracle between the dorsal position on 11-flagellomered genera to the lateral position on 10-flagellomered genera, in particular the propodeal spiracle becomes lateral in the 11-flagellomered genera with aptery or body flattening and persists in that location through the clade D.

The wing venation patterns described illustrate an array of convergent strategies suitable to live in different degrees of fossorial and cryptic micro-environments. In Scleroderminae all of them are different expressions of secondary losses that, from the general pattern of the three closed cells plus the r-rs&Rsc vein, includes the following variations: i) the loss of the C vein, ii) loss of the r-rs&Rsc vein, iii) the reduction of the 1Cu cell, iv) the loss of the 1Cu cell, v) the reduction of the 1cu-a vein, v) the loss of the R cell and vi) the loss of the Sc+R vein (Table 1). Then, this subfamily could be defined as a suprageneric taxa that exhibit several complex convergent patterns of morphological reduction, mixed with structure allocation changes (e.g. eye position, propodeal spiracle displacement) and distinct types of shape transformations (e.g. robust vs. depressed body, winged vs. apterous), and the appearance vs. disappearance of cuticular details (e.g. veins, carinae, sutures, hamuli, hairs).

Scleroderminae need several additional alpha-taxonomic works, mainly revisions of the speciose genera *Sclerodermus* and *Cephalonomia*, and the paraphyletic clades, through the analysis of the types, specialized sampling field works and improved efforts of coding its morphological and molecular attributes in order to discover synapomorphies and to describe the way the groups has explored the range of available 'design' options. By now, we did not get useful synapomorphies Scleroderminae due to their large phenotypic plasticity, which hampers the more accurate delimitation of homology hypotheses. Some non-monophyletic groups found in this study, such as *Cephalonomia*, *Plastanoxus*, *Allobethylus* and *Nothepyris*, reflect the poor state of existing taxonomic studies for such taxa, which Ebach et al. (2006) call "bad taxonomy".

Scleroderminae are rare in collections and rarely caught in traps during field

expeditions when compared with other bethylid subfamilies, that is an additional difficult the improvement of their Systematics.

Taxonomic accounts

Key to genera of Scleroderminae

1. Antenna with 11 flagellomeres...2
 - Antenna with 10 flagellomeres, very rarely with eight or seven...15
2. Forewing with complete venation, with three closed cells...3
 - Forewing venation somewhat reduced, at least without costal vein...6
3. Head as wide as mesothorax in dorsal view; female occipital carina inconspicuous or absent; pronotal disc with anterior margin straight; forewing with 1Cu cell somewhat shorter than R cell and 1cu-a vein straight...4
 - Head distinctly wider than mesothorax; occipital carina present; pronotal disc with anterior margin arched; forewing with 1Cu cell equal or longer than R cell and 1cu-a vein angled...5
4. Mandible long with three distal teeth; forewing with r-rs vein and Rsc vein; metasomal ventral modifications absent...*Allobethylus* (♀)
 - Mandible short with four distal teeth; forewing without r-rs vein and Rsc vein; metasomal ventral modifications present...*Galodoxa* (♀♂)
5. Eye elongate and subtriangular; mandible short with two or three distal teeth; frontal line present; stigma large; metapectal-propodeal disc shorter than wide... *Chilepyris* (♀♂)
 - Eye circular; mandible long with five or seven distal teeth; frontal line absent; stigma narrow; metapectal-propodeal disc longer than wide...*Glenosema* (♀♂)
6. Head globoid and/or body not depressed...7
 - Head and body depressed...10
7. Brachypterous...*Bethylopsis carinatus* (♀)
 - Fully winged...8
8. Propodeal declivity with medial longitudinal carina; forewing with r-rs&Rsc vein ...*Nothepyris*
 - Propodeal declivity without medial longitudinal carina; forewing without r-rs&Rsc vein ...9
9. Metasoma with dorsal processes present on segments III or IV to V and last two segments directed upwards or at least posteriorly...*Discleroderma*
 - Metasoma without dorsal processes and last two segments directed downwards...*Sclerodermus*
10. Micropterous; propleural anterior corners not visible in dorsal view...*Platepyris* (♀)
 - Macropterous; propleural anterior corners visible in dorsal view...11
11. Prosternum small, area of prosternum in ventral view about 1x or less of procoxa ...12

- Prosternum large, area of prosternum in ventral view about 2x of procoxa ...14
- 12. Forewing venation extremely reduced to Sc+R1a vein and A vein, or with R and 1Cu cells partially outlined but totally fused...*Tuberepyris*
- Forewing venation not extremely reduced, with R and 1Cu cells divided by tubular M+Cu vein...13
- 13. Forewing with M+Cu vein incomplete, then R and 1Cu cells partially fused...*Thlastepyris* (♀)
- Forewing with M+Cu vein complete, then R and 1Cu cells totally divided...*Alongatepyris* (♀)
- 14. Prosternum pentagonal, forewing venation extremely reduced with R and 1Cu closed cells absent and, at most, Sc+R1a vein and basal stub of A vein present...*Megaprosternum* (♀♂)
- Prosternum subtriangular, forewing venation not extremely reduced, with R and 1Cu cells fused or partially divided by nebulous incomplete M+Cu vein...*Solepyris* (♀)
- 15. Antenna with less than 10 flagellomeres...16
- Antenna 10 flagellomeres...17
- 16. Antenna 8-flagellomeres...*Cephalonomia cisidophaga*
- Antenna 7-flagellomeres...New genus F sp. nov. 08
- 17. Forewing with two closed cells...18
- Forewing with one closed cell or less...26
- 18. Forewing with r-rs&Rsc vein ...19
- Forewing without r-rs&Rsc vein ...New genus B sp. nov. 02 and 04
- 19. Propodeal spiracle huge and circular, body densely hairy...New genus A
- Propodeal spiracle small...20
- 20. Head with short anterior frontal process; forewing with M+Cu incomplete...New genus D
- Head without frontal process; forewing with M+Cu complete...21
- 21. Head trapezoidal in dorsal view with lateral margins divergent anteriorly, anterior frons strongly depressed; mesopleural pit with posterior tubercle...New genus C
- Head not as above, lateral margins subparallel or convex, anterior frons not depressed; mesopleural pit without posterior tubercle...22
- 22. Head rectangular in dorsal view; notauli absent...23
- Head subsquadrated in dorsal view; notauli present... 25
- 23. Malar suture absent; forewing with Rsa&M vein widened at Rsa segment with Rs+M as an outer angulation...*Israelius* (♀♂)
- Malar suture present; forewing with Rsa&M vein evenly wide at Rsa segment, Rs+M absent...24

24. Clypeus with anterior margin as wide plate evenly projected anteriorly, median and lateral lobes subequal; eye large; posterior margin of metapectal-propodeal disc strongly concave... *Proplastanoxus* (♀)
- Clypeus truncated, not widely projected anteriorly; eye small; posterior margin of metapectal-propodeal disc straight to convex... *Plastanoxus* (♀) part (*P. laevis* and *P. incompletus*).
25. Body depressed in lateral view; head quadrate in dorsal view, depressed and flat in lateral view, posterior ocelli widely separated; forewing with 1cu-a inconspicuous and directed proximad; metapectal-propodeal disc longer than wide, sides converging posteriorly; propodeal spiracle rounded... *Alloplastanoxus* (♀♂)
- Body robust in lateral view; head trapezoidal in dorsal view, anterior margin longer than posterior margin, subgloboid in lateral view; forewing with 1cu-a conspicuous and directed antero-posteriorly; metapectal-propodeal disc wider than long, sides subparallel; propodeal spiracle elliptical... New genus E. (♀)
26. Forewing with one closed cell and r-rs&Rsc present...27
- Forewing usually without closed cells, if with any then r-rs&Rsc absent...29
27. Head subrounded, lateral margins convex, eye well separated from mandibular base and vertex; if head subtriangular then body slender and mainly alutaceous to polished... *Plastanoxus* (♀♂) part.
- Head not as above...28
28. Head strongly triangular in dorsal view, subgloboid in lateral view; eye large, in contact with vertex; malar spaces convergent anteriorly; pronotal disc not depressed forward; body sculpture rugous or scabrous... *Pararhabdepyris* (♀)
- Head subquadrate in dorsal view, elliptical in lateral view; eye medium sized, widely separated from vertex; malar spaces subparallel; pronotal disc depressed forward; body alutaceous to polished... New genus B, sp. nov. 03. (♀)
29. Total body length about 3.5mm; brachypterous (forewing only surpassing transverse posterior carina of metapectal-propodeal disc)... *Bethylopsis fullawayi* (♀)
- Total body length, total length 0.7-2.5mm; fully winged or apterous...29
29. Head with frontal anterior projection between toruli; clypeus not visible in dorsal view... *Prorops* (♀♂)
- Head without frontal anterior projection between toruli; clypeus visible in dorsal view...30
30. Body not depressed; prosternum small and subrectangular; metapectal-propodeal disc carinate... *Cephalonomia* (♀♂)
- Body extremely flat; prosternum large and pentagonal; metapectal-propodeal disc not carinate... *Megaprosternum* (♀♂)

New Genus A

Type species. – ***New Genus A sp. nov. 01*** by present designation.

Description. Female. Large wasp. Body robust, densely setose. Head subgloboid in lateral view. Mandible slender with two small distal teeth. Malar space shorter than mandibular proximal width. Malar sulcus thin, subparallel to mandibular proximal

margin. Mandible robust with two large distal teeth, upper margin not denticulate. Gena visible behind eye in dorsal view, occipital-genal lateral margin obtusely angled in lateral view. Anterior ocellus located between eyes. Pronotal disc not depressed forward. Notauli present. Scutellar process evenly thick, without rounded foveae. Metapectal-propodeal disc subquadrate, reticulate to alutaceous, metapostnotal median carina incomplete, transverse posterior carina straight and metapleural carinae not outlining propodeal spiracle; propodeal spiracle large, circular, lateral. Forewing with two closed cells; M+Cu vein complete; stigma linear, r-rs&Rsc vein present; A vein tubular; 1cu-a vein present; 1Cu cell shorter R cell. Hind wing with 3 hamuli irregularly spaced. Mesopleural pit with posterior surface elevated. Femora with transverse section subcylindrical. Metasoma robust, cross section subcylindrical, densely setose at the posterior half, sternum VI with lateral margins exposed dorsally. **Male.** Unknown.

Remarks. This genus is considered new due to the combination of the following characters: robust body, quadrate head with lateral margins straight, 10-flagellomered antenna, malar sulcus subparallel to mandibular proximal margin, eyes small and far from anterior margin of head in dorsal view, leaving the gena exposed, pronotal disc as long as wide, forewing with two closed cells subequal in length, proximal venation longer than $0.25\times$ the forewing length, r-rs&Rsc vein present, notauli present, subquadrate and reticulous metapectal-propodeal disc and huge rounded and lateral propodeal spiracle.

The genus is very different from the known genera with 10-flagellomered antenna by having a particular forewing venation, somewhat similar to *Alloplastanoxus* because of the in the two closed cells. However the remaining characters are so different. In general, the 10-flagellomered genera appear to have a extremely short median clypeal lobe.

New Genus A sp. nov. 01

Fig. 13. A-D

Description, female. – Body length 3.34 mm. LFW 1.09 mm. LH 0.62 mm. WH 0.58 mm. WF 0.34 mm. HE 0.25 mm. WOT 0.14 mm. OOL 0.09 mm. WH $0.95\times$ LH; WF $0.58\times$ WH; WF $1.38\times$ HE; OOL $0.67\times$ WOT. Body dense setose. Head subquadrate, lateral margin convex in dorsal view, globoid in lateral view. Mandible Mandibular upper margin not denticulate. Malar space midsize. Malar sulcus inconspicuous. Median clypeal lobe truncated, without angulation in anterior view, lateral lobe not outlined. Toruli not covering anterior clypeal margin. Hypostomal carina not angulate, emarginate medially. Antenna with 10 flagellomeres, pedicel as long as last flagellomere. Frontal line present. Eye elliptical in full view, densely setose, setae longer than ommatidium, eye contour not protruding. Ocellar triangle with right frontal angle. VOL shorter than HE. Ocellar triangle far from vertex crest. Pronotal collar conspicuous. Propleural neck and anterior propleural angles not visible in dorsal view. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum and mesoscutellum median lengths subequal. Notauli complete, very convergent backward, straight, evenly wide. Mesoscutellar apex shape widely rounded. Scutellar process conspicuous, linear, continuous. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior and metapleural carinae; median and posterior carinae not connected; lateral margins straight, subparallel; metapleural carina not outlining propodeal spiracle. Propodeal spiracle located below metapleural carina. Metapectal-propodeal pleural posterolateral corners rounded. Propodeal declivity without median carina. Mesotibia without setae. Forewing anterior margin incurved; M+Cu vein tubular; Rsa&M vein not widened at Rsa segment; fusion Sc&R1a vein short; r-rs&Rsc vein tubular; A vein present; 1cu-a vein straight, oriented anterior-posteriorly; 1Cu cell shorter than R cell; longitudinal fold distally simple; proximal venation reaching more

than 0.25x of total length of forewing; membrane color infusate. Mesopleural subtegular fovea long, widened anteriorly, subdivided. Metasomal segment II as long as remaining segments, apical segments oriented downward.

Material examined. Holotype female, THAILAND, Chaiyaphum, Tat Tone NP, Chaiyapoom forest, fire station, 16°0.809'N 102°1.335'E, 195m, Malaise trap, 26.xii.2006-2.i.2007, Tawit Jaruphan & Orawan Budsawong leg. T1376. (QSBG).

New Genus B

Type species. – *Israelius amputatus* Barbosa, Kawada & Azevedo, 2014.

Description. Female. Small wasp. Body glabrous. Head oval to subglobose in lateral view. Malar space inconspicuous to midsize. Malar sulcus present or absent, if present perpendicular to mandibular proximal margin. Mandible robust with two small distal teeth. Eye glabrous to setose. Gena hidden by eye in dorsal view, occipital-genal lateral margin rounded in lateral view. Anterior ocellus located between eyes or nearly so. Pronotal disc depressed forward. Scutellar process wider laterally with subrounded deeper foveae. Notauli present or absent, if present then short, not strongly convergent posteriorly. Metapectal-propodeal disc subquadrate, alutaceous, metapostnotal median carina complete, transverse posterior concave and metapleural carinae outlining propodeal spiracle; propodeal spiracle lateral, small, rounded to elliptical. Forewing with one or two closed cells; M+Cu vein complete, Rsa&M vein widened at Rsa segment; rs&Rsc vein absent; A vein present or absent; 1cu-a vein present or absent, if present short to inconspicuous; 1Cu cell shorter R cell when last cell present. Hind wing with three hamuli irregularly spaced. Metasomal cross section subcylindrical. **Male.** Unknown.

Remarks. This genus is considered new due to the combination of the following characters: robust body; subquadrate head with lateral margins convex, 10-flagellomered antenna, malar sulcus perpendicular to mandibular proximal margin, eyes large and close to anterior margin of head in dorsal view covering the gena, pronotal disc shorter than wide, forewing with proximal venation shorter than 0.20x the forewing length, one or two closed cells with 1Cu cell shorter than R cell, notauli present or absent; subquadrate and carinated metapectal-propodeal disc and a small rounded to elliptical, lateral propodeal spiracle.

This genus have two closed cells with 1Cu cell shorter than R cell, this could be seen as similar to *Alloplastanoxus*, *Proplastanoxus*, *Israelius* and two species of *Plastanoxus*. However the robust body and the absence of r-rs&Rsc is an important difference with those genera. The widening of Rsa&M in some species does not show angulation and here we consider it different from that in *Israelius*. Several characters with gradual variation, like the head shape, are similar with *Plastanoxus* but only the revision of the latter genus should clarify this situation.

New Genus B comb. nov. (to be proposed for *Israelius amputatus*)

Description, female. – Body length 2.31 mm. LFW 1.21 mm. LH 0.38 mm. WH 0.43 mm. WF 0.23 mm. HE 0.18 mm. WOT 0.12 mm. OOL 0.12 mm. WH 1.12× LH; WF 0.54× WH; WF 1.25× HE; OOL 1.0× WOT. Head with lateral margins straight. Malar space as long as proximal mandibular width. Median clypeal lobe truncate, as long as lateral ones, separated by emargination from lateral lobes, anterior margin not angled in anterior view. Clypeal carina present. Toruli not reaching anterior clypeal margin. Gena hidden by eye in dorsal view. Mandible intercondylar lobe present. Hypostomal carina emarginated, angulate medially. Antenna with ten flagellomeres, pedicel shorter than last flagellomere. Frontal line present. Eye elliptical in full view, glabrous, contour slightly

protruding. Ocellar triangle with frontal angle right or nearly so. VOL longer than HE, ocellar triangle close to vertex crest, only anterior ocellus located between eyes. Pronotum collar conspicuous, disc surface not depressed forward. Neck and propleural anterior angles hidden in dorsal view. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum shorter than scutellum. Scutellar apex widely rounded. Scutellar process conspicuous, broadly interrupted medially, not evenly wide, evenly depth, lateral, foveae subcircular. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior and metapleural carinae, median and posterior carinae connected, disc lateral margins straight, divergent posteriorly. Propodeal spiracle fully visible in lateral view, elliptical, located above carina. Forewing anterior margin angulate; M+Cu vein tubular, complete; Rsa&M vein with segment Rsa not widened; fusion of Sc&R1a vein long; stigma short; A vein present; 1cu-a vein inconspicuous, not angulate, directed anterior-posteriorly; 1Cu as long as R cell, or nearly so; longitudinal fold simple or inconspicuous; proximal venation length short; membrane infuscate yellow to brown. Hind wing with three hamuli irregularly spaced. Mesopleural pit posteriorly in contact with posterior tubercle or elevation. Subtegular fovea long, evenly linear, U shaped. Metasomal tergite I lateral margins separated each other ventrally, apical segments directed downward.

Material examined. Holotype female, UNITED ARAB EMIRATES, al-Ajban, 24.36N 55.01E, Malaise trap, 27.v-26.vi.2006, A. van Harten col. (UFES N° 118737).

Remarks. We transferred this species to *Israelius* because it has the pronotal disc carinate and the forewing does not present any angulation on the Rsa+M.

New Genus B sp. nov. 02

Fig. 13. E-H

Description, female. – Body length 2.25 mm. LFW 1.68 mm. LH 0.40 mm. WH 0.40 mm. WF 0.20 mm. HE 0.18 mm. WOT 0.11 mm. OOL 0.12 mm. WH 1.0× LH; WF 0.50× WH; WF 1.08× HE; OOL 1.14× WOT. Head with lateral margins convex. Malar space as long as proximal mandibular width. Malar sulcus present. Median clypeal lobe longer than lateral ones, truncate, not separated by emargination from lateral lobes, anterior margin not angled in anterior view. Toruli covering anterior clypeal margin or nearly so. Gena visible behind eye in dorsal view, at least partially. Hypostomal carina emarginated, not angulate medially. Antenna with ten flagellomeres, pedicel as long as last flagellomere. Eye subtriangular in full view, glabrous, contour not protruding. Ocellar triangle with frontal angle right or nearly so. VOL shorter than HE, ocellar triangle far from vertex crest, only anterior ocellus located between eyes. Pronotum collar conspicuous, disc surface not depressed forward, disc without median line (carina or groove). Neck and propleural anterior angles hidden in dorsal view. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum medially shorter than scutellum. Notauli straight, incomplete, drop-shaped posteriorly, posterior convergence faint. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, not evenly wide, evenly depth with lateral subcircular foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior and metapleural carinae; median and posterior carinae connected; lateral margins straight divergent posteriorly. Propodeal spiracle elliptical, located below carina. Forewing anterior margin angulate; M+Cu vein tubular complete; Rsa&M vein present; fusion of Sc&R1a vein inconspicuous; stigma short; A vein present; 1cu-a vein inconspicuous, not angulate directed proximally; 1Cu shorter than R cell; longitudinal fold simple or inconspicuous; proximal venation length short; membrane infuscate yellow to brown. Hind wing with three hamuli irregularly spaced. Mesopleural

pit posteriorly in contact with posterior tubercle or elevation. Subtegular fovea long, widened anteriorly and subdivided. Metasomal tergite I lateral margins separated each other ventrally, metasomal apex directed downward.

Material examined. Holotype female, MADAGASCAR, Mahajanga Province, Parc National de Namoroka, 16.9km 317° NNW Vilanandro, 12-16 Nov[ember] 2002, 16°24'24"S 45°18'36"E, Coll. Fisher, Griswold et al., sifted litter (leaf mold, rotten wood), in tropical dry forest, elev. 100m. CASENT 2064947 (CASC).

Remarks. This species is new by having the R and 1Cu cells present, notauli present and r-rs&Rsc absent.

New Genus B sp. nov. 03

Fig. 14. A-D

Description, female. – Body length 1.62 mm. LFW 1.0 mm. LH 0.35 mm. WH 0.32 mm. WF 0.18 mm. HE 0.14 mm. WOT 0.08 mm. OOL 0.14 mm. WH 0.91× LH; WF 0.57× WH; WF 1.33× HE; OOL 1.80× WOT. Head oval in lateral view, lateral margins straight. Malar space as long as proximal mandibular width. Malar sulcus present. Median clypeal lobe as long as lateral ones, truncate, not separated by emargination from lateral lobes, anterior margin not angled in anterior view. Toruli not reaching anterior clypeal margin. Gena visible behind eye in dorsal view visible, at least partially. Hypostomal carina emarginated, not angulate medially. Antenna with 10 flagellomeres, pedicel as long as last flagellomere. Eye subtriangular in full view, setose, contour not protruding. Ocellar triangle with frontal angle acute. VOL subequal than HE, ocellar triangle close to vertex crest far from imaginary line between anterior top of eyes. Pronotum collar conspicuous, disc surface not depressed forward, disc without median line (carina or groove). Neck and propleural anterior angles hidden in dorsal view. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum medially shorter than scutellum. Notauli straight, complete, evenly wide, posterior convergence faint. Scutellar apex widely rounded. Scutellar process conspicuous, continuous. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, first metapostnotal, transverse posterior and metapleural carinae, median and posterior carinae connected, lateral margins straight divergent posteriorly. Propodeal spiracle fully visible in lateral view, circular, located below carina. Forewing anterior margin angulate; M+Cu vein tubular; Rsa&M vein present; fusion of Sc&R1a vein inconspicuous; stigma short; longitudinal fold simple or inconspicuous; proximal venation length short; membrane infusate yellow to brown. Hind wing with three hamuli irregularly spaced. Mesopleural pit posteriorly in contact with posterior tubercle or elevation. Subtegular fovea long, widened anteriorly and subdivided. Metasomal tergite I lateral margins separated each other ventrally, metasomal apex directed downward.

Material examined. Holotype female, MADAGASCAR, Mahajanga Province, Parc National de Baie de Baly, 12.4km 337° NNW Soalala, elev 10m, 26-30 November 2002, 16°00'36"S 45°15'54"E, Coll. Fisher, Griswold et al., sifted litter- in tropical dry forest coll., CASENT 2111436 (CASC).

Remarks. This species is new by having the R cell in the forewing, notauli and missing r-rs&Rsc in the forewing. It is similar to sp. nov 02 by having notauli. However this species lacks the 1Cu cell in the forewing and has the head rectangular with lateral margins straight.

New Genus B sp. nov. 04

Fig. 14. E-H

Description, female. – Body length 2.25 mm. LFW 1.33 mm. LH 0.49 mm. WH 0.45 mm. WF 0.23 mm. HE 0.23 mm. WOT 0.09 mm. OOL 0.17 mm. WH $0.91 \times$ LH; WF $0.52 \times$ WH; WF $1.0 \times$ HE; OOL $1.83 \times$ WOT. Head globoid in lateral views subquadrate in dorsal view, lateral margins convex. Malar space short or inconspicuous with sulcus present. Clypeus projected anteriorly as a truncate wide plate, with median lobe not separated from lateral ones by emarginations, not angled in anterior view. Toruli not covering anterior clypeal margin in dorsal view. Gena visible behind eye, at least partially. Mandible robust with two large distal teeth, Mandibular upper margin not denticulate, median lobe present. Hypostomal carina emarginate, and angulate medially. Antenna with ten flagellomeres, pedicel as long as last flagellomere. Frontal line present. Eye subtriangular in full view. Eye contour not protruding, glabrous. Ocellar triangle anterior angle acute. VOL shorter than HE. Ocellar triangle close to vertex crest. Anterior ocellus located between eyes top. Pronotum collar conspicuous, disc surface depressed forward. Neck and anterior angles hidden in dorsal view. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum subequal in length than mesoscutellum. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, not evenly wide, deeper at lateral ends with lateral subcircular foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc depressed with transverse anterior, metapostnotal median, transverse posterior and metapleural carinae present; median and posterior carinae connected. Propodeal spiracle circular, located below metapleural carina and fully visible in lateral view, metapleural carina not outlining propodeal spiracle. Metapectal-propodeal complex lateral margins straight, subparallel. Mesotibia without spines. Forewing anterior margin angulated, M+Cu vein tubular, complete, Rsa&M vein not abruptly widened at Rsa segment, fusion Sc&R1a vein long, stigma short, A vein present, 1cu-a vein inconspicuous, 1Cu cell shorter than R cell, longitudinal fold simple or inconspicuous distally, proximal venation long, reaching more than $0.25x$ of forewing total length or more, membrane color hyaline. Hind wing with three hamuli irregularly spaced. Mesopleural pit conspicuous without posterior elevation. Subtegular fovea long, simple, evenly linear. Metasomal tergite I lateral margins separated each other ventrally, sternites V and VI with paired calli, second segment longer than remains, metasomal apex orientated downward.

Material examined. Holotype female, MADAGASCAR, Toliara Prov., Fiherenana, el. 100m, $23^{\circ}10.37'S$ $43^{\circ}57.39'E$, 21-24 October 2002, colls: Frontier Wilderness Project, sifted litter (leaf, mold, rotten wood) gallery forest, MGF 040, CASENT 2083233 (CASC). Paratype: 1 female, MADAGASCAR, Antsiranana, Forêt de Bekaraoka, 6.8km, $60^{\circ}NE$ Daraina, elev. 150m, 7 December 2003, $13^{\circ}10'00''S$ $49^{\circ}42'36''E$, collector: B.L. Fisher, general collection night spider, tropical dry forest, CASENT 2103988 (CASC).

Remarks. This species is new by having the forewing with R and 1Cu cells present, the notauli absent and the forewing with r-rs&Rsc absent. It is similar to *Plastanoxus* by having the head with lateral margins convex and to *Proplastanoxus* by having large eyes. However this species lacks the r-rs&Rsc vein in the forewing and bear paired tubercles on metasomal sternum VI, whereas these features are different in the compared genera and in the remaining species in the New genus B.

New Genus C

Type species. – *New Genus C sp. nov. 05* by present designation.

Description. Female. Large wasp. Body with scattered short setae. Head subquadrate in dorsal view, elliptical in lateral view. Head wider anteriorly in dorsal view, frons depressed anteriorly. Mandible slender with three large distal teeth. Malar space inconspicuous. Malar sulcus present, perpendicular to mandibular proximal margin. Toruli widely separated each other by at least 3x torular diameter. Eye glabrous, subtriangular in full view. Gena hidden by eye in dorsal view. Ocellar triangle far from vertex crest, anterior ocellus located between eyes. Frontal line extending from clypeus to anterior ocellus. Pronotal disc not depressed forward. Neck and propleural anterior angles hidden in dorsal view. Scutellar process evenly wide, evenly deep, without rounded foveae. Metapectal-propodeal disc transverse rectangular, with metapleural margins diverging posteriorly; disc surface mainly polished, anteriorly with irregular carinae; transverse anterior carina wide, metapostnotal median carina complete, transverse posterior carina concave, paraspircular carina divergent, metapleural carinae divergent; area between paraspircular and metapleural carinae trabeculate; propodeal spiracle dorsal, elliptical, slit shaped, located between metapleural and paraspircular carinae. Forewing with two closed cells; anterior margin subtly incurved; M+Cu vein complete; Rsa&M vein not abruptly widened at Rsa segment; stigma short and subtriangular; r-rs&Rsc vein present; 1cu-a vein directed distad; 1Cu subequal than R cell; 1cu-a vein not angulate, directed distally; proximal venation longer than 2.5x the forewing length; longitudinal fold simple. Mesopleural pit with posterior tubercle or projection. Metasomal cross section subcylindrical. **Male.** Unknown.

Remarks. This genus is considered new due to the combination of the following characters: robust body; trapezoidal head with lateral margins diverging anterad; 10-flagellomered antenna; malar sulcus perpendicular to proximal mandibular margin; eyes almost in touch with anterior margin of head, covering the gena; pronotal disc shorter than wide; forewing with two closed cells subequal in length; 1cu-a diverging posterad, the forewing with r-rs&Rsc vein; notauli absent; metapectal-propodeal disc rectangular with metapleural and transverse posterior carinae, lateral margins strongly diverging posterad and small propodeal spiracle slit-shaped.

This genus bears a similarity with *Chilepyris* head in dorsal view and with *Glenosema* in forewing venation; the robust body is not common among the 10-flagellomered genera and only present, by now, in *Pararhabdepyris*.

New Genus C sp. nov. 05

Fig. 15. A-D

Description, female. – Body length 3.36 mm. LFW 2.55 mm. LH 0.86 mm. WH 0.92 mm. WF 0.54 mm. HE 0.43 mm. WOT 0.20 mm. OOL 0.26 mm. WH 1.07× LH; WF 0.58× WH; WF 1.25× HE; OOL 1.31× WOT. Head elliptical, depressed anteriorly in lateral view, lateral margins convex. Mandible with upper margin not denticulate, intercondylar lobe present. Median clypeal lobe truncate, as long as lateral ones, not separated by emargination from lateral lobes, anterior margin not angled in anterior view. Toruli not reaching anterior clypeal margin. Hypostomal carina straight. Antenna with ten flagellomeres, pedicel as long as last flagellomere. Frontal line present. Eye with contour slightly protruding. Ocellar triangle with frontal angle acute or nearly so. VOL shorter than HE. Pronotum collar conspicuous. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum medially subequal than mesoscutellum. Scutellar apex widely rounded. Scutellar process conspicuous,

continuous. Metanotal inter-flap space wide. Metapectal-propodeal disc with metapostnotal median complete, disc lateral margins straight, divergent posteriorly, metapleural carina outlining propodeal spiracle. Propodeal spiracle fully visible dorsally, elliptical, located below metapleural carina. Forewing infusate yellow to brown; M+Cu vein tubular; fusion of Sc&R1a vein present; r-rs&Rsc vein tubular; A vein present; 1cu-a vein conspicuous; 1Cu subequal than R cell; longitudinal fold simple or inconspicuous; proximal venation long. Hind wing with four hamuli irregularly spaced. Mesopleural pit posteriorly in contact with posterior tubercle or elevation. Subtegular fovea short and isolated. Metasomal tergite I with lateral margins separated each other ventrally, metasomal apex directed downward.

Material examined. Holotype female, MADAGASCAR, Toamasina, Montagne d'Anjanaharibe, 18.0km, 21°NNE Ambinanitelo, elev. 470m, 8-12 March 2003, 15°11'18"S 49°36'54"E, Coll: Fisher, Griswold et al., Malaise trap, in rainforest, CASENT 2087370 (CASC).

New Genus D

Type species. – *New Genus D sp. nov. 06* by present designation.

Description. Female. Large wasp. Body glabrous. Head long, depressed in lateral view. Mandible robust with three small distal teeth. Malar space shorter than mandibular proximal width. Malar sulcus perpendicular to mandibular proximal margin. Eye glabrous, high, elliptical in full view. Frons projected anteriorly, projection defined laterally by short ledges, projection not covering clypeus. Frontal line deep, polished, extending from clypeus to anterior ocellus. Toruli separated at least by 2x the torular diameter, covering anterior clypeal margin or nearly so. Gena hidden by eye in dorsal view. Pronotal collar conspicuous, disc polished, depressed forward. Mesonotum 0.5x as long as scutellum. Propleural anterior angles exposed in dorsal view. Metapectal-propodeal disc longitudinally rectangular, disc reticulate rugose, transverse anterior carina elevated, metapostnotal median carina incomplete, transverse posterior carinae straight; metapleural carina inconspicuous. Propodeal spiracle lateral and slit shaped. Forewing with two closed cells, anterior margin subtly incurved; M+Cu vein incomplete, tubular; r-rs&Rsc vein tubular; 1Cu shorter than R cell; 1cu-a vein inconspicuous; proximal venation long. Hind wing with three hamuli irregularly spaced. Metasomal cross section elliptical. **Male.** Fully winged, smaller than female with general morphology alike with it.

Remarks. This genus is considered new due to the combination of the following characters: slender body; rectangular head with lateral margins straight to slightly convex; 10-flagellomered antenna; malar sulcus perpendicular to mandibular proximal margin; frons projected anteriorly between the toruli; WF shorter than HE; VOL shorter than HE; anterior ocellus located between eyes posterior margin; eyes large and elongated covering the gena in dorsal view; pronotal disc depressed forward in lateral view and longer than wide in dorsal view; forewing with cells R and 1Cu present but fused due to the incompleteness of M+Cu vein; proximal venation longer than 0.25x the forewing length; r-rs&Rsc vein present; notauli absent; rectangular, elongated and reticulous metapectal-propodeal disc and small, lateral and propodeal spiracle slit-shaped.

This genus is so unique among the 10-flagellomered genera because of the incompleteness of the M+Cu vein in the forewing and the presence of head frontal projection although shorter than in *Prorops*; the only genus that has the forewing with M+Cu incomplete is *Solepyris* but we consider this similarity homoplastic.

New Genus D sp. nov. 06

Fig. 15. E-H, Fig. 16. A-H

Description, female. – Body length 2.82 mm. LFW 1.61 mm. LH 0.77 mm. WH 0.58 mm. WF 0.28 mm. HE 0.32 mm. WOT 0.11 mm. OOL 0.15 mm. WH $0.75\times$ LH; WF $0.47\times$ WH; WF $0.86\times$ HE; OOL $1.43\times$ WOT. Head lateral margins straight. Malar space conspicuous. Malar sulcus present. Median clypeal lobe longer than lateral ones, truncate, not separated by emargination from lateral lobes, anterior margin not angled in anterior view. Hypostomal carina straight. Antenna with ten flagellomeres, pedicel as long as last flagellomere. Frontal line present. Eye contour not protruding. Ocellar triangle with frontal angle acute. VOL shorter than HE, ocellar triangle far from vertex crest, anterior ocellus located between eyes. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, not evenly wide with deeper lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median and transverse posterior carinae; median and posterior carinae separated; lateral margins straight, divergent posteriorly; metapleural carina outlining propodeal spiracle. Propodeal spiracle fully visible in lateral position, elliptical, located below metapleural angulation. Forewing anterior M+Cu vein distal segment present; Rsa&M vein with segment Rsa not widened; fusion of Sc&R1a vein long; stigma short; r-rs&Rsc vein present; A vein present; 1cu-a vein not angulate, directed proximally; 1Cu cell shorter than R cell; longitudinal fold simple or inconspicuous; proximal venation long; membrane infusate yellow to brown. Hind wing with three hamuli irregularly spaced. Mesopleural pit posteriorly in contact with posterior tubercle or elevation. Subtegular fovea short and isolated. Metasomal tergite I lateral margins separated each other ventrally, metasomal apex directed downward.

Description, male. – Body length 2.14 mm. LFW 1.19 mm. LH 0.55 mm. WH 0.46 mm. WF 0.23 mm. HE 0.29 mm. WOT 0.10 mm. OOL 0.11 mm. WH $0.84\times$ LH; WF $0.50\times$ WH; WF $0.79\times$ HE; OOL $1.10\times$ WOT. Head lateral margins straight. Malar space conspicuous. Malar sulcus present. Median clypeal lobe longer than lateral ones, truncate, not separated by emargination from lateral lobes, anterior margin not angled in anterior view. Hypostomal carina straight. Antenna with ten flagellomeres, pedicel as long as last flagellomere. Frontal line present. Eye contour somewhat protruding. Ocellar triangle with frontal angle straight. VOL shorter than HE, ocellar triangle far from vertex crest, anterior ocellus located between eyes. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum, mesocutum shorter than mesoscutellum. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, not evenly wide with deeper lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc rugulose with transverse anterior, metapostnotal median and transverse posterior carinae; median and posterior carinae separated; lateral margins straight and subparallel; metapleural angle not outlining propodeal spiracle. Propodeal spiracle fully visible in lateral position, elliptical, located below metapleural angulation. Forewing anterior M+Cu vein distal segment present; Rsa&M vein with segment Rsa not widened; fusion of Sc&R1a vein long; stigma short; r-rs&Rsc vein present; A vein present; 1cu-a vein inconspicuous and not angulate, directed proximally; 1Cu cell shorter than R cell; longitudinal fold simple; proximal venation long; membrane infusate brown. Hind wing with three hamuli irregularly spaced. Mesopleural pit posteriorly in contact with posterior tubercle or elevation. Subtegular fovea short and isolated. Metasomal tergite I lateral margins separated each other ventrally, metasomal apex directed downward. Genitalia with parameres simple, short with apical end somewhat truncate; aedeagus longer than parameres, deeply divided apically with acute paired lobes, cuspis wide with margin

rounded, shorter than digitus, digitus margin sawed apically (genital capsule exposed, not dissected).

Material examined. Holotype female, MADAGASCAR, Province Fianarantsoa, Parc National Ranomafana, radio tower at Forest edge, elev. 1130m, 24 Dec. 2001-2 Jan. 2002, 21°15.05'S 47°24.43'E, Collector: R. Harin'Hala, Malaise, mixed tropical forest, MA-02-09B-09, CASENT 2063390 (CASC). Allotype: 1 male, MADAGASCAR, Toliara Prov., Parc Nat. d'Anfohahela, Forêt d'Ambohibory, 1.7km 61° ENE Tsomelahy, 36.1km 308° NW Tolagnaro, 16-20.i.2002, 24°55'48"S 46°38'44"E, coll: Fisher, Griswold et al., Malaise trap in tropical dry forest, elev. 300m, BLF4917, CASENT 2086477 (CASC). Paratype: 1 female, MADAGASCAR, Toliara Prov., Parc Nat. de Tsimanampetsotsa, Forêt de Bemanatiza, 20.7km 81° E Efoetse, 23.0km 131° SE Beheloka, 22-26 March 2002, 23°59'32"S 43°52'50"E, coll: Fisher, Griswold et al., Malaise trap in spiny forest thicket, elev. 90m, CASENT 2111557 (CASC).

New Genus E

Type species. – *New Genus E sp. nov. 07* by present designation.

Description. Female. Body glabrous. Head subquadrate in dorsal view, subglobose in lateral view, anterior margin wider than posterior in dorsal view. Mandible robust with three large distal teeth. Malar space shorter than mandibular proximal width. Malar sulcus perpendicular to mandibular proximal margin. Eye glabrous, elliptical in full view. Gena partially visible behind eye in dorsal view. Toruli widely spaced at least 2.0x torular diameter. Notauli present. Mesonotum shorter than scutellum. Metapectal-propodeal disc constricted anteriorly, sculpture mainly reticulate coriaceous, transverse anterior carina thin, metapostnotal median carina complete, transverse posterior carinae somewhat concave medially. Propodeal spiracle lateral, elliptical, located below metapleural carina. Forewing with two close cells, M+Cu vein complete; Rsa&M vein abruptly widened at Rsa segment; r-rs&Rsc vein present; 1cu-a vein conspicuous, not angulate, directed antero-posteriorly; 1Cu shorter than R cell; proximal venation long. Hind wing with three hamuli irregularly spaced. Mesopleural pit with posterior tubercle or elevation. Metasomal cross section depressed. **Male.** Unknown.

Remarks. This genus is considered new due to the combination of the following characters: robust body; trapezoidal head with lateral margins straight and diverging anterad; posterior margin of head shorter than anterior margin; 10-flagellomered antenna; malar sulcus perpendicular to proximal mandibular margin; eyes far from anterior margin of head, covering the gena; pronotal disc not depressed forward in lateral view, wider than long in dorsal view; forewing with two closed cells, 1Cu cell shorter than R cell and 1cu-a oriented posterad; notauli present; mesoscutum shorter than mesoscutellum; metapectal-propodeal disc transversely rectangular with metapleural and transverse posterior carinae, lateral margins converging posteriorly and small elliptical propodeal spiracle.

This genus shows a head shape in dorsal view similar with the new genus C because the anterior margin wider than posterior, the forewing with r-rs&Rsc vein complete is a similarity shared with *Pararhabdepyris*, *Prorops*, *Plastanoxus*, *Alloplastanoxus*, *Proplastanoxus*, New genera A, C, D and F.

New Genus E sp. nov. 07

Fig. 15. A-E

Description, female. – Body length 1.98 mm. LFW 1.07 mm. LH 0.46 mm. WH 0.45 mm. WF 0.23 mm. HE 0.23 mm. WOT 0.12 mm. OOL 0.11 mm. WH 0.97× LH; WF

0.52× WH; WF 1.0× HE; OOL 0.88× WOT. Head subgloboid in lateral view. Malar space inconspicuous. Malar sulcus present. Clypeus median clypeal lobe as long as lateral ones, median clypeal lobe truncate, lobes not delimited by emarginations, median lobe anterior margin not angled in anterior view. Head lateral margin convex. Mandibular upper margin not denticulate, basal intercondylar lobe present. Hypostomal carina not emarginate medially. Antenna, with ten flagellomeres 10, pedicel as long as last flagellomere. Frontal line present. Eyes setose, elliptical in full view, contour not protruding. Ocellar triangle anterior angle right or nearly so. VOL shorter than HE. Ocellar triangle far from vertex crest, Anterior ocellus located between eyes. Pronotum collar conspicuous, surface not depressed forward. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum medially shorter than scutellum. Notauli straight, subparallel, complete, uniform, posterior convergence faint. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, evenly wide, with lateral deeper subcircular foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior and metapleural carinae; median and posterior carinae connected; lateral margins straight, subparallel. Metapleural carina outlining propodeal spiracle. Mesotibia without setae like spines. Forewing anterior margin angulated; M+Cu vein tubular; fusion Sc&R1a vein short; stigma short; r-rs&Rsc vein tubular; A vein present; longitudinal fold simple. Forewing proximal venation long, membrane color hyaline to whitish. Mesopleural pit with posterior tubercle or elevation. Subtegular fovea short and isolated, evenly linear, subdivided. Metasomal second segment short, apex orientation downward.

Material examined. Holotype female, MADAGASCAR, Mahajanga Province, Parc National de Namoroka, 16.9km 317°NW Vilanandro, elev. 100m, 12-16 November 2002, 16°24'24"S 45°18'36"E, Coll: Fisher, Griswold et al., Malaise trap, tropical dry forest, CASENT 2103330 (CASC).

New Genus F

Type species. – *New Genus F sp. nov. 08* by present designation.

Description. Female. Body glabrous. Head elongated, subcylindrical. Malar sulcus present. Antenna with seven flagellomeres. Inter-torular space present. Gena visible behind eye in dorsal view. Mandible with two distal teeth. Pronotal collar conspicuous, disc surface depressed forward. Metapectal-propodeal disc polished with transverse anterior, transverse posterior and metapleural carinae; propodeal spiracle circular, visible in lateral position, located below metapleural carina. Forewing with two closed cells, r-rs&Rsc vein tubular, Rs+M vein as stub. Hind wing with three hamuli. **Male.** Unknown.

Remarks. This genus is considered new due to the combination of the following characters: robust body; rectangular head with lateral margins slightly convex; 7-flagellomered antenna; malar sulcus perpendicular to proximal mandibular margin; eyes close to anterior margin, leaving exposed the gena in dorsal view; VOL longer than HE; clypeal lobe anteriorly projected with median lobe separated from lateral lobes by acute emarginations; pronotal disc depressed forward in lateral view and longer than wide in dorsal view; forewing with one closed cell and r-rs&Rsc vein present; notauli absent; metapectal-propodeal disc rugulous to polished with faint median, metapleural and posterior carinae, lateral margins converging posterad; propodeal spiracle small, lateral and rounded.

This genus is similar to *Proplastanoxus* because of the clypeal lobe projected anteriorly; however, the 7-flagellomered antenna is new in Scleroderminae and even in Bethyilidae. The wing venation is similar to that in *Pararhabdepyris* and *Plastanoxus* by the absence of 1Cu cell and to *Israelius* by the widening of Rs&M vein.

New Genus F sp. nov. 08

Fig. 17. F-H, Fig. 18. A-D

Description, female. – Body length 1.99 mm. LFW 1.02 mm. LH 0.42 mm. WH 0.37 mm. WF 0.15 mm. HE 0.14 mm. WOT 0.08 mm. OOL 0.15 mm. WH $0.89\times$ LH; WF $0.42\times$ WH; WF $1.11\times$ HE; OOL $2.0\times$ WOT. Head oval in lateral view, lateral margin straight. Malar space inconspicuous. Malar sulcus present. Clypeus truncate, median clypeal lobe as long as lateral ones with lobe delimitation distinct. Inter-torular space present. Toruli not reaching anterior margin of clypeus. Gena visible behind eye in dorsal view. Mandible robust with two large distal teeth; intercondylar lobe present. Hypostomal carina emarginate medially, not angulate. Antenna with seven flagellomeres, pedicel as long as flagellomere I. Eyes elliptical in full view, setose with contour not protruding. Ocellar triangle anterior angle acute. VOL longer than HE. Ocellar triangle close to vertex crest. Ocellus far from imaginary line between eyes. Pronotum collar conspicuous, disc surface depressed forward. Prosternum small. Mesoscutum medially subequal than scutellum. Scutellar apex widely rounded. Scutellar process inconspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc polished with transverse anterior, transverse posterior and metapleural carinae, lateral margins convex, subparallel. Propodeal spiracle circular, visible in lateral position, located below metapleural carina. Metapectal-propodeal declivity with median carina. Forewing anterior margin angulated; M+Cu vein type tubular, complete; fusion Sc&R1a vein short; stigma short; r-rs&Rsc vein tubular; Rs+M vein present; A vein present; 1cu-a vein inconspicuous, directed anterior-posteriorly; 1Cu cell shorter than R cell, longitudinal fold simple; proximal venation long; membrane hyaline to whitish. Hind wing with three hamuli irregularly spaced. Mesopleural pit conspicuous. Subtegular fovea long, evenly linear, anterior segment U shaped like in *Cephalonomia*, subdivided. Metasomal second segment short. Metasomal apex directed downward.

Material examined. Holotype female, MADAGASCAR, Antsiranan,. Rés. Analameranana, 28.4km, 99° Anivorano-Nord, elev. 60 m, 5 December 2004, 12° 44'48"S 49° 29'41"E, Coll: B.L. Fisher, sifted litter (leaf, mold, rotten wood) tropical dry forest, CASENT 2089809 (CASC).

Allobethylus sp. nov. 09

Fig. 18. E-H

Description, female. – Body length 3.70 mm. LFW 2.04 mm. LH 0.92 mm. WH 0.62 mm. WF 0.32 mm. HE 0.28 mm. WOT 0.12 mm. OOL 0.38 mm. WH $0.67\times$ LH; WF $0.53\times$ WH; WF $1.17\times$ HE; OOL $3.13\times$ WOT. Head depressed in lateral view, with lateral margin straight. Malar space short or inconspicuous. Malar sulcus absent. Clypeus truncate, median clypeal lobe longer than lateral ones, lobe delimitation not distinct, median lobe anterior margin shape (anterior view) not angled, clypeal carina absent. Inter-torular space absent or nearly so. Toruli covering anterior clypeal margin. Frontal process absent. Gena visible behind eye in dorsal view, at least partially. Mandible slender with four large distal teeth, upper margin not denticulate, basal intercondylar lobe present. Hypostomal carina emarginate but not angulate medially. Antenna with 11 flagellomeres, pedicel as long as distal flagellomere. Frontal line present. Eye subtriangular in full view. Eye contour not protruding. Eyes with distinct setae longer than ommatidium. Ocellar triangle with frontal angle right or nearly so. VOL longer than HE or at least as long as eye in dorsal view. Ocellar triangle far from vertex crest by more than basal width WOT.

Ocellus separated from imaginary line of eye top. Occipital carina present. Pronotal collar conspicuous, pronotal surface not depressed forward. Propleural epicoxal sulcus present, propleural neck and anterior angles not visible in dorsal view. Prosternum small. Mesoscutum medially shorter than scutellum. Notauli complete, straight, wider anteriorly. Scutellar apex sharp. Scutellar process conspicuous, continuous, evenly wide, evenly depth, with lateral linear foveae. Metanotum inter-flap space wide. Metapectal-propodeal disc flat with prevailing basal cuticular micro-sculpture rugulose; transverse anterior, transverse posterior and metapleural carinae present; lateral margins straight, subparallel; metapleural carina outlining propodeal spiracle. Propodeal spiracle dorsal, elliptical located above metapleural carina. Metapectal-propodeal pleural posterolateral angle angulate. Metapectal-propodeal declivity without median carina. Mesotibia without thick setae like spines. Forewing anterior margin straight; C vein present; M+Cu vein tubular, complete; R₅₊₆ vein complete; Sc+R_{1a} vein longer than wide; stigma short; r-rs+R₅₊₆ vein tubular; A vein present; 1cu-a vein long, straight, oriented posteriorly; 1Cu cell shorter than R cell; longitudinal fold forked distally, proximal venation reaching more than 0.25x of forewing total length. Forewing color infusate yellow to brown. Hind wing with four hamuli irregularly spaced. Mesopleuron without prepectal carina or groove. Mesopleural pit conspicuous, displaced posterodorsally. Upper mesopleural fovea anteriorly open. Subtegular fovea evenly linear, simple, short, isolated. Metasoma with second segment short, metasomal apex oriented downward.

Material examined. Holotype female, New Hebrides {=Republic of Vanuatu}, Shepherd Group, Tongariki I, 0-300 m, 29.VIII.1979 (BPBM).

Remarks. This species is considered new due to the combination of the following characters: head elongated with lateral margins straight; VOL almost twice the HE; eyes small and subrounded; median clypeal lobe transverse rectangular without teeth; mandible with four apical teeth and dorsal margin diminutively toothed; mandible elongated reaching the opposite proximal mandibular margin; pronotal anterior margin straight and strongly angulated with the collar, disc elongated and trapezoidal in dorsal view; notauli evenly narrow; forewing with 1Cu cell shorter than R cell, r-rs+R₅₊₆ vein present and tubular; metapectal-propodeal disc with lateral margins straight.

The species is similar to *A. korystus* from Thailand but differs in several features like clypeus shape, clypeal tooth presence, head shape, head margins, pronotal crest presence.

Alloplastanoxus sp. nov. 10

Fig. 19. A-E

Description, female. – Body length 1.80 mm. LFW 1.07 mm. LH 0.40 mm. WH 0.37 mm. WF 0.22 mm. HE 0.17 mm. WOT 0.11 mm. OOL 0.14 mm. WH 0.92× LH; WF 0.58× WH; WF 1.27× HE; OOL 1.29× WOT. Head depressed in lateral view, lateral margin convex. Malar space inconspicuous. Malar sulcus present. Clypeus median lobe truncate, median clypeal lobe longer than lateral ones, lobe delimitation not distinct, median lobe not angled in anterior view. Clypeal carina absent. Inter-totular space absent or nearly so. Toruli not covering anterior clypeal margin. Frontal process absent. Gena not visible behind eye in dorsal view. Mandible slender with three small or inconspicuous distal teeth, Mandibular upper margin not denticulate, with basal intercondylar lobe. Hypostomal carina emarginate, angulate medially. Antenna with 10 flagellomeres, pedicel as long as distal flagellomere. Frontal line present. Eye subtriangular in full view. Eye contour protruding slightly. Eyes glabrous. Ocular triangle anterior angle obtuse. VOL shorter than HE in dorsal view. Ocular triangle close to vertex crest (separated by about one ocular triangle length). Anterior ocellus separated from imaginary line of eye top. Occipital carina absent. Pronotal collar conspicuous. Pronotal surface not depressed

forward, median line (carina or groove) absent. Propleural epicoxal sulcus absent, propleural neck and anterior angles not visible in dorsal view. Prosternum small. Mesonotum divided into mesocutum and mesoscutellum. Mesoscutum medially shorter than scutellum. Notauli complete, concave laterad, uniform width with strong posterior convergence. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, evenly wide, evenly depth, with lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior and metapleural discal carinae; median and posterior carinae connected; basal micro-sculpture polished; lateral margins straight, strongly convergent posteriorly; metapleural carina outlining propodeal spiracle. Propodeal spiracle lateral, circular, located below metapleural carina. Metapectal-propodeal complex pleuron posterolaterally rounded. Forewing anterior margin angulated or conspicuously curve near prostigma; M+Cu vein tubular, complete; Rsa&M vein complete; Sc&R1a vein longer than wide; stigma size short; r-rs&Rsc vein complete, tubular; A vein present; 1cu-a vein present, length inconspicuous, straight, oriented proximally; 1Cu cell shorter than R cell; longitudinal fold distally simple or inconspicuous; proximal venation reaching more than 0.25x of wing total length, color hyaline to whitish. Hind wing with three hamuli irregularly spaced. Mesopleural pit conspicuous, central, with posterior tubercle or elevation. Subtegular fovea long, connected with episternal groove, widened at least anteriorly and subdivided. Metasomal second segment short, apical segments oriented downward.

Material examined. Holotype female, MADAGASCAR, Mahajanga Prov., Parc National Tsingy de Bemaraha, 3.4 km 93°E Bekopaka Tombeau Vazimba, Elev. 50m, 6-10 Nov. 2001. 19°8'31"S 44°49'41"E. California Acad. of Sciences. Coll. Fisher. Griswold et al., Malaise trap, in tropical dry forest, CASENT 2116531 (CASC).

Remarks. This is the second species of this genus. It differs *A. unexpectatus* by having the quadrate head; VOL shorter than HE; antenna light testaceous and body dark brown, whereas *A. unexpectatus* bears elongated black head; VOL longer than HE; antennal proximal half yellow and apical half dark testaceous and body black with legs light yellow.

In the original description Terayama (2006) listed the absence of basal vein (Rs&M) which is in fact present and the presence of costa (C vein) that is absent in the specimen observed and identified as *A. unexpectatus* in the present study.

Alloplastanoxus sp. nov. 11

Fig. 19. F-H, Fig. 20. A-B

Description, female. – Body length 1.94 mm. LFW 1.19 mm. LH 0.38 mm. WH 0.38 mm. WF 0.23 mm. HE 0.17 mm. WOT 0.11 mm. OOL 0.15 mm. WH 1.0× LH; WF 0.60× WH; WF 1.36× HE; OOL 1.43× WOT. Head depressed in lateral view, with lateral margin convex. Malar space inconspicuous. Malar sulcus present. Clypeus truncate, median clypeal lobe longer than lateral ones, lobe delimitation not distinct, median lobe anterior margin shape not angled in anterior view, clypeal carina absent. Inter-totular space absent. Toruli covering anterior clypeal margin. Gena not visible behind eye in dorsal view. Mandible slender with three small distal teeth, Mandibular upper margin not denticulate. Hypostomal carina emarginate, angulate medially. Antenna with 10 of flagellomeres, pedicel as long as distal flagellomere. Eye elliptical in full view, contour protruding slightly. Eyes glabrous. Ocular triangle with anterior angle right or nearly so. VOL shorter than HE. Ocular triangle from vertex close to vertex crest. Anterior oculus separated form imaginary line of eye top. Pronotal collar conspicuous, surface depressed forward. Prosternum small. Mesoscutum medially shorter than scutellum. Notauli

complete, straight, width uniform, strongly convergent posteriorly. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotum inter-flap space wide. Metapectal-propodeal disc polished with transverse anterior, metapostnotal median, transverse posterior and metapleural carinae; median and posterior carinae joining present; lateral margins convex; metapleural carina outlining propodeal spiracle. Propodeal spiracle circular, lateral, located below carina. Metapectal-propodeal pleura posterolaterally rounded. Forewing anterior margin angulated or conspicuously curve near prostigma. Forewing with M+Cu vein complete, tubular; Rsa&M vein complete; Sc&R1a vein longer than wide; stigma short, r-rs&Rsc vein complete, tubular; A vein present; 1cu-a vein short, oriented proximally; 1Cu cell shorter than R cell; longitudinal fold distally simple; proximal venation reaching more than 0.25x of FW total length, membrane color hyaline to whitish. Hind wing with three hamuli irregularly spaced. Mesopleural pit conspicuous, central with posterior tubercle or elevation. Subtegular fovea, long, simple, widened anteriorly, connected with episternal groove. Metasomal second segment short, apical segments oriented downward.

Material examined. Holotype female, BRAZIL, Brasília, D.F., Reserva Ecológica do IBGE, 15°55'58"S 47°51'02"W, 18-25.VII.1980, Campo limpo, janela, Col. B.F.S. Dias e outros (IBGE).

Remarks. This is the third species of this genus. It differs *A. unexpectatus* by having the quadrate head; VOL shorter than HE; antenna yellow and body brown with legs tectaceous, whereas *A. unexpectatus* bears elongated black head; VOL longer than HE; antennal proximal half yellow and apical half dark testaceous and body black with legs light yellow.

Discleroderma sp. nov. 12

Fig. 20. C-H

Description, female. – Body length 2.74 mm. LFW 1.19 mm. LH 0.48 mm. WH 0.48 mm. WF 0.29 mm. HE 0.22 mm. WOT 0.12 mm. OOL 0.14 mm. WH 1.0× LH; WF 0.61× WH; WF 1.36× HE; OOL 1.13× WOT. Head globoid in lateral view, lateral margin convex. Malar space about as long as proximal mandibular width. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct, anterior margin angled in anterior view. Clypeal carina present. Clypeus with two parallel carinae along margin in anterior view. Gena visible behind eye in dorsal view. Mandible robust with two large distal teeth, Mandibular upper margin not denticulate, basal intercondylar lobe present. Hypostomal carina emarginate, not angulate medially. Antenna with 11 flagellomeres, pedicel as long as flagellomere I. Eye rounded in full view, glabrous, contour not protruding. Ocular triangle anterior angle acute. VOL shorter than HE. Ocular triangle far from vertex crest by more than one time WOT, anterior ocellus anterad to imaginary line of eye top. Pronotal collar inconspicuous, surface depressed forward. Prosternum small. Mesoscutum medially subequal than scutellum. Scutellar apex sharp. Scutellar process conspicuous, continuous, evenly wide, evenly depth, with lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior, first metapostnotal and metapleural carinae; lateral margins straight, subparallel; metapleural carina not outlining propodeal spiracle. Propodeal spiracle elliptical located dorsally above metapleural carina. Metapectal-propodeal complex pleural anterior dorso-ventral concavity present. Metapectal-propodeal pleura posterolaterally angulate. Mesotibia with thick setae like spines. Forewing anterior margin straight. Forewing with M+Cu vein complete, tubular; Rsa&M vein complete;

Sc&R1a vein longer than wide; stigma short; Cua vein present; A vein present; 1cu-a vein conspicuously long, orientated distally; 1Cu cell subequal than R cell; longitudinal fold distally forked; proximal venation long, membrane color hyaline to whitish. Hind wing with three hamuli irregularly spaced. Mesopleural prepectal carina, depression faint. Mesopleural pit displaced posterodorsally. Subtegular fovea simple, short, isolated, evenly linear. Metasomal segment II short, paired short blunt tubercles on tergites IV and V and metasomal ventral surface strongly convex with segments VI-VIII oriented upward.

Material examined. Holotype female, INDONESIA, Nceram, 9 km E Wahai, nr PHPA-Q coastal rainforest, 28.II-21.III.1997, Mal. trap 6, C. v. Achterberg & R. de Vries (RMNH).

Remarks. This species is considered new due to the combination of the following characters: small size of body; head subrounded in dorsal view; eye covering the gena; notauli absent; parapsidal lines complete; propodeal declivity without median carina and short and blunt metasomal processes on terga IV-V.

Discleroderma sp. nov. 13

Fig. 21. A-E

Description, female. – Body length 4.26 mm. LFW 1.99 mm. LH 0.65 mm. WH 0.71 mm. WF 0.38 mm. HE 0.31 mm. WOT 0.14 mm. OOL 0.20 mm. WH 1.10× LH; WF 0.54× WH; WF 1.25× HE; OOL 1.44× WOT. Head in globoid in lateral view, lateral margins convex. Malar space about as long as proximal mandibular width. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct, angled medially in anterior view, clypeal carina present. Clypeus in anterior view with two parallel carinae along margin. Toruli not reaching anterior clypeal margin absent. Gena visible behind eye in dorsal view. Mandible robust with two large distal teeth, upper margin not denticulate, basal intercondylar lobe present. Hypostomal carina emarginate, not angulate medially. Antenna with 11 flagellomeres, pedicel as long as flagellomere I. Frontal line present. Eye rounded in full view, setose with contour not protruding. Ocular triangle anterior angle acute. VOL shorter than HE. Ocular triangle close to vertex crest. Anterior ocellus anterad to imaginary line between eyes top. Occipital carina present. Pronotal collar inconspicuous. Pronotal disc surface depressed forward. Prosternum small. Mesoscutum medially subequal than scutellum. Scutellar apex sharp. Scutellar process conspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior, first metapostnotal and metapleural carinae, median and posterior carinae connected; lateral margins convex; metapleural carina not outlining propodeal spiracle. Propodeal spiracle dorsal, elliptical, located above metapleural carina. Metapectal-propodeal pleura posterolaterally angulate. Mesotibia pilosity with thick setae like spines. Forewing anterior margin straight. Forewing M+Cu vein complete, tubular; Rsa&M vein complete; Sc&R1a vein longer than wide; stigma short; Cua vein present; A vein present, 1cu-a vein conspicuously long, oriented distally; 1Cu subequal then R cell; longitudinal fold distally forked; proximal cells long; membrane color infusate yellow to brown. Hind wing with three hamuli, irregularly spaced. Mesopleuron prepectal carina present. Mesopleural pit conspicuous, central. Subtegular fovea short, isolated, evenly linear, simple. Metasomal segment II short, paired flat modifications on terga III, paired short spine-like tubercles on terga IV - V, metasomal ventral surface slightly convex with segments VI-VIII oriented upward.

Variations. Measurements of paratype: body length 4.15 mm. LFW 1.97 mm. LH 0.72 mm. WH 0.72 mm. WF 0.38 mm. HE 0.31 mm. WOT 0.15 mm. OOL 0.18 mm. WH 1.0× LH; WF 0.53× WH; WF 1.25× HE; OOL 1.20× WOT.

Material examined. Holotype female, THAILAND, Nakhon, Ratchasima Khao Yai NP, Moist evergreen forest at Dan Chang, 14°28.285'N 101°22.570'E, 751m, Malaise trap, 5-12.xii.2006, Wirat Sook kho leg. T1304 (QSBG). Paratype: 1 female, same locality T1305 (QSBG).

Remarks. This species is considered new due to the combination of the following characters: large size of body; head trapezoidal in dorsal view; eyes leaving exposed the gena; notauli absent; parapsidal lines complete; propodeal declivity without median carina and paired metasomal flat modifications on tergum III and paired short and acute processes on terga IV-V.

Discleroderma sp. nov. 14

Fig. 21. F-H, Fig. 22. A-B

Description, female. – Body length 4.41 mm. LFW 2.36 mm. LH 0.74 mm. WH 0.74 mm. WF 0.35 mm. HE 0.31 mm. WOT 0.15 mm. OOL 0.20 mm. WH 1.0× LH; WF 0.48× WH; WF 1.15× HE; OOL 1.30× WOT. Head shape globoid in lateral view. Head lateral margin convex. Malar space about as long as proximal mandibular width. Malar sulcus absent. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct, median lobe anterior margin angled in anterior view. Clypeal carina present. Clypeus in anterior view with two parallel carinae along margin. Gena visible behind eye in dorsal view. Mandible robust with two large distal teeth. Mandibular upper margin not denticulate. Mandible basal intercondylar lobe present. Hypostomal carina emarginate but not angulate medially. Antenna with 11 flagellomeres, pedicel as long as distal flagellomere. Frontal line present. Eye glabrous, rounded in full view, contour not protruding. Ocular triangle anterior angle acute. VOL shorter than HE. Ocular triangle far from vertex crest by more than 1x WOT. Anterior ocellus anterad to imaginary line of eyes top. Occipital carina present. Pronotal collar inconspicuous, disc surface depressed forward. Propleural epicoxal sulcus present. Prosternum size small. Mesoscutum median length subequal than scutellum. Notauli complete, S-shaped, evenly wide, faint posterior convergence. Scutellar apex sharp. Scutellar process conspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotum inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior, first metapostnotal, paraspicular and metapleural carinae, median and posterior carinae connected; lateral margins convex; metapleural carina not outlining propodeal spiracle. Spiracle elliptical, located dorsally above metapleural carina. Metapectal-propodeal pleura with anterior transverse uniform concavity, angulate posterolaterally. Mesotibia with thick setae. Forewing anterior margin straight. Forewing with M+Cu vein complete, tubular, Rsa&M vein complete, Sc&R1a vein longer than wide, stigma short, Cua vein present, A vein present, 1cu-a vein long oriented distally, strongly convex, 1Cu subequal then R cell, longitudinal fold distally forked, proximal venation long. Hind wing with three hamuli irregularly spaced. Mesopleural prepectal carina present. Mesopleural pit conspicuous, central. Subtegular fovea short, isolated, evenly linear, simple. Metasomal ventral segment II short, paired flat modifications connected medially on tergite III, paired long spine-like tubercles on tergites IV and V, metasomal ventral surface slightly convex with segments VI-VIII strongly oriented upward.

Material examined. Holotype female, THAILAND, Phetchabun, Khao Kho NP, Mix deciduous near office, 16°39.479'N 101°08.105'E, 260m, Malaise trap, 5-12.ii.2007, Somchai Chachumnan & Saink Singtong leg., T1600 (QSBG).

Remarks. This species is considered new due to the combination of the following characters: large body size; head subquadrate in dorsal view; eyes leaving exposed the gena; occipital carina present; notauli present; parapsidal lines incomplete and paired metasomal acute modifications on tergum III and paired long and acute processes on terga IV-V.

Glenosema sp. nov. 15

Fig. 22. C-H

Description, male. – Body length 1.32 – 1.85 mm. LH 0.37 mm. WH 0.31 mm. WF 0.20 mm. HE 0.09 mm. WOT 0.05 mm. OOL 0.17 mm. WH $0.83 \times$ LH; WF $0.65 \times$ WH; WF $2.17 \times$ HE; OOL $3.67 \times$ WOT. Head oval in lateral view, lateral margin convex. Malar space absent. Median clypeal lobe longer than lateral ones, shape of median clypeal lobe truncate with delimitation distinct, anterior margin (anterior view) not angled, clypeal carina absent. Inter-torular space absent or nearly so. Torulus covering anterior clypeal margin or nearly so. Gena not visible behind eye in dorsal view. Mandible slender with five large distal teeth, upper margin not denticulate, basal intercondylar lobe present. Hypostomal carina emarginate medially, not angulate. Antenna with 11 flagellomeres, pedicel as long as flagellomere I. Eye rounded in full view, glabrous, contour protruding slightly. Ocular triangle with anterior angle acute. VOL longer than HE. Posterior ocelli far from vertex crest, anterior ocellus separated from imaginary line of eye top. Occipital carina present. Pronotum with conspicuous collar, disc surface depressed forward. Propleuron with epicoxal sulcus. Mesoscutellum not divided into scutum and scutellum. Scutellar apex widely rounded. Scutellar process absent. Metanotal inter-flap space wide. Metapectal-propodeal disc polished with lateral margins subparallel. Propodeal spiracle circular, lateral. Metapectal-propodeal pleura without posterolateral carina or angulation. Wings absent. Metasomal segment II short, apex orientated downward. Hypopygium rhomboid, median stalk short, $1.0 \times$ as long as plate, lateral stalk absent, anterior margin angled, posterior and lateral margin angled between them, lateral margins converging posterad. Genitalia longer than wide. Paramere deeply divided in two lobes subequal in length, dorsal slender lobe, ventral wide lobe with apical margin rounded. Cuspis bifid, dorsal arms wide, progressively slightly narrowing apicad, apex rounded, ventral arm as short as stub. Digitus small, distally sharpening, upper margin denticulate. Basiparamere and basivolsella widely separated. Aedeagus bottle-shaped, swollen, apex not surpassing paramere apex, with subapical constriction, apex rounded. Genital ring elliptical. Basal ring small, subcircular.

Material examined. Holotype male, [FRANCE], F-46-CAHORS, 26-IX., Col. Tussac UQIC material, No. ENT 13.39. SP.G1e.2 (UQIC). Paratype: 1 male, same locality (UQIC).

Remarks. This species is considered new due to the combination of the following characters: body colour yellow to light brown; oblong head; eye contour projected; aptery; mandibular dorsal margin not toothed; occipital carina absent and scutellar process absent.

Israelius sp. nov. 16

Fig. 23. A-F

Description, female. – Body length 2.14 mm. LFW 1.09 mm. LH 0.42 mm. WH 0.34 mm. WF 0.20 mm. HE 0.15 mm. WOT 0.09 mm. OOL 0.18 mm. WH $0.81 \times$ LH; WF $0.59 \times$ WH; WF $1.30 \times$ HE; OOL $2.0 \times$ WOT. Malar space short or inconspicuous. Malar sulcus absent. Median clypeal lobe truncate, longer than lateral ones, lobe delimitation not distinct, median lobe anterior margin not angled in anterior view. Toruli not reaching anterior clypeal margin. Head oval in lateral view, lateral margin straight. Gena not visible behind eye in dorsal view. Mandible robust with three large distal teeth. Mandibular upper margin not denticulate. Hypostomal carina emarginate and angulate medially. Antenna 10 flagellomeres and pedicel as long as flagellomere I. Eyes elliptical in full view and setose with contour not protruding. Ocular triangle anterior angle right or nearly so. VOL longer than HE or at least as long as eye in dorsal view. Ocular triangle close to vertex crest. Anterior oculus separated from imaginary line between eyes top. Occipital carina absent. Pronotal collar conspicuous and disc surface depressed forward. Prosternum large and rhomboid. Mesoscutum median length subequal than scutellum. Scutellar apex widely rounded. Scutellar process conspicuous, continuous, evenly wide, evenly depth. Metanotum inter-flap space wide. Metapectal-propodeal disc flat, polished, lateral margins subparallel. Metapectal-propodeal pleura posterolateral corner rounded. Metapectal-propodeal dorso-lateral angle outlining propodeal spiracle. Propodeal spiracle lateral, circular. Forewing anterior margin angulated. Forewing M+Cu vein complete, tubular; Rsa&M vein complete, abruptly widened at Rsa segment; Sc&R1a vein longer than wide; r-rs segment tubular; Rs+M vein angled; A vein present; 1cu-a vein short, oriented antero-posteriorly; 1Cu cell shorter than R cell; longitudinal fold distally simple; proximal venation reaching more than $0.25 \times$ of forewing total length, membrane color hyaline to whitish. Hind wing with three hamuli evenly spaced. Subtegular fovea widened anteriorly, short, isolated, simple. Metasomal second segment short, apical segments oriented downward.

Material examined. Holotype female, UNITED ARAB EMIRATES, Al-Ajban, 24.36N 55.01E, 12-19.09.2006, light trap. A. van Harten (UFES).

Remarks. This species is considered new due to the combination of the following characters: head rectangular and elongated; VOL almost twice the HE; body colour brown; antenna and legs yellow; pronotal disc as long as wide; r-rs vein segment present and tubular; Rs&M widened at M segment but not conspicuously angulated so Rs+M appears inconspicuous.

Israelius sp. nov. 17

Fig. 24. G-H, Fig. 25. A-B

Description, female. – Body length 2.25 mm. LFW 1.45 mm. LH 0.52 mm. WH 0.37 mm. WF 0.22 mm. HE 0.58 mm. WOT 0.09 mm. OOL 0.22 mm. WH $0.71 \times$ LH; WF $0.60 \times$ WH; WF $1.36 \times$ HE; OOL $2.33 \times$ WOT. Head depressed in lateral view. Head lateral margin straight. Malar space short. Malar sulcus present. Clypeal median truncate, as long as lateral ones, lobe delimitation not distinct. Toruli covering anterior clypeal margin. Gena visible behind eye in dorsal view. Mandible robust with two large distal teeth, basal intercondylar lobe. Hypostomal carina emarginate, not angulate medially. Antenna with 10 flagellomeres, pedicel as long as distal flagellomere. Eye subtriangular in full view, setose with contour not protruding. Ocular triangle with anterior angle right or nearly so. VOL longer than HE or at least as long as eye in dorsal view. Ocular triangle close to vertex crest. Oculus posteriorly separated from imaginary line between eyes top. Pronotal collar conspicuous. Propleural anterior angles visible in dorsal view. Prosternum small. Mesoscutum medially shorter than scutellum. Scutellar apex widely rounded. Metanotum inter-flap space wide. Metapectal-propodeal disc flat, polished. Propodeal spiracle lateral,

circular, located below dorso-lateral angle. Metapectal-propodeal pleural posterior-lateral angle rounded. metapectal-propodeal disc lateral margins subparallel. Forewing anterior margin angulated. Forewing venation M+Cu vein complete, tubular; Rsa&M vein complete, abruptly widened at Rsc segment; Sc&R1a vein wider than long; r-rs&Rsc vein nebulous; Rs+M vein present; A vein present; 1cu-a vein present; inconspicuous and oriented antero-posteriorly; longitudinal fold simple or inconspicuous; proximal venation reaching more than 0.25x of forewing total length and membrane color infusate yellow to brown. Hind wing with three hamuli irregularly spaced. Subtegular fovea short, isolated, evenly linear and subdivided with anterior segment U shaped. Metasomal segment II short and apical segments oriented downward.

Material examined. Holotype female, SOUTH AFRICA, W. Cape, Koeberg Nature Reserve, 33°37.622'S 18°24.259'E, 17 April - 15 May 1998, S van Noort, Malaise trap, KO97 - M32, West Coast Strandveld (ISAM). Paratypes: SOUTH AFRICA, W. Cape, 1 female, West Coast Fossil Park, (5.5km 270° W Langebaanweg), 32°58.156'S 18°05.878'E, 11-18 Sept 2002, S van Noort, Malaise trap, LW02-R3-M26, Rehabilitated mine dump (ISAM); 1 female, Langeberg Farm, (3 km 270°W. Langebaanweg) 32°58.461'S 18°07.344'E, 20-27 Nov 2002, S. van Noort, Malaise trap, LW02-N2-M143, Sand Plain Fynbos (ISAM).

Remarks. This species is considered new due to the combination of the following characters: head rectangular and elongated; VOL twice the HE; body colour black; antenna testaceous; pronotal disc longer than wide; Rsc vein segment spectral to nebulous; Rs&M widened and angulated at M segment so Rs+M appears conspicuous; 1cu-a conspicuous.

Israelius sp. nov. 18

Fig. 25. C-F

Description, female. – Body length 1.82 mm. LFW 1.14 mm. LH 0.42 mm. WH 0.28 mm. WF 0.14 mm. HE 0.14 mm. WOT 0.06 mm. OOL 0.22 mm. WH 0.67× LH; WF 0.50× WH; WF 1.0× HE; OOL 3.50× WOT. Head depressed in lateral view. Head lateral margin straight. Malar space short. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct. Toruli covering anterior clypeal margin or nearly so. Gena not visible behind eye in dorsal view. Mandible robust with three distal teeth. Hypostomal carina emarginate medially, not angulate. Antenna with 10 flagellomeres, pedicel as long as distal flagellomere. Eyes rounded in full view, setose with contour not protruding. Ocular triangle anterior angle obtuse. VOL longer than HE or at least as long as eye in dorsal view. Ocular triangle close to vertex crest. Pronotum collar conspicuous. Pronotal surface depressed forward. Prosternum small. Mesoscutum medially subequal than scutellum. Scutellar apex shape widely rounded. Metanotal inter-flap space wide. Metapectal-propodeal disc flat, polished; lateral margins subparallel, strongly convergent posteriorly. Spiracle circular, lateral outlined by metapleural lateral margin. Metapectal-propodeal pleura posterolateral corner rounded. Forewing anterior margin angulated. Forewing with M+Cu vein complete, tubular; M+Cu vein complete; Rsa&M complete, abruptly widened at Rsa segment; Sc&R1a vein longer than wide; stigma short; r-rs&Rsc vein with r-rs spectral, Rsc tubular; Rs+M vein present; A vein present; 1cu-a vein inconspicuous, oriented antero-posteriorly; 1Cu cell shorter than R cell; longitudinal fold simple or inconspicuous; proximal venation reaching more than 0.25x of forewing total length, membrane color hyaline to whitish. Hind wing with three hamuli evenly spaced. Mesopleural pit conspicuous, central. Subtegular fovea short, simple, isolated, evenly linear with anterior segment U shaped. Metasoma second segment size short, apical segments oriented downward.

Material examined. Holotype female, MADAGASCAR, Province of d'Antsiranana, Orangea, 3 km E of Ramena near fort., elev. 65m, 23-27 Jan 2001, 12°14'49"S 49°22'17"E, M.E. Irwin, E.I. Schinger & R. Harin'Hara collectors, Malaise trap, littoral forest on sand, MA-01-05-02, CASN 2103138 (CASC).

Remarks. This species is considered new due to the combination of the following characters: head rectangular, elongated and with lateral margins diverging anteriorly; VOL more than twice the HE; body colour dark brown; antenna yellow to light testaceous; pronotal disc longer than wide; Rsc vein apical segment nebulous; Rs&M widened and angulated at M segment so Rs+M appears conspicuous; 1cu-a inconspicuous.

***Megaprosternum longiceps* Azevedo, 2006**

Fig. 29. E-H

Description, female. – Body length 4.63 mm. LFW 2.58 mm. LH 0.92 mm. WH 0.51 mm. WF 0.25 mm. HE 0.26 mm. WOT 0.12 mm. OOL 0.51 mm. WH $0.55 \times$ LH; WF $0.48 \times$ WH; WF $0.94 \times$ HE; OOL $4.13 \times$ WOT. Head depressed in lateral view. Head lateral margin straight. Malar space short. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct. Toruli covering anterior clypeal margin or nearly so. Gena not visible behind eye in dorsal view. Mandible slender with three large distal teeth, upper margin not denticulate, intercondylar lobe present. Hypostomal carina emarginate, not angulate medially. Antenna with 11 flagellomeres, pedicel as long as flagellomere I. Frontal line present. Eye subtriangular in full view, setose with contour not protruding. Ocular triangle anterior angle acute. VOL longer than HE or at least as long as eye in dorsal view. Ocular triangle close to vertex crest. Anterior ocellus posteriorly separated from imaginary line between eyes top. Pronotal collar inconspicuous. Pronotal disc depressed forward. Propleural neck and anterior angles visible in dorsal view. Prosternum large, pentagonal. Propleural sternal inner margins extending posteriorly beyond half length of prosternum. Mesoscutum medially longer than scutellum. Scutellar apex widely rounded. Metanotum inter-flap space wide. Metapectal-propodeal disc flat, polished with lateral margins strongly convergent posteriorly. Propodeal spiracle circular, lateral. Metapectal-propodeal pleura posterolateral corner rounded. Forewing with anterior margin angulated; Sc&R1a vein wider than long; stigma short; longitudinal fold simple; proximal venation reaching at most 0.2x of forewing total length, membrane color infusate yellow to brown. Hind wing with four hamuli evenly spaced. Mesopleural pit conspicuous, central. Upper mesopleural fovea open. Subtegular fovea simple, long, evenly linear, connected with episternal groove. Metasomal second segment short, apical segments orientated downward.

Material examined. Female, FIJI, Viti-levu, Navai-Nasonga, trail IX/12/[19]38, Tholo North, summit 3400', In dead Cyahea fronds, EC Zimmerman collection (BPBM).

Remarks. This specimen is identified as *M. longiceps* due to head about 1.8x as long as wide, rectangular, sides subparallel; ocelli nearly touching one another.

***Megaprosternum* sp. nov. 19**

Fig. 24. G-H, Fig. 25. A-C

Description, female. – Body length 1.51 mm. LFW 0.85 mm. LH 0.32 mm. WH 0.26 mm. WF 0.18 mm. HE 0.11 mm. WOT 0.08 mm. OOL 0.14 mm. WH $0.81 \times$ LH; WF $0.71 \times$ WH; WF $1.71 \times$ HE; OOL $1.80 \times$ WOT. Head shape in lateral view oval. Head lateral margin straight. Malar space about as long as proximal mandibular width. Malar sulcus present. Median clypeal lobe truncate, longer than lateral ones, lobe delimitation

not distinct. Toruli widely separated, covering anterior clypeal margin. Gena not visible behind eye in dorsal view. Mandible slender with four small distal teeth, upper margin not denticulate. Hypostomal carina emarginate, not angulate medially. Antenna with 10 flagellomeres with pedicel as long as flagellomere I. Eye glabrous, elliptical in full view, slightly protruding. Ocular triangle anterior angle obtuse. VOL longer than HE or at least as long as eye in dorsal view. Ocular triangle close to vertex crest. Anterior oculus anterad to imaginary line between anterior eyes margin. Pronotal collar inconspicuous, disc depressed forward. Propleural neck and anterior angles visible in dorsal view. Prosternum large, pentagonal. Propleural sternal inner margins extending posteriorly beyond half length of prosternum. Mesoscutum medially subequal than scutellum. Scutellar apex widely rounded. Metanotal inter-flap space wide. Metapectal-propodeal disc flat, polished with transverse anterior, metapostnotal median and metapleural carinae; lateral margins straight, strongly convergent posteriorly. Propodeal spiracle lateral, circular located below metapleural carina. Metapectal-propodeal pleura posterolateral corner rounded. Forewing anterior margin angulated; Sc+R vein present; Sc&R1a vein inconspicuous; stigma short; longitudinal fold simple; proximal venation reaching more than 0.25x of forewing total length, membrane color hyaline to whitish. Hind wing with three hamuli evenly spaced. Mesopleural pit conspicuous, central. Metasomal second segment short, apical segments oriented downward. **Male.** Head sides convex.

Material examined. Holotype female, Tinian, I[slas] Marianas, Mt. Lasso NW slope, 17:III:[19]45, Col. & press. by Henry S. Dybas Lot 864 (BPBM); Allotype male, Australia, SE Q[weens]l[an]d. W. of Brisbane, Moggill Farm, 25m, 23-27.X.1961, J.L. Gressitt. Malaise trap (BPBM). Paratypes: 2 females, Saipan, I[slas] Marianas, As Mahetog area, 19:I:[19]45. Col. & press. by Henry S. Dybas Lot 544. Under bark (BPBM); 1 female, Saipan, I[slas] Marianas, Mt. Tagpochau, alt. 1250 ft, 15:II:[19]45, Col. & press. by Henry S. Dybas Lot 715, under bark (BPBM).

Remarks. This species is considered new due to the combination of the following characters: small body size; head about 1.2x as long as wide, rectangular; sides subparallel; ocelli not touching each other; 10-flafellomered antenna; pronotal disc anterior margin conspicuous; propleural sternal sides not embracing the pentagonal large prosternum. The male is in bad condition, the apex of the metasoma is missing, so that it is not possible to study the genitalia.

***Megaprosternum* sp. nov. 20**

Fig. 25. D-H

Description, female. – Body length 2.98 mm. LFW 1.59 mm. LH 0.55 mm. WH 0.40 mm. WF 0.25 mm. HE 0.22 mm. WOT 0.09 mm. OOL 0.29 mm. WH $0.72 \times$ LH; WF $0.62 \times$ WH; WF $1.14 \times$ HE; OOL $3.17 \times$ WOT. Head depressed in lateral view. Head lateral margin straight. Malar space absent. Median truncate, clypeal lobe as long as lateral ones, lobe delimitation not distinct. Toruli covering anterior clypeal margin or nearly so. Gena not visible behind eye in dorsal view. Mandible slender with three large distal teeth, upper margin not denticulate, intercondylar lobe present. Hypostomal carina emarginate, not angulate medially. Antenna with 11 flagellomeres, pedicel as long as flagellomere I. Eye elliptical in full view, setose with contour not protruding. Ocular triangle anterior angle acute. VOL longer than HE or at least as long as eye in dorsal view. Ocular triangle close to vertex crest. Anterior oculus separated posteriorly from imaginary line between eyes top. Pronotal collar inconspicuous. Pronotal disc depressed forward. Propleural and anterior angles visible in dorsal view. Prosternum large, pentagonal. Propleural sternal inner margins extending posteriorly beyond half length of prosternum. Mesoscutum medially longer than scutellum. Scutellar apex shape widely rounded. Metapectal-

propodeal complex disc flat, polished with lateral margins strongly convergent posteriorly. Propodeal spiracle lateral, circular. Metapectal-propodeal pleura posterolateral corner rounded. Forewing with anterior margin angulated. Forewing Sc+R vein present; stigma short; longitudinal fold simple; proximal venation reaching at most 0.2x of forewing total length, membrane color infusate yellow to brown. Hind wing with three hamuli evenly spaced. Metasomal second segment short, apical segments oriented upward.

Material examined. Holotype female, LAOS, Sayaboury Prov., Sayabouri, 12.XII.1965, Native collector RONDON (BPBM).

Remarks. This species is considered new due to the combination of the following characters: small body size; head about 1.4x as long as wide, rectangular; sdes subparallel; ocelli not touching each other; 11-flafellomered antenna; pronotal disc anterior margin inconspicuous; propleural sternal sides embracing the pentagonal large prosternum and metapectal-propodeal disc polished. This species is very similar with *M. pentagonal* but with different propodeal sculpture.

Nothepyrus sp. nov. 21

Fig. 26. A-F

Description, female. – Body length 3.06 mm. LFW 2.04 mm. LH 0.63 mm. WH 0.65 mm. WF 0.34 mm. HE 0.31 mm. WOT 0.15 mm. OOL 0.17 mm. WH 1.02× LH; WF 0.52× WH; WF 1.10× HE; OOL 1.10× WOT. Head globoid in lateral view. Head lateral margin convex. Malar space about as long as proximal mandibular width. Malar sulcus absent. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct. Clypeus in anterior view medially angled with two parallel carinae along margin. Clypeal carina present. Gena visible behind eye in dorsal view. Mandible robust with two large distal teeth, upper margin not denticulate, intercondylar lobe present. Mandible, shape. Hypostomal carina emarginate medially, not angulate. Antenna with 11 flagellomeres, pedicel length as long as distal flagellomere. Eye setose, subtriangular in full view, contour not protruding. Ocular triangle anterior angle acute. VOL shorter than HE. Ocular triangle far from vertex crest. Anterior ocellus located between eyes. Pronotal collar conspicuous. Propleural epicoxal sulcus present. Prosternum small. Mesoscutum medially shorter than scutellum. Notauli straight, complete, width uniform with faint posterior convergence. Scutellar apex sharp. Scutellar process conspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior, first metapostnotal, paraspiracular and metapleural carinae; median and posterior carinae connected; metapleural carina not outlining propodeal spiracle; lateral margins straight, subparallel. Propodeal spiracle dorsal, elliptical, located above metapleural carina. Metapectal-propodeal pleura with anterior transverse uniform concavity, posterolateral corner angulate. Metapectal-propodeal declivity with median carina. Mesotibia with setae like spines. Forewing anterior margin straight. Forewing venation with M+Cu vein complete, tubular, Rsa&M vein complete, Sc&R1a vein longer than wide, stigma short, Cua vein present, A vein present, 1cu-a vein conspicuous,, oriented distally, 1Cu cell subequal than R cell, longitudinal fold forked, proximal venation reaching more than 0.25x of FW total length, membrane color infusate yellow to brown. Hind wing with 3 hamuli irregularly spaced. Mesopleuron prepectal carina or groove present. Mesopleural pit conspicuous, displaced posterodorsally. Upper mesopleural fovea open. Subtegular fovea connected at least with episternal groove, evenly linear, simple. Metasomal paired calli located ventrally on sternite VI. Metasomal second segment medium-sized, apical segments orientated downward.

Material examined. Holotype female, BRAZIL (MA), Carolina, PARNA Chapada das Mesas, Riacho Cancela, 225 m, 07°06'44.2"S / 47°17'56.8"W, Armadilha de Malaise, 01-15.vii.2013, J.A. Rafael, F. Limeira de Oliveira & T.T.A. Silva, cols. (CZMA).

Remarks. This species is considered new due to the combination of the following characters: head subrounded, anterior margin length subequal than posterior margin; head and pronotum light brown; eyes covering the gena in dorsal view; forewing with distal half dark infusate; r-rs&Rsc vein absent; notauli present and subparallel; propodeal paraspiracular carina complete and metasomal sternum VI with paired lateral blunt tubercles.

Nothepyris sp. nov. 22

Fig. 26. G-H, Fig. 27. A-C

Description, female. – Body length 2.92 mm. LFW 2.16 mm. LH 0.49 mm. WH 0.48 mm. WF 0.25 mm. HE 0.23 mm. WOT 0.11 mm. OOL 0.14 mm. WH 0.97× LH; WF 0.52× WH; WF 1.07× HE; OOL 1.29× WOT. Head globoid in lateral view. Head lateral margin convex. Malar space about as long as proximal mandibular width. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct. Clypeus in anterior view medially angled with two parallel carinae along margin. Clypeal carina present. Gena visible behind eye in dorsal view. Mandible robust with two large distal teeth. Hypostomal carina emarginate medially, not angulate. Antenna with 11 flagellomeres, pedicel as long as flagellomere I. Frontal line present. Eye setose, rounded in full view, contour not protruding. Ocular triangle anterior angle acute. VOL shorter than HE. Ocular far from vertex crest. Anterior ocellus anterad to imaginary line between top of eyes. Pronotal collar conspicuous. Propleural epicoxal sulcus present. Prosternum. Mesoscutum medially subequal than scutellum. Notauli straight, complete, uniform, faintly convergent. Scutellar apex sharp. Scutellar process conspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotum inter-flap space wide. Metapectal-propodeal disc with transverse anterior, transverse posterior, first metapostnotal and metapleural carinae; metapleural carina not outlining propodeal spiracle; lateral margins convex, oriented subparallel. Propodeal spiracle dorsal, elliptical located above metapleural carina. Metapectal-propodeal pleura with anterior transverse uniform concavity (apparently to receive mesofemur when retracted). Metapectal-propodeal pleura posterolateral corner angulate. Metapectal-propodeal declivity with median carina. Mesotibia pilosity with setae like spines. Forewing anterior margin straight. Forewing venation with M+Cu vein complete, tubular, Rsa&M vein complete, Sc+R present, Sc&R1a vein longer than wide; Rsc segment tubular, Cua vein present, A vein present, 1cu-a vein conspicuous, oriented distally, 1Cu cell subequal than (R) cell, longitudinal fold forked, proximal venation reaching more than 0.25x of forewing length, membrane color infusate yellow to brown. Hind wing with three hamuli irregularly spaced. Mesopleural prepectal carina or groove present. Mesopleural pit conspicuous, displaced posterior-dorsally. Upper mesopleural fovea open. Subtegular fovea long, connected at least with episternal groove; evenly linear, simple. Metasomal paired calli located on sternites VI, second segment medium-sized, apical segments oriented downward.

Material examined. Holotype female, REP. DOMINICANA, La Cumbre, 400m, 21.III.1978, L. Masner (CNCI).

Remarks. This species is considered new due to the combination of the following characters: head subtrapezoidal, anterior margin shorter than posterior margin, lateral margin converging anteriorly; head and pronotum dark brown; r-rs vein segment absent,

Rsc vein segment present and nebulous to tubular distally; notauli present and subparallel; propodeal paraspiracular carina incomplete, submedian carinae inconspicuous; legs light yellow; metasomal sternum VI with paired lateral blunt tubercles.

Nothepyrus brasiliensis

Fig. 30. A-G

Description, male. – Body length 2.8 mm; LFW 2.0 mm. WH $1 \times$ LH; WF $0.55 \times$ WH; WF $1.2 \times$ HE; OOL $0.82 \times$ WOT. Body, antenna, clypeus, coxae, trochanters, femora, and meso- and metatibiae dark castaneous; mandible, palpi, protibia, tarsi light castaneous; wings hyaline, venation light castaneous to castaneous. Head globoid in lateral view, about $0.68 \times$ as high as long, subcircular in dorsal view, malar space, temple converging anterad, posterad respectively, lateral margin convex. Malar space about as long as proximal mandibular width. Mandible robust basally, narrow apically, with four large apical distal teeth, intercondylar lobe present. Clypeus with truncate subtrapezoidal median lobe, longer than lateral ones, lobe delimitation not distinct, anterior margin angled in anterior view; median carina high, straight in profile; apical margin thick, triangular in lateral view. Antenna with 11 flagellomeres, subfiliform-filiform, scape thick, slightly curved, progressively thickened apicad; pedicel barrel-shaped, longer than flagellomere I; antennal sockets closed each other; toruli not reaching anterior clypeal margin. Eye setose, subtriangular, about only $1.2 \times$ as high as wide, contour protruding slightly. Frons coriaceous, with very sparse inconspicuous punctures, frontal carina shorter than scape, not conspicuous, line between frontal carina, anterior ocellus with very faint sulcus. Posterior ocelli distant from vertex $1.87 \times$ DAO. Vertex evenly convex, corner rounded. Palpal formula apparently 6:3. Hypostomal area short, broad, Hypostomal carina emarginate but not angulate medially. Occipital carina absent. Gena not visible visibility behind eye in dorsal view. Ocular triangle between eyes, anterior angle acute. VOL shorter than HE. Ocular triangle far from vertex crest. Pronotum collar conspicuous, disc trapezoidal, ecarinate, slightly depressed forward, so that anterior corner in lower level, coriaceous progressively weakening posterad. Prosternum small. Mesoscutum medially longer than scutellum. Notauli complete, well impressed, straight, progressively wider posterad, strongly converging posteriorly. Parapsidal signal complete, but progressively weakening anterad. Scutellum not well delimited posteriorly with apex sharp, Scutellar process continuous, evenly wide, evenly depth. Surface of axilla with very deep pit. Metanotal inter-flap space wide. Metapectal-propodeal disc with transverse anterior, metapostnotal median, transverse posterior, paraspiracular and metapleural carinae; lateral margins straight, subparallel. Metapectal-propodeal declivity with median carina. Metapectal-propodeal pleura with anterior transverse uniform concavity, posterior-lateral angle angulate. Propodeal spiracle dorsal, elliptical located above metapleural carina, metapleural carina not outlining propodeal spiracle. Mesopleuron subtegular fovea deep, progressively shallower posterad, simple, connected with episternal groove, widened anteriorly; upper mesopleural fovea open; central pit small, displaced posterior-dorsally; anterior fovea fused with upper fovea, reaching episternal sulcus, trans-episternal line carinate, carina strong anteriorly, progressively weakening posterad, sulcus arched, well impressed on its anterior half; prepectal carina present. Mesotibia pilosity with thick setae. Forewing anterior margin straight with R and 1Cu cells closed, both cells almost same-sized; M+Cu vein tubular, complete; Rsa&M complete; Sc+R present; Sc&R1a vein longer than wide; stigma short, wide; r-rs&Rsc vein tubular, short, much shorter than submedian vein; Cua vein present; A vein present; 1cu-a vein present, length conspicuous, oriented distally, strongly convex; 1Cu cell subequal than R cell; longitudinal fold forked; proximal venation reaching more than

0.25x of forewing total length; membrane color hyaline to whitish. Hind wing with three hamuli irregularly spaced. Metasomal cross section subcircular, tergum I polished, segment II short, other terga weakly coriaceous; sternum I flat, coriaceous, other sterna distinctly weakly coriaceous; sternum II sulcate anteriorly. Posterior margins of sterna IV-VI not emarginated, metasomal apical segments oriented downward. Hypopygium subtriangular, median stalk short, $0.62 \times$ as long as plate, lateral stalk absent, anterior margin evenly straight, posterior and lateral margin not angled between them, evenly concave. Paramere divided in two lobes, minute dorsal lobe, large ventral, wide, short lobe with apical margin rounded, dorsal margin straight, ventral margin slightly convex. Cuspis subquadrate, wide, short, apical margin almost truncate, base of ventral margin with small expansion. Digitus small, distally sharpening, upper margin denticulate. Basiparamere and basivolsella fused, without any suture between them. Aedeagus bottle-shaped but not constricted medially, apical lobe rounded. Genital ring elliptical. Basal ring conspicuous but small, subcircular, opening smaller than opening of genital ring.

Material examined. Male, BRAZIL, Nova Teutonia, IV-5-1941, F. Plaumann. C.O. Azevedo det. 2013, American Ent. Institute coll. (AEIC).

Remarks. This specimen has the same data labels of the type series collected by F. Plaumann in April of 1941. The similarities with female includes head subrounded, anterior margin shorter than posterior margin, lateral margin converging anteriorly; r-rs&Rsc vein present and thin; notauli present and convergent posteriorly; paraspiracular carina incomplete.

Prorops sp. nov. 23

Fig. 27. D-H

Description, female. – Body length 2.71 mm. LFW 1.87 mm. LH 0.49 mm. WH 0.60 mm. WF 0.43 mm. HE 0.25 mm. WOT 0.14 mm. OOL 0.18 mm. WH $1.22 \times$ LH; WF $0.72 \times$ WH; WF $1.75 \times$ HE; OOL $1.33 \times$ WOT. Head globoid in lateral view, lateral margin convex. Malar space short. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct, anterior margin not angled in anterior. Toruli covering anterior clypeal margin. Frontal process present. Gena not visible behind eye in dorsal view. Mandible robust with three large distal teeth, upper margin not denticulate, basal intercondylar lobe present. Hypostomal carina emarginate, not angulate medially. Antenna with 10 flagellomeres, pedicel as long as distal flagellomere. Frontal line present. Eye glabrous, subtriangular in full view, contour protruding slightly. Ocular triangle anterior angle right or nearly so. VOL shorter than HE. Ocular triangle close to vertex crest. Anterior ocellus located between eyes. Pronotal collar conspicuous. Prosternum, size small. Mesoscutum medially longer than scutellum. Scutellar apex shape widely rounded. Scutellar process conspicuous, continuous, evenly wide, evenly depth. Metanotal inter-flap space wide. Metapectal-propodeal disc polished; lateral margins straight, subparallel; metapleural carina not outlining propodeal spiracle. Propodeal spiracle lateral, circular located below carina. Metapectal-propodeal pleura posterolateral corner rounded. Mesotibia with thick setae. Forewing anterior margin angulated. Forewing venation with Sc+R present; Rsa&M vein complete; Sc&R1a vein longer than wide; stigma short; r-rs&Rsc vein tubular; longitudinal fold simple; proximal venation reaching more than 0.25x of forewing total length; membrane color infusate yellow to brown. Upper mesopleural fovea open. Subtegular fovea simple, long, widened anteriorly, connected with episternal groove. Metasomal second segment short, apical segments oriented downward.

Material examined. Holotype female, THAILAND, Nakhon Si Thammarat Namtok Yong NP, TV aerial, 8°14.262'N 99°48.289'E, 966m. Malaise trap, 5-12.xi.2008, Paiboon leg. T4246 (QSBG).

Remarks. This species is considered new due to the combination of the following characters: head short, transverse and rectangular, surface alutaceous; eye subtriangular; VOL shorter than HE; short frontal process, shorter than HE, with apex bifid, arms narrowly separated and curved dorsad; Sc, Sc+R1a and r-rs&Rsc veins present and tubular.

Prorops sp. nov. 24

Fig. 28. A-E

Description, female. – Body length 2.82 mm. LFW 1.85 mm. LH 0.51 mm. WH 0.60 mm. WF 0.45 mm. HE 0.18 mm. WOT 0.11 mm. OOL 0.18 mm. WH 1,18× LH; WF 0.74× WH; WF 2.42× HE; OOL 1.71× WOT. Head oval in lateral view, lateral margin convex. Malar space short. Median clypeal lobe truncate, as long as lateral ones, lobe delimitation not distinct, anterior margin not angled in anterior view. Toruli not reaching anterior clypeal margin. Frontal process present. Gena, visibility behind eye in dorsal view not visible. Mandible robust with three large distal teeth, upper margin not denticulate. Hypostomal carina emarginate, not angulate medially. Antenna with 10 flagellomeres, pedicel as long as flagellomere I. Frontal line present. Eye rounded in full view, glabrous, contour protruding slightly. Ocular triangle anterior angle acute. VOL shorter than HE. Ocular triangle close to vertex crest. Anterior ocellus located between eyes. Pronotal collar conspicuous. Prosternum small. Mesoscutum medially subequal than scutellum. Scutellar apex widely rounded. Scutellar process inconspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc polished with lateral margins subparallel. Metapectal-propodeal dorso-lateral angulation not outlining propodeal spiracle. Propodeal spiracle lateral, circular. Metapectal-propodeal pleura posterolateral corner rounded. Mesotibia with thick setae. Forewing anterior margin angulated. Forewing venation with Sc+R vein present; Sc&R1a vein longer than wide; stigma short; r-rs&Rsc vein tubular; longitudinal fold simple; proximal venation reaching more than 0.25x of forewing total length; membrane color infusate yellow to brown. Hind wing with three hamuli evenly spaced. Mesopleural pit conspicuous, central. Subtegular fovea simple, long, connected at least with episternal groove evenly linear with anterior segment U shaped. Metasomal segment II short, apical segments oriented downward.

Material examined. Holotype female, VIETNAM, Viet Try nr Thanh Son, Thuong Cuu, 20°59'N 105°8'[E], 350-400m, 11-16.x.1999, Malaise traps, R. de Vries (RMNH).

Remarks. This species is considered new due to the combination of the following characters: head short, transverse and rectangular, surface polished; eye rounded; VOL as long as HE; vertex deeply concave; frontal process medium sized, longer than HE, arms narrowly separated and curved dorsad; Sc, Sc+R1a and r-rs&Rsc veins present and tubular.

Prorops sp. nov. 25

Fig. 28. F-H

Description, female. – Body length 2.11 mm. LFW 1.35 mm. LH 0.42 mm. WH 0.52 mm. WF 0.35 mm. HE 0.18 mm. WOT 0.12 mm. OOL 0.28 mm. WH 1.26× LH; WF 0.68× WH; WF 1.92× HE; OOL 2.25× WOT. Head depressed in lateral view, lateral margin straight. Malar space short. Median clypeal lobe truncate, as long as lateral ones

with lobe delimitation not distinct, anterior margin not angled in anterior view. Toruli not reaching anterior clypeal margin. Frontal process present. Gena not visible behind eye in dorsal view. Mandible robust with three large distal teeth, upper margin not denticulate. Hypostomal carina emarginate, angulate medially. Antenna with 10 flagellomeres, pedicel as long as distal flagellomere. Frontal line present. Eye rounded in full view, setose with contour protruding slightly. Ocular triangle close to vertex crest with anterior angle acute. VOL longer than HE or at least as long as eye in dorsal view. Anterior oculus anterad to imaginary line between anterior eyes margin. Pronotum collar conspicuous. Prosternum small. Mesoscutum medially longer than scutellum. Scutellar apex widely rounded. Scutellar process inconspicuous, continuous, evenly wide, evenly depth with lateral linear foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc flat, polished with lateral margins subparallel. Metapectal-propodeal dorso-lateral angulation not outlining propodeal spiracle. Propodeal spiracle lateral, circular. Metapectal-propodeal pleura posterolateral corner rounded. Mesotibia with thick setae. Forewing anterior margin angulated. Forewing venation with Sc+R vein; Sc&R1a vein longer than wide; Rsc vein spectral. proximal venation reaching more than 0.25x of forewing total length; membrane color infusate yellow to brown. Hind wing with two hamuli. Mesopleural pit conspicuous, central. Subtegular fovea long, subdivided, connected at least with episternal groove, evenly linear with anterior segment U shaped. Metasomal second segment size short, apical segments oriented downward.

Material examined. Holotype female, UNITED ARAB EMIRATES, Al-Ajban, 24.36N 55.01E, 12-19.09.2006, light trap, A. van Harten (UFES).

Remarks. This species is considered new due to the combination of the following characters: head elongated rectangular, surface polished; eye rounded; VOL about twice HE; vertex slightly concave; frontal process medium sized, as long as HE, arms narrowly separated apically and curved dorsad; Sc and Sc+R1a veins present and nebulous.

Thlastepyrus marquisensis (Fullaway, 1935) *stat. et comb. nov.*

Fig. 28.A-D

Description, female. – Body depressed. Body length 2.35 mm. LFW 1.40 mm. LH 0.58 mm. WH 0.43 mm. WF 0.25 mm. HE 0.23 mm. WOT 0.12 mm. OOL 0.26 mm. WH 0.74× LH; WF 0.57× WH; WF 1.07× HE; OOL 2.13× WOT. Head depressed, oval in lateral view, lateral margin straight, frons strongly coriaceous. Malar space absent. Medial clypeal lobe truncate, not carinate, longer than lateral ones, lobe delimitation not distinct, anterior margin shape (anterior view) not angled. Inter-totular space absent or nearly so. Toruli covering anterior clypeal margin or nearly so. Gena not visible behind eye in dorsal view. Mandible slender with basal intercondylar lobe, four small distal teeth, upper margin not denticulate. Hypostomal carina not emarginate medially. Antenna with 11 flagellomeres, pedicel as long as distal flagellomere. Frontal line present. Eye subtriangular in full view, setose with contour not protruding. Ocular triangle anterior angle obtuse. VOL longer than eye. Ocular triangle close to vertex crest. Oculus anterad to imaginary line between eyes anterior margin. Occipital carena absent. Pronotal collar inconspicuous. Pronotal disc flat, longer than wide with anterior margin semicircular. Propleural neck and anterior angles visible in dorsal view. Prosternum size small. Mesoscutum medial length subequal than scutellum. Scutellum apex widely rounded. Scutellar process conspicuous, continuous, not evenly wide, deeper at lateral ends with lateral subcircular foveae. Metanotal inter-flap space wide. Metapectal-propodeal disc flat, rugulose to areolated with transverse anterior, metapostnotal median and metapleural carinae; lateral margins straight, strongly convergent posteriorly; metapleural carina outlining propodeal spiracle. Propodeal spiracle lateral, circular, located below

metapleural carina. Metapectal-propodeal pleural postero-lateral corner rounded. Forewing anterior margin angulated near prostigma. Forewing venation with Sc+R vein; M+Cu tubular, basally incomplete; Rsa&M complete; fusion Sc&R1a longer than wide; stigma short; r-rs vein segment tubular; A vein present; 1cu-a vein present, length conspicuous, oriented proximally; 1Cu cell length less than half of R cell length; longitudinal fold simple; proximal venation reaching at most 0.2x of forewing total length; membrane color hyaline to whitish. Mesopleural prepectal carina, two anterior small foveae present. Upper mesopleural fovea open. Subtegular fovea simple, long, connected with episternal groove, widened anteriorly. Metasomal tergite I lateral margins in contact each other ventrally. Metasomal second segment size short, apical segments oriented downward.

Material examined. Holotype of *Sierola depressa* var. *marquinensis* Fullaway, 1935, female, Marquesas Islands, Tapeata, E. Slope, Mt. Ootva, 5–25–29, Hiva[Oa], 2500 ft, On *Paspalum conjugatum*, Mumford & Adamson, Type 777, Pacific Entomological Survey (BPBM).

Remarks. This species is considered a new combination of the following characters: *Thlastepyris* due to the absence of clypeal carina; front strongly alutaceous; R and 1Cu cells present, proximally fused due to the incompleteness of M+Cu and r-rs&Rsc present.

***Tuberepyris* sp. nov. 26**

Fig. 29. A-D

Description, male. – Body length 2.72 mm. LFW 1.92 mm. LH 0.46 mm. WH 0.52 mm. WF 0.31 mm. HE 0.22 mm. WOT 0.23 mm. OOL 0.20 mm. WH 1.13× LH; WF 0.59× WH; WF 1.43× HE; OOL 0.87× WOT. Head depressed in lateral view, lateral margin convex. Malar space short. Clypeus truncate, medial clypeal lobe longer than lateral ones, lobe delimitation distinct, anterior margin not angled in anterior view. Toruli covering anterior clypeal margin or nearly so. Gena not visible behind eye in dorsal view. Mandible slender with four small distal teeth, basal intercondylar lobe. Hypostomal carina not emarginate medially. Antenna with 11 flagellomeres with pedicel length as long as distal flagellomere. Frontal line present. Eye rounded in full view, glabrous, contour protruding slightly. Ocular triangle close to vertex with anterior angle obtuse. VOL longer than HE or at least as long as eye in dorsal view. Anterior oculus anterad to imaginary line between anterior eyes margin. Pronotal collar inconspicuous. Pronotal surface depressed forward. Propleural neck and anterior angles visible in dorsal view. Prosternum small. Mesoscutum medially longer than scutellum. Scutellar apex widely rounded. Metanotal inter-flap space wide. Metapectal-propodeal disc flat, polished with anterior transverse carina, lateral margins strongly convergent posteriorly. Propodeal spiracle lateral, circular. Metapectal-propodeal pleura postero-laterally rounded. Forewing anterior margin angulated. Forewing venation with Sc+R vein present; Rsa&M vein complete; fusion Sc&R1a vein wider than long; stigma size short; r-rs&Rsc vein present, r-rs spectral, Rsc nebulous; A vein presence incomplete; longitudinal fold inconspicuous; proximal venation reaching more than 0.25x of forewing total length; membrane color hyaline to whitish. Hind wing with three hamuli evenly spaced. Mesopleural pit conspicuous, central. Upper mesopleural fovea open. Subtegular fovea short, isolated, simple, widened anteriorly. Metasomal second segment short, apical segments oriented downward. Genitalia with paramere longer than basiparamere, about twice as long as wide, dorsal half with apical margin somewhat rounded, dorsal and ventral margins subparallel to slightly convex in lateral view; digitus slender, progressively narrowing apicad, apex acute; cuspis basally wide, apically narrow, rounded, slightly longer than digitus; aedeagus bottled-shaped, with pair of rounded apical lobes, apex not surpassing

cuspid apex, not reaching paramere apex; hypopygium trapezoidal, median stalk absent; genital ring elliptical; basal ring subcircular, smaller than basal ring.

Material examined. Holotype male, SOUTH AFRICA, W. Cape, Koeberg Nature Reserve, 33°37.622'S 18°24.259'E, 16-May[V]-3 June[VI]-1997, S. van Noort, Malaise trap, KO97-M02, West Coast Strandveld (ISAM).

Remarks. This species is considered new of *Tuberepyris* due to the head quadrate; posterior ocelli widely separated each other by twice the space between anterior and posterior ocelli; mesoscutum twice the scutellum length; scutellar process absent; forewing with Sc, Sc+R1a, Rsa+M veins and small rounded stigma tubular, r-rs&Rsc present and hyaline spectral. The wing venation is similar to *T. hamus* by the presence of Rsa&M but differs in mesoscutum length, scutellar process presence and metapectal-propodeal disc with metapostnotal median carina.

References

- Agnarsson, I. & Miller, J.A. (2008) Is ACCTRAN better than DELTRAN? *Cladistics* **24**: 1-7.
- 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.
- Ashmead, W.H. (1900) Notes on some New Zealand and Australian parasitic Hymenoptera, with description of new genera and new species. *Proceedings of the Linnean Society of New Wales* **3**: 327-360.
- Azevedo, C.O. (2003) Synopsis of the Neotropical *Dissomphalus* (Hymenoptera, Bethylidae). *Zootaxa* **338**: 1-74.
- Azevedo, C.O. (2006) Two new genera of Sclerodermini (Hymenoptera: Bethylidae; Epyrinae) with large, scolebythid-like prosternums. *Zootaxa* **1191**: 35-47.
- 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.
- 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 Leiden* **83**: 841-851.
- Barbosa, D.N. & Azevedo, C.O. (2011a) Taxonomy of *Allobethylus* Kieffer (Hymenoptera, Bethylidae) from southeastern Asia. *Journal of Asia-Pacific Entomology* **14**: 89-94.
- Barbosa, D.N. & Azevedo, C.O. (2011b) Order Hymenoptera, family Bethylidae, subfamily Mesitiinae. In: van Harten, A. (Ed.). *Arthropod Fauna of UAE*. Volume 4. Abu Dhabi: Dar Al Ummah Printing, Publishing, Distribution & Advertising: pp. 375-404.
- Berland, L. (1928) *Faune de France 19. Hyménoptères Vespiformes II*. Office Central de Faunistique, Paris: 215 pp.
- Blanke, A; Greve, C; Wipfler, B, Beutel, R.G., Holland, B.R. & Misof, B. (2013) The Identification of Concerted Convergence in Insect Heads Corroborates Palaeoptera. *Systematic Biology* **62**: 250-263.
- Brothers, D.J. (1975) Phylogeny and classification of the Aculeate Hymenoptera, with special reference to Mutillidae. *The University of Kansas Science Bulletin*, **11**: 483-648.
- Brothers, D.J. & Carpenter, J.M. (1993) Phylogeny of aculeata: Chrysoidea and Vespoidea (Hymenoptera). *Journal of Hymenoptera Research* **2**: 227-302.
- Carpenter, J. (1986) Cladistics of the Chrysoidea (Hymenoptera). *Journal of the New York Entomological Society* **94**: 303-330.
- Carpenter, J. (1999) What do we know about chrysidoid (Hymenoptera) relationships? *Zoologica Scripta* **28**: 215-231.
- 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.
- De Pinna, M.G.G. (1991) Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**: 367-394.
- Eady, R.D. (1968) Some illustrations of microsculpture in the Hymenoptera. *Proceedings of the Royal Entomological Society of London* **43**: 66-72.
- Ebach, M.C., Williams, D.M. & Morrone, J.J. (2006) Paraphyly is bad taxonomy. *Taxon* **55**: 831-832.
- 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. (1966) A revision of the genus *Anisepyrus* Kieffer (Hymenoptera, Bethyridae). *Studia Entomologica* **9**: 1-120.
- Evans, H.E. (1973) Further studies on South American Bethyridae (Hymenoptera). *Proceedings of the Entomological Society of Washington* **75**: 194-204.
- Evans, H.E. (1978) The Bethyridae of America North of Mexico. *Memoirs of the American Entomological Institute* **27**: 1-332.
- Farris, J.S. (1989) The Retention Index and The Rescaled Consistency Index. *Cladistics* **5**: 417-419.
- Florence, J., Chevillotte, H., Ollier C. & Meyer, J.Y. (2013) Base de données botaniques Nadeaud de l'Herbier de la Polynésie Française (PAP). (online resource). <http://www.hear.org/pier/scientificnames/scinamep.htm> (accessed 01 Apr 2017).
- Fouts, R.M. (1935) New serphoid, bethyrid, and anteonid wasps from the Marquesas and Society Islands. *Pacific Entomological Survey Publication* **8**: 151-157.
- Gahan, A.B. (1931) On certain hymenopterous parasites of stored-grain insects. *Journal of Academy of Sciences* **21**: 213-221.
- Goloboff, P.A. (1993) Character optimization and calculation of tree lengths. *Cladistics* **9**: 433-436.
- 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.
- Goloboff, P.A., Carpenter, J.M., Arias, S., & Miranda, E.D.R. (2008) Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* **24**: 758-773.
- Goulet, H., & J. Huber, T. (eds.), Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada; Ottawa, Canada: vii+668 pp.
- Gordh, G. & Móczár, L. (1990) A catalog of the world Bethyridae (Hymenoptera: Aculeata). *Memoirs of the American Entomological Institute* **46**: 1-364.
- Harris, S.R., Gower, D.J. & Wilkinson, M. (2003) Intraorganismal Homology, Character construction, and the Phylogeny of Aetosaurian Archosaurs (Reptilia, Diapsida). *Systematic Biology* **52**: 239-252.
- Hawkins, J.A., Hughes, C.E. & Scotland, R.W. (1997) Primary Homology Assessment, Characters and Character States. *Cladistics* **13**: 275-283.
- Hedqvist, K.J. (1975) Notes on Embolemidae and Bethyridae in Sweden with Description of a New Genus and Species (Hym., Bethyloidea). *Entomologisk Tidskrift* **96**: 121-132.
- Heraty, J.M., et al. (2013) A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera). *Cladistics* **29**: 466-542.
- Heuzé, V., Tran, G. & Baumont, R. (2016) Buffalo grass (*Paspalum conjugatum*). *Feedipedia*, INRA, CIRAD, AFZ and FAO. <http://www.feedipedia.org/node/407>. (accessed 01 Apr 2017).
- Jiang, Y., Yang, Z., Wang, X. & Hou, Y. (2015) Molecular identification of sibling species of *Sclerodermus* (Hymenoptera: Bethyridae) 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. doi:10.1371/journal.pone.0119573.
- Kawada, R., Lanes, G.O. & Azevedo, C.O. (2015) Evolution of metapostnotum in flat wasps (Hymenoptera, Bethyridae): implications for homology assessments in Chrysidoidea. *PLoS ONE*, 10(10): e0140051. DOI:10.1371/journal.pone.0140051.
- Kieffer, J.J. (1914d) Bethyridae. *Das Tierreich* **41**: 228-595.
- Lanes, G.O. & Azevedo, C.O. (2008) Phylogeny and Taxonomy of Sclerodermini

- (Hymenoptera, Bethylidae, Epyrinae). *Insect Systematic and Evolution* **39**: 55-86.
- Móczár, L. (1984) Oriental Mesitiinae (Hymenoptera: Bethylidae). *Folia Entomologica Hungarica* **45**: 109-150.
- Móczár, L. (1986) New and little known Mesitiinae (Hymenoptera: Bethylidae). *Folia Entomologica Hungarica* **47**: 127-133.
- Nixon, K. C. (1999-2002) Winclada version 1.00.08. Computer program and documentation published and distributed by the author. http://www.millersville.edu/academics/scma/biology/courses/471/19_WC_24oct03.pdf (accessed 01 Feb 2015).
- Ramos, M.S. & Azevedo, C.O. (2012) Revision of *Eupsenella* Westwood, 1874 (Hymenoptera, Bethylidae). *Zootaxa* **3539**: 1-80.
- Rasnitsyn A.P. (1980) Origin and evolution of Hymenoptera. Trans. Paleontol. Inst. Acad. Sci. USSR. 174. Nauka Press, Moscow: 192 pp. (in Russian).
- Richards, O.W. (1952) A new species of Bethylidae (Hymenoptera) from Palestine. *Annals and Magazine of Natural History* **5**: 409-410.
- Ronquist, F. (1999) Phylogeny of the Hymenoptera (Insecta): The state of the art. *Zoologica Scripta* **28**: 3-11.
- 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.
- Terayama, M. & Tachikawa, T. (1987) A new species of the genus *Plastanoxus* (Hymenoptera: Bethylidae) from Japan. *Transactions of the Shikoku Entomological Society* **18**: 311-314.
- Terayama, M. (1995) The phylogeny of the bethylid wasps tribe Sclerodermini (Hymenoptera, Bethylidae). *Proceedings of the Japanese Society of Systematic Zoology* **54**: 65-73.
- Terayama, M. (2005) Descriptions of new taxa and distribution records of the family Bethylidae (Insecta, Hymenoptera). III Subfamily Epyrinae. *Liberal Arts* **13**: 51-112.
- Terayama, M. (2006) *Insects of Japan Bethylidae (Hymenoptera)*. Touka Shobo Co, Fukuoka, Japan: 317pp.
- Vargas, J.M. & Azevedo, C.O. (2016a) Three new species of *Pararhabdepyris* Gorbатовsky (Hymenoptera, Bethylidae) from Central Africa and the Arabian Peninsula. *Zootaxa* **4117**: 429-439. <http://doi.org/10.11646/zootaxa.4117.3.10>
- Vargas, J. M. & Azevedo, C.O. (2016b) Discovery of the male of *Galodoxa* Nagy (Hymenoptera: Bethylidae), with emended generic diagnosis. In: Robillard, T., Legendre, F., Villemant, C. & Leponce, M. (eds). Insects of Mount Wilhelm, Papua New Guinea. Muséum national d'Histoire naturelle, Paris, (Mémoires du Muséum national d'Histoire naturelle ; 209): pp. 393-406.
- Wiens, J.J. (2001) Character Analysis in Morphological Phylogenetics: Problems and Solutions. *Systematic Biology* **50**: 689-699.
- Wiley, E.O. & Lieberman, B.S. (2011) Phylogenetics, The Theory of Phylogenetic Systematics. 2nd edition. Wiley-Blackwell, New Jersey, USA: 406 pp.
- Yoder, M.J., Mikó, I., Seltmann, K.C., Bertone, M.A. & Deans, A.R. (2010) A Gross Anatomy Ontology for Hymenoptera. PLoS ONE **5** (12): e15991. doi:10.1371/journal.pone.0015991

Figures

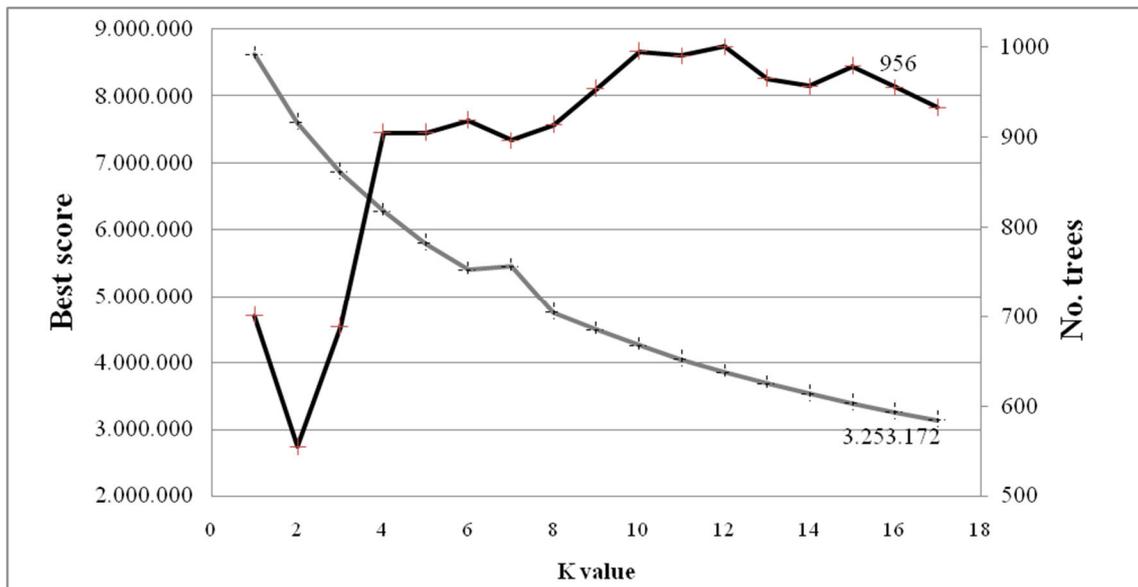


Figure 1. Test of k values with implied weighting, primary axis (gray line) and secondary axis (black line).

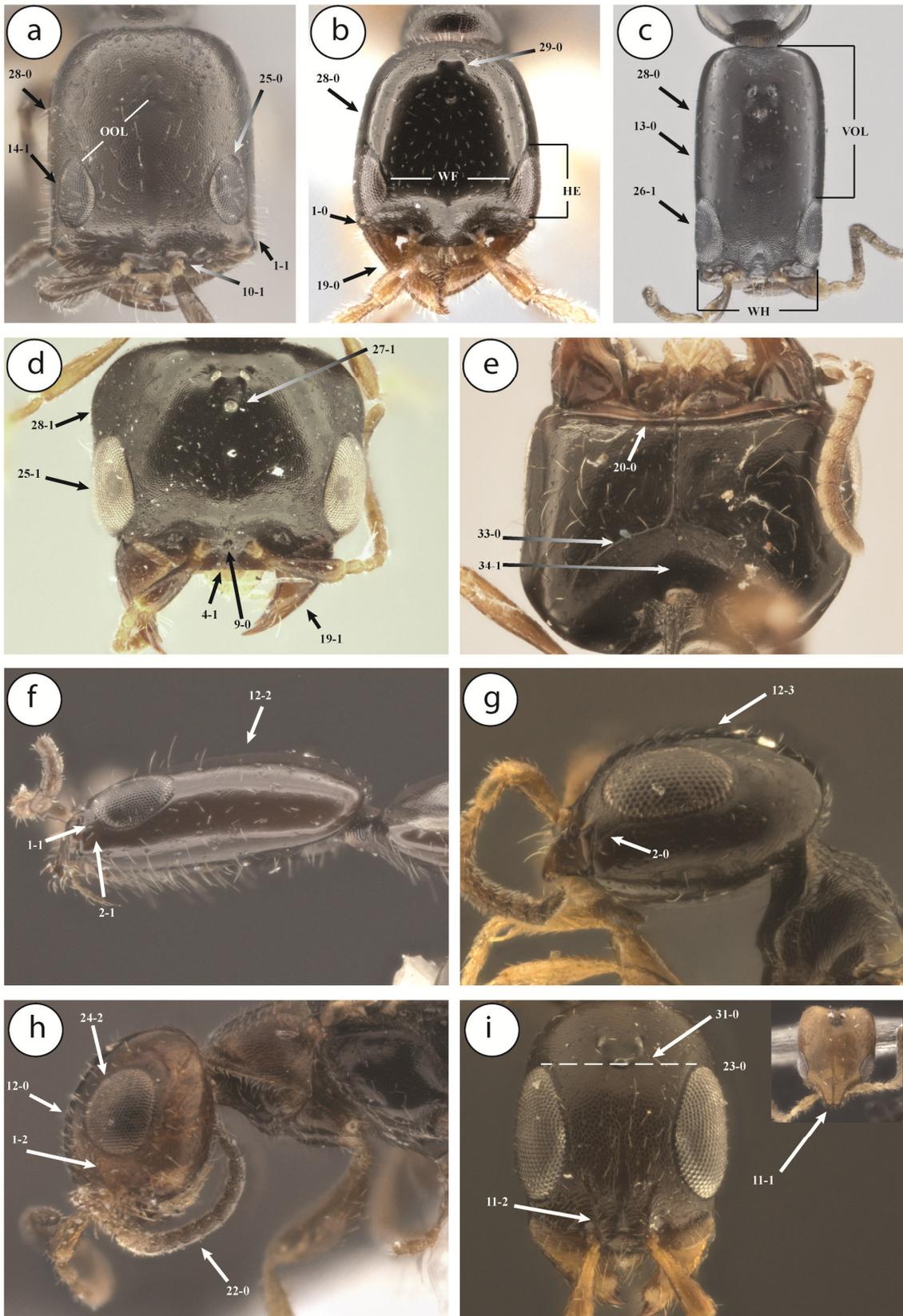


Figure 2. Morphological characters. Head. A. *Bethylopsis fulawayi*, dorsal; B. *Glenosema*, dorsal view; C. *Megaprosternum*, dorsal view; D. *Chilepyris*, dorsal view; E. *Chilepyris*, ventral view; F. *Megaprosternum*, lateral view; G. New genus E, lateral view; H. *Nothepyris*, lateral view; I. New genus D, dorsal view (dotted line shows an imaginary border between anterior margins of the eyes, left box *Prorops*, dorsal view).

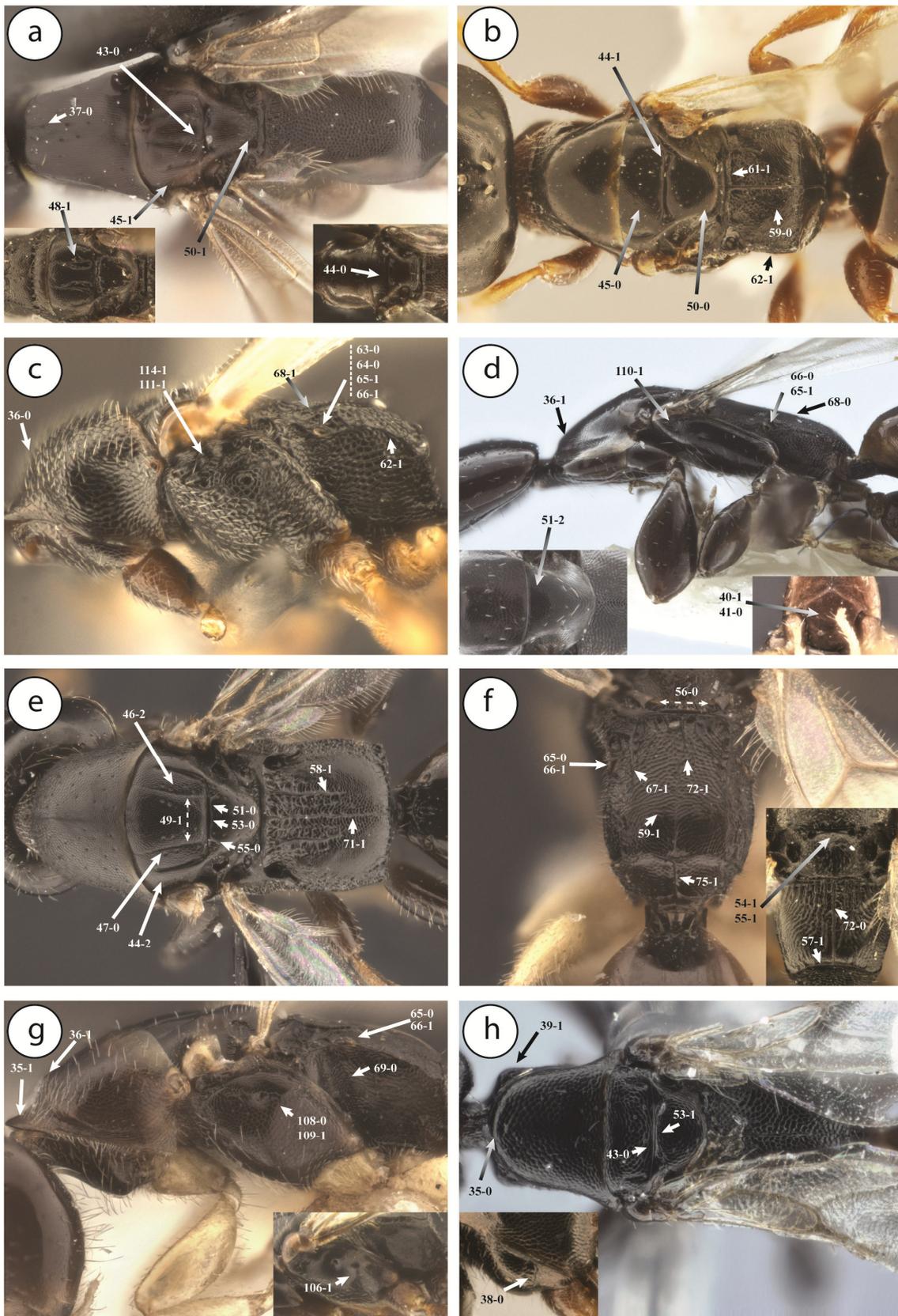


Figure 3. Morphological characters. Thorax. A. *Galodoxa* female, dorsal view (left box *Galodoxa* male, right box New genus D male); B. *Chilepyris*, dorsal view; C. *Pararhabdepyris*, lateral view; D. *Megaprosternum*, lateral view (left square dorsal mesothorax; right box prosternum detail); E. *Discleroderma*, dorsal view; F. *Nothepyris*, metapectal-propodeal complex (right box *Pararhabdepyris*); G. *Nothepyris*, lateral view (right box New genus A; H. *Thlastepyris*, dorsal view (left box *Glenosema* propleural detail).

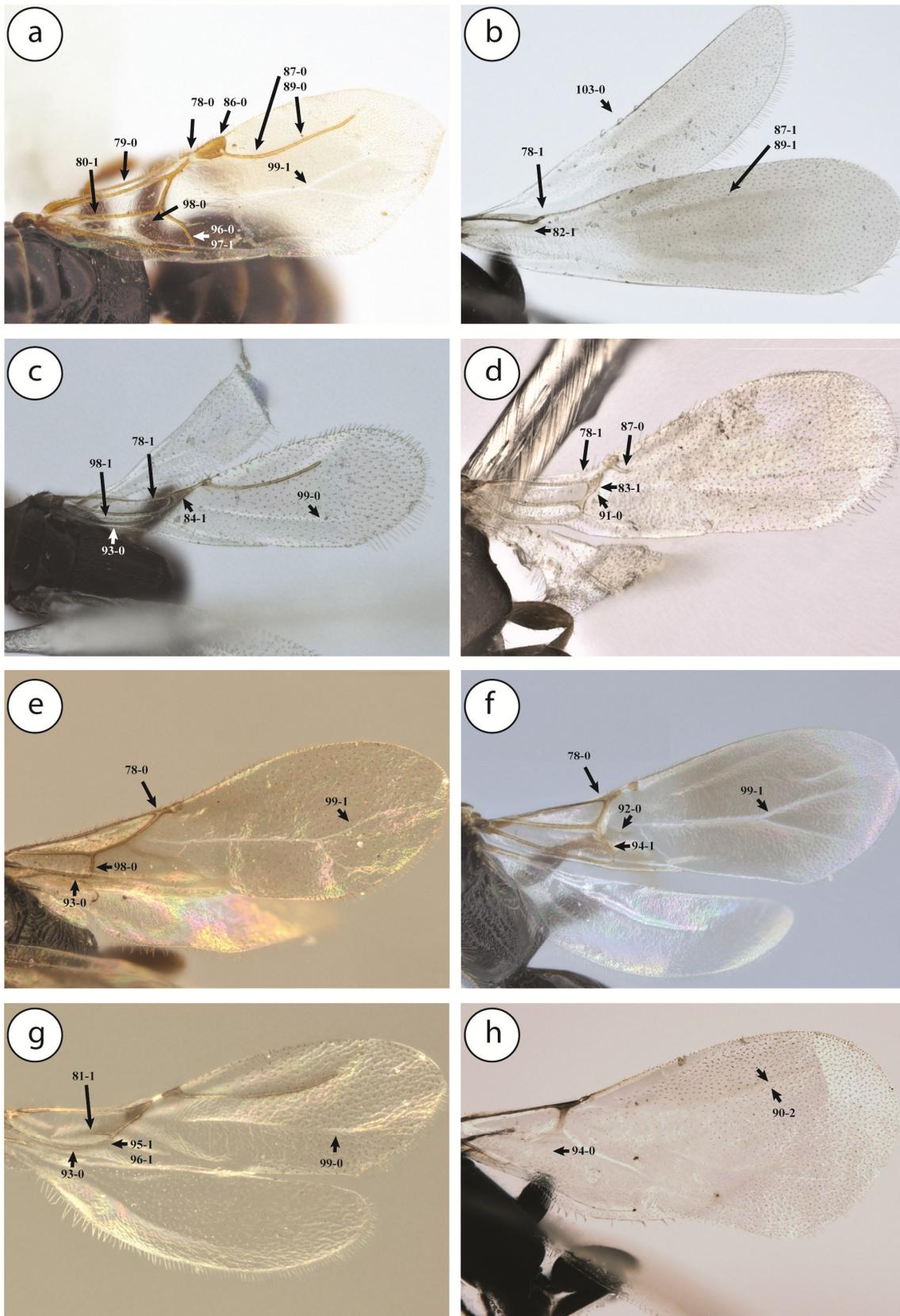


Figure 4. Morphological characters. Wings. A. *Chilepyris*; B. *Megaprosternum*; C. *Alloplastanoxus*; D. *Israelius*; E. *Galodoxa*; F. *Nothepyris*; G. New genus D; H. *Tuberepyris*.

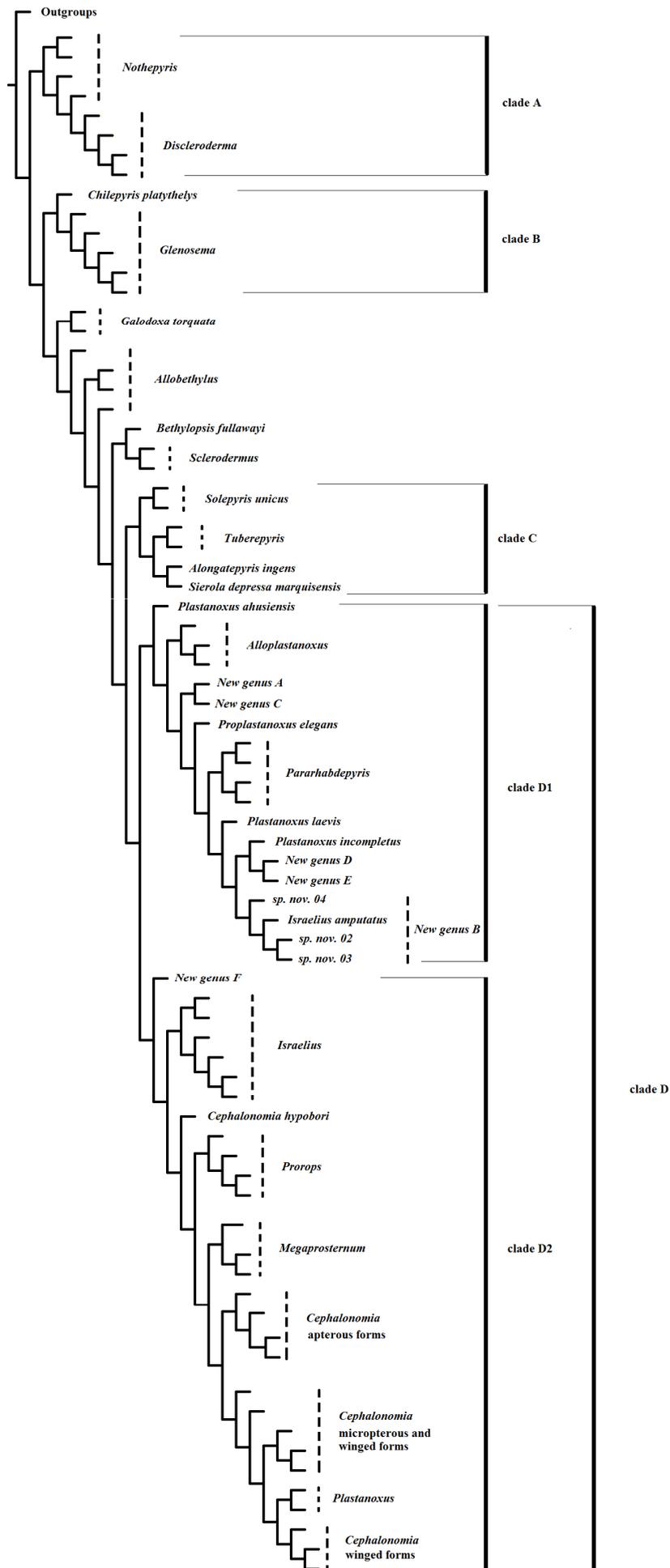


Figure 5. MPT under implied weighting. Dotted lines: genera and some minor clades or groups; solid lines: major clades or groups (clades A and B). Detailed MPT on appendix.

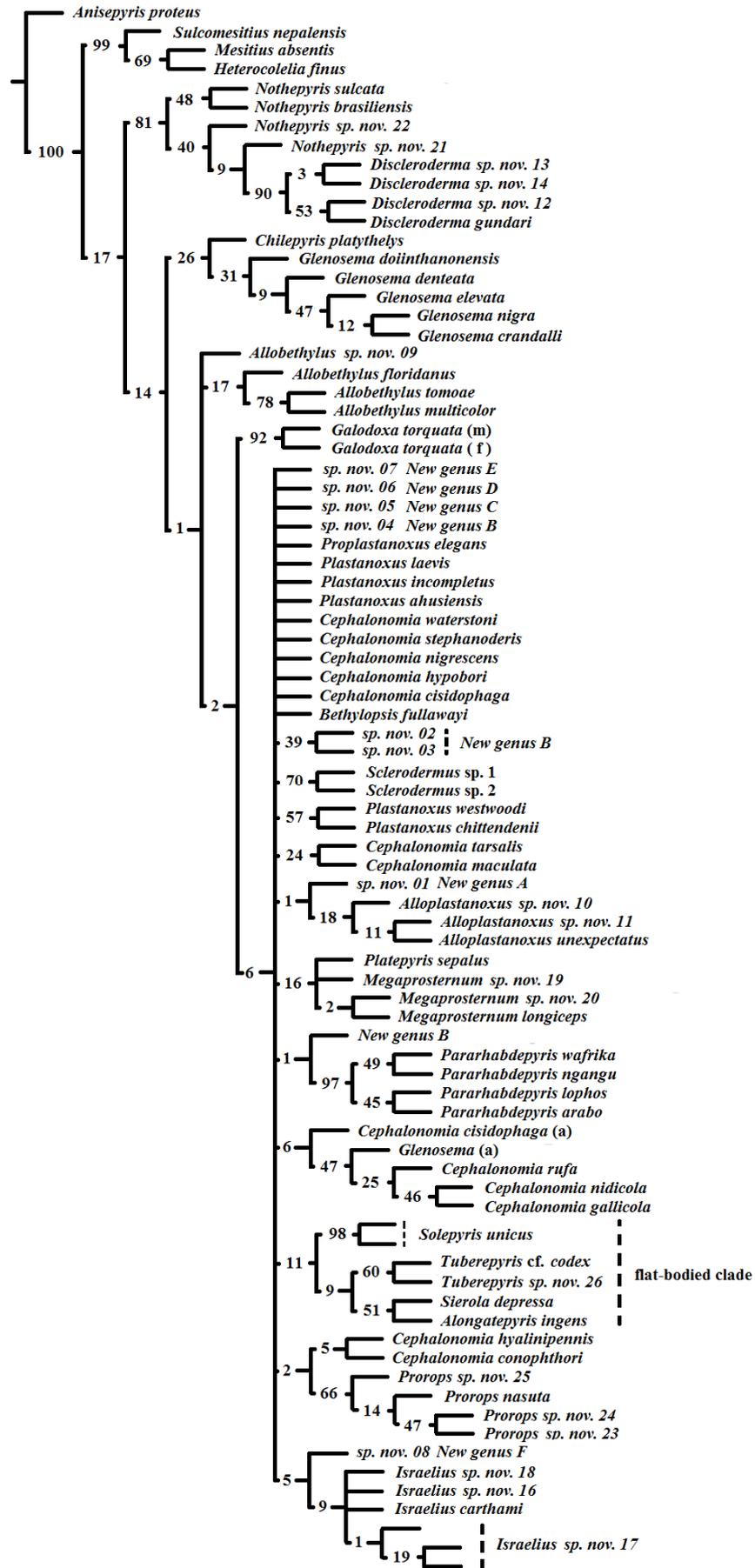


Figure 6. Symmetric resampling support, GC values, 2,000 replicates, cut=1, (P=33).

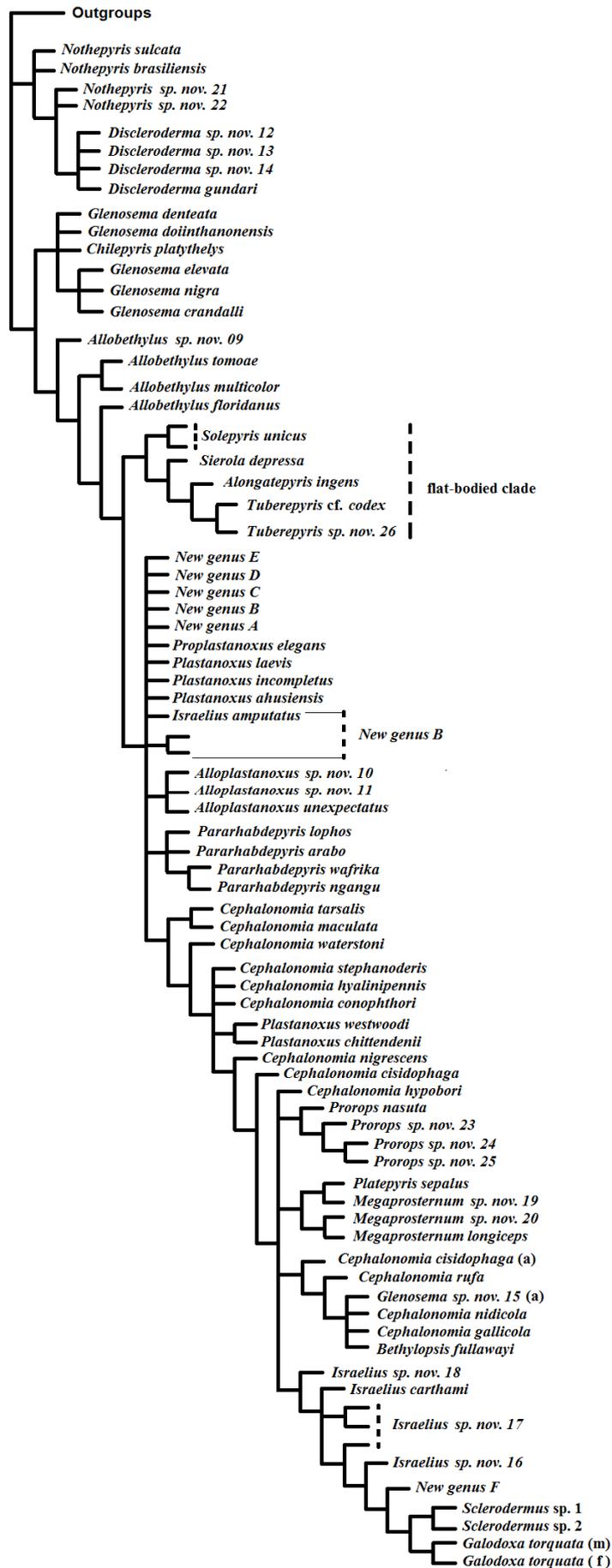


Figure 7. Morphology consensus, based on 30 MPTs obtained by New Technologies and EW with 2,000 replicates.



Figure 8. Mapping of selected characters. A. character 22 (number of antennal flagellomeres); B. character 45 (notauli presence).

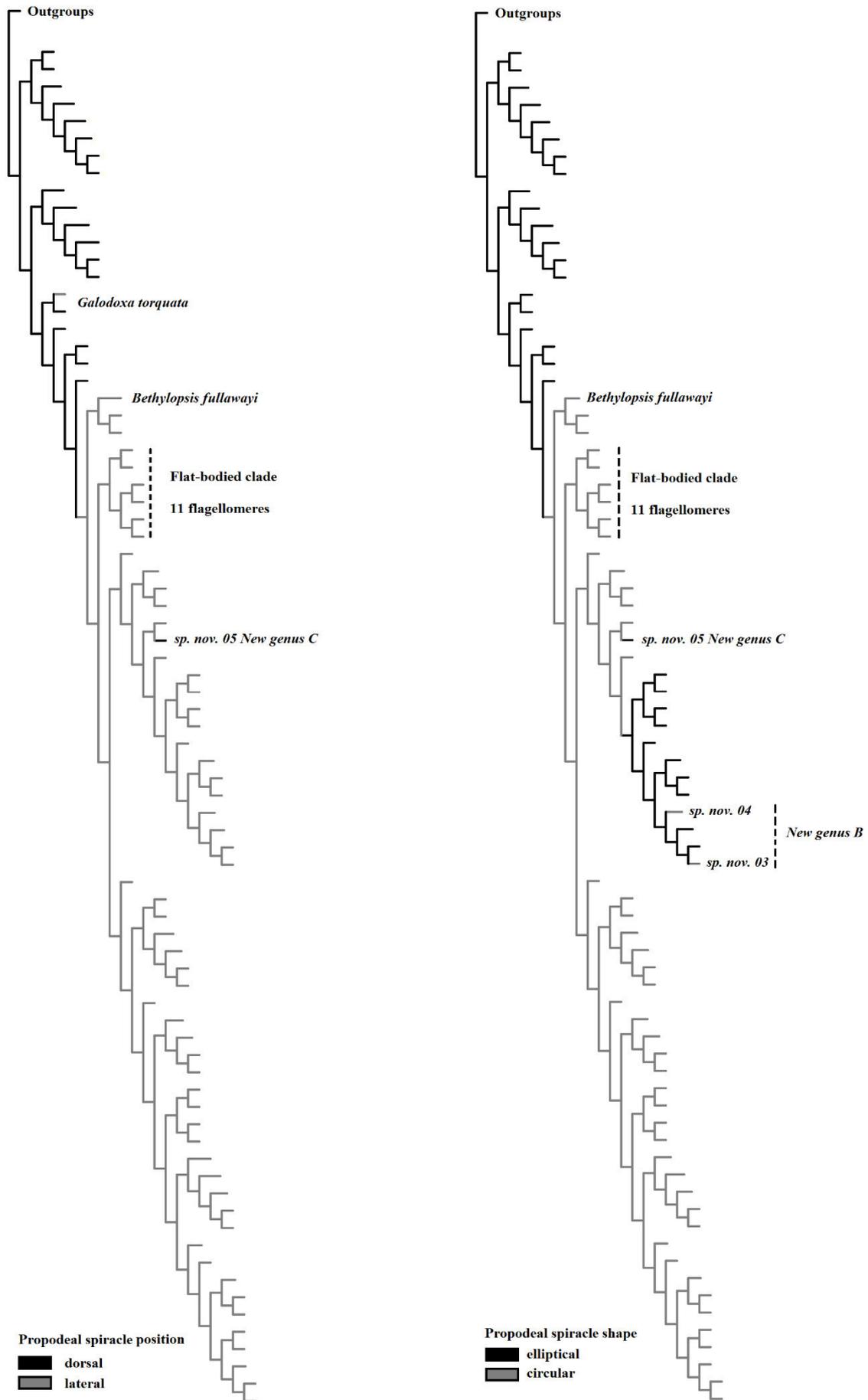


Figure 9. Mapping of selected characters. A. character 65 (spiracle position); B. character 66 (spiracle shape).



Figure 10. Mapping of selected characters. A. character 79 (presence of C vein); B. character 87 (presence of r-rs vein).

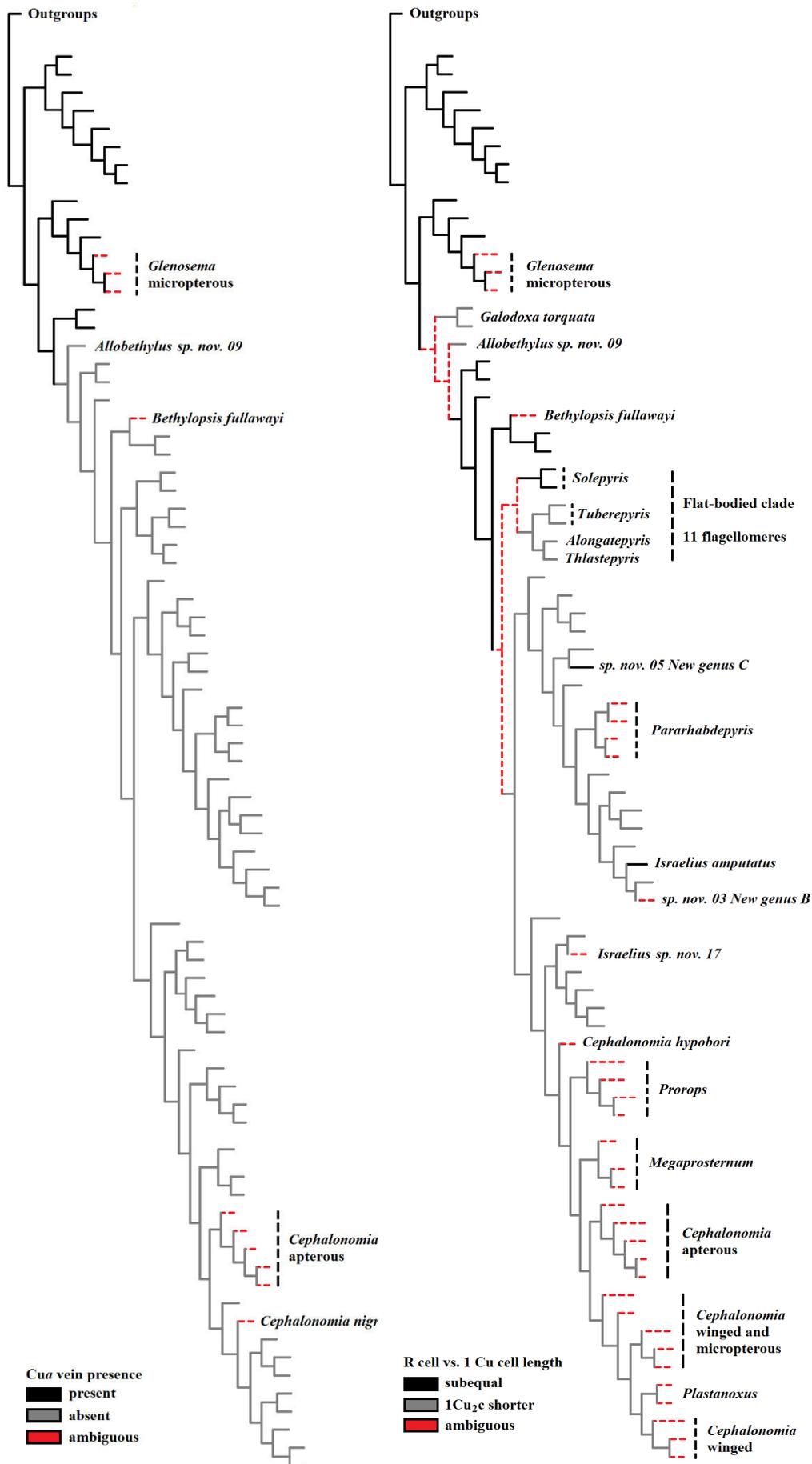
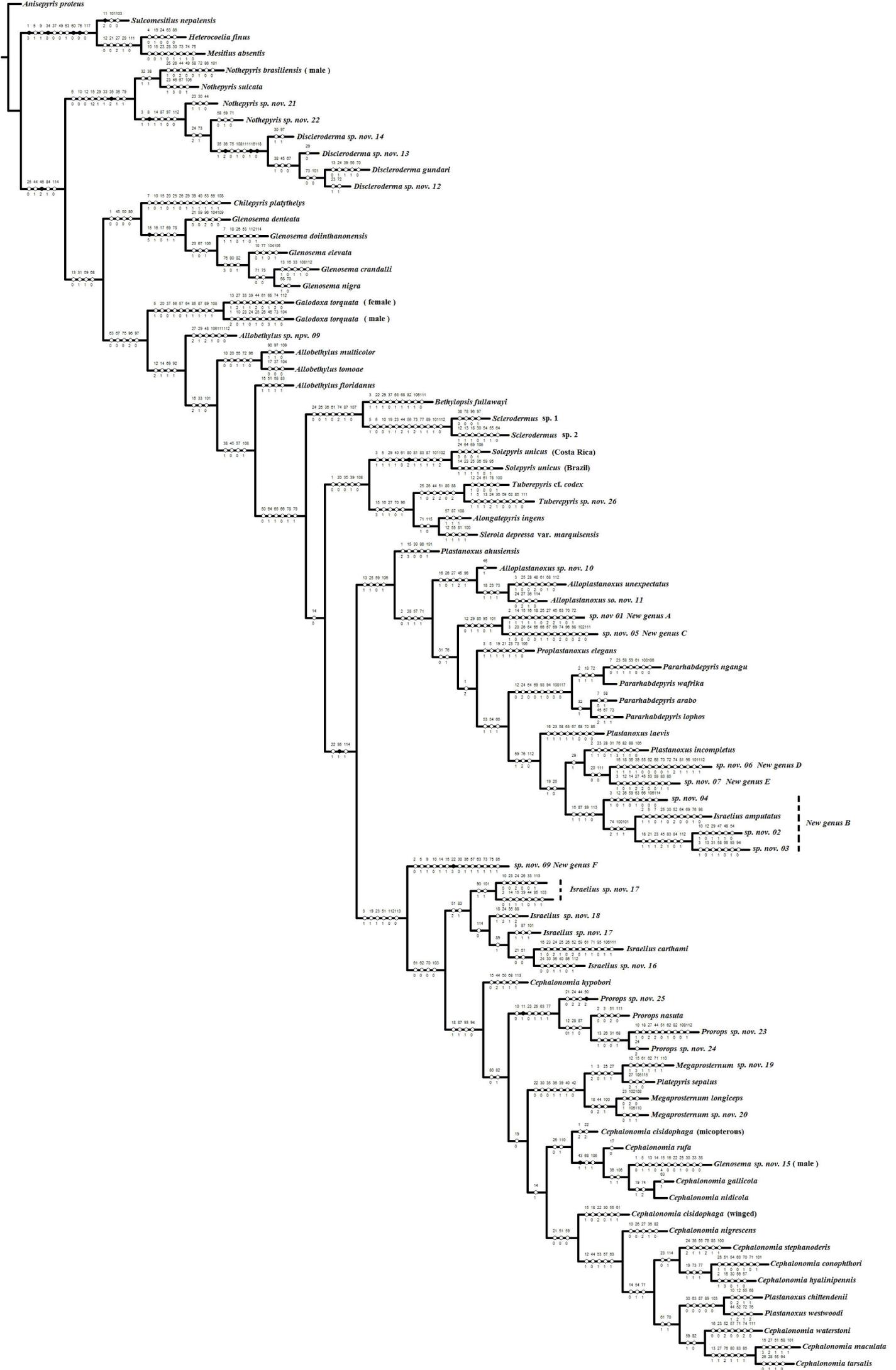


Figure 11. Mapping of selected characters. A. character 92 (presence of Cua vein); B. character 98 (R cell vs. 1Cu cell length).

Figure 12. MPT under implied weighting with characters and states of character (next page).



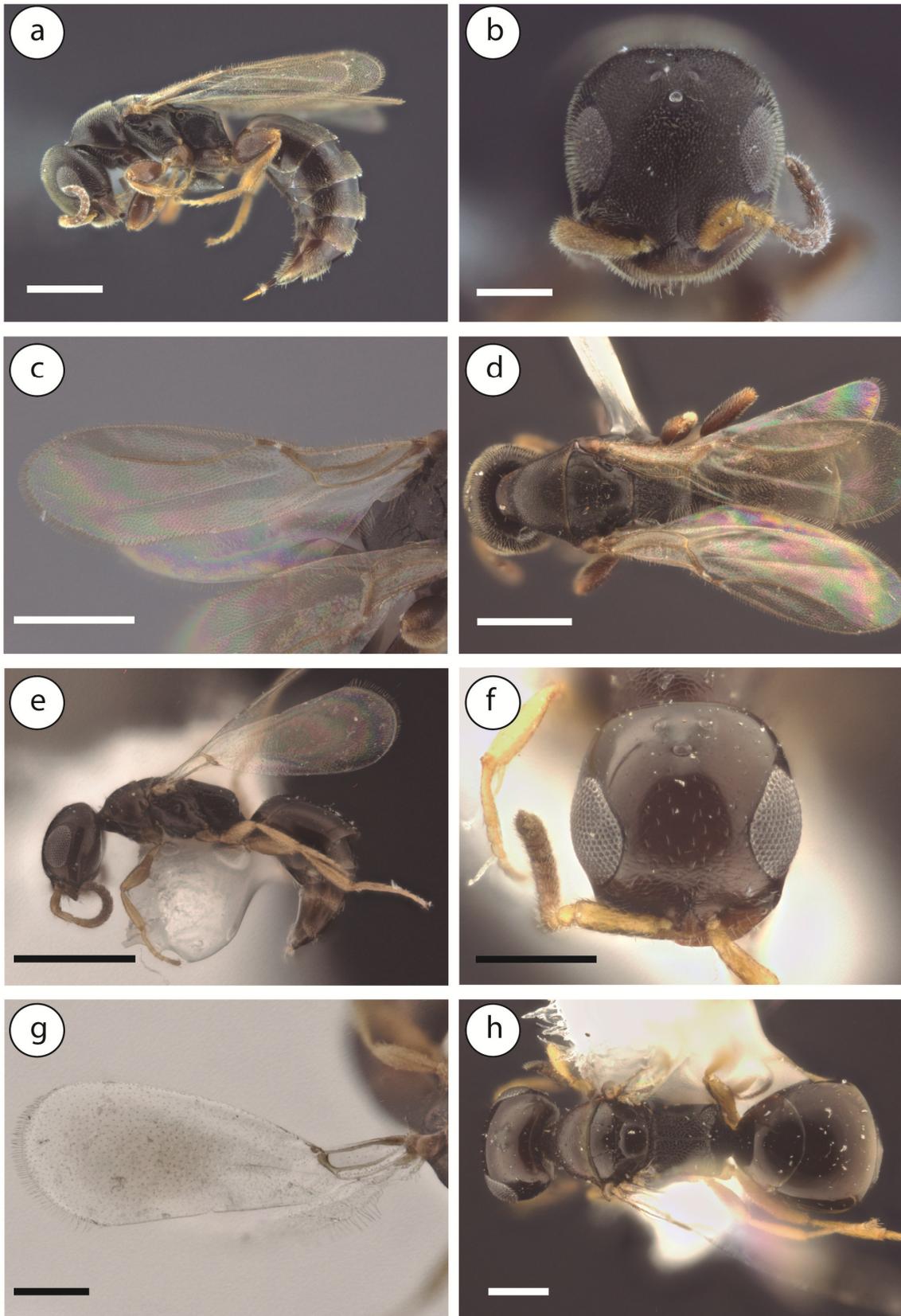


Figure 13. New genus A, sp. nov. 01. A. habitus, lateral (500 μm); B. head, dorsal (200 μm); C. forewing (500 μm); D. thorax, dorsal (500 μm). New genus B, sp. nov. 02. E. habitus, lateral (500 μm); F. head, dorsal (200 μm), G. forewing (200 μm); H. thorax, lateral (200 μm).

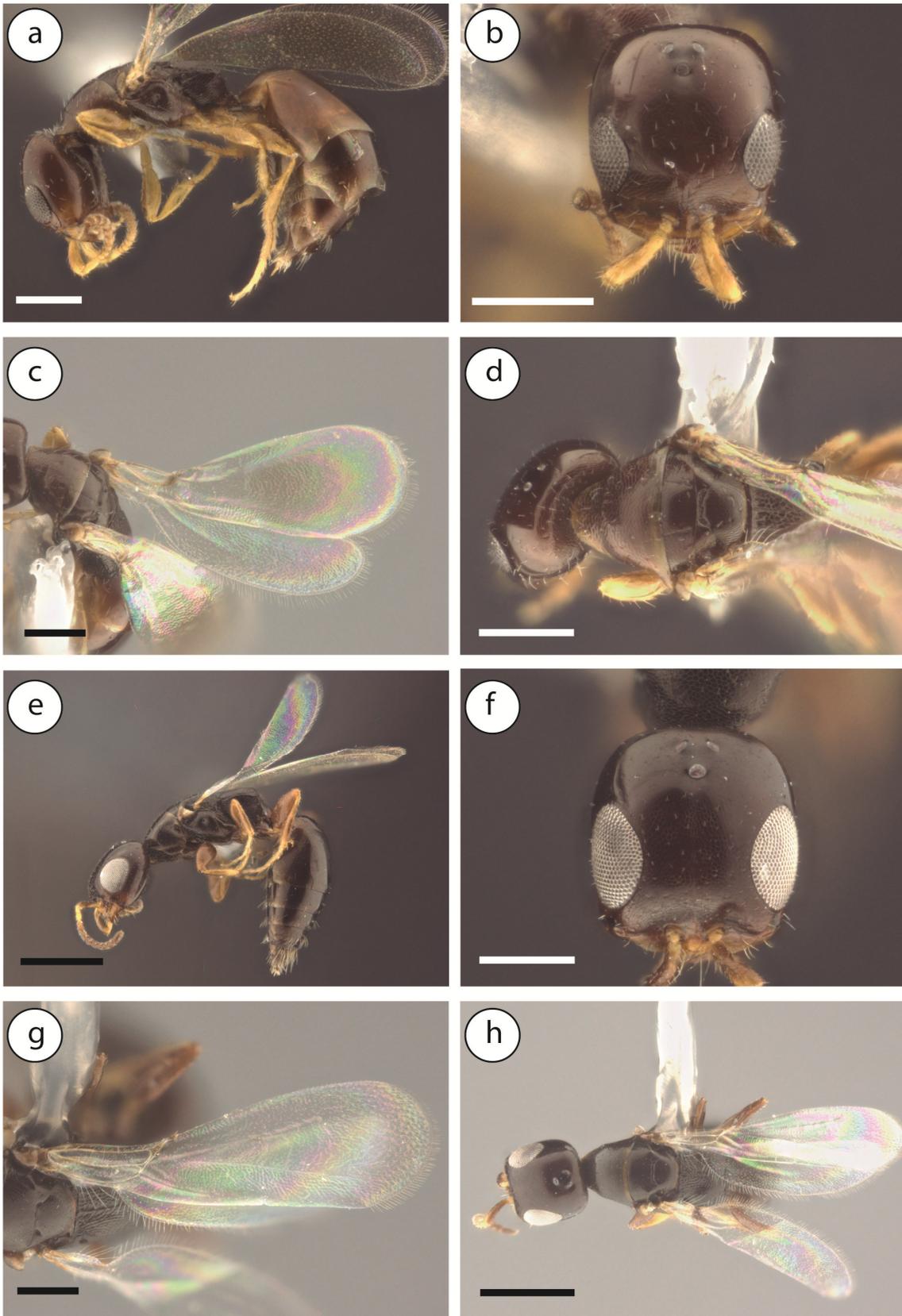


Figure 14. New genus B, sp. nov. 03. A. habitus, lateral (200 μ m); B. head, dorsal (200 μ m); C. forewing (200 μ m); D. thorax, dorsal (200 μ m). New genus B, sp. nov. 04. E. habitus, lateral (500 μ m); F. head, dorsal (200 μ m), G. forewing (200 μ m); H. thorax, dorsal (500 μ m).

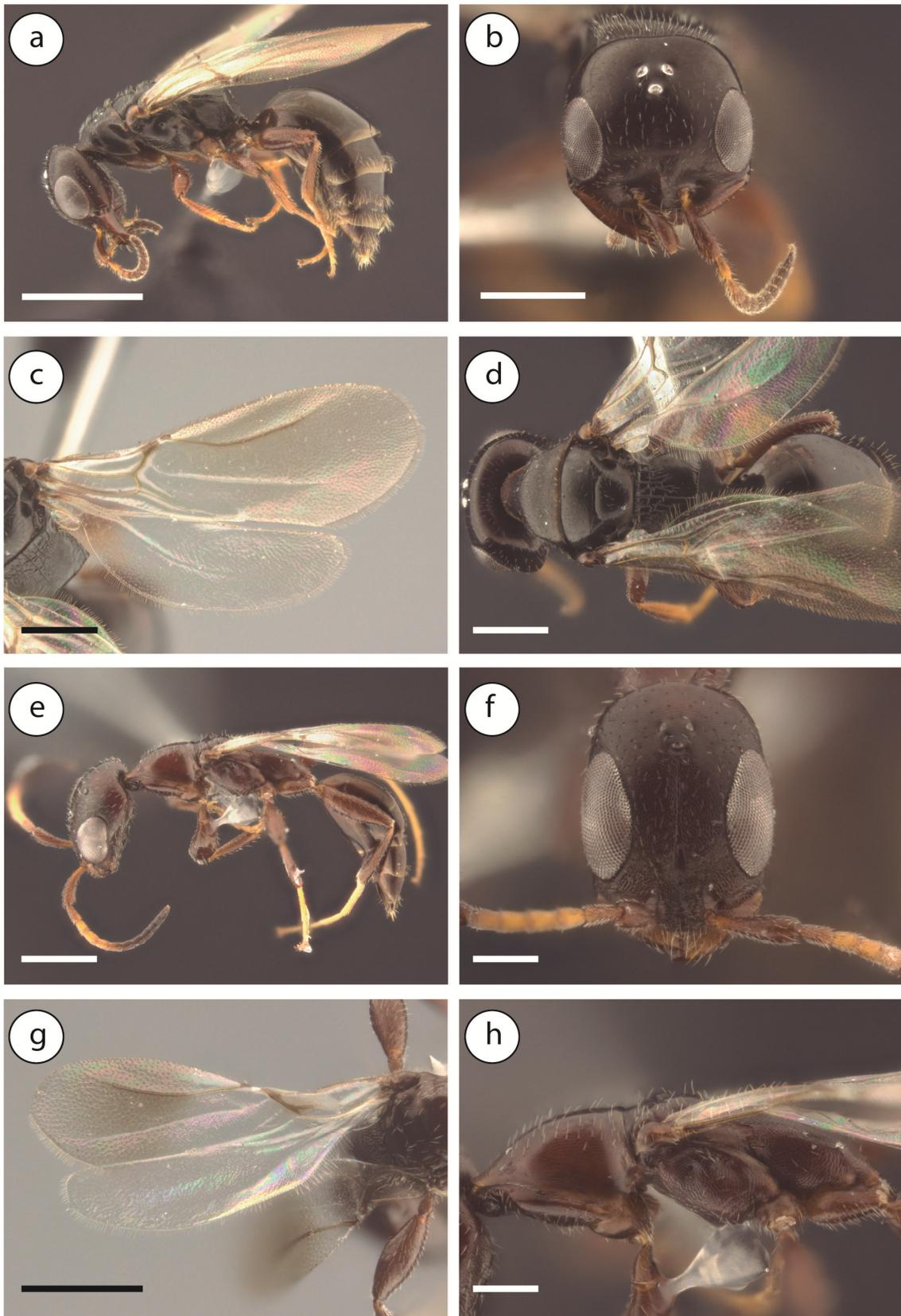


Figure 15. New genus C, sp. nov. 05. A. habitus, lateral (1mm); B. head, dorsal view (500 μ m); C. forewing (500 μ m); D. thorax, dorsal (500 μ m). New genus D, sp. nov. 06. E. habitus, lateral (500 μ m); F. head, dorsal (200 μ m), G. forewing (500 μ m); H. thorax, lateral (200 μ m).

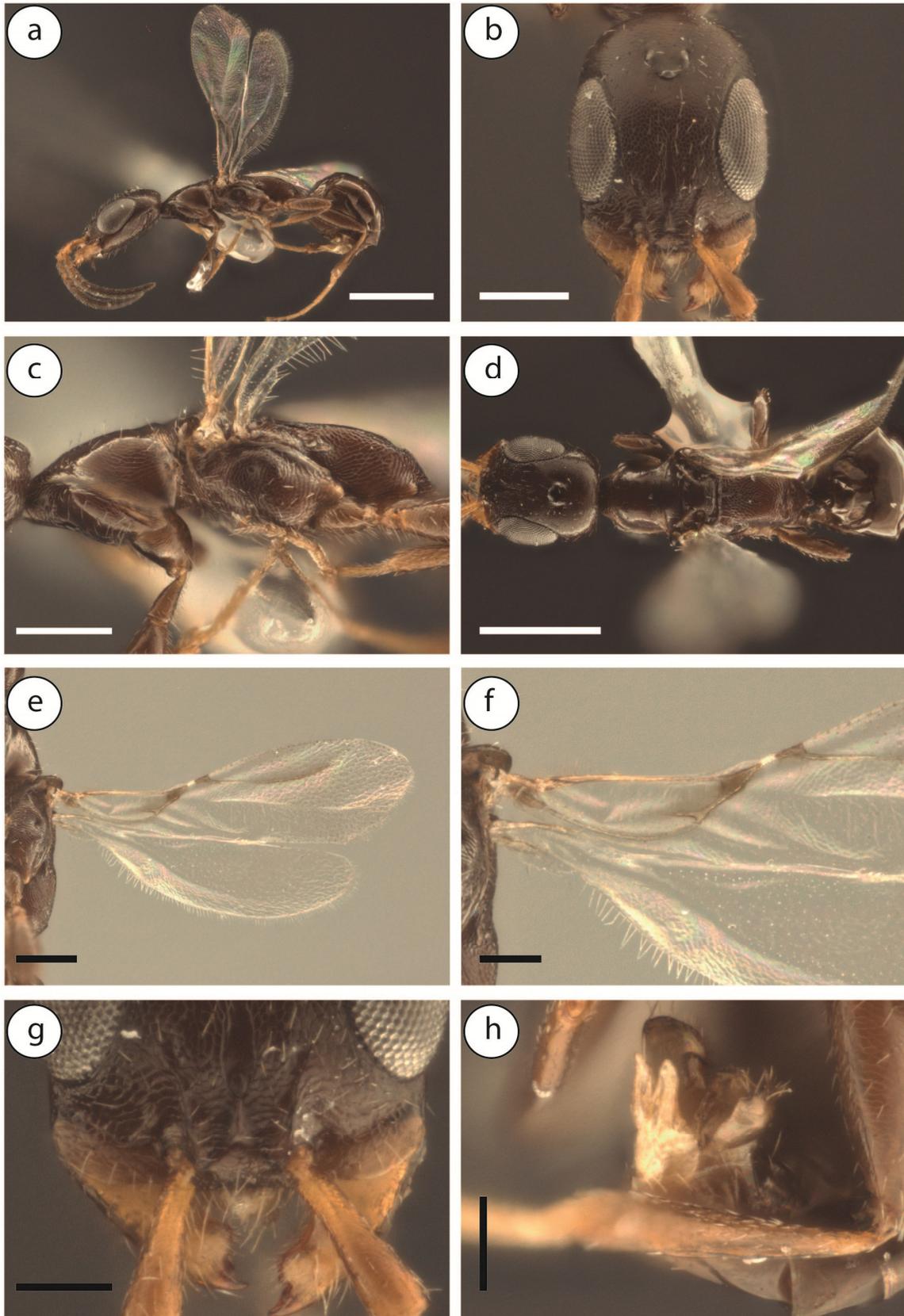


Figure 16. New genus D, sp. nov. 06. Male. A. habitus, lateral (500 μm); B. head, dorsal (200 μm); C. forewing (200 μm); D. thorax, dorsal (500 μm); E. forewing (200 μm); F. forewing cells, detail (100 μm); G. frontal process, detail (100 μm); H. genitalia, dorso-lateral view (100 μm).

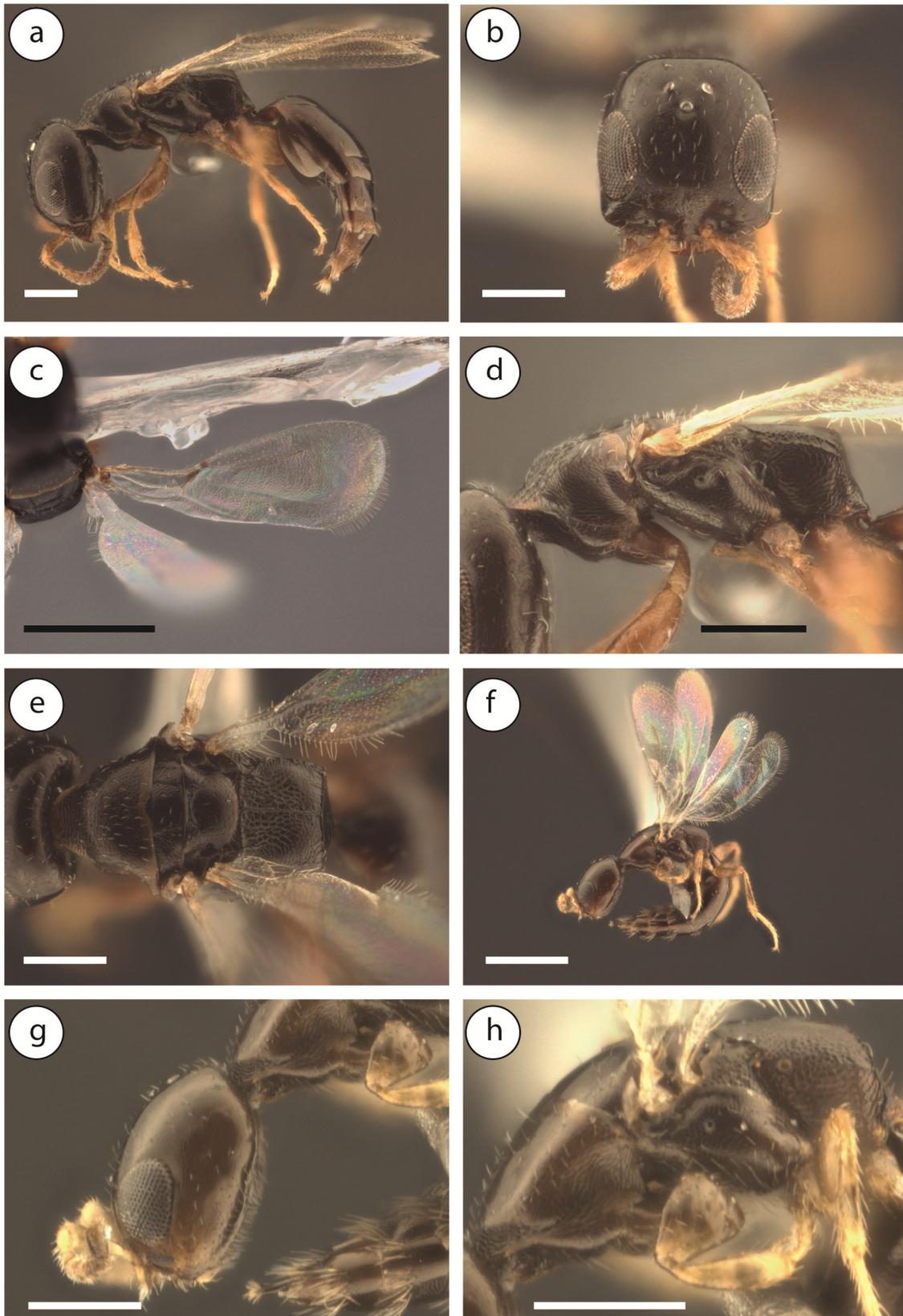


Figure 17. New genus E, sp. nov. 07. A. habitus, lateral (200 μm); B. head, dorsal (200 μm); C. forewing (500 μm); D. thorax, lateral (200 μm); E. thorax, dorsal (200 μm). New genus F, sp. nov. 06. F. habitus, lateral (500 μm); G. head, lateral (200 μm), H. thorax, lateral (200 μm).

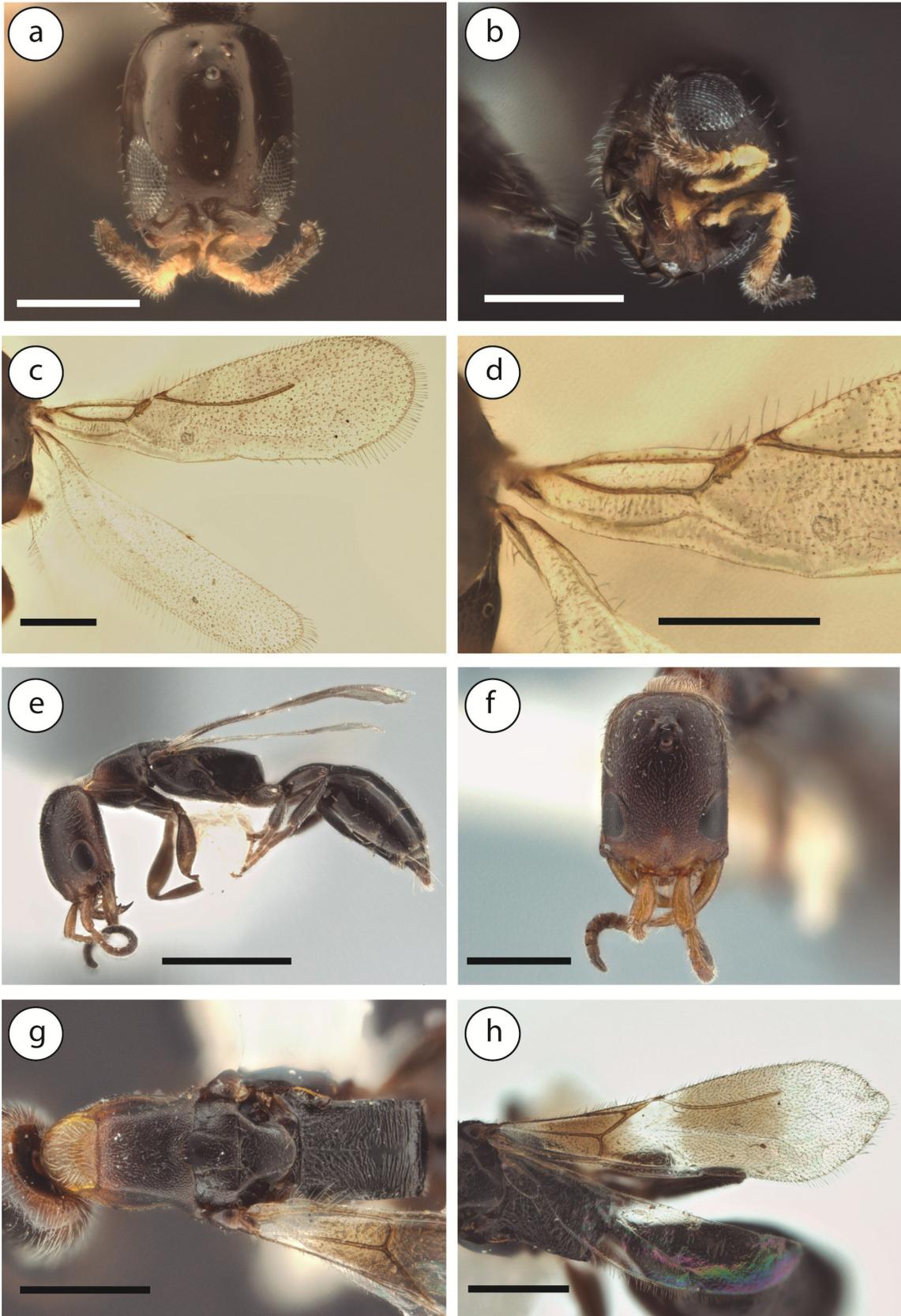


Figure 18. New genus *F*, sp. nov. 08. **A.** head, dorsal (1mm); **B.** antenna, detail seven flagellomeres (200 μ m); **C.** wings (200 μ m); **D.** forewing cell, detail (200 μ m). *Allobethylus* sp. nov. 09. **E.** habitus, lateral (1 mm), **F.** head, dorsal (500 μ m); **G.** thorax, dorsal (500 μ m); **H.** wings (500 μ m).

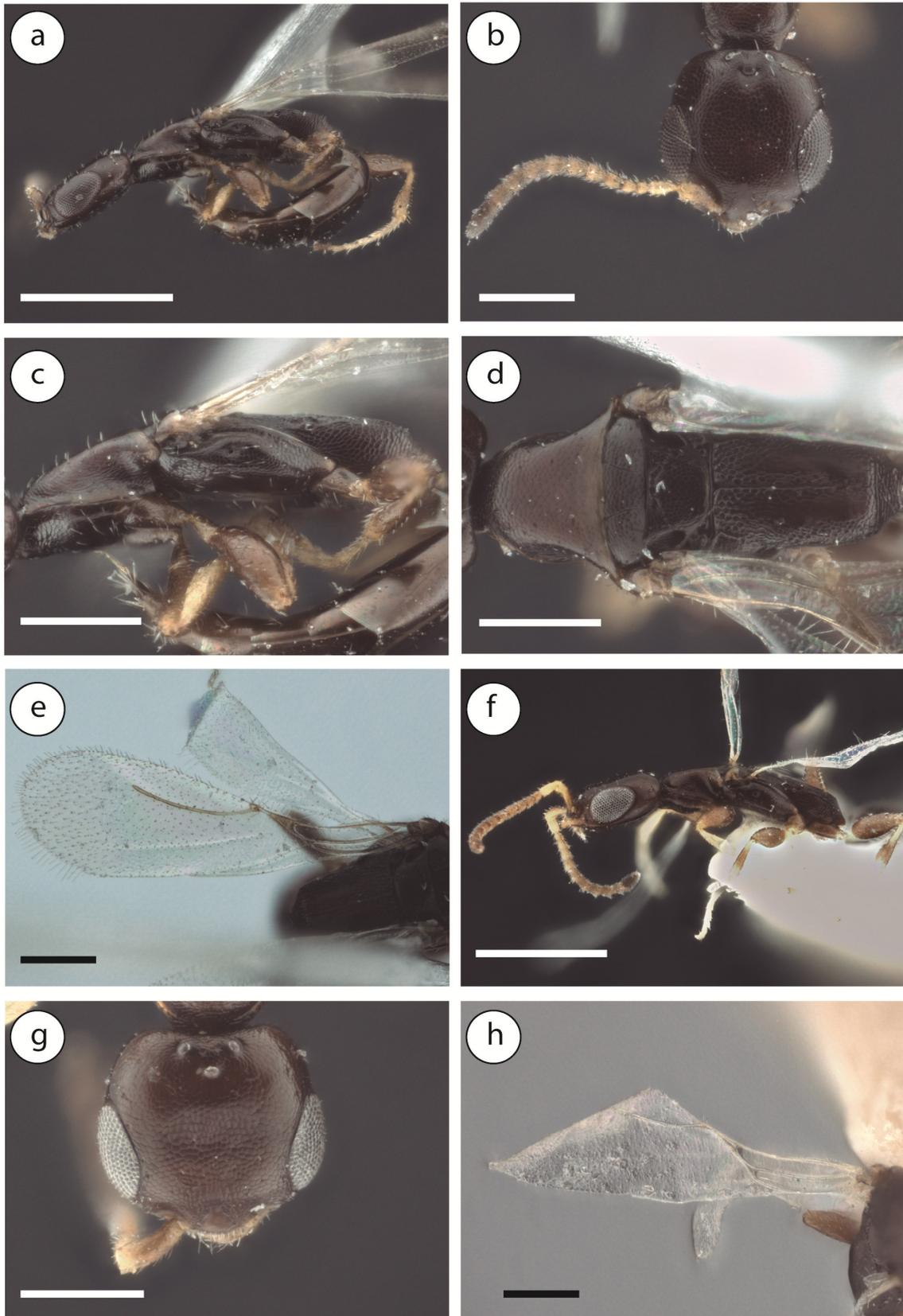


Figure 19. *Alloplastanoxus* sp. nov. 10. A. habitus, lateral (500 μ m); B. head, dorsal (200 μ m); C. thorax, lateral (200 μ m); D. thorax, dorsal (200 μ m); E. forewing (200 μ m). *Alloplastanoxus* sp. nov. 11. F. habitus, lateral (500 μ m); head, dorsal (200 μ m), forewing (200 μ m).

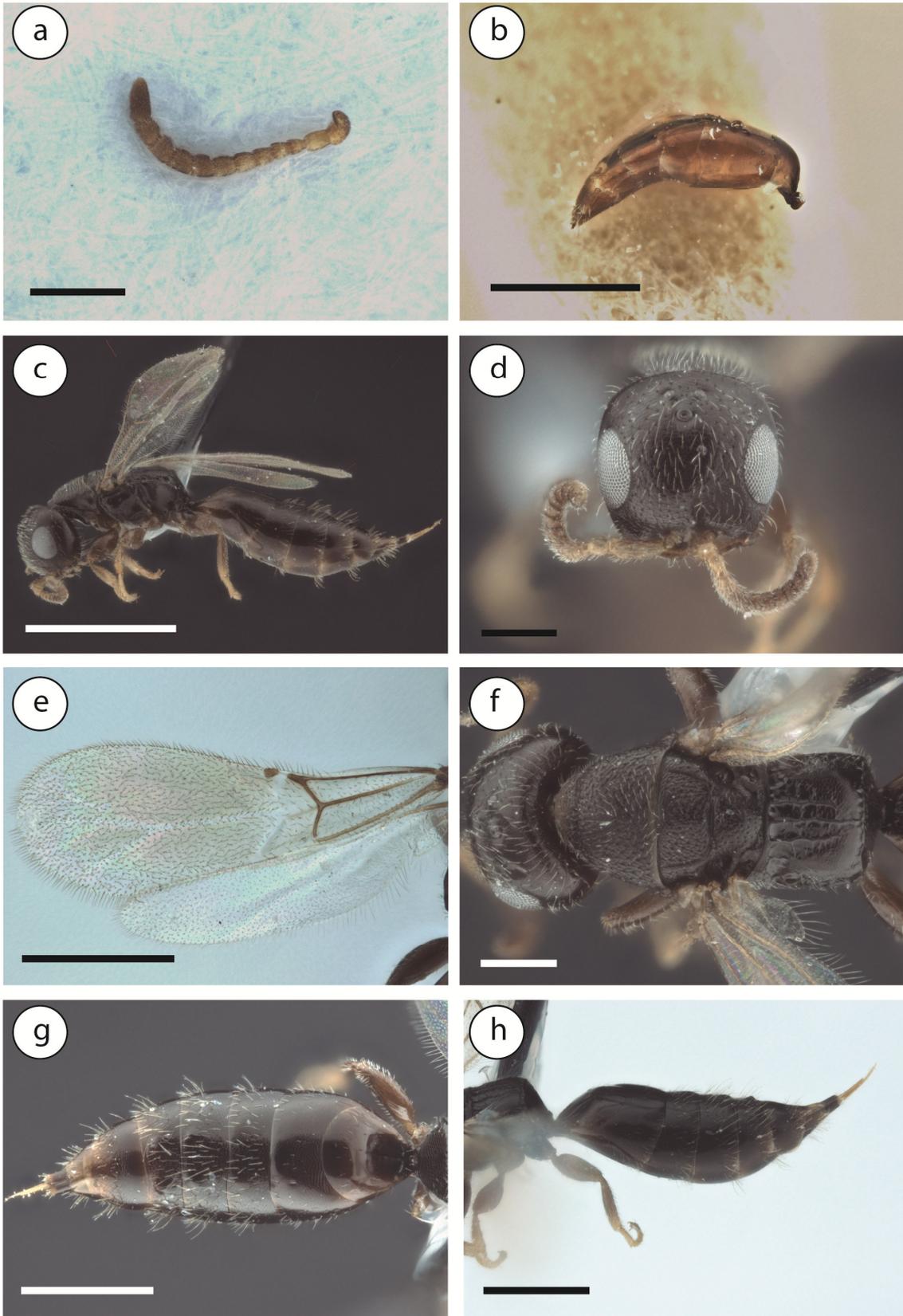


Figure 20. *Alloplastanoxus* sp. nov. 11. A. antenna (200 μm); B. metasoma (500 μm). *Discleroderma* sp. nov. 12.; C. habitus, lateral (500 μm); D. head, dorsal (200 μm); E. wings (500 μm); F. thorax, dorsal (200 μm); G. metasoma, dorsal (500 μm); H. metasoma, lateral (250 μm).

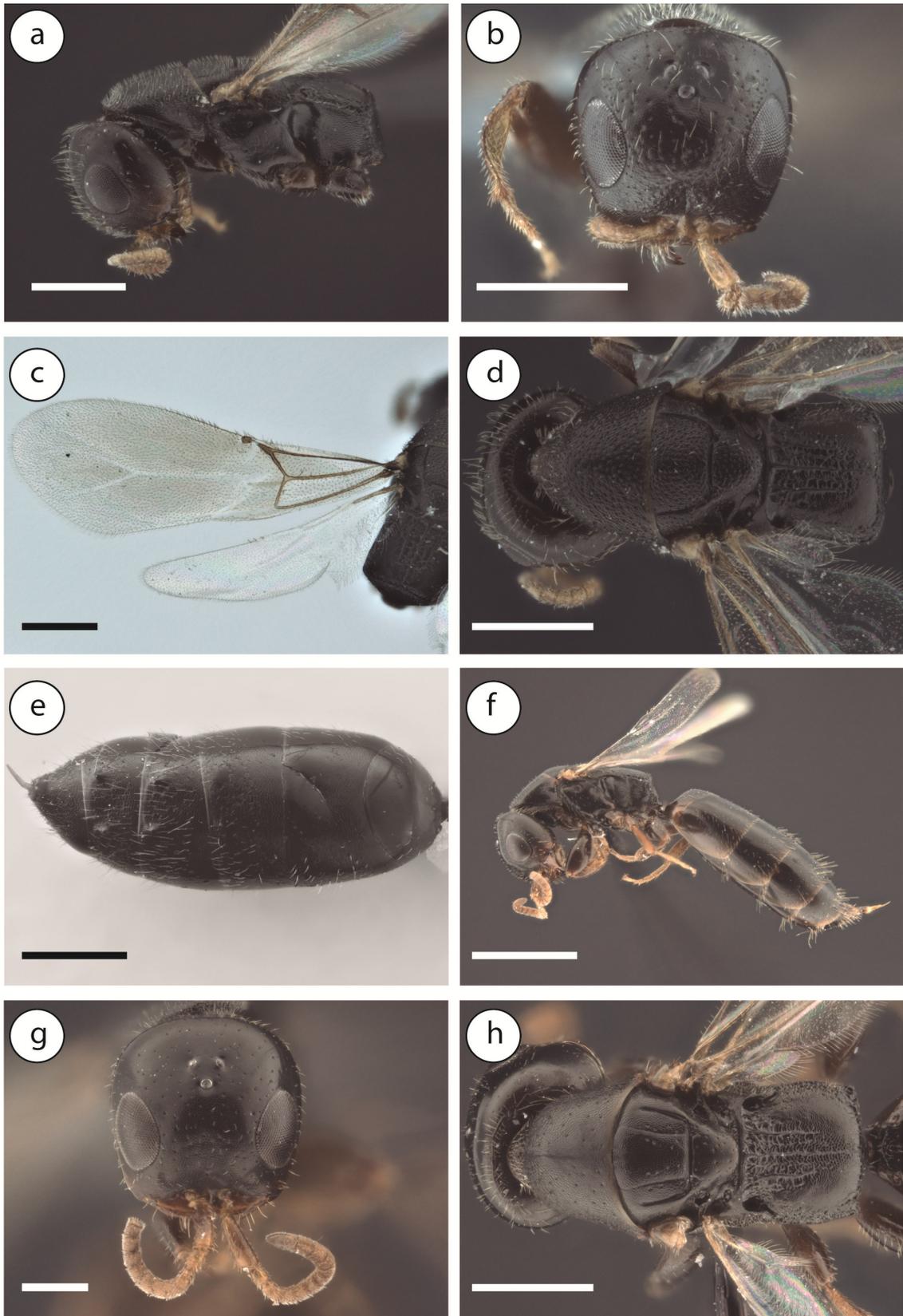


Figure 21. *Discleroderma* sp. nov. 13. A. habitus, lateral (500 μ m); B. head, dorsal (500 μ m); C. forewing (500 μ m); D. thorax, dorsal (500 μ m). E. metasoma, dorsal (500 μ m). *Discleroderma* sp. nov. 14. F. habitus, lateral (1 mm); G. head, dorsal (500 μ m); H. thorax, dorsal (500 μ m).

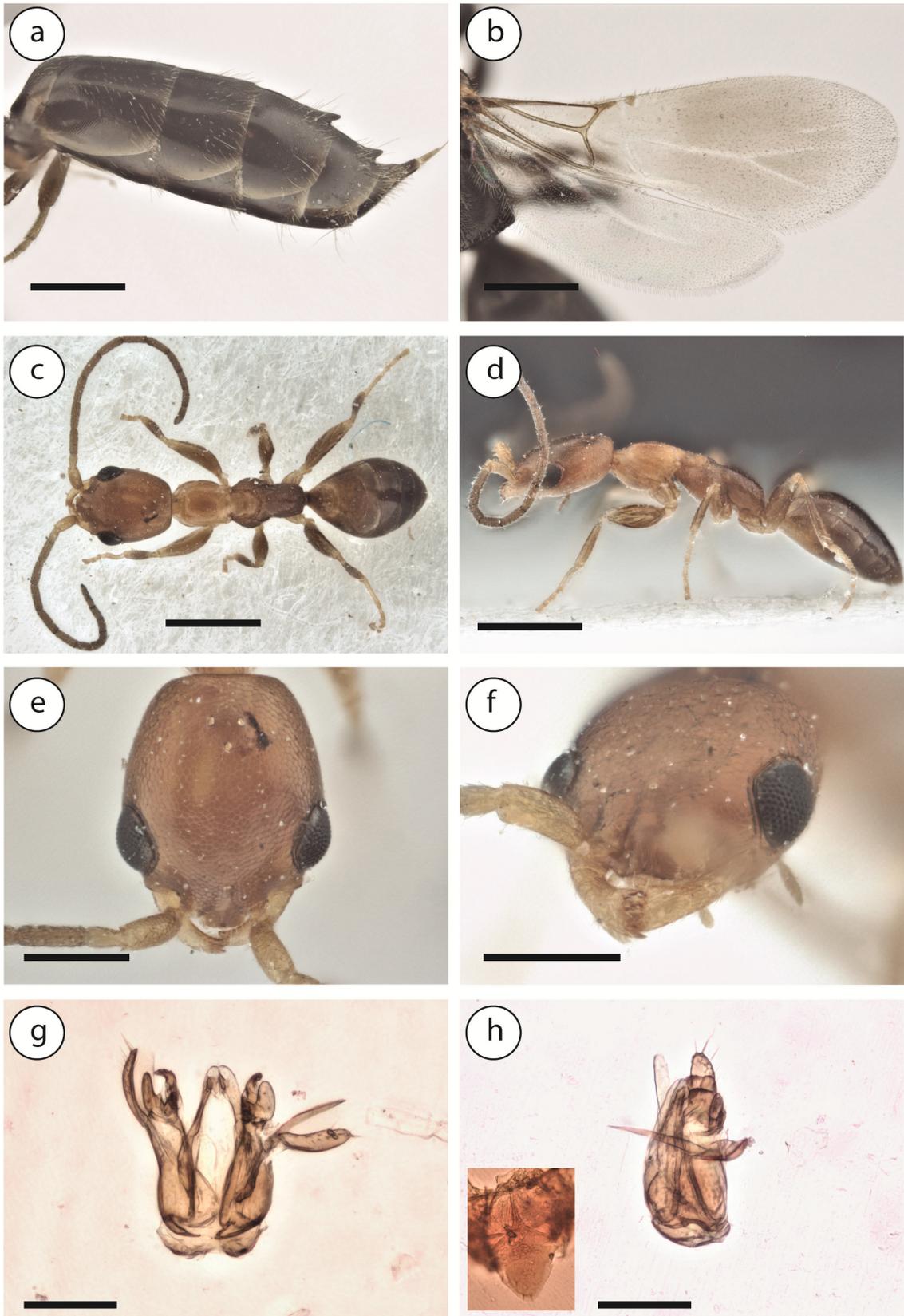


Figure 22. *Discleroderma* sp. nov. 14. A. metasoma, lateral (500 μm); B. wings (500 μm). *Glenosema* sp. nov. 15, male. C. habitus, dorsal (500 μm); D. habitus, lateral (500 μm); E. head, dorsal (200 μm); F. mandible, detail (200 μm); G. genitalia, ventral (85 μm); H. genitalia, lateral (85 μm); subgenital plate (left box).

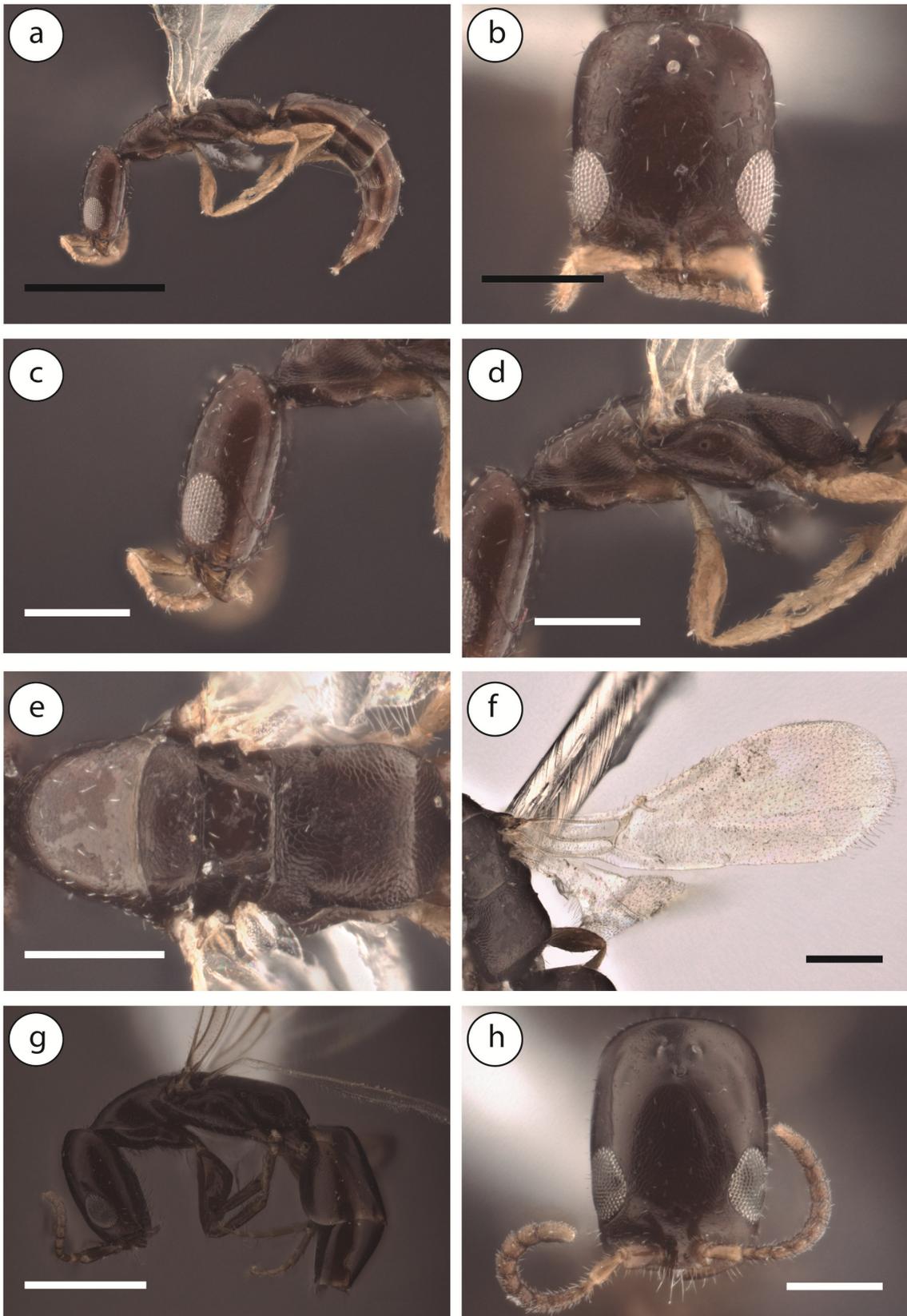


Figure 23. *Israelius* sp. nov. 16. A. habitus (200 μ m); B. head dorsal view (200 μ m); C. head, lateral (200 μ m); D. thorax lateral (200 μ m); E. thorax, dorsal (200 μ m); F. forewing (200 μ m). *Israelius* sp. nov. 17. G. habitus, lateral (500 μ m); H. head, dorsal (200 μ m).

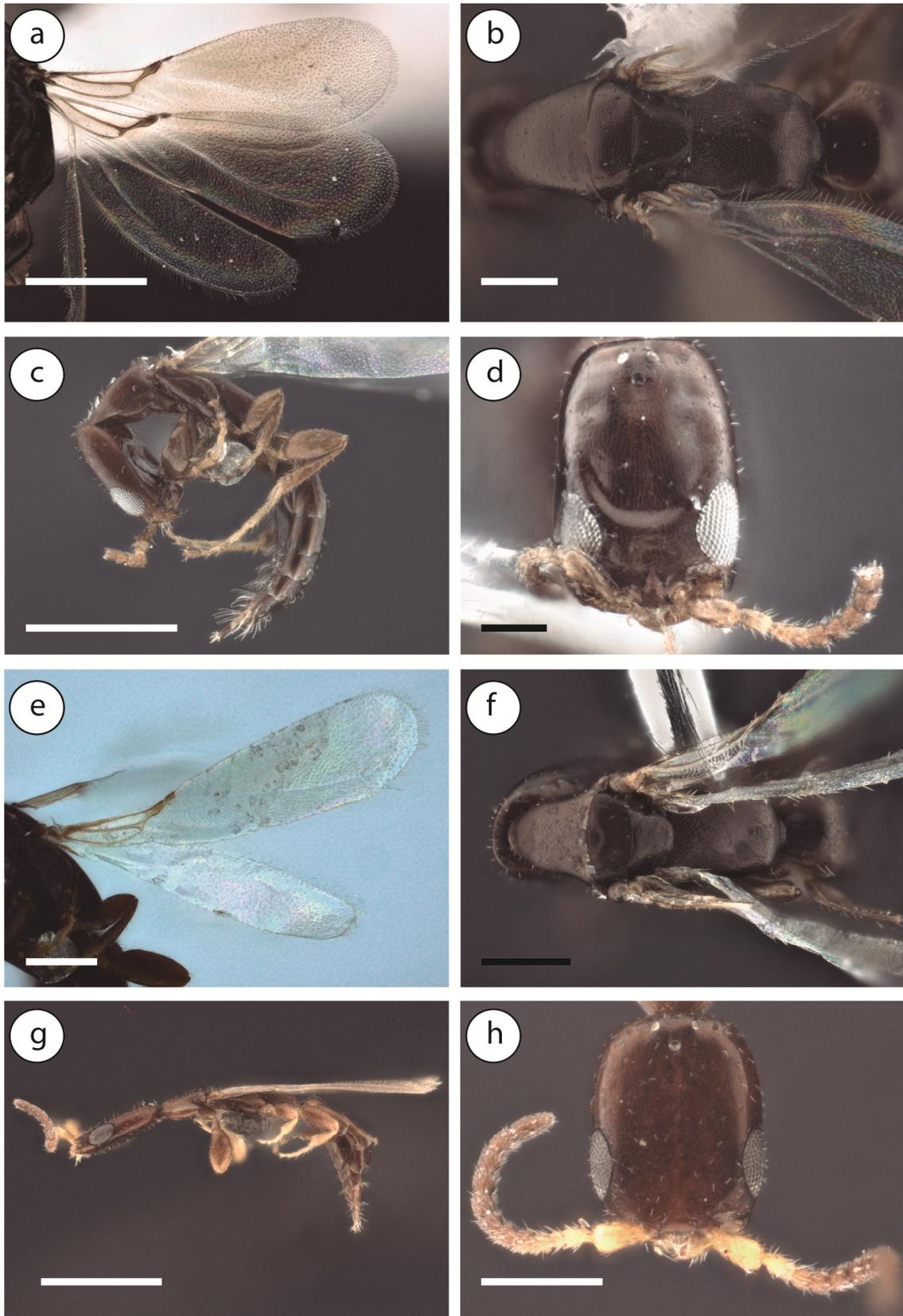


Figure 24. *Israelius* sp. nov. 17. A. wings (500 μm); B. thorax, dorsal (200 μm). *Israelius* sp. nov. 18. C. habitus (500 μm); D. head, dorsal (100 μm); E. wings (200 μm); F. thorax, dorsal (200 μm). *Megaprosternum* sp. nov. 19. G. habitus, lateral (500 μm); H. head dorsal view (200 μm).

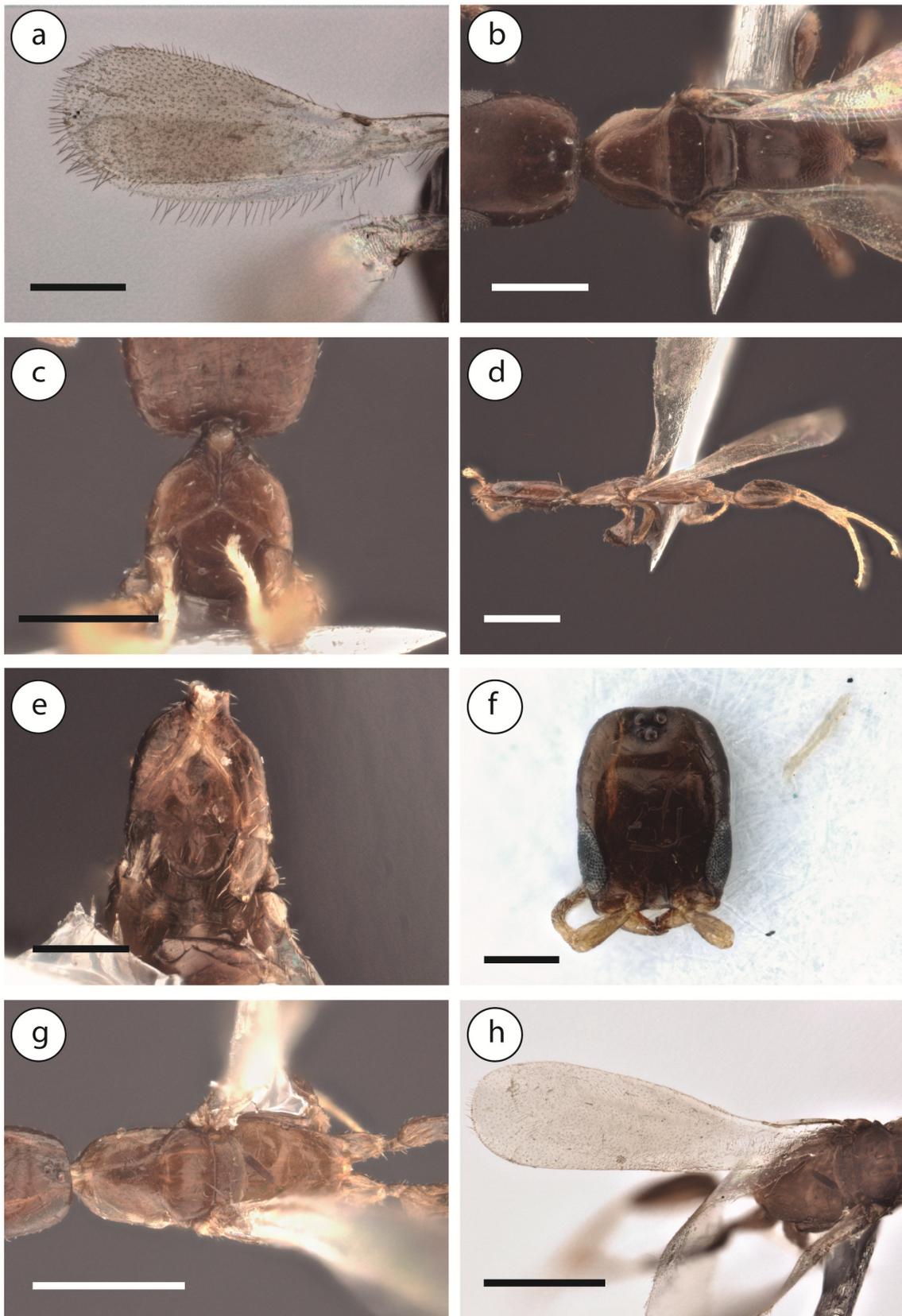


Figure 25. *Megaprosternum* sp. nov. 19. A. forewing (200 μ m); B. thorax, dorsal (200 μ m); C. prosternum (200 μ m). *Megaprosternum* sp. nov. 20. D. habitus, lateral (500 μ m); E. prosternum (200 μ m); F. head, dorsal (200 μ m); G. thorax, lateral (500 μ m); H. forewing (200 μ m).

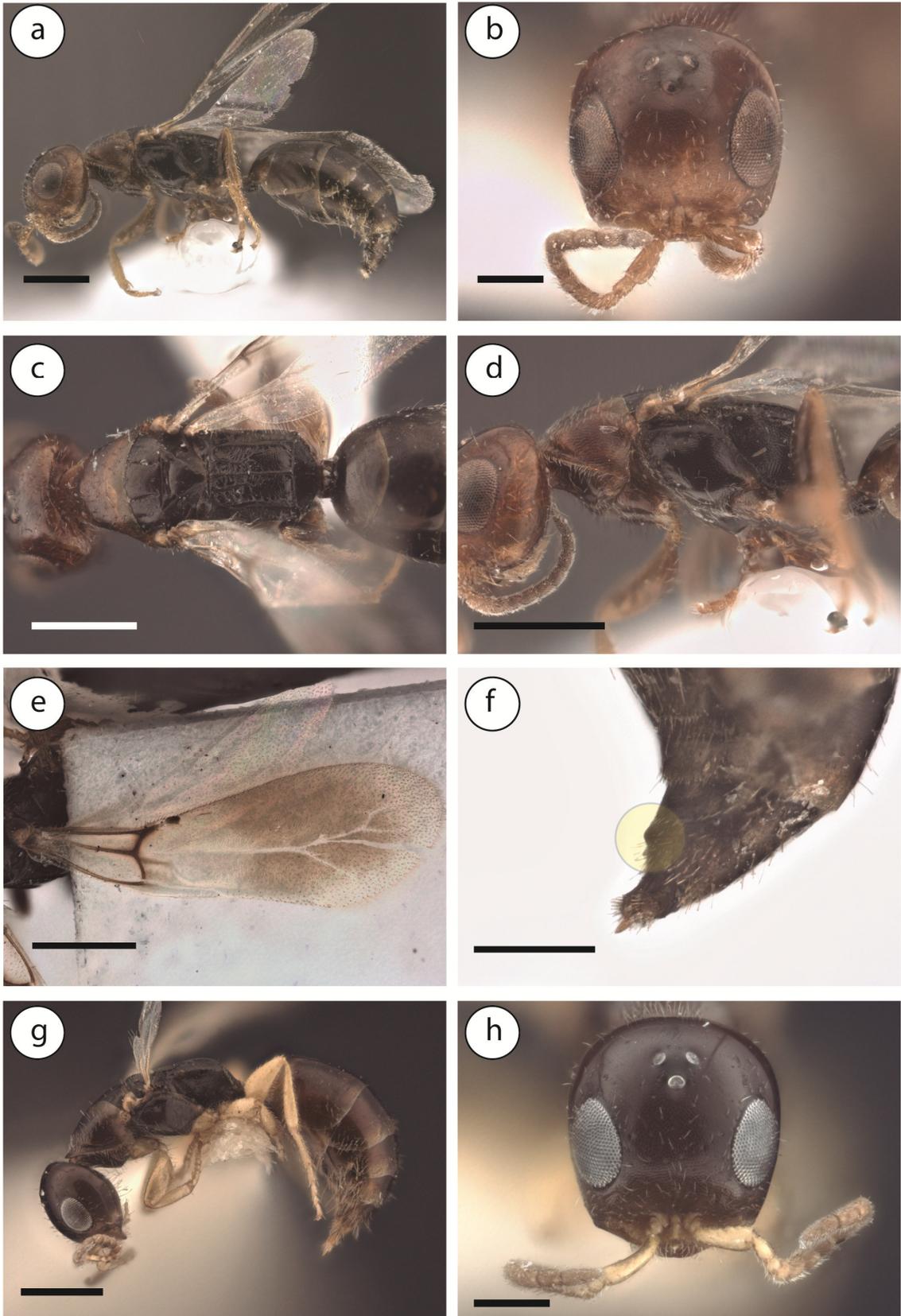


Figure 26. *Nothepyris* sp. nov. 21. A. habitus (500 μ m); B. head dorsal view (200 μ m); C. thorax, dorsal (500 μ m); D. thorax lateral (500 μ m); E. forewing (500 μ m); F. metasomal apex, sternal tubercle (yellow circle) (200 μ m). *Nothepyris* sp. nov. 22. G. habitus, lateral (500 μ m); H. head, dorsal (200 μ m).

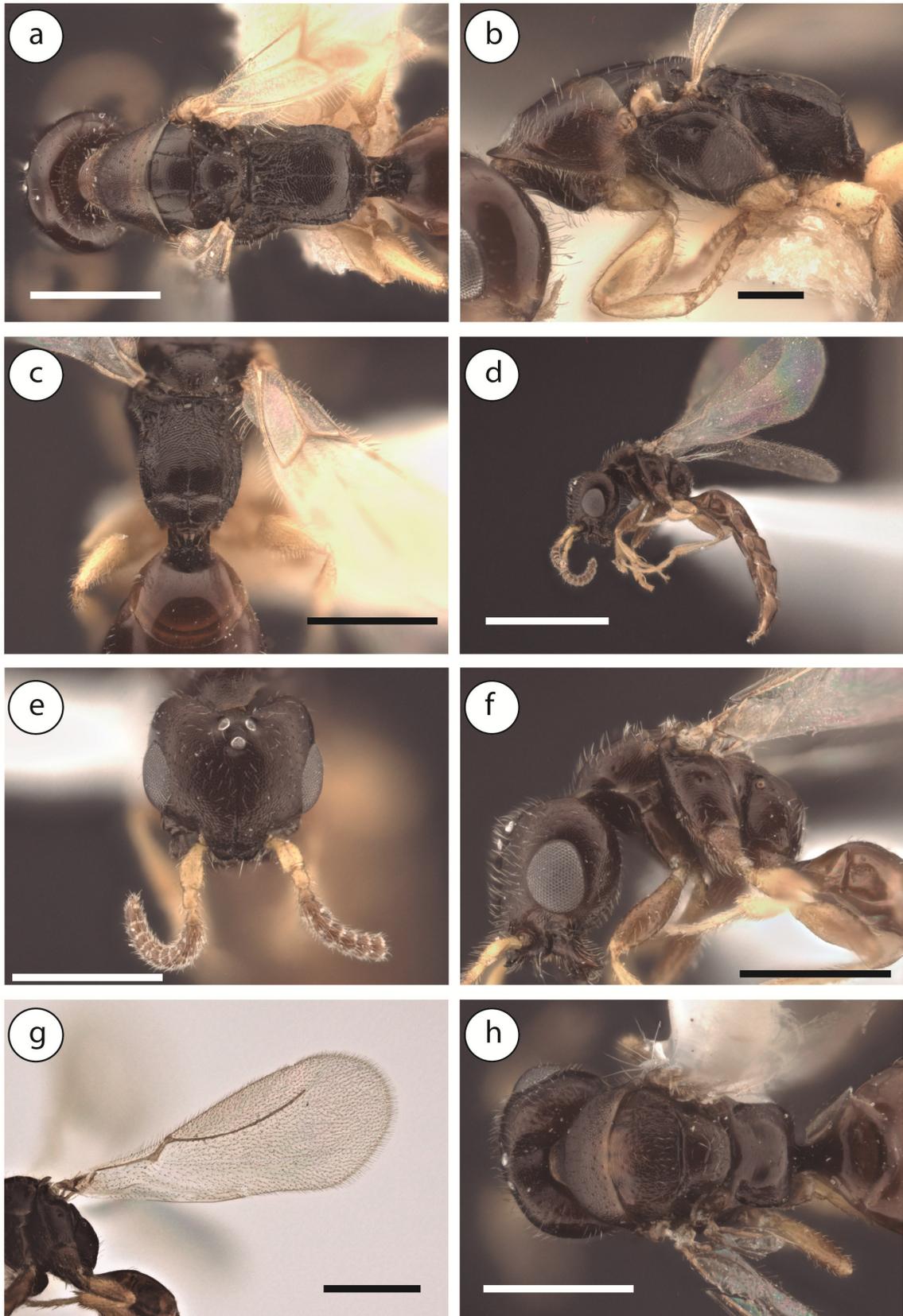


Figure 27. *Nothepyrus* sp. nov. 22. A. thorax, dorsal (500 μm); B. thorax, lateral (200 μm); C. metapectal-propodeal complex (500 μm). *Prorops* sp. nov. 23; D. habitus, lateral (1 mm); E. head, dorsal (500 μm); F. thorax, lateral (500 μm); G. forewing (500 μm); H. thorax,

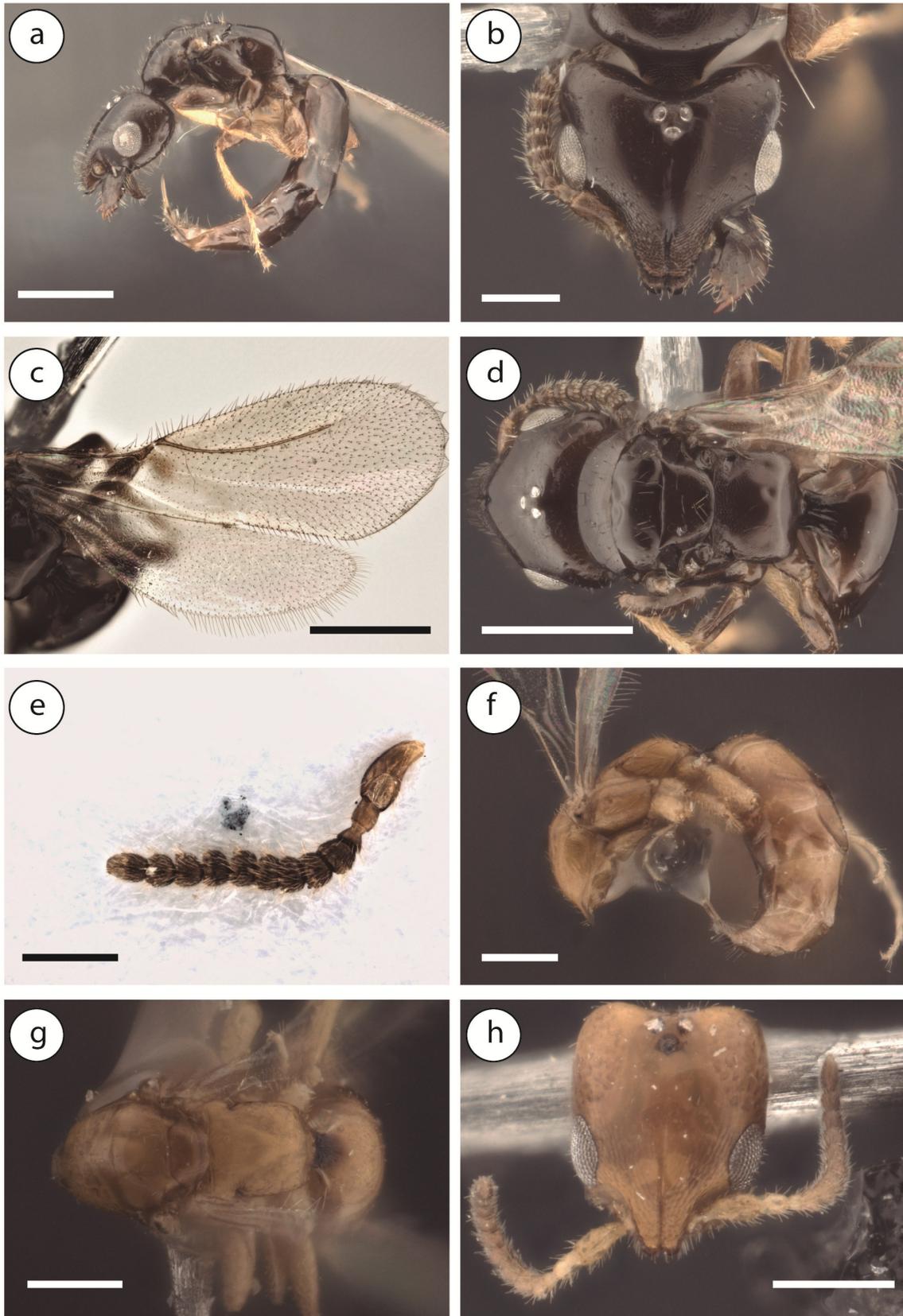


Figure 28. *Prorops* sp. nov. 24. A. habitus, lateral (500 μ m); B. head, dorsal (200 μ m); C. forewing (500 μ m); D. thorax, dorsal (500 μ m); E. antenna (200 μ m). *Prorops* sp. nov. 25. F. habitus, lateral (200 μ m), G. thorax, dorsal (200 μ m); H. head, dorsal (200 μ m).

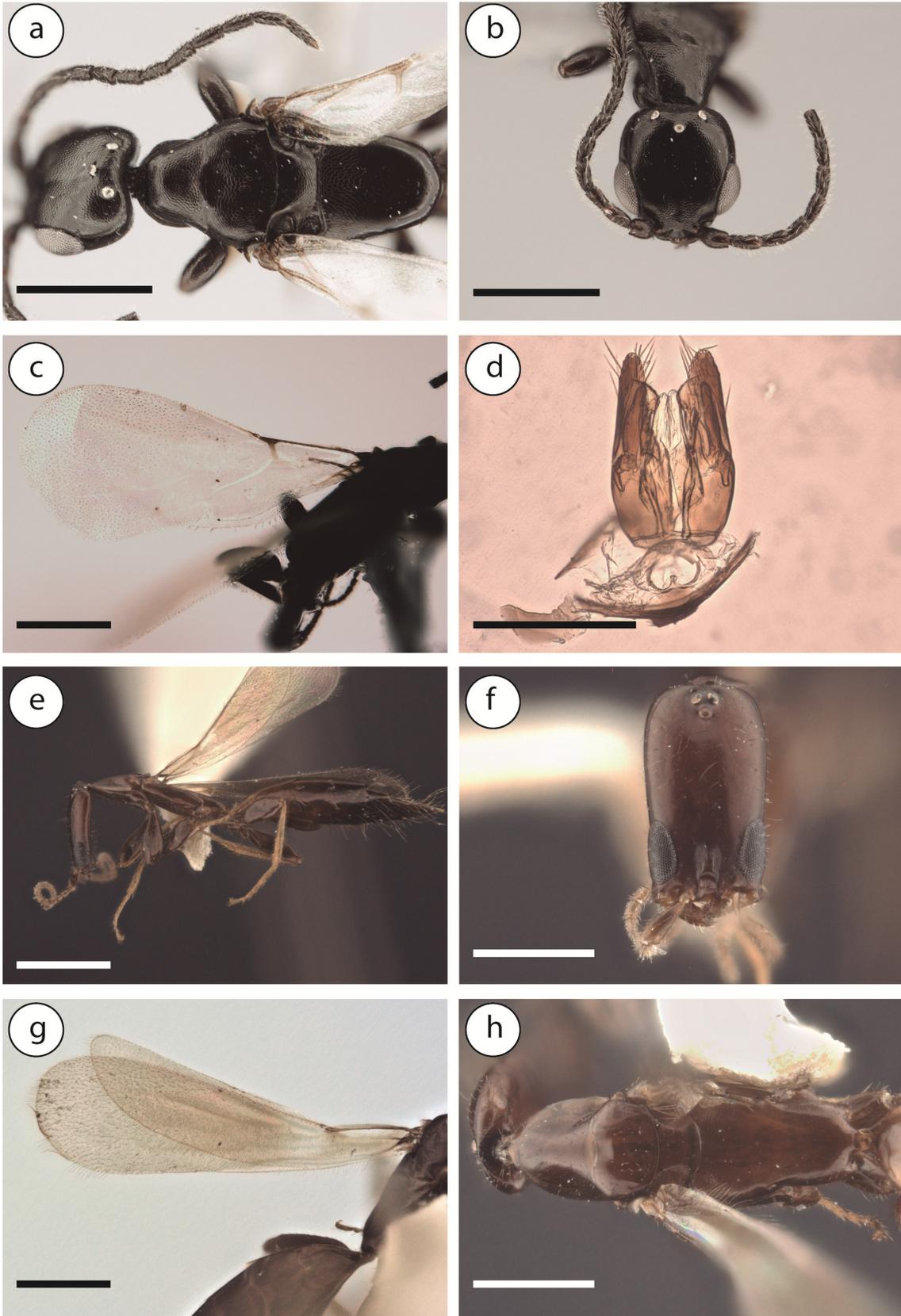


Figure 29. *Tuberepyris* sp. nov. 26. A. habitus, dorsal (500 μ m); B. head, dorsal (500 μ m); C. forewing (500 μ m); D. genitalia, ventral (200 μ m). *Megaprosternum longiceps*, female. E. habitus, lateral (1 mm); F. head, dorsal (500 μ m); G. forewing (250 μ m); H. thorax, dorsal (500 μ m).

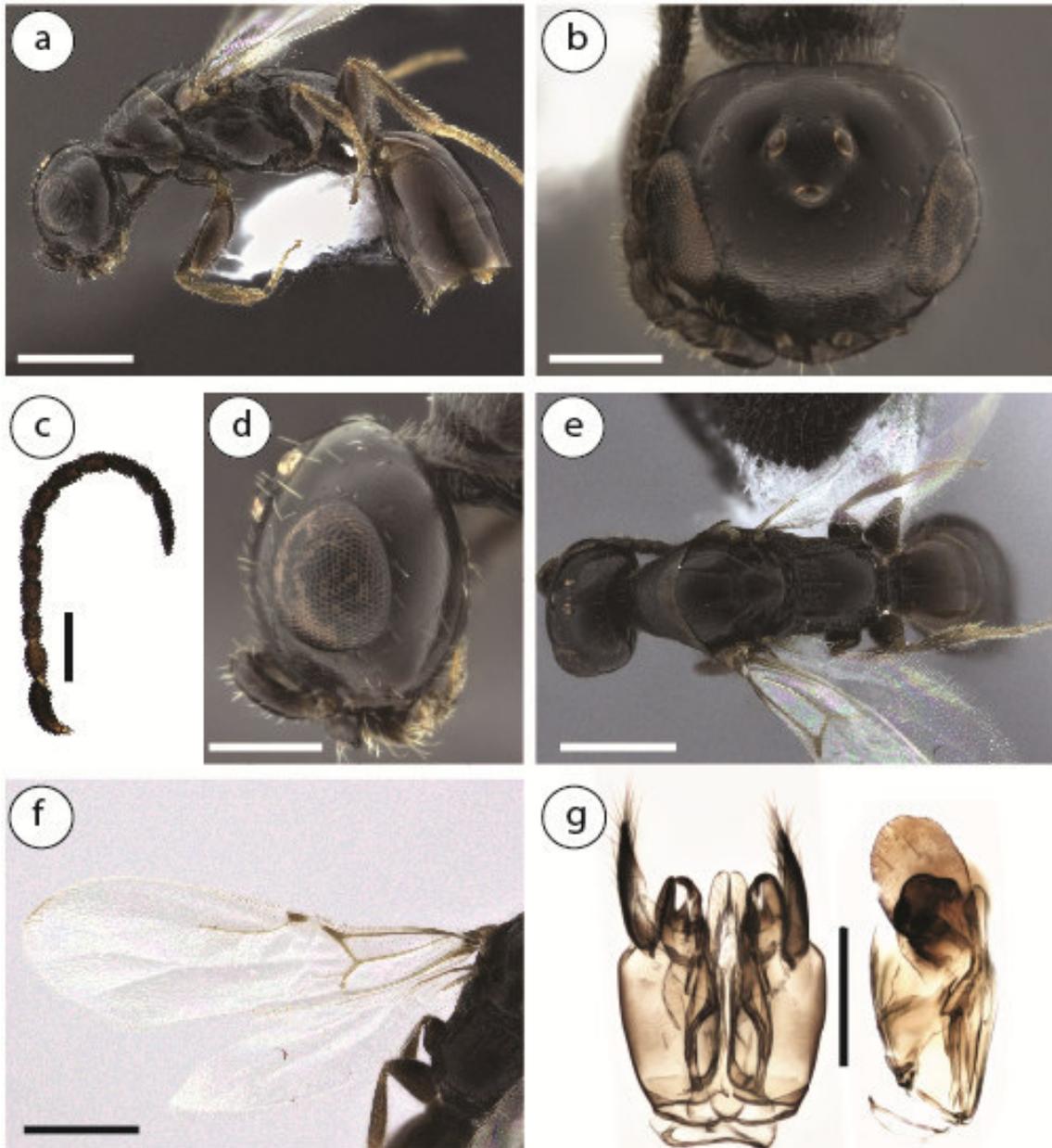


Figure 30. *Nothepyris brasiliensis*, male. A. lateral habitus (500 µm); head, dorsal (200 µm); C. antenna (1800 µm), detail; D. head, lateral (200 µm); E. habitus, dorsal (500 µm); F. wings (500 µm); G. genitalia (left, dorsal; right, lateral; 240 µm).

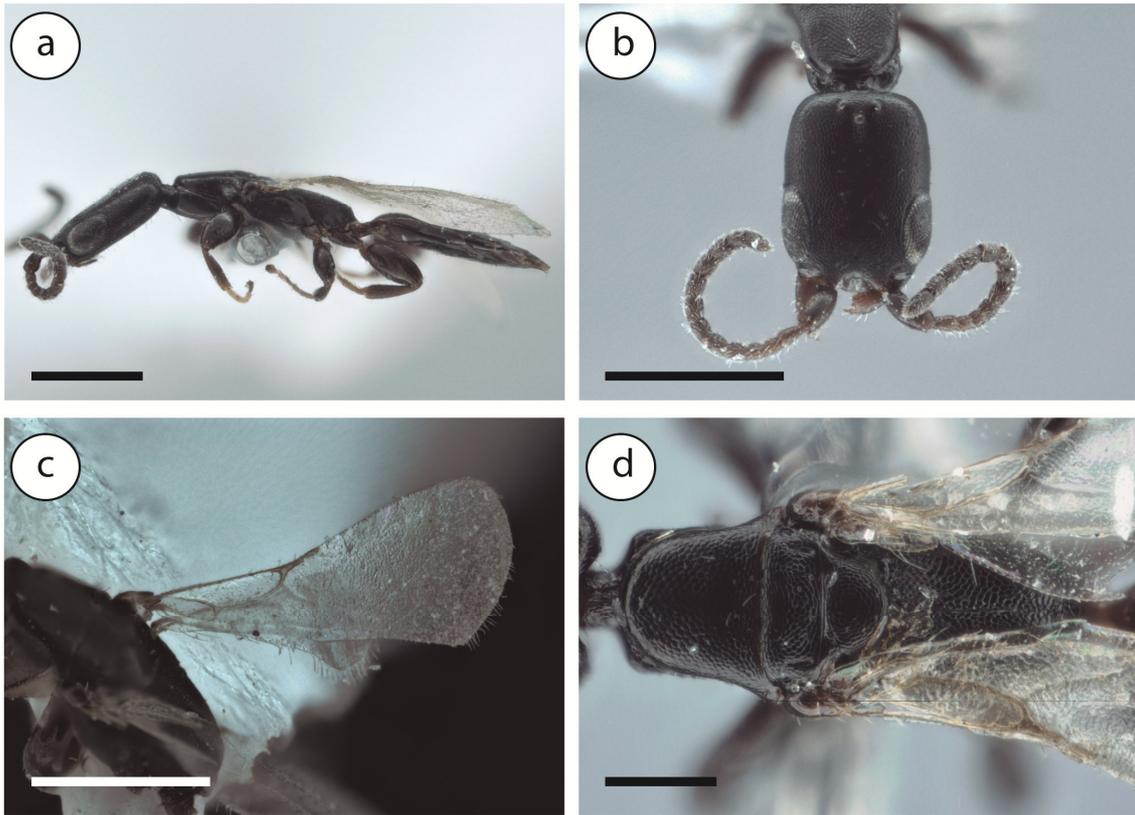


Figure 31. *Thlastepyrus marquisensis*. A. habitus, lateral (1mm); B. head, dorsal (200 μm); C. forewing (500 μm); D. thorax dorsal (200 μm).

Appendix 1. List of OTU's (^H = holotype, ^P = paratype).

Terminal	Sex	Locality	Deposit.
<i>Anisepyrus proteus</i> Evans, 1966	♀	Brazil	UFES
<i>Heterocoelia finus</i> ^P Barbosa & Azevedo, 2011	♀	Russia	UFES
<i>Heterocoelia nikolskajae</i> Móczár, 1984	♀	Russia	UFES
<i>Mesitius absentis</i> Barbosa & Azevedo, 2011	♀	U.A.E.	UFES
<i>Sulcomesitius nepalensis</i> Móczár, 1986	♀	Nepal	UFES
<i>Allobethylus</i> sp. nov. 09	♀	Vanuatu	BPBM
<i>Allobethylus floridanus</i> (Evans, 1964)	♀	U.S.A.	UFES
<i>Allobethylus multicolor</i> (Kieffer, 1905)	♀	Mariana Islands	BPBM
<i>Allobethylus tomoae</i> Terayama, 1999	♀	Hong Kong	BPBM
<i>Alloplastanoxus unexpectatus</i> Terayama, 2006	♀	Thailand	QSBG
<i>Alloplastanoxus</i> sp. nov. 10	♀	Madagascar	CASC
<i>Alloplastanoxus</i> sp. nov. 11	♀	Brazil	IBGE
<i>Alongatepyris ingens</i> ^H Vargas & Azevedo, 2008	♀	Colombia	IAVH
<i>Bethylopsis fullawayi</i> ^H Fouts, 1939	♀	Marquesas Islands	BPBM
<i>Cephalonomia cisidophaga</i> (Strejček, 1990)	♀	Mariana Islands	BPBM
<i>Cephalonomia cisidophaga</i> (Strejček, 1990)	♀	Italia	MNHN
<i>Cephalonomia conophthori</i> Evans, 1978	♀	U.S.A.	UFES
<i>Cephalonomia gallicola</i> (Ashmead 1887)	♀	Australia	UQIC
<i>Cephalonomia hypobori</i> Kieffer, 1919	♀	Iran	MCSN
<i>Cephalonomia hyalinipennis</i> Ashmead, 1893	♀	U.S.A.	UFES
<i>Cephalonomia maculata</i> ^H Maneval, 1935	♀	France	MNHN
<i>Cephalonomia nidicola</i> ^P Szelenyi, 1944	♀	Hungary	UFES
<i>Cephalonomia nigrescens</i> ^H Kieffer, 1906	♀	France	MNHN
<i>Cephalonomia rufa</i> ^H Kieffer, 1906	♀	France	MNHN
<i>Cephalonomia stephanoderis</i> Betrem, 1961	♀	Colombia	UFES
<i>Cephalonomia tarsalis</i> (Ashmead, 1893)	♀	Iran	UFES
<i>Cephalonomia waterstoni</i> Gahan, 1931	♀	U.S.A.	UFES
<i>Chilepyris platythelys</i> Sorg & Walker, 1988	♀	Australia	UFES
<i>Discleroderma gundari</i> Terayama, 2006	♀	Japan	UFES
<i>Discleroderma</i> sp. nov. 12	♀	Indonesia	RMNH
<i>Discleroderma</i> sp. nov. 13	♀	Thailand	QSBG
<i>Discleroderma</i> sp. nov. 14	♀	Thailand	QSBG
<i>Galodoxa torquata</i> Nagy, 1974	♀	Malaysia	AEIC
<i>Galodoxa torquata</i> Nagy, 1974	♂	Laos	BPBM
<i>Glenosema</i> sp. nov. 15	♂	France	UQIC
<i>Glenosema crandalli</i> Evans 1964	♀	U.S.A.	UFES
<i>Glenosema doiinthanonensis</i> Terayama, 1996	♀	Vietnam	RMNH
<i>Glenosema denteata</i> Lanes & Azevedo, 2008	♀	Madagascar	CASC
<i>Glenosema nigra</i> ^H Kieffer, 1906	♀	France	MNHN
<i>Glenosema elevata</i> Lanes & Azevedo, 2008	♀	Madagascar	CASC
<i>Israelius amputatus</i> ^H Barbosa, Kawada & Azevedo, 2014	♀	U.A.E.	UFES
<i>Israelius carthami</i> ^P Richards, 1952	♀	Palestina	UFES
<i>Israelius</i> sp. nov. 16	♀	U.A.E.	UFES
<i>Israelius</i> sp. nov. 17	♀	South Africa	ISAM
<i>Israelius</i> sp. nov. 17	♀	South Africa	ISAM
<i>Israelius</i> sp. nov. 17	♀	South Africa	ISAM
<i>Israelius</i> sp. nov. 18	♀	Madagascar	CASC
<i>Megaprosternum longiceps</i> Azevedo, 2006	♀	Fiji	BPBM
<i>Megaprosternum</i> sp. nov. 19	♀	Central African Rep.	ISAM
<i>Megaprosternum</i> sp. nov. 20	♀	Laos	BPBM

<i>Nothepyrus sulcata</i> (Azevedo, 1999)	♀	Brazil	MPEG
<i>Nothepyrus brasiliensis</i> Evans, 1973	♂	Brazil	AEIC
<i>Nothepyrus</i> sp. nov. 21	♀	Brazil	CZMA
<i>Nothepyrus</i> sp. nov. 22	♀	Dominican Rep.	CNCI
<i>Pararhabdepyris arabo</i> Vargas & Azevedo, 2016	♀	U.A.E.	UFES
<i>Pararhabdepyris lophos</i> ^P Azevedo & Barbosa, 2010	♀	Thailand	UFES
<i>Pararhabdepyris ngangu</i> ^H Vargas & Azevedo, 2016	♀	Central African Rep.	ISAM
<i>Pararhabdepyris wafrika</i> ^H Vargas & Azevedo, 2016	♀	Central African Rep.	ISAM
<i>Plastanoxus ahusiensis</i> ^H (Hedqvist, 1975)	♀	Sweden	NHRS
<i>Plastanoxus chittendenii</i> (Ashmead, 1893)	♀	U.S.A.	UFES
<i>Plastanoxus incompletus</i> Evans 1964	♀	U.S.A.	UFES
<i>Plastanoxus laevis</i> Ashmead, 1893	♀	Brazil	CNCI
<i>Plastanoxus westwoodi</i> Kieffer, 1914	♀	Brazil	UFES
<i>Platepyris sepalus</i> Lanes & Azevedo, 2008	♀	South Africa	BMNH
<i>Proplastanoxus elegans</i> Terayama, 2005	♀	Thailand	QSBG
<i>Prorops nasuta</i> Waterston, 1923	♀	Colombia	UFES
<i>Prorops</i> sp. nov. 23	♀	Thailand	QSBG
<i>Prorops</i> sp. nov. 24	♀	N. Vietnam	RMNH
<i>Prorops</i> sp. nov. 25	♀	U.A.E.	UFES
<i>Sclerodermus</i> sp. 1	♀	Papua-New Guinea	BPBM
<i>Sclerodermus</i> sp. 2	♀	Thailand	QSBG
<i>Sierola depressa marquisensis</i> ^H Fullaway, 1920	♀	Marquesas Islands	BPBM
<i>Solepyris unicus</i> Azevedo, 2006	♀	Costa Rica	PMAE
<i>Solepyris unicus</i> Azevedo, 2006	♀	Brazil	UFES
<i>Tuberepyris</i> cf. codex	♀	South Africa	ISAM
<i>Tuberepyris</i> sp. nov. 26	♀	South Africa	ISAM
New genus A sp. nov. 01	♀	Thailand	QSBG
New genus B sp. nov. 02	♀	Madagascar	CASC
New genus B sp. nov. 03	♀	Madagascar	CASC
New genus B sp. nov. 04	♀	Madagascar	CASC
New genus C sp. nov. 05	♀	Madagascar	CASC
New genus D sp. nov. 06	♀	Madagascar	CASC
New genus E sp. nov. 07	♀	Madagascar	CASC
New genus F sp. nov. 08	♀	Madagascar	CASC

Appendix 2. Character list

Head

1. Malar space size: 0. absent, eye touching mandible; 1. short or inconspicuous; 2. median-sized (about as long as proximal mandibular width); 3. long (twice as long as proximal mandibular width). From Carpenter (1999, char. 8) used this character to analyze relationships among chrysidoid families; Alencar & Azevedo (2013) referred to the malar space coding the shape of profile (char. 76), surface (char. 77) and the area sculpturing (char. 90).

2. Malar sulcus: 0. present; 1. absent. This character has been used for Chrysoidea by Carpenter (1999).

3. Relative size of median clypeal lobe in dorsal view: 0. longer than lateral ones; 1. as long as lateral ones. This character is defined as the anterior projection length of the median clypeal lobe compared with the lateral lobes. From Lanes & Azevedo (2008, char. 10).

4. Shape of anterior margin of median clypeal lobe in dorsal view: 0. angulate; 1. truncate. From Alencar & Azevedo (2013, char 54).

5. Median clypeal lobe delimitation: 0. not distinct; 1. distinct. The lobe delimitation in the clypeus is defined by the presence of emarginations that separates the median lobe from lateral ones.

6. Shape of median clypeal lobe in anterior view: 0. angled; 1. not angled (angulation does not include clypeal carina). The description of most structures is usually made from a few standard points of view, which disregard other ways of perceiving the object of study. The shape of the clypeus has, in addition to variations in dorsal view, variations that can be perceived if alternative views such as the anterior view of the head are assumed. From this point of view it was possible to discover that the anterior margin of the clypeus of genera such as *Sclerodermus*, *Nothepyris* and *Discleroderma* can be angulated medially, a characteristic that is atypical in the generality of the subfamily.

7. Median clypeal carina: 0. present (at least as a sharp line); 1. absent. The character states order this primary hypothesis is contrary to that in Sorg (1988) because our preliminary perception is that, in Scleroderminae, the presence of clypeal carina is interpreted as a plesiomorphic character being more commonly present in groups like *Nothepyris* and *Discleroderma* and generally absent in genera with structural reduction, that is considered apomorphic, as is the case of *Sclerodermus* and *Cephalonomia*. From Sorg (1988, char. 10), Terayama (2003a, char. 3), Lanes & Azevedo (2008, char. 12) and Alencar & Azevedo (2013, char. 49).

8. Clypeus in anterior view with two parallel carinae along margin in anterior view: 0. present; 1. absent.

9. Inter-torular junction: 0. inconspicuous; 1. conspicuous.

10. Anterior margin of torulus reaching the anterior margin of clypeus: 0. absent; 1. present.

11. Frontal process: 0. absent; 1. present; 2. projected but not covering the clypeus. This character has been regarded as an autapomorphy of *Prorops*. However the presence of a similar morphology on the genus *D* make us to think in a possible homologous relationship between them.

12. Head capsule shape in lateral view: 0. globoid; 1. oval (neither globoid nor depressed); 2. depressed; 3. subgloboid (wedge-shaped anteriorly in lateral view). The head globoid is particularly evident in the genera *Nothepyris* and *Discleroderma*. From Lanes & Azevedo (2008, char. 2).

13. Lateral margins of head: 0. straight; 1. convex. The shape of lateral margin of head was selected as an alternative to the character head in dorsal view used by Lanes &

Azevedo (2008, char. 1) that seems more difficult to be homologous. From Terayama (1995a, char. 3) and Lanes & Azevedo (2008, char. 3).

14. Gena visibility behind the eye in dorsal view: 0. not visible; 1. visible, at least partially. From Lanes & Azevedo (2008, char. 21) and Alencar & Azevedo (2013, char. 62).

15. Number of mandibular teeth: 0. one; 1. two; 2. three; 3. four; 4. five; 5. seven. This character has been encoded as multistate to include all the possible alternatives that this quantitative discrete feature may have. From Terayama (1995a, char. 3) and Lanes & Azevedo (2008, char. 7).

16. Mandibular teeth size: 0. large; 1. small. From Alencar & Azevedo (2013, char. 39)

17. Mandibular upper margin: 0. denticulate; 1. not denticulate. From Terayama (1995a, char. 6), Lanes & Azevedo (2008, char. 8).

18. Intercondilar lobe of mandibular base: 0. present; 1. absent. This character was observed by the first time in *Galodoxa* and named by Azevedo & Lanes (2009) as basal callus, in the present study it was scored along the remaining genera in Scleroderminae.

19. Shape of mandible: 0. slender; 1. robust. The general appearance of mandible was coded by Terayama (1995) as a composite character with the mixture of two more or less dependent characters, here we interpret this general shape as a single character. From Terayama (1995, char. 4).

20. Hypostomal carina: 0. not emarginate medially; 1. emarginate medially.

21. Hypostomal carina: 0. angulate; 1. not angulate.

22. Number of antennal flagellomeres: 0. eleven; 1. ten; 2. eight; 3. seven. The reduction on number of antennal segments is one of the patterns of structure reduction cited by Evans (1964) and in *Bethylus* (Evans, 1978), and the old 10-flagellomeres a true reduction; in *Anisepyris* there is kind of intermediate state in which the third segment appears as an inconspicuous ring attached to the fourth segment. From Carpenter (1986), Alencar & Azevedo (2013, char. 4).

23. Frontal line: 0. present; 1. absent. From Lanes & Azevedo (2008, char. 18), Alencar & Azevedo (2013, char. 87).

24. Eye shape in full view in lateral view: 0. elliptical; 1. subtriangular; 2. rounded. From Alencar & Azevedo (2013, char. 61).

25. Eye contour: 0. not protruding (eye/head junction not forming angle); 1. protruding slightly (eye/head junction not forming angle); 2. protruding strongly anteriorly. From Lanes & Azevedo (2008, char. 23) and Alencar & Azevedo (2013, char. 59).

26. Setae on eyes: 0. absent or indistinct, at most as long as diameter of ommatidium; 1. distinct setae longer than ommatidium present on at least part of eye. From (Vilhelmsen 2011, char. 4) and Alencar & Azevedo (2013, char. 63).

27. Frontal angle of ocellar triangle: 0. acute; 1. obtuse; 2. nearly right.

28. Vertex-ocellar line (VOL), longer than eye or at least as long as eye in dorsal view: 0. present; 1. absent.

29. Position of posterior ocelli: 0. close to vertex crest (separated by about one ocellar triangle length); 1. far from vertex crest (separated from eyes by more than ocellar triangle basal width WOT). From Alencar & Azevedo (2008, char. 67).

30. Length of pedicel: 0. short (as long as flagellomere I); 1. long (as long as distal flagellomere). From Alencar & Azevedo (2013, char. 16).

31. Space between anterior ocellus and an imaginary line between the anterior top of the eyes: 0. absent; 1. present. From Lanes & Azevedo (2008, char. 68).

32. Ocellar triangle position between the eyes: 0. only anterior ocellus anterad to an imaginary line of eye top; 1. both anterior and posterior ocelli anterior to imaginary line of eye

33. Occipital carina: 0. present; 1. absent. From Terayama (1995, char. 10), Lanes & Azevedo (2008, char. 26), Alencar & Azevedo (2013, char. 78-81)

34. Anterior occipital surface: 0. not depressed; 1. depressed

Prothorax

35. Pronotal collar: 0. inconspicuous; 1. conspicuous. From Alencar & Azevedo (2013, char. 93).

36. Pronotal surface depressed forward, anterior profile not angled: 0. absent; 1. present

37. Median line of pronotal disc (carina or groove): 0. present; 1. absent. From Móczár (1984) and Alencar & Azevedo (2013, char. 108).

38. Epicoxal sulcus on propleuron in lateral view: 0. present; 1. absent. From Alencar & Azevedo (2013, char. 120).

39. Neck and propleural anterior angles visible in dorsal view: 0. absent; 1. present. Generally the neck and anterior angles of the propleuron are covered dorsally by the pronotal collar. However in Scleroderminae there are some genera whose pronotal collar is extremely inconspicuous, which allows appreciating these structures in dorsal view.

40. Prosternum size: 0. small, procoxa touching, or separated by less than its own width; 1. large, procoxa separated by more than its width. From Lanes & Azevedo (2008, char. 31).

41. Shape of large prosternum: 0. pentagonal; 1. quadrangular.

42. Sternal inner margins of propleuron, extending posteriorly beyond half of the length of prosternum: 0. present; 1. absent.

Mesothorax

43. Mesonotum divided into scutum and scutellum: 0. present; 1. absent. Terayama (1995, char. 14).

44. Mesoscutum median length: 0. short (shorter than mesoscutellum); 1. midsize (subequal than mesoscutellum); 2. long (longer than mesoscutellum). From Terayama (1995, char. 14), Lanes & Azevedo (2008, char. 35) and Alencar & Azevedo (2013, char. 137).

45. Notauli presence (dorsal view): 0. absent; 1. inconspicuous or faint; 2. present. From Terayama (1995, char. 11), Lanes & Azevedo (2008, char. 33), Alencar & Azevedo (2013, char. 132).

46. Notauli shape: 0. concave mesad; 1. concave laterad; 2. straight; 3. S-shaped. The character proposed by Alencar & Azevedo (2013) considers two states not encompassing the variability present in Scleroderminae. From Alencar & Azevedo (2013, char. 134).

47. Extension of the notauli: 0. complete; 1. incomplete. The completeness of the notauli line is interpreted here to include the anterior end. From Alencar & Azevedo (2013, char. 133).

48. Notauli line shape variation: 0. uniform; 1. drop-shaped posteriorly; 2. wider anteriorly.

49. Posterior convergence of notauli: 0. strong; 1. faint. Here we reinterpret the character proposed by Alencar & Azevedo (2013) in order to include the strength of the expression of the convergence. From Alencar & Azevedo (2013, char. 134)

50. Mesoscutellar apex shape: 0. widely rounded; 1. sharp.

51. Mesoscutellar process presence: 0. conspicuous; 1. inconspicuous; 2. absent. This character was modified to avoid the ambiguous quantitative delimitation among states. From Terayama (1995, chars. 15-16), Lanes & Azevedo (2008, char. 36), Alencar & Azevedo (2013, char. 142).

52. Shape of scutellar process: 0. continuous; 1. shortly interrupted medially; 2.

broadly interrupted medially. This character was modified to avoid the ambiguous quantitative delimitation among states. From Alencar & Azevedo (2013, char. 138).

53. Scutellar process width: 0. evenly wide; 1. not evenly wide. Alencar & Azevedo (2013) consider the presence of fovea and sulcus, on the anterior margin of scutellum, as part of a single modification, to avoid the difficulties in classifying the wide variation of sulcus presence/absence used in previous studies. In the present study this coding was used to interpret the variation. From Lanes & Azevedo (2008, 37), Alencar & Azevedo (2013, char. 140).

54. Scutellar process depth: 0. evenly deep; 1. deeper laterally. From Alencar & Azevedo (2013, char. 141).

55. Scutellar process, lateral foveae shape: 0. linear; 1. subcircular.

Metathorax and metapectal-propodeal complex

56. Inter-flap space of metanotum: 0. wide; 1. narrow. From Lanes & Azevedo (pers. comm.)

57. Transverse posterior carina of metapectal-propodeal complex: 0. absent or inconspicuous; 1. present.

58. First metapostnotal carina: 0. absent; 1. present.

59. Basal triangle of metapectal-propodeal complex: 0. present; 1. absent.

60. Basal triangle sculpture of metapectal-propodeal complex: 0. depression deep and carinate; 1. depression shallow and not carinate.

61. Transverse anterior carina of metapectal-propodeal complex: 0. absent or inconspicuous; 1. present. From Terayama (1995, char. 19).

62. Metapleural carina: 0. absent; 1. present. From Terayama (1995, char. 18).

63. Metapleural carina association with spiracle: 0. outlined; 1. not outlined.

64. Spiracle position vs. metapleural carina on metapectal-propodeal complex in lateral view: 0. above carina or distinctly not below; 1. below carina.

65. General position of spiracle on metapectal-propodeal complex: 0. dorsal; 1. lateral.

66. Shape of metapectal-propodeal complex spiracle: 0. circular; 1. elongated.

67. Paraspircular carina: 0. absent; 1. present.

68. Metapectal-propodeal disc: 0. flat; 1. depressed.

69. Pleural anterior transverse uniform concavity on metapectal-propodeal complex: 0. present posteriorly to the junction between mesopleural and metapectal-propodeal complex; 1. absent.

70. Junction of lateral and posterior flanges of metapectal-propodeal complex: 0. rounded; 1. angulate.

71. Median metapostnotal-propodeal carina: 0. absent; 1. present. From Terayama (1995, char. 20).

72. Length of median metapostnotal-propodeal carina. 0. Complete. 1. Incomplete.

73. Shape of lateral margins of metapectal-propodeal complex: 0. straight; 1. convex; 2. concave.

74. Orientation of lateral margins of metapectal-propodeal complex: 0. parallel or subparallel; 1. strongly convergent posteriorly; 2. divergent posteriorly.

75. Median carina of metapectal-propodeal complex declivity: 0. absent; 1. present.

76. Main texture of metapectal-propodeal disc: 0. scabrous; 1. carinate; 2. rugulose; 3. polished.

Leg

77. Mesotibial bristles: 0. absent; 1. present (at least a few distal ones). From Azevedo & Lanes (2009).

Forewing

78. Shape of anterior margin: 0. straight; 1. incurved on proximal portion. From Alencar & Azevedo (2013, char. 250).

79. C vein: 0. present (at least as nebulous vein); 1. absent. Terayama (1995) coded this character by focusing on the cell, that is defined by the presence of C vein, later Lanes & Azevedo (2008) coded it taking into account only the C vein. From Terayama (1995, char. 26), Lanes & Azevedo (2008, char. 61) and Alencar & Azevedo (2013, char. 253).

80. M+Cu vein type: 0. absent; 1. tubular; 2. spectral. From Lanes & Azevedo (2008, char. 62).

81. M+Cu vein completeness: 0. complete; 1. incomplete.

82. Presence of M segment. 0. present; 1. absent. : In genera like *Tuberepyris* and *Megaprosternum* the vein Rsa&M vein could be represented only by the Rsa anterior segment.

83. Rsa&M vein abruptly widened at Rsa segment: 0. absent; 1. present. Richards (1952) used this character to describe the main feature of *Israelius*.

84. Presence of fusion Sc&R1a vein: 0. absent or inconspicuous; 1. present. From Alencar & Azevedo (2013, chars. 262 and 263). In *Goniozus* or *Pristocera* this junction of veins could be present but without real fusion. This is our interpretation of the enlarged vein before the pterostigma or which Terayama calls prostigma.

85. Length of fusion Sc&R1a vein: 0. long (longer than wide); 1. short (wider than long). This character is related with the chars 262 in Alencar & Azevedo (2013) that refers to the pterostigma length, this because the character 264 refers to the stigma length. From Alencar & Azevedo (2013, chars 262 and 263).

86. Size of stigma on forewing: 0. long; 1. short. From Alencar & Azevedo (2013, chars. 264).

87. Presence of r-rs segment: 0. present; 1. absent. This is the proximal segment of the traditional radial vein. From Alencar & Azevedo (2013, chars. 265).

88. Type of r-rs segment: 0. tubular; 1. nebulous; 2. spectral.

89. Presence of Rsc segment: 0. present; 1. absent. This is the distal segment of the radial vein *sensu* Evans (1964). From Alencar & Azevedo (2013, chars. 265).

90. Type of Rsc segment: 0. tubular; 1. nebulous; 2. spectral.

91. Rs+M vein as angulation on Rsa&M: 0. present; 1. absent. This vein is especially common in Bethylinae and appears as a perpendicular stub arising from Rsa&M vein. From Ramos & Azevedo (2012, char. 116).

92. Cua vein: 0. present; 1. absent.

93. A vein: 0. present; 1. absent. If the submedian cell is closed, this vein is obligatorily present. From Terayama (1995, char. 24) and Lanes & Azevedo (2008, char. 64).

94. 1cu-a vein: 0. absent; 1. present. It is the transverse median vein *sensu* Evans (1964). From Lanes & Azevedo (2008, char. 65).

95. 1cu-a vein: 0. conspicuous; 1. inconspicuous.

96. 1cu-a vein orientation from M+Cu vein: 0. distad; 1. proximad; 2. antero-posterad.

97. 1cu-a vein strongly convex or angulate: 0. absent; 1. present.

98. 1Cu cell length compared with R cell length: 0. subequal or larger (cubital cell length at least 4/5 of radial cell); 1. shorter. From Terayama (1995, char. 24) and Lanes & Azevedo (2008, char. 68).

99. Shape of longitudinal folding: 0. simple or inconspicuous; 1. forked. Mason (1986) referred to the fold line present in Hymenoptera as the only fold line present; however Danforth & Michener (1988) identified a longitudinal folding present in several hymenopteran families. In Bethylinidae there is a longitudinal folding in the forewing whose variation could be phylogenetically informative (Kawada, pers. comm.).

100. Proximal venation length: 0. long ($\frac{1}{4}$ of forewing length); 1. short ($\frac{1}{5}$ forewing

length).

101. Color: 0. hyaline to whitish; 1. infusate yellow to brown.

Hind wing

102. Quantity of hamuli : 0. two; 1. three; 2. four. From Lanes & Azevedo (2008, char. 69).

103. Distance among hamuli: 0. evenly spaced; 1. irregularly spaced. From Lanes & Azevedo (2008, char. 70).

Mesopleuron

104. Epicnemium: 0. present (at least as an angulation of mesopleural-sternal surface); 1. absent. From Lanes & Azevedo (2008, char. 40).

105. Mesopleural pit: 0. present; 1. absent. From Alencar & Azevedo (2013, char. 197).

106. Tubercle or elevation posterior to mesopleural pit: 0. absent; 1. present.

107. Position of mesopleural pit: 0. posterodorsal; 1. central. From Alencar & Azevedo (2013, char. 197).

108. Upper mesopleural fovea presence: 0. present; 1. absent. From Alencar & Azevedo (2013, char. 192)

109. Delimitation of upper mesopleural fovea: 0. closed; 1. open. From Alencar & Azevedo (2013, char. 193).

110. Subtegular fovea: 0. present; 1. absent. From Lanes & Azevedo (2008, char. 38).

111. Development of subtegular fovea: 0. short and isolated; 1. long, connected at least with episternal groove. From Alencar & Azevedo (2013, char. 187).

112. Shape of subtegular fovea: 0. evenly linear; 1. widened, at least anteriorly.

113. Anterior segment of subtegular fovea U-shaped: 0. present; 1. absent. We observed this condition in *Cephalonomia* and but in other 10-flagellomered genera.

114. Subdivision of subtegular fovea: 0. simple; 1. subdivided.

Metasoma

115. Lateral margins of first metasomal tergite in contact each other ventrally: 0. present; 1. absent. This was also observed in *Alongatepyris*, in which the metasoma is extremely flat with ventral margins of tergite I and surface of sternite I closely attached. This character maybe coincides with an autapomorphy of *Platepyris* (type not observed), that refers to the first metasomal sternite visible beyond the petiole with posterior margin divided in two lobe (Lanes & Azevedo 2008; Fig. 8k), therefore this emargination could be an artifact of the ventral junction between the lateral margins of tergite I. From Lanes & Azevedo (2008, item 9 of the key to genera).

116. Position of metasomal paired projections: 0. ventral; 1. dorsal. We call here modifications to any type of paired and conspicuous projections of the cuticle in the metasoma, associated with at least one sternite or a tergite. Nagy (1974) call as appendages the ventral projections of sternum IV and later Azevedo & Lanes (2009) refers to the same character as expansions; Terayama (2006) and Lanes & Azevedo (2008) use the term tubercles for paired projection on terga III to V in *Discleroderma*. In the present analysis we register the presence of sternal minute paired projections on metasomal sternites in, at least, one species of *Nothepyris* and one species of the new genus D, so we decide to use generically the term “paired projections”. From Nagy (1974), Terayama (2006), Lanes & Azevedo (2008) and Azevedo & Lanes (2009).

117. Size of metasomal second segment: 0. longer than the remaining segments together.; 1. shorter than two segments together. Barbosa & Azevedo (2010) use this character in the diagnosis of the genus *Pararhabdepyris*.

118. Metasomal apex orientation: 0. upward; 1. downward. This is regarded as a synapomorphy of *Discleroderma*.

Appendix 3. Matrix (next page).

OTU	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
<i>Anisepyris proteus</i>	1	1	0	0	0	1	0	2	0	1	0	1	1	0	4	1	1	0	0	0	?	0	1	0	1	1	0	1	0	0
<i>Heterocoelia finus</i>	3	1	0	0	1	1	0	2	1	1	0	0	1	0	3	1	1	0	1	1	0	0	0	0	1	1	2	1	1	0
<i>Mesitius absentis</i>	3	1	0	1	1	1	0	2	1	0	0	0	1	0	0	1	1	0	0	1	0	0	1	2	1	1	2	0	1	1
<i>Sulcomesitius nepalensis</i>	1	1	0	1	0	1	1	2	0	1	0	2	0	1	3	0	1	0	0	1	1	0	0	1	0	1	2	0	1	1
<i>Allobethylus floridanus</i>	1	1	0	1	0	1	0	2	0	1	0	2	0	1	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1
<i>Allobethylus multicolor</i>	1	1	0	1	0	1	0	2	0	0	0	2	0	1	2	0	1	0	0	0	?	0	0	1	0	1	0	0	0	1
<i>Allobethylus tomoae</i>	1	1	0	1	0	1	1	2	0	0	0	2	0	1	2	0	0	0	0	0	?	0	0	1	0	1	0	0	0	1
<i>Alloplastanoxus unexpectatus</i>	1	0	1	1	0	1	1	2	0	1	0	2	1	0	2	1	1	1	0	1	0	1	1	1	0	0	1	0	0	1
<i>Alloplastanoxus</i> sp. 1	1	0	0	1	0	1	1	2	0	0	0	2	1	0	2	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1
<i>Alloplastanoxus</i> sp. 2	1	0	0	1	0	1	1	2	0	1	0	2	1	0	2	1	1	1	0	1	0	1	1	0	1	0	2	1	0	1
<i>Alongatepyris ingens</i>	0	0	0	1	0	1	1	2	0	1	0	2	0	0	3	1	1	0	0	0	?	0	0	1	0	1	1	0	0	1
<i>Bethylopsis fullawayi</i>	1	1	1	1	0	1	1	2	0	1	0	2	0	1	2	0	1	0	0	1	1	1	0	0	0	0	0	0	1	1
<i>Cephalonomia cisidophaga</i> (w)	1	0	1	1	0	1	0	2	0	1	0	2	0	1	1	1	?	0	0	1	0	2	1	0	0	1	0	0	0	0
<i>Cephalonomia cisidophaga</i> (a)	2	0	1	1	0	1	1	2	0	1	0	2	0	1	2	1	?	1	0	?	?	2	1	2	0	0	0	0	0	1
<i>Cephalonomia conophthori</i>	1	0	1	1	0	1	1	2	0	1	0	1	0	0	2	0	?	0	1	1	0	1	0	0	1	1	0	0	0	1
<i>Cephalonomia gallicola</i>	1	1	1	1	0	1	1	2	0	1	0	2	0	1	2	1	?	0	1	1	1	1	1	2	0	0	0	0	1	1
<i>Cephalonomia hypobori</i>	1	1	1	1	0	1	1	2	0	1	0	2	0	0	0	1	1	1	1	1	1	1	1	0	0	1	2	0	0	1
<i>Cephalonomia hyalinipennis</i>	1	1	1	1	0	1	0	2	0	1	0	1	0	0	3	1	1	?	1	1	0	1	0	1	0	1	0	0	0	0
<i>Cephalonomia maculata</i>	2	0	0	1	0	1	1	2	0	1	0	1	1	0	3	?	?	1	0	?	?	1	1	1	1	1	2	0	0	1
<i>Cephalonomia nidicola</i>	1	1	1	1	0	1	1	2	0	1	0	2	0	1	2	1	1	1	1	?	?	1	1	2	0	0	0	0	1	1
<i>Cephalonomia nigrescens</i>	2	0	1	1	0	1	0	2	0	0	0	1	0	1	?	?	?	?	?	?	?	1	1	0	0	0	2	0	0	1
<i>Cephalonomia rufa</i>	1	0	0	1	0	1	1	2	0	1	0	1	0	1	2	?	0	1	0	?	?	1	1	1	0	0	?	0	?	1
<i>Cephalonomia stephanoderis</i>	1	0	1	1	0	1	1	2	0	1	0	1	0	0	2	0	1	1	0	1	0	1	0	2	0	1	0	0	0	1
<i>Cephalonomia tarsalis</i>	2	0	0	1	0	1	1	2	0	1	0	1	1	0	2	1	1	1	0	1	0	1	1	1	0	0	1	1	0	1
<i>Cephalonomia waterstoni</i>	2	0	0	1	0	1	1	2	0	1	0	1	0	0	2	0	1	1	0	1	0	1	0	0	1	1	0	0	0	1
<i>Chilepyris platythelys</i>	0	1	1	1	0	1	1	2	0	0	0	1	0	0	1	0	1	0	1	0	?	0	0	1	1	0	0	0	1	1
<i>Discleroderma gundari</i>	2	1	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	1	0	0	0	1	1	0
<i>Discleroderma</i> sp. 1	2	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	1	1	0	1	2	0	0	0	1	1	0
<i>Discleroderma</i> sp. 2	2	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	1	1	0	0	2	0	1	0	1	0	0
<i>Discleroderma</i> sp. 3	2	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	1	1	0	0	2	0	0	0	1	1	1
<i>Galodoxa torquata</i> (f)	1	1	0	1	1	1	0	2	0	1	0	1	1	0	3	0	1	0	1	0	?	0	0	1	0	1	2	1	0	0
<i>Galodoxa torquata</i> (m)	2	1	0	1	1	1	0	2	0	0	0	1	0	0	3	0	1	0	1	0	?	0	1	0	1	0	1	1	0	0
<i>Glenosema</i> sp. (m)	0	?	0	1	1	1	1	2	0	1	0	1	1	0	4	0	1	0	0	1	1	0	1	2	1	0	0	0	1	0
<i>Glenosema crandalli</i>	0	?	0	1	0	1	0	2	0	1	0	1	1	0	5	0	0	0	0	1	0	0	1	2	0	1	0	0	0	1
<i>Glenosema doiinthanonensis</i>	0	0	1	1	0	1	1	2	0	1	0	1	0	0	5	1	0	1	0	1	1	0	1	1	0	0	0	0	0	1

OTU	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
<i>Glenosema denteata</i>	0	?	0	1	0	1	0	2	0	1	0	1	0	0	5	1	0	0	0	1	0	0	0	2	0	1	0	0	0	1
<i>Glenosema nigra</i>	0	?	0	1	0	1	0	2	0	1	0	1	0	0	5	1	0	?	?	?	?	0	1	1	0	1	0	0	0	1
<i>Glenosema elevata</i>	0	?	1	1	0	1	0	2	0	0	0	1	0	0	5	1	0	0	0	1	1	0	1	2	0	1	0	0	0	1
<i>Israelius carthami</i>	1	0	1	1	0	1	1	2	0	1	0	2	0	0	2	1	1	0	1	1	0	1	0	2	1	0	2	0	0	1
<i>Israelius</i> sp. 1	1	1	0	1	0	1	1	2	0	0	0	1	0	0	2	0	1	?	1	1	0	1	1	0	0	1	2	0	0	0
<i>Israelius</i> sp. 2	1	1	1	1	0	1	1	2	0	0	0	2	0	0	2	0	1	0	1	?	?	1	0	2	0	0	2	0	0	1
<i>Israelius</i> sp. 3	1	0	0	1	1	1	1	2	0	0	0	1	0	0	2	0	?	0	1	1	1	1	1	1	0	1	2	0	0	1
<i>Israelius</i> sp. 4	1	0	1	1	0	1	1	2	0	1	0	2	0	1	1	0	1	0	1	1	1	1	1	1	0	1	2	0	0	1
<i>Israelius</i> sp. 5	1	1	1	1	0	1	1	2	0	1	0	2	0	0	2	?	?	1	1	1	1	1	1	2	0	1	1	0	0	1
<i>Israelius amputatus</i>	2	1	0	1	1	1	0	2	0	0	0	1	1	0	?	?	?	0	1	1	0	1	0	0	1	?	2	0	0	0
<i>Megaprosternum longiceps</i>	1	1	1	1	0	1	1	2	0	1	0	2	0	0	2	0	1	0	0	1	1	0	0	1	0	1	0	0	0	0
<i>Megaprosternum</i> sp. 1	2	0	0	1	0	1	1	2	0	1	0	1	0	0	3	1	1	1	0	1	1	0	1	0	1	0	1	0	0	0
<i>Megaprosternum</i> sp. 2	0	?	1	1	0	1	1	2	0	1	0	2	0	0	2	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0
<i>Nothepyris brasiliensis</i>	2	1	0	1	0	0	0	2	0	0	0	0	1	0	2	0	1	0	1	1	1	0	0	1	1	0	0	1	1	0
<i>Nothepyris sulcata</i>	2	1	0	1	0	0	0	2	0	0	0	0	1	0	1	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0
<i>Nothepyris</i> sp. 1	2	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	1	1	0	1	1	0	1	0	1	1	1
<i>Nothepyris</i> sp. 2	2	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	?	0	1	1	1	0	0	2	0	1	0	1	1	0
<i>Pararhabdepyris arabo</i>	2	0	0	1	0	1	0	2	0	0	0	0	1	0	2	0	1	0	0	1	0	1	0	2	1	1	2	1	0	1
<i>Pararhabdepyris ngangu</i>	2	1	0	1	0	1	0	2	0	0	0	0	1	0	?	0	?	1	0	?	?	1	1	2	1	1	2	1	0	1
<i>Pararhabdepyris lophos</i>	2	0	0	1	0	1	1	2	0	0	0	0	1	0	2	0	?	0	0	?	?	1	0	2	1	1	0	1	0	1
<i>Pararhabdepyris wafrika</i>	2	1	0	1	0	1	1	2	0	0	0	0	1	0	2	0	1	1	0	?	?	1	0	2	1	1	2	1	0	1
<i>Platepyris sepalus</i>	2	?	0	1	0	1	1	2	0	1	0	2	0	0	2	1	?	?	0	?	?	0	?	0	1	?	2	0	0	0
<i>Plastanoxus ahusiensi</i>	2	1	0	1	0	1	1	2	0	1	0	1	1	0	3	?	1	?	0	?	?	1	0	1	1	1	0	0	0	0
<i>Plastanoxus chittendenii</i>	2	0	1	1	0	1	0	2	0	0	0	2	0	0	2	1	1	1	0	1	0	1	1	0	0	1	0	0	0	0
<i>Plastanoxus incompletus</i>	1	1	0	1	0	1	1	2	0	1	0	2	0	0	2	0	?	0	1	1	0	1	1	0	0	1	0	0	1	1
<i>Plastanoxus laevis</i>	2	0	0	1	0	1	1	2	0	0	0	1	1	0	2	1	1	0	0	1	0	1	1	0	1	0	0	1	0	1
<i>Plastanoxus westwoodi</i>	2	0	0	1	0	1	0	2	0	1	0	1	0	0	2	1	1	1	0	?	?	1	1	1	0	1	0	0	0	0
<i>Proplastanoxus elegans</i>	2	0	1	1	1	1	1	2	0	0	0	1	1	0	2	0	1	0	1	1	1	1	1	0	1	1	0	1	0	1
<i>Prorops</i> sp. 1	1	1	1	1	0	1	1	2	0	1	1	0	1	0	2	0	1	0	1	1	1	1	0	1	1	0	2	1	0	1
<i>Prorops</i> sp. 2	1	1	1	1	0	1	1	2	0	0	1	1	1	0	2	0	1	1	1	1	1	1	0	2	1	0	0	1	0	0
<i>Prorops</i> sp. 3	1	1	1	1	0	1	1	2	0	0	1	2	0	0	2	0	1	1	1	1	0	1	0	2	1	1	0	0	0	1
<i>Prorops nasuta</i>	1	0	0	1	0	1	1	2	0	0	1	0	0	0	2	0	1	1	1	?	?	1	0	1	1	1	0	1	0	0
<i>Sclerodermus</i> sp. 1	1	1	0	1	1	0	0	2	0	0	0	2	0	1	2	0	?	0	1	1	1	0	1	0	0	0	0	0	0	1
<i>Sclerodermus</i> sp. 2	1	1	0	1	1	0	0	2	0	0	0	1	1	1	2	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0
<i>Sierola depressa</i>	0	?	0	1	0	1	1	2	0	1	0	1	0	0	3	1	1	0	0	0	?	0	0	1	0	1	1	0	0	1

OTU	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
<i>Solepyris unicus 1</i>	0	?	1	1	1	1	1	2	0	1	0	2	0	0	2	0	1	0	0	0	?	0	0	0	0	1	0	0	1	1
<i>Solepyris unicus 2</i>	0	?	1	1	1	1	1	2	0	1	0	2	0	1	2	0	1	0	0	0	?	0	1	1	1	1	0	0	1	1
<i>Tuberepyris sp.</i>	0	?	0	1	0	1	1	2	0	1	0	1	0	0	3	1	1	0	0	0	?	0	0	0	1	0	1	0	0	1
<i>Tuberepyris cf hamus</i>	1	1	0	1	1	1	1	2	0	1	0	2	1	0	3	1	?	0	0	0	?	0	0	2	1	0	1	0	0	1
UG 1	1	1	0	1	0	1	1	2	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0	0	0	1	2	1	1	1
UG 2	2	0	0	1	0	1	1	2	0	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	0	0	2	1	1	1
UG 3	2	0	1	1	0	1	1	2	0	0	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0	1
UG 5	1	0	1	1	0	1	1	2	0	0	0	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	0	1
UG 6	1	0	1	1	0	1	1	2	0	0	0	0	1	0	2	0	1	0	0	0	?	1	0	1	1	0	0	1	1	1
UG 7	1	0	0	1	0	1	1	2	0	1	0	2	0	0	2	1	1	1	1	0	?	1	0	0	0	0	0	1	1	1
UG 8	1	0	1	1	0	1	1	2	0	0	0	0	1	1	2	0	1	0	1	0	?	1	0	0	0	1	2	1	1	1
UG 9	1	0	1	1	1	1	1	2	1	0	0	1	0	1	1	0	?	0	1	1	1	3	1	0	0	1	0	0	0	0

OTU	.31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60			
<i>Anisepyris proteus</i>	0	0	0	1	1	0	1	0	0	0	?	0	0	2	2	0	1	1	1	1	0	0	0	0	0	0	1	1	0	1			
<i>Heterocoelia finus</i>	0	0	0	0	1	0	0	0	0	0	?	1	0	2	2	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0			
<i>Mesitius absentis</i>	0	0	0	0	1	0	0	0	0	0	?	1	0	2	2	1	0	0	0	1	0	0	1	0	1	0	1	1	0	0			
<i>Sulcomesitius nepalensis</i>	1	?	0	1	1	0	1	0	0	0	?	1	0	0	2	2	0	2	?	1	0	0	0	0	0	0	1	0	1	1			
<i>Allobethylus floridanus</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	1	1	0	1	1	0	0	0	1	1	1			
<i>Allobethylus multicolor</i>	1	?	1	1	1	0	1	0	0	0	?	1	0	0	2	2	0	0	0	1	0	0	1	1	1	0	1	0	1	1			
<i>Allobethylus tomoae</i>	1	?	1	1	1	0	0	0	0	0	?	1	0	0	2	2	0	0	0	1	0	0	1	1	1	0	1	0	1	1			
<i>Alloplastanoxus unexpectatus</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	2	2	0	2	0	0	0	0	0	0	0	0	0	1	0	0	1		
<i>Alloplastanoxus sp. 1</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1		
<i>Alloplastanoxus sp. 2</i>	1	?	1	1	1	1	1	1	0	0	?	1	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1		
<i>Alongatepyris ingens</i>	1	?	1	1	0	0	1	1	1	0	?	1	0	1	0	?	?	?	?	?	0	0	0	1	1	0	0	1	0	1	1		
<i>Bethylopsis fullawayi</i>	1	?	1	1	1	1	0	1	0	0	?	1	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	1	1		
<i>Cephalonomia cisidophaga (w)</i>	1	?	1	1	1	0	1	1	0	?	?	?	?	0	1	0	?	?	?	?	?	0	0	0	0	0	1	0	0	0	1		
<i>Cephalonomia cisidophaga (a)</i>	1	?	1	1	1	0	1	1	0	?	?	?	?	0	1	0	?	?	?	?	?	0	2	?	?	?	?	?	0	0	1	1	
<i>Cephalonomia conophthori</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	?	0	1	0	1	0	0	0	1	0	0	1		
<i>Cephalonomia gallicola</i>	1	?	1	1	1	1	1	1	0	?	?	?	?	1	?	0	?	?	?	?	?	0	2	?	?	?	?	?	0	0	1	1	
<i>Cephalonomia hypobori</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	2	0	?	?	?	?	?	1	1	0	0	0	0	0	0	0	1	1		
<i>Cephalonomia hyalinipennis</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	?	0	0	0	1	1	0	1	0	0	0	1		
<i>Cephalonomia maculata</i>	1	?	1	1	1	0	1	1	0	?	?	?	?	0	0	0	?	?	?	?	?	0	1	0	1	1	0	0	1	0	1	1	
<i>Cephalonomia nidicola</i>	1	?	1	1	?	1	1	1	0	?	?	?	?	1	?	0	?	?	?	?	?	0	2	?	?	?	?	?	?	0	0	1	1
<i>Cephalonomia nigrescens</i>	1	?	1	1	1	1	1	1	0	?	?	?	?	0	0	0	?	?	?	?	?	0	0	0	1	0	?	0	1	0	0	1	
<i>Cephalonomia rufa</i>	?	?	1	1	1	0	1	1	0	?	?	?	?	1	?	0	?	?	?	?	?	0	2	?	?	?	?	?	?	0	0	1	1
<i>Cephalonomia stephanoderis</i>	1	?	1	1	1	1	1	1	0	0	?	1	0	0	0	?	?	?	?	?	?	0	0	0	1	1	1	0	1	0	0	1	
<i>Cephalonomia tarsalis</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	?	?	0	0	0	1	1	1	0	1	0	1	1	
<i>Cephalonomia waterstoni</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	?	?	0	0	2	?	?	0	0	0	0	1	1	
<i>Chilepyris platythelys</i>	1	?	0	1	1	0	1	0	1	1	?	1	0	0	0	?	?	?	?	?	?	0	0	0	1	0	?	1	1	0	1	1	
<i>Discleroderma gundari</i>	0	0	1	1	1	2	1	1	1	0	?	1	0	1	0	?	?	?	?	?	?	1	0	0	0	0	0	1	1	1	0	1	
<i>Discleroderma sp. 1</i>	0	0	1	1	1	2	1	1	0	0	?	1	0	1	0	?	?	?	?	?	?	1	0	0	0	0	0	0	1	1	0	1	
<i>Discleroderma sp. 2</i>	0	0	0	1	1	2	1	1	0	0	?	1	0	1	0	?	?	?	?	?	?	1	0	0	0	0	0	0	1	1	0	1	
<i>Discleroderma sp. 3</i>	0	0	0	1	1	2	1	0	0	0	?	1	0	1	2	3	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	
<i>Galodoxa torquata (f)</i>	1	?	1	1	1	0	0	0	1	0	?	1	0	2	2	2	?	1	1	1	0	0	0	0	0	?	1	0	0	1	1		
<i>Galodoxa torquata (m)</i>	1	?	0	1	1	0	0	0	0	0	?	1	0	1	2	3	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1		
<i>Glenosema sp. (m)</i>	1	?	0	1	1	1	1	0	0	?	?	?	?	1	?	0	?	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Glenosema crandalli</i>	1	?	1	1	1	0	1	0	0	0	?	1	0	0	0	?	?	?	?	?	?	0	0	0	0	0	0	0	1	0	1	1	
<i>Glenosema doiinthanonensis</i>	1	?	0	1	1	0	1	0	0	0	?	1	0	0	0	?	?	?	?	?	?	0	0	0	1	0	0	0	1	1	1	1	

OTU	.31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	
<i>Glenosema denteata</i>	1	?	0	1	1	0	1	0	0	0	?	1	0	0	0	?	?	?	?	0	0	0	0	0	0	0	1	1	0	1	
<i>Glenosema nigra</i>	1	?	0	1	1	0	1	0	0	0	?	1	0	0	0	?	?	?	?	0	0	0	0	0	?	0	1	0	1	1	
<i>Glenosema elevata</i>	1	?	0	1	1	0	1	0	0	0	?	1	0	0	0	?	?	?	?	0	0	0	0	0	0	0	1	0	1	1	
<i>Israelius carthami</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	2	?	?	?	0	0	0	0	1	
<i>Israelius</i> sp. 1	1	?	1	1	1	1	1	1	0	1	?	1	0	1	0	?	?	?	?	0	0	0	0	0	?	0	0	0	1	1	
<i>Israelius</i> sp. 2	1	?	0	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Israelius</i> sp. 3	1	?	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Israelius</i> sp. 4	1	?	1	1	1	0	1	1	1	0	?	1	0	0	0	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Israelius</i> sp. 5	?	?	1	1	1	1	1	1	0	0	?	1	0	1	0	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Israelius amputatus</i>	0	0	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	0	0	2	?	?	1	0	1	0	1	1	
<i>Megaprosternum longiceps</i>	1	?	1	1	0	1	1	1	1	1	0	0	0	2	0	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Megaprosternum</i> sp. 1	1	?	1	1	0	1	1	1	1	1	0	0	0	1	0	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Megaprosternum</i> sp. 2	1	?	1	1	0	1	1	1	1	1	0	0	0	2	0	?	?	?	?	0	2	?	?	?	?	?	?	0	0	1	1
<i>Nothepyris brasiliensis</i>	0	1	1	1	2	1	1	1	0	0	?	1	0	2	2	2	0	0	0	1	0	0	0	0	?	0	1	0	0	1	
<i>Nothepyris sulcata</i>	0	1	1	1	2	1	1	1	0	0	?	1	0	1	2	3	?	1	1	1	0	0	0	0	?	0	1	1	0	1	
<i>Nothepyris</i> sp. 1	0	0	1	1	2	1	1	0	0	0	?	1	0	0	2	2	0	0	1	1	0	0	0	0	0	0	1	1	0	1	
<i>Nothepyris</i> sp. 2	0	0	1	1	2	1	1	0	0	0	?	1	0	1	2	2	0	0	1	1	0	0	0	0	0	0	1	0	1	1	
<i>Pararhabdepyris arabo</i>	0	1	1	?	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	0	1	1	?	0	1	1	0	1	
<i>Pararhabdepyris ngangu</i>	0	0	1	?	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	0	1	1	1	0	1	1	1	1	
<i>Pararhabdepyris lophos</i>	0	1	1	?	1	0	1	1	0	0	?	1	0	1	2	0	0	2	0	0	0	0	1	1	1	0	1	0	0	1	
<i>Pararhabdepyris wafrika</i>	0	0	1	?	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	0	1	1	1	0	1	0	0	1	
<i>Platepyris sepalus</i>	1	?	1	1	0	?	1	?	?	?	?	?	0	1	0	?	?	?	?	0	2	?	?	?	?	?	?	0	0	1	1
<i>Plastanoxus ahusiensi</i>	1	?	1	1	1	?	1	1	0	?	?	?	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	1
<i>Plastanoxus chittendenii</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	0	0	0	1	1	1	0	1	0	0	1	
<i>Plastanoxus incompletus</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	0	0	?	?	?	?	0	0	0	1	1	1	0	1	0	1	1	
<i>Plastanoxus laevis</i>	0	0	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	0	1	1	0	0	1	1	1	1	
<i>Plastanoxus westwoodi</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	2	?	?	?	?	0	0	1	0	1
<i>Proplastanoxus elegans</i>	0	0	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	0	0	0	0	0	0	1	0	0	1
<i>Prorops</i> sp. 1	0	0	1	1	1	0	1	1	0	0	?	1	0	2	0	?	?	?	?	0	0	0	0	0	?	0	0	0	1	1	
<i>Prorops</i> sp. 2	0	0	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	1	0	0	0	0	0	0	0	0	1	1
<i>Prorops</i> sp. 3	1	?	1	1	1	0	1	1	0	0	?	1	0	2	0	?	?	?	?	0	1	0	0	0	0	0	0	0	0	1	1
<i>Prorops nasuta</i>	1	?	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	2	?	?	?	?	?	0	0	0	1	1
<i>Sclerodermus</i> sp. 1	1	?	1	1	1	1	1	0	0	0	?	1	0	2	0	?	?	?	?	0	0	0	0	0	0	0	1	0	0	1	1
<i>Sclerodermus</i> sp. 2	1	?	1	1	1	1	1	1	0	0	?	1	0	2	0	?	?	?	?	0	0	0	0	1	1	1	0	0	1	1	
<i>Sierola depressa</i>	1	?	1	1	0	0	1	1	1	0	?	1	0	1	0	?	?	?	?	0	0	0	1	1	1	0	0	0	1	1	

OTU	.31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	
<i>Solepyris unicus 1</i>	1	?	1	1	0	0	1	1	1	1	1	1	0	1	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	1
<i>Solepyris unicus 2</i>	1	?	1	1	0	1	1	1	1	1	1	1	0	1	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	1
<i>Tuberepyris sp.</i>	1	?	1	1	0	0	1	1	1	0	?	1	0	2	0	?	?	?	?	0	2	?	?	?	?	0	0	0	1	1	
<i>Tuberepyris cf hamus</i>	1	?	1	1	0	1	1	1	1	0	?	1	0	2	0	?	?	?	?	0	2	?	?	?	?	0	0	0	0	1	
UG 1	0	0	1	1	1	0	1	1	0	0	?	1	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
UG 2	0	0	1	1	1	0	1	1	0	0	?	1	0	0	2	2	1	1	1	0	0	0	1	0	1	0	1	0	1	1	
UG 3	1	?	1	1	1	0	1	1	0	0	?	1	0	0	2	2	0	0	1	0	0	0	1	1	1	0	1	1	1	1	
UG 5	0	0	1	1	1	1	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	0	1	1	1	0	1	0	0	1	
UG 6	0	0	1	1	1	0	1	1	0	0	?	1	0	1	0	?	?	?	?	0	0	0	0	0	0	0	0	1	0	0	1
UG 7	0	0	1	1	1	1	1	1	1	0	?	1	0	0	0	?	?	?	?	0	0	0	1	1	0	0	1	0	1	1	
UG 8	0	0	1	1	1	0	1	1	0	0	?	1	0	0	2	2	0	0	1	0	0	0	0	1	1	0	1	0	0	1	
UG 9	1	?	1	1	1	1	1	1	0	0	?	1	0	1	0	?	?	?	?	0	1	0	0	0	0	0	0	1	0	1	1

OTU	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	
<i>Anisepyris proteus</i>	1	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	0	0	1	0	0	0	?	1	0	0	0	0		
<i>Heterocoelia finus</i>	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	?	0	0	0	0		
<i>Mesitius absentis</i>	1	1	1	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	?	1	0	0	0		
<i>Sulcomesitius nepalensis</i>	1	1	0	0	0	1	0	0	1	1	0	?	0	0	0	2	0	0	0	1	0	0	0	1	0	1	0	0	0		
<i>Allobethylus floridanus</i>	1	1	0	0	0	1	0	0	1	1	1	?	0	0	0	2	0	0	0	1	0	0	1	1	0	1	0	0	0		
<i>Allobethylus multicolor</i>	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	2	0	0	0	1	0	0	0	1	0	1	0	0	0		
<i>Allobethylus tomoae</i>	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	2	0	0	0	1	0	0	0	1	0	1	0	0	0		
<i>Alloplastanoxus unexpectatus</i>	0	1	0	1	1	0	0	1	1	1	1	0	1	0	0	3	0	1	1	1	0	0	0	1	0	1	0	0	0		
<i>Alloplastanoxus</i> sp. 1	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0	3	0	1	1	1	0	0	0	1	0	1	0	0	0		
<i>Alloplastanoxus</i> sp. 2	1	1	0	1	1	0	0	0	1	0	1	0	1	0	0	3	0	1	1	1	0	0	0	1	0	1	0	0	0		
<i>Alongatepyris ingens</i>	1	1	1	1	1	0	0	0	1	0	1	0	0	1	0	3	0	1	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Bethyloopsis fullawayi</i>	0	1	1	1	1	0	0	1	1	0	0	?	0	2	0	3	0	1	1	1	0	1	?	?	?	?	?	1	?	0	0
<i>Cephalonomia cisidophaga</i> (w)	1	1	0	1	1	0	0	0	1	0	0	?	0	1	0	3	0	1	1	0	0	1	?	1	0	1	1	?	1	?	
<i>Cephalonomia cisidophaga</i> (a)	0	0	?	?	1	0	0	0	1	0	0	?	?	0	0	3	0	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Cephalonomia conophthori</i>	0	1	0	1	1	0	0	1	1	1	0	?	1	0	0	3	1	1	1	0	0	1	?	1	0	1	1	?	1	?	
<i>Cephalonomia gallicola</i>	0	1	1	1	1	0	0	1	1	0	0	?	2	2	0	3	0	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Cephalonomia hypobori</i>	0	0	?	?	1	0	0	1	1	0	0	?	?	1	0	3	0	1	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Cephalonomia hyalinipennis</i>	0	1	1	1	1	0	0	0	1	0	1	?	1	0	0	3	1	1	1	0	0	1	?	1	0	1	1	?	1	?	
<i>Cephalonomia maculata</i>	1	1	1	1	1	0	0	1	1	1	1	?	0	0	0	2	0	1	1	1	0	0	1	1	1	1	1	?	1	?	
<i>Cephalonomia nidicola</i>	0	1	0	1	1	0	0	1	1	0	0	?	2	2	0	3	0	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Cephalonomia nigrescens</i>	0	1	1	1	1	0	0	0	1	0	0	?	0	1	0	3	0	?	1	0	0	0	?	?	?	?	?	?	?	?	
<i>Cephalonomia rufa</i>	0	1	0	1	1	0	0	1	1	0	0	?	1	?	0	3	0	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Cephalonomia stephanoderis</i>	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	2	0	1	1	0	0	1	?	1	1	1	1	?	1	?	
<i>Cephalonomia tarsalis</i>	1	1	1	0	1	0	0	0	1	1	1	0	0	0	0	2	0	1	1	1	0	0	1	1	1	1	1	?	1	?	
<i>Cephalonomia waterstoni</i>	1	1	1	1	1	0	0	0	1	1	0	?	0	2	0	3	?	1	1	0	0	0	0	1	0	1	1	?	1	?	
<i>Chilepyris platythelys</i>	1	1	1	0	0	1	1	0	0	1	1	0	0	0	1	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
<i>Discleroderma gundari</i>	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Discleroderma</i> sp. 1	1	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Discleroderma</i> sp. 2	1	1	1	0	0	1	0	1	0	1	1	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Discleroderma</i> sp. 3	1	1	1	0	0	1	1	1	0	1	1	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Galodoxa torquata</i> (f)	0	1	0	1	1	1	0	0	0	1	0	?	0	2	0	2	1	0	0	1	0	0	0	1	1	?	1	?	1	?	
<i>Galodoxa torquata</i> (m)	1	1	0	1	0	1	0	0	0	1	0	?	1	0	0	2	1	0	0	1	0	0	0	1	1	1	1	?	1	?	
<i>Glenosema</i> sp. (m)	0	0	?	?	1	0	0	1	1	0	0	?	?	0	0	3	0	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Glenosema crandalli</i>	1	1	1	0	0	1	0	0	1	1	0	?	0	0	0	3	0	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Glenosema doiinthanonensis</i>	1	1	0	0	0	1	0	0	1	1	1	0	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	

OTU	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	
<i>Glenosema denteata</i>	1	1	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	1	0	1	0	0	0	1	0	?	0	0	?	0	
<i>Glenosema nigra</i>	0	1	1	0	0	1	0	1	1	0	0	?	0	2	0	3	0	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Glenosema elevata</i>	0	1	0	0	0	1	0	0	1	1	1	0	0	2	1	3	1	?	?	0	0	1	?	?	?	?	?	?	?	?	
<i>Israelius carthami</i>	1	0	0	?	1	0	0	0	1	0	1	?	?	0	0	3	0	1	1	1	0	0	1	1	0	1	0	0	1	?	
<i>Israelius</i> sp. 1	0	0	0	?	1	0	0	0	1	0	0	?	?	0	0	3	0	1	1	1	0	0	1	1	0	0	0	0	0	1	?
<i>Israelius</i> sp. 2	0	0	0	?	1	0	0	0	1	0	0	?	?	0	?	3	0	1	1	1	0	0	1	1	0	1	0	1	0	1	
<i>Israelius</i> sp. 3	0	0	0	?	1	0	0	0	1	0	0	?	?	0	0	3	0	1	1	1	0	0	1	1	0	1	1	?	1	?	
<i>Israelius</i> sp. 4	0	0	0	?	1	0	0	0	1	0	0	?	?	0	0	3	0	1	1	1	0	0	1	1	1	1	0	1	0	1	
<i>Israelius</i> sp. 5	0	0	0	?	1	0	0	0	1	0	0	?	?	1	0	3	0	1	1	1	0	0	1	1	0	1	0	2	0	0	
<i>Israelius amputatus</i>	1	1	0	0	1	1	0	0	0	1	1	0	0	2	0	1	0	1	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Megaprosternum longiceps</i>	0	0	?	?	1	0	0	0	1	0	0	?	?	1	0	3	0	1	1	0	0	1	?	1	1	1	1	?	1	?	
<i>Megaprosternum</i> sp. 1	1	1	?	1	1	0	0	0	1	0	1	?	0	1	0	3	0	1	1	0	0	1	?	0	?	1	1	?	1	?	
<i>Megaprosternum</i> sp. 2	0	0	?	?	1	0	0	0	1	0	0	?	?	1	0	3	0	1	1	0	0	1	?	0	?	1	1	?	1	?	
<i>Nothepyris brasiliensis</i>	1	1	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	
<i>Nothepyris sulcata</i>	1	1	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	0	1	0	0	0	0	
<i>Nothepyris</i> sp. 1	1	1	1	0	0	1	1	1	0	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	0	1	1	?	1	?	
<i>Nothepyris</i> sp. 2	1	1	1	0	0	1	1	1	0	1	0	?	1	0	1	1	1	0	1	1	0	0	0	1	0	?	1	?	0	0	
<i>Pararhabdepyris arabo</i>	1	1	0	0	1	1	0	1	0	1	1	0	0	1	0	1	0	1	1	1	0	0	1	1	0	1	0	0	0	0	
<i>Pararhabdepyris ngangu</i>	0	1	0	0	1	1	0	1	0	1	1	1	0	1	0	1	0	1	1	1	0	0	1	1	0	1	0	0	0	0	
<i>Pararhabdepyris lophos</i>	1	1	0	0	1	1	1	1	0	1	1	0	1	1	0	1	0	1	1	1	0	0	1	1	0	1	0	0	0	0	
<i>Pararhabdepyris wafrika</i>	1	1	0	0	1	1	0	1	0	1	1	1	0	1	0	1	0	1	1	1	0	0	1	1	0	1	0	0	0	0	
<i>Platepyris sepalus</i>	0	0	?	?	1	0	0	?	?	0	0	?	?	0	0	3	?	?	?	0	0	1	?	?	?	?	?	1	?	?	?
<i>Plastanoxus ahusiensi</i>	1	1	?	1	1	0	0	0	1	1	0	?	0	0	0	2	0	1	1	1	0	0	0	1	0	0	0	0	0	0	
<i>Plastanoxus chittendenii</i>	1	1	0	1	1	0	0	1	1	1	1	0	0	0	0	3	0	1	1	0	0	1	?	1	0	1	0	0	0	0	
<i>Plastanoxus incompletus</i>	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	3	0	1	1	1	0	1	?	1	0	1	0	1	0	0	
<i>Plastanoxus laevis</i>	1	1	1	1	1	1	1	0	1	0	1	0	0	1	0	2	0	1	1	1	0	0	0	1	0	0	0	0	0	0	
<i>Plastanoxus westwoodi</i>	1	1	0	1	1	0	0	0	1	?	1	1	0	0	0	2	0	1	1	0	0	1	?	1	0	1	0	0	0	0	
<i>Proplastanoxus elegans</i>	1	1	0	1	1	0	0	1	1	1	1	0	1	1	0	1	0	1	1	1	0	0	1	1	0	1	0	0	0	0	
<i>Prorops</i> sp. 1	0	1	1	1	1	0	0	1	1	0	0	?	0	0	0	3	1	1	1	0	0	0	0	1	0	1	0	0	0	0	
<i>Prorops</i> sp. 2	0	0	1	?	1	0	0	1	1	0	0	?	?	0	0	3	1	1	1	0	0	1	?	1	0	1	0	0	0	0	
<i>Prorops</i> sp. 3	0	0	1	?	1	0	0	0	1	0	0	?	?	0	0	3	1	1	1	0	0	1	?	1	0	?	1	?	0	2	
<i>Prorops nasuta</i>	0	0	1	?	1	0	0	0	1	0	0	?	?	0	0	3	1	1	1	0	0	1	?	1	0	1	0	0	0	0	
<i>Sclerodermus</i> sp. 1	0	1	0	1	1	0	0	0	1	0	0	?	2	2	0	3	1	0	1	1	0	0	0	1	1	1	1	?	1	?	
<i>Sclerodermus</i> sp. 2	0	1	0	0	1	0	0	0	1	1	0	?	2	2	0	3	1	1	1	1	0	0	0	1	1	1	1	?	1	?	
<i>Sierola depressa</i>	1	1	0	1	1	0	0	0	1	0	1	?	0	1	0	2	0	1	1	1	1	0	0	1	0	1	0	0	1	?	

OTU	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
<i>Solepyris unicus 1</i>	0	1	0	0	1	0	0	0	0	1	0	?	0	1	0	2	0	1	1	2	1	0	1	1	0	1	1	?	1	?
<i>Solepyris unicus 2</i>	0	1	0	1	1	0	0	0	1	1	0	?	0	1	0	2	0	1	1	2	1	0	1	1	1	1	1	?	1	?
<i>Tuberepyris sp.</i>	0	1	1	1	1	0	0	0	1	0	0	?	0	1	0	3	0	0	1	0	0	0	0	1	0	1	0	2	0	1
<i>Tuberepyris cf hamus</i>	1	0	1	?	1	0	0	0	1	0	0	?	?	1	0	3	0	1	1	0	0	0	0	1	1	1	0	2	0	1
UG 1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	0
UG 2	1	1	0	1	1	1	0	0	1	1	1	0	0	2	0	2	0	1	1	1	0	0	1	0	?	1	1	?	1	?
UG 3	1	1	0	1	1	0	0	1	1	1	1	0	0	2	0	2	0	1	1	1	0	0	1	0	?	?	1	?	1	?
UG 5	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	2	0	1	1	1	0	0	0	1	0	1	1	?	1	?
UG 6	1	1	0	0	0	1	1	1	0	1	1	0	0	2	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	0
UG 7	1	0	0	?	1	1	0	0	1	0	1	1	?	2	0	2	0	1	1	1	1	0	0	1	0	1	0	0	0	0
UG 8	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	2	0	1	1	1	0	0	1	1	1	1	0	0	0	0
UG 9	1	1	1	1	1	0	0	0	1	1	0	?	1	0	1	3	0	1	1	1	0	0	0	1	1	1	0	0	0	0

OTU	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	
<i>Anisepyris proteus</i>	1	1	0	1	0	0	1	0	1	0	1	2	1	0	0	1	1	0	0	0	1	1	?	1	1	?	1	1	
<i>Heterocoelia finus</i>	1	0	0	1	0	0	1	0	1	0	1	1	1	1	0	0	1	0	1	0	0	1	?	1	1	?	0	1	
<i>Mesitius absentis</i>	1	0	0	1	0	0	1	0	1	0	1	1	1	1	0	0	1	0	1	0	0	1	?	1	1	?	0	1	
<i>Sulcomesitius nepalensis</i>	1	1	0	1	0	2	0	1	1	0	1	2	1	1	0	1	0	0	1	0	0	0	1	0	1	?	1	1	
<i>Allobethylus floridanus</i>	1	1	0	1	0	2	0	0	1	0	0	1	1	1	0	0	1	1	?	0	1	1	?	0	1	?	1	1	
<i>Allobethylus multicolor</i>	1	1	0	1	0	0	1	0	1	0	0	1	1	1	0	0	1	0	0	0	1	1	?	0	1	?	1	1	
<i>Allobethylus tomoae</i>	1	1	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	1	1	?	0	1	?	1	1	
<i>Alloplastanoxus unexpectatus</i>	1	1	0	1	1	?	?	1	0	0	0	1	1	1	0	1	1	1	?	0	1	0	1	1	1	?	1	1	
<i>Alloplastanoxus</i> sp. 1	1	1	0	1	1	1	0	1	0	0	0	1	1	1	0	1	1	1	?	0	1	1	?	1	1	?	1	1	
<i>Alloplastanoxus</i> sp. 2	1	1	0	1	1	1	0	1	0	0	0	1	1	1	0	1	1	1	?	0	1	1	?	0	1	?	1	1	
<i>Alongatepyris ingens</i>	1	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	1	?	0	1	1	?	0	0	?	1	1	
<i>Bethylopsis fullawayi</i>	1	?	0	?	?	?	?	?	?	?	0	?	?	1	0	1	0	1	?	0	0	1	?	0	1	?	1	1	
<i>Cephalonomia cisidophaga</i> (w)	1	1	1	0	?	?	?	?	0	0	1	1	1	1	0	0	1	1	?	0	1	0	0	0	1	?	1	1	
<i>Cephalonomia cisidophaga</i> (a)	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1	?	1	?	?	?	?	1	?	1	1	
<i>Cephalonomia conophthori</i>	1	1	1	0	?	?	?	?	0	0	1	1	1	1	0	0	1	1	?	0	1	0	0	1	1	?	1	1	
<i>Cephalonomia gallicola</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	1	?	1	?	?	?	?	?	1	?	1	1
<i>Cephalonomia hypobori</i>	1	1	1	0	?	?	?	?	0	0	0	1	0	1	0	0	1	1	?	0	0	0	1	1	1	?	1	1	
<i>Cephalonomia hyalinipennis</i>	1	1	1	0	?	?	?	?	0	0	0	1	1	1	0	0	1	1	?	0	1	0	0	1	1	?	1	1	
<i>Cephalonomia maculata</i>	1	1	1	0	?	?	?	?	0	0	1	1	1	1	0	0	1	1	?	?	?	?	?	?	1	?	1	1	
<i>Cephalonomia nidicola</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	1	?	1	?	?	?	?	?	1	?	1	1
<i>Cephalonomia nigrescens</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	1	?	?	?	?	?	?	?	1	?	1	1
<i>Cephalonomia rufa</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	?	1	?	1	?	?	?	?	?	1	?	1	1
<i>Cephalonomia stephanoderis</i>	1	1	1	0	?	?	?	?	0	1	0	1	1	1	0	0	1	1	?	0	1	0	0	1	1	?	1	1	
<i>Cephalonomia tarsalis</i>	1	1	1	0	?	?	?	?	0	0	0	1	1	1	0	0	1	1	?	0	1	0	0	0	0	1	?	1	1
<i>Cephalonomia waterstoni</i>	1	1	1	0	?	?	?	?	0	0	0	1	1	1	0	0	1	1	?	0	0	0	0	0	0	1	?	1	1
<i>Chilepyris platythelys</i>	?	0	0	1	0	0	1	0	1	0	1	2	0	1	?	0	?	1	?	?	?	?	?	?	?	1	?	1	1
<i>Discleroderma gundari</i>	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	0	0	1	0	1	1	1	0	
<i>Discleroderma</i> sp. 1	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	0	0	1	0	1	1	1	0	
<i>Discleroderma</i> sp. 2	1	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	1	1	?	0	0	0	1	0	1	1	1	0	
<i>Discleroderma</i> sp. 3	1	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	1	1	?	0	0	0	1	0	1	1	1	0	
<i>Galodoxa torquata</i> (f)	1	0	0	1	0	2	0	1	1	0	1	1	0	1	?	0	?	1	?	0	1	0	1	0	1	0	1	1	
<i>Galodoxa torquata</i> (m)	1	0	0	1	0	2	0	1	1	0	1	1	0	0	0	0	0	1	?	0	1	1	?	0	1	?	1	1	
<i>Glenosema</i> sp. (m)	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	1	?	1	?	?	?	?	?	1	?	1	1
<i>Glenosema crandalli</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	?	0	0	0	1	0	1	?	1	1	
<i>Glenosema doiinthanonensis</i>	1	0	0	1	0	0	1	0	0	0	1	2	0	1	0	1	1	0	1	0	1	0	1	1	1	?	1	1	

OTU	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	
<i>Glenosema denteata</i>	1	0	0	1	0	2	1	0	1	0	1	2	0	0	0	0	1	0	0	0	0	1	?	0	1	?	1	1	
<i>Glenosema nigra</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	0	?	0	1	1	?	?	1	?	1	1	
<i>Glenosema elevata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	?	0	1	0	0	1	?	0	1	?	1	1	
<i>Israelius carthami</i>	0	1	0	1	0	2	0	1	0	0	0	1	0	1	0	1	1	1	?	0	1	0	0	0	1	?	1	1	
<i>Israelius</i> sp. 1	0	1	0	1	1	2	0	1	0	0	0	1	0	1	?	0	?	1	?	0	0	1	?	0	1	?	1	1	
<i>Israelius</i> sp. 2	0	1	0	1	1	2	0	1	0	0	1	1	0	1	0	0	1	1	?	0	1	0	1	1	1	?	1	1	
<i>Israelius</i> sp. 3	0	1	0	1	1	?	0	1	0	0	1	1	0	1	0	0	1	1	?	0	0	0	0	0	1	?	1	1	
<i>Israelius</i> sp. 4	0	1	0	1	1	2	0	?	0	0	1	1	1	1	?	0	?	1	?	0	0	0	0	1	1	?	1	1	
<i>Israelius</i> sp. 5	0	1	0	1	1	2	0	1	0	0	0	1	0	1	0	0	1	1	?	0	0	0	0	0	1	?	1	1	
<i>Israelius amputatus</i>	1	1	0	1	1	2	0	0	0	1	1	1	1	1	0	1	1	1	?	0	1	0	0	1	1	?	1	1	
<i>Megaprosternum longiceps</i>	1	1	1	0	?	?	?	?	?	0	1	1	2	0	1	0	0	1	0	1	0	1	0	1	0	1	?	1	1
<i>Megaprosternum</i> sp. 1	1	1	1	0	?	?	?	?	?	0	0	0	1	0	1	0	0	1	1	?	1	?	?	?	?	1	?	1	1
<i>Megaprosternum</i> sp. 2	1	1	1	0	?	?	?	?	?	0	1	1	1	0	1	1	0	?	1	?	1	?	?	?	?	1	?	1	1
<i>Nothepeyris brasiliensis</i>	1	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	1	1	?	0	1	?	1	1	
<i>Nothepeyris sulcata</i>	1	0	0	1	0	0	1	0	1	0	1	1	1	0	0	1	0	0	1	0	1	1	?	0	1	?	1	1	
<i>Nothepeyris</i> sp. 1	1	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	
<i>Nothepeyris</i> sp. 2	1	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	
<i>Pararhabdepyris arabo</i>	1	1	1	0	?	2	0	?	0	0	0	1	1	1	0	1	1	0	0	0	1	1	?	1	1	?	0	1	
<i>Pararhabdepyris ngangu</i>	1	1	1	0	?	?	?	?	?	0	0	0	1	0	1	0	0	1	0	0	0	1	1	?	1	1	?	0	1
<i>Pararhabdepyris lophos</i>	1	1	1	0	?	?	?	?	?	0	0	0	1	1	1	0	1	1	0	0	0	1	1	?	1	1	?	0	1
<i>Pararhabdepyris wafrika</i>	1	1	1	0	?	?	?	?	?	0	0	0	1	1	1	0	1	1	0	0	0	1	1	?	1	1	?	0	1
<i>Platepyris sepalus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	?	1	?	?	0	?	?	?	?	0	?	?	1
<i>Plastanoxus ahusiensi</i>	1	1	0	1	1	?	?	?	1	0	0	1	?	?	?	?	1	?	?	?	?	?	?	?	?	1	?	1	1
<i>Plastanoxus chittendenii</i>	1	1	1	0	?	?	?	?	?	0	0	0	1	0	1	0	0	1	1	?	0	1	0	0	0	1	?	1	1
<i>Plastanoxus incompletus</i>	1	1	0	1	1	2	0	1	0	0	0	1	1	1	0	0	1	1	?	0	1	0	1	1	1	1	?	1	?
<i>Plastanoxus laevis</i>	1	1	0	1	1	2	0	1	0	0	0	1	1	1	0	1	1	1	?	0	1	0	1	1	1	1	?	1	1
<i>Plastanoxus westwoodi</i>	1	1	1	0	?	?	?	?	?	0	0	0	1	0	1	0	0	1	1	?	0	1	0	0	0	1	?	1	1
<i>Proplastanoxus elegans</i>	1	1	0	1	1	2	0	1	0	0	0	1	1	1	0	0	1	1	?	0	1	1	?	1	1	?	1	1	
<i>Prorops</i> sp. 1	1	1	1	0	?	?	?	?	?	0	0	1	?	?	1	?	0	?	0	1	0	1	1	?	0	1	?	1	1
<i>Prorops</i> sp. 2	1	1	1	0	?	?	?	?	?	0	0	1	1	0	1	0	0	1	1	?	0	1	0	0	0	1	?	1	1
<i>Prorops</i> sp. 3	1	1	1	0	?	?	?	?	?	0	1	0	?	1	0	0	1	1	?	0	1	0	0	1	1	?	1	1	
<i>Prorops nasuta</i>	1	1	1	0	?	?	?	?	?	0	0	0	0	?	1	0	0	1	1	?	0	0	0	0	0	1	?	1	1
<i>Sclerodermus</i> sp. 1	1	1	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	1	?	0	1	0	1	0	1	?	1	1	
<i>Sclerodermus</i> sp. 2	1	1	0	1	0	2	0	0	0	1	1	1	1	1	0	0	0	1	?	0	1	0	1	0	1	?	1	1	
<i>Sierola depressa</i>	1	1	0	1	0	1	0	1	0	1	0	?	?	0	?	0	?	0	1	0	1	1	?	0	0	?	1	1	

OTU	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118
<i>Solepyris unicus 1</i>	1	1	0	1	0	2	0	0	0	0	1	2	0	0	0	1	1	0	1	0	1	1	?	0	1	?	1	1
<i>Solepyris unicus 2</i>	1	1	0	1	0	2	0	0	0	0	1	2	0	0	0	0	1	0	1	0	1	1	?	0	1	?	1	1
<i>Tuberepyris sp.</i>	1	1	0	1	0	1	0	1	0	1	0	1	0	1	?	0	?	0	1	0	1	1	?	0	1	?	1	1
<i>Tuberepyris cf hamus</i>	1	1	0	1	0	?	?	1	0	0	0	1	0	1	0	0	1	0	1	0	0	1	?	0	1	?	1	1
UG 1	1	1	0	1	0	2	0	1	0	0	1	1	1	1	?	1	?	1	?	0	1	1	?	1	1	?	1	1
UG 2	1	1	0	1	1	1	0	1	0	1	1	1	1	1	?	1	?	1	?	0	1	1	?	1	1	?	1	1
UG 3	1	1	1	0	?	?	?	?	0	1	1	1	1	1	?	1	?	1	?	0	1	1	?	1	1	?	1	1
UG 5	1	1	0	1	1	1	0	1	0	0	0	1	1	1	?	0	?	1	?	0	1	0	0	0	1	0	1	1
UG 6	1	1	0	1	0	0	0	0	0	0	1	2	1	1	?	1	?	1	?	0	0	1	?	1	1	?	1	1
UG 7	1	1	0	1	1	1	0	1	0	0	1	1	1	1	?	1	?	1	?	0	0	1	?	1	1	?	1	1
UG 8	1	1	0	1	1	2	0	1	0	0	0	1	1	1	?	1	?	1	?	0	0	0	1	1	1	?	1	1
UG 9	0	1	0	1	1	2	0	1	0	0	0	1	1	1	0	0	1	1	?	0	1	0	0	1	1	?	1	1