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HOLOPOTHRIPS HOOD, 1914 (THYSANOPTERA: PHLAEOTHRIPIDAE): RELAÇÕES FILOGENÉTICAS E DIVERSIDADE

PORTO ALEGRE
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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.
Área de concentração: Biologia Comparada
Orientador: Prof. Dr. Adriano Cavalleri
Co-orientador: Prof. Dr. Augusto Ferrari

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Sumário

Resumo

Holopothrips (Thysanoptera: Phlaeothripidae) é um gênero Neotropical de tripes frequentemente associados a galhas. Dez das 36 espécies atualmente descritas foram coletadas de galhas, em sua maioria indutores destas estruturas, mas pelo menos duas espécies são invasoras de galhas abandonadas de Cecidomyiidae. Duas espécies do gênero foram coletadas causando danos em plantas cultivadas: *Holopothrips ananasi* em abacaxi, e *Holopothrips fulvus* em caju, e uma nova espécie descrita neste trabalho é referida como praga em feijoa. Apesar do interesse ecológico do hábito galhador e do potencial interesse econômico, *Holopothrips* ainda é um grupo pouco estudado, com muitas espécies conhecidas apenas da série tipo, e diversos espécimes sem identificação em coleções ao redor do mundo. Além disso, a diagnose do grupo é limitada, com várias espécies apresentando exceções ou modificações dos caracteres usados para identificar o gênero. Com isso, questionamentos acerca da monofilia de *Holopothrips* têm sido feitos nos últimos 20 anos. Neste trabalho buscamos preencher algumas destas lacunas no conhecimento de *Holopothrips*, descrevendo 24 novas espécies, realizando um estudo comparativo da variação morfológica existente no grupo (principalmente interespecífica), elaborando uma chave de identificação ilustrada, e realizando uma análise filogenética do gênero. A partir deste trabalho, o gênero passa a ter 60 espécies reconhecidas, das quais 30 possuem registro de associação com galhas, muitas das quais são ilustradas neste trabalho. Os estudos morfológicos serviram de base para a criação de uma matriz com 140 caracteres e 87 terminais, que foi analisada com base em um critério de parcimônia. Apesar dos valores de suporte obtidos nas análises serem muito baixos para uma revisão da classificação do gênero, foi possível observar algumas tendências nas topologias e otimizações dos caracteres diagnósticos do grupo, que são discutidos. Assim, esperamos prover a base taxonômica e sistemática necessária para a correta identificação do gênero, e para futuros estudos ecológicos e evolutivos desses tripes galhadores.

Abstract

Holopothrips Hood (Thysanoptera: Phlaeothripidae) is a Neotropical genus of thrips frequently associated to plant galls. Ten out of 36 known species were collected from galls, most of them being the inducers of such structures, but at least two species are invaders of Cecidomyiidae abandoned galls. Two species of the genus were collected damaging crops: *Holopothrips ananasi* in pineapple, and *Holopothrips fulvus* in cashew; and a new species described in this work is recorded as a pest in feijoa. Despite the ecological interest in the galling habit and the potential economic importance of the group, the genus *Holopothrips* is still poorly studied, with several species known only from the type series, and many specimens without identification in collections across the world. Moreover, the diagnosis of the group is limited, with several species having exceptions or modifications of the characters used to identify the genus. With this, questions about the monophyly of *Holopothrips* have been made in the last twenty years. In this work we attempt to fill in some of these gaps in the knowledge about *Holopothrips*, describing 24 new species, performing a comparative study of the morphological variation observed in the group (mainly interspecific), proposing an illustrated identification key, and perform a phylogenetic analysis of the genus. With this work, the genus now comprises 60 known species, 30 of them recorded in association with galls, several of which are illustrated here. The morphological studies served as the basis for the creation of a matrix with 140 characters and 87 terminals, which was analyzed using parsimony. Despite the very low support values obtained in the analyses, which do not allow the revision of the systematics of the group, it was possible to observe some tendencies in the topologies and optimization of diagnostic characters of *Holopothrips*, which are discussed. Thus, we hope to provide the needed taxonomical and systematic basis for the correct identification of the genus, and for future ecological and evolutive studies of these galling thrips.

Introdução Geral

A ordem Thysanoptera é composta por pouco mais de 6000 espécies descritas de insetos diminutos, popularmente conhecidos como tripes. Suas principais características diagnósticas são a presença de asas franjadas, tarsos com arólios eversíveis e aparelho bucal assimétrico, sendo esta última uma sinapomorfia da ordem (Mound & Marullo 1996).

Thysanoptera é dividida em duas subordens, Terebrantia (oito famílias e cerca de 2500 espécies) e Tubulifera (uma família e quase 3700 espécies) (ThripsWiki 2018), e evidências filogenéticas indicam que estes são grupos-irmãos (Mound & Morris 2007; Buckman *et al*. 2013). A única família de Tubulifera, Phlaeothripidae Uzel, 1895, é dividida em duas subfamílias: Idolothripinae Bagnall, 1908 (cerca de 700 espécies), que parece ser um grupo monofilético, e Phlaeothripinae Uzel, 1895 (quase 3000 espécies), que é provavelmente um grupo parafilético (Buckman *et al*. 2013). A classificação em gênero e espécie é ainda mais complexa, com alguns poucos gêneros muito diversos e de definição inadequada. Cerca de 47% dos gêneros de tripes são monotípicos, e as relações de parentesco entre estes grupos permanecem pouco estudadas (ThripsWiki 2018).

Os tripes apresentam uma grande variedade de hábitos, com espécies predadoras, fungívoras, fitófagas e ectoparasitas. Devido à variação em seu hábito alimentar, estes insetos ocupam diversos habitats, tais como: flores e folhas de inúmeras espécies vegetais, serapilheira, bulbos armazenados, cascas de árvores e galhas induzidas por eles ou outros insetos (Mound 2005).

O hábito galhador é registrado para cerca de 300 espécies de Thysanoptera, a grande maioria pertencentes à família Phlaeothripidae (Ananthakrishnan & Raman 1989). Existe uma grande variedade de morfologias de galhas, desde simples dobramentos e enrolamentos das folhas a rosetas e intumescimentos caulinares (Ananthakrishnan & Raman 1989; Mound 1994). Os tripes também exibem outros hábitos associados a estas estruturas, como espécies invasoras de galhas, desde simples inquilinos a cleptoparasitas; e espécies que vivem em galhas abandonadas (Crespi *et al*. 2004). Esta variedade está presente no gênero Neotropical *Holopothrips* (Phlaeothripidae: Phlaeothripinae), que compreende diversas espécies galhadoras e invasoras de galhas.

Holopothrips é atualmente composto por 36 espécies, distribuídas desde o México até a Argentina, com uma espécie descrita da Flórida (ThripsWiki 2018). Todas as espécies são fitófagas, e algumas foram descritas de galhas ou causando alterações no tecido vegetal de

plantas diversas (Cavalleri & Kaminski 2007). O gênero não é definido por uma única característica, mas sim por uma combinação de caracteres morfológicos, sendo os mais frequentemente usados: presença de um terceiro par de cerdas retentoras das asas nos tergitos abdominais II–VII; presença de cerdas discais anteriores no metanoto; machos com placas porosas múltiplas e de estrutura complexa; fêmeas com espermateca bem desenvolvida e visível após a maceração (Mound & Marullo 1996, Zamora *et al*. 2015).

Porém, muitas destas características não são estáveis entre as espécies. Modificações e exceções à diagnose do gênero ocorrem com alguma frequência, como ausência do terceiro par de cerdas retentoras das asas em alguns tergitos, ou ausência de placas porosas nos machos de algumas espécies (Mound & Marullo 1996; este trabalho). Outras características comumente encontradas no grupo, mas também com variabilidade, são às vezes utilizadas para auxiliar na identificação (Mound & Marullo 1996).

O gênero *Holopothrips* foi descrito em 1914 por J. D. Hood, para abrigar duas espécies encontradas em galhas de *Hura crepitans* (Euphorbiaceae) no Panamá, porém não foi confirmado se estas espécies eram as indutoras das galhas. Na descrição original, o gênero foi considerado relacionado com o gênero asiático *Gynaikothrips*, também com espécies indutoras de galhas. Diversos outros gêneros relacionados foram descritos após este trabalho, a princípio sendo tratados como grupos distintos, mas muitos deles são hoje considerados sinônimos de *Holopothrips*, de acordo com a revisão feita por Mound & Marullo (1996). Estes autores também descreveram seis novas espécies para o gênero e elaboraram uma chave de identificação, a única disponível para *Holopothrips*. Após isto, outras cinco espécies, três do Brasil (Cavalleri & Kaminski 2007, Lindner *et al.* 2016, Jorge *et al.* 2016) e duas da região do Caribe foram descritas (Cabrera & Segarra 2008; Zamora *et al*. 2015).

Atualmente o gênero *Holopothrips* tem sido relacionado com cinco gêneros Neotropicais (Mound & Marullo 1996; Retana-Salazar & Nishida 2007; Retana-Salazar & Soto-Rodríguez 2008; Soto-Rodríguez *et al*. 2012; Mound 2013). *Plagiothrips* é um gênero cuja única espécie foi inicialmente descrita como pertencente a *Gynaikothrips*, sendo encontrada induzindo galhas em *Eugenia* (Mound & Marullo 1996); compartilha com *Holopothrips* a presença de um terceiro par de cerdas retentoras das asas nos tergitos abdominais, mas foi diferenciado deste por possuir um dente tarsal bem desenvolvido e hamus aparente nas pernas anteriores (Mound & Marullo 1996). *Mixothrips* atualmente possui duas espécies, uma delas descrita como possuindo duas formas, mas uma destas formas foi mais tarde reconhecida como uma espécie pertencente a *Holopothrips* (Mound & Marullo 1996); o

gênero foi distinguido pela presença de um hamus bem desenvolvido no primeiro par de pernas e ausência de um terceiro par de cerdas retentoras das asas na maioria dos espécimes (Mound & Marullo 1996). *Jersonithrips* foi descrito como um galhador em uma espécie de pteridófita, sendo considerado um gênero próximo a *Holopothrips,* mas com estiletes maxilares muito curtos e afastados entre si e cones sensoriais pequenos e robustos (Retana-Salazar & Nishida 2007). *Johansenthrips* foi comparado a *Plagiothrips,* mas considerado como um gênero distinto por apresentar uma projeção na parte posterior da cabeça e áreas de esculturação diferenciadas nos tergitos abdominais (Retana-Salazar & Soto-Rodríguez 2008). *Fourbethrips* foi inicialmente tratado como um gênero próximo a espécies Neotropicais de tripes fungívoros (Soto-Rodríguez *et al*. 2012), mas Mound (2013) apontou as semelhanças morfológicas e de hábito de vida entre *Fourbethrips* e espécies de *Holopothrips* e *Mixothrips*. A exata relação entre estes gêneros não é conhecida, e Mound & Marullo (1996) sugerem que *Plagiothrips* e *Mixothrips* possam ser parafilético com respeito a *Holopothrips*.

No Brasil, 19 espécies de *Holopothrips* são registradas, porém a maioria destas são conhecidas apenas do material tipo (ThripsWiki 2018). Mesmo com poucos estudos neste gênero, material presente na coleção de Thysanoptera da UFRGS, provenientes de diversas coletas das mais variadas partes do Brasil, indicam uma diversidade muito maior que a registrada. A coleção potencialmente possui diversas espécies novas, muitas delas coletadas em grande quantidade em galhas. Descrever esta diversidade pouco explorada, e compreender melhor a definição de *Holopothrips* e suas relações com outros gêneros, são os principais objetivos deste trabalho.

No capítulo 1, a diversidade de *Holopothrips* é explorada: 24 espécies, baseadas principalmente no material não identificado depositado na UFRGS, são descritas, junto com informações de suas galhas sempre que possível. Neste capítulo tecemos comentários e observações sobre a variação morfológica de *Holopothrips*, com base em observações de material tipo de diversas espécies, informações na literatura, e espécimes previamente identificados por comparação com tipos ou descrições originais. Além disso, toda esta informação da diversidade morfológica do gênero é ricamente ilustrada com fotos da maioria das espécies mencionadas no trabalho. Por fim, provemos uma chave de identificação para 56 das 60 espécies agora reconhecidas para *Holopothrips*, para facilitar futuros trabalhos que requerem a correta identificação de espécimes do gênero.

No capítulo 2, os estudos morfológicos realizados no capítulo 1 servem como ponto de partida para a criação de uma matriz de caracteres, que é analisada filogeneticamente. Além de

incluir 55 das 60 espécies de *Holopothrips* reconhecidas no capítulo 1, a análise também compreende todas as espécies dos cinco gêneros propostos como relacionados, e espécies de outros 25 gêneros de Phlaeothripinae, de diversas partes do mundo e de hábitos variados. Ao todo, são analisados 140 caracteres, 109 discretos e 31 contínuos, a maior parte deles propostos para um enfoque filogenético pela primeira vez aqui. Esta análise objetiva explorar a monofilia de *Holopothrips* como é atualmente reconhecido, e estabelecer seu possível relacionamento com os outros gêneros de galhadores Neotropicais.

Objetivos

Objetivo geral:

Testar a monofilia de *Holopothrips* e descrever a diversidade taxonômica desse grupo de tripes.

Objetivos específicos:

(1) Testar a monofilia de *Holopothrips* com base na morfologia e estabelecer as relações filogenéticas entre as espécies com base na morfologia;

(2) Compilar o conhecimento já existente de *Holopothrip*s: distribuição, plantas hospedeiras, hábitos, variedade morfológica, com ênfase em material coletado no Brasil;

(3) Descrever novas espécies de *Holopothrips*, com base principalmente no material depositado na coleção de Thysanoptera da UFRGS;

(4) Produzir uma chave de identificação para as espécies de *Holopothrips*.

Referências

Ananthakrishnan, T.N. & Raman, A. (1989) *Thrips and gall dynamics*. Oxford & IBH Publishing Company, Janpath, New Delhi, 120 pp.

Bournier, A. (1993) Thysanoptere de Martinique et de Guadeloupe. *Zoology (Journal of Pure and Applied Zoology)*, 3 (3), 227–240.

Buckman, R.S., Mound, L.A. & Whiting, M.F. (2013) Phylogeny of thrips (Insecta: Thysanoptera) based on five molecular loci. *Systematic Entomology*, 38, 123–133.

Cabrera, I. & Segarra, A. (2008) A new gall-inducing species of *Holopothrips* (Thysanoptera: Phlaeothripinae) from *Tabebuia* trumpet trees in the Caribbean region. *Florida Entomologist*, 91 (2), 232-236.

Cavalleri, A. & Kaminski, L.A. (2007) A new *Holopothrips* species (Thysanoptera: Phlaeothripidae) damaging *Mollinedia* (Monimiaceae) leaves in Southern Brazil. *Zootaxa*, 1625, 61–68.

Crespi, B.J., Morris, D.C. & Mound, L.A. (2004) *Evolution of ecological and behavioural diversity: Australian Acacia thrips as model organisms*. Australian Biological Resources Study & Australian National Insect Collection, CSIRO, Canberra, 328pp.

Hood, J.D. (1914) Two new Thysanoptera from Panama. *Insecutor inscitiae menstruus*, 2, 49–53.

Hood, J.D. (1954) Brasilian Thysanoptera IV. *Proceedings of the Biological Society of Washington*, 67, 17–54.

Jorge, N.C., Cavalleri, A., Bedetti, C.S. & Isaias, R.M. (2016) A new leaf-galling *Holopothrips* (Thysanoptera: Phlaeothripidae) and the structural alterations on *Myrcia retorta* (Myrtaceae). *Zootaxa* 4200(1), 174–180.

Lindner, M.F., Mendonça Jr., M.S. & Cavalleri, A. (2016) *Holopothrips molzi* **sp.n**. (Thysanoptera, Phlaeothripidae): natural history and interactions in Myrtaceae galls. *Zootaxa* 4114(2), 139–148.

Mound, L.A. (1994) Thrips and gall induction: a search for patterns. *In:* Williams, M.A.J. (Ed), *Plant Galls: Organisms, Interactions, Populations*. Systematics Association Special Volume 49. Clarendon Press, Oxford, pp. 131–149.

Mound, L.A. (2005) Thysanoptera – Diversity and Interactions. *Annual Review of Entomo*logy, 50, 247–269.

Mound, L.A. (2013) Homologies and host-plant specificity: recurrent problems in the study of

thrips. *Florida Entomologist*, 96 (2), 318–322.

Mound, L.A. & Marullo, R. (1996) The thrips of Central and South America: an introduction (Insecta: Thysanoptera). *Memoirs on Entomology, International*, 6, 1–488.

Mound, L.A. & Morris, D.C. (2007) The insect Order Thysanoptera: classification versus systematics. *In:* Zhang, Z.Q. & Shear, W.A. (eds), Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. *Zootaxa*, 1668, 1-766

Priesner, H. (1921) Neue und wenig bekannte Thysanopteren der neotropischen Fauna aus der Sammlung des Berliner Zoologischen Museums. *Deutsche entomologische Zeitung*, 1921, 187–223.

Retana-Salazar, A.P. & Nishida, K. (2007) First gall-inducing thrips on *Elaphroglossum* ferns: a new genus and species of thrips, *Jersonithrips galligenus* from Costa Rica (Insecta, Thysanoptera, Phlaeothripidae). *Senckenbergiana biologica*, 87, 143–148.

Retana-Salazar, A.P. & Soto-Rodriguez, G.A. (2008) A new genus and species of gall-inducing thrips (Thysanoptera: Tubulifera) from the neotropical region. *Brenesia*, 69, 59–64.

Soto-Rodríguez, G.A., Nishida, K. & Retana-Salazar, A.P. (2012) A new genus of gall-dwelling thrips from Costa Rica (Thysanoptera: Phlaeothripidae: Phlaeothripinae). *Revista Mexicana de Biodiversidad*, 83, 606–610.

ThripsWiki (2018) ThripsWiki – providing information on the World's thrips. Disponível em http://thrips.info/wiki/Main_Page (Acesso em 21 de Fevereiro)

Zamora, S., Hanson, P. & Mound, L.A. (2015) On the biology of *Holopothrips chaconi* sp.n. (Thysanoptera, Phlaeothripinae) from leaf-vein galls on Piper species in Costa Rica. *Revista de Biologia Tropical*, 63 (4), 1035–1042.

Capítulo 1

HOLOPOTHRIPS DIVERSITY - A NEOTROPICAL GENUS OF GALL-INDUCING INSECTS (THYSANOPTERA, PHLAEOTHRIPIDAE)

Artigo a ser submetido para o periódico Zootaxa

Holopothrips diversity - a Neotropical genus of gall-inducing insects (Thysanoptera, Phlaeothripidae)

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Abstract

The genus *Holopothrips* represents the main Neotropical group of thrips associated to plant galls. Several of the 36 currently described species are known to induce galls or invade them, but we lack information on host plants and habits for many other species. Moreover, *Holopothrips* presents a high morphological diversity, which blurs the delimitations of the genus and makes difficult to identify possible phylogenetic relationships. The existence of several *Holopothrips* specimens in collections that do not belong to any of the already described species, allied to the absence of basic biological information for several species, such as host plants and habit, shows that the current knowledge on the genus is severely lacking. Here we start addressing these problems, by describing 24 new species: *H. acrioris*, *H. atlanticus*, *H. bicolor*, *H. brevicapitatum*, *H. cardosoi*, *H. clarisetis*, *H. curiosus*, *H. graziae*, *H. inconspicuus*, *H. infestans*, *H. irregularis*, *H. johanseni*, *H. kaminskii*, *H. longihamus*, *H. longisetus*, *H. magnus*, *H. maiae*, *H. nigrisetis*, *H. nigrum*, *H. punctatus*, *H. reticulatus*, *H. singularis*, *H. spermathecus*, *H. varicolor*. This study also includes information on galls for several of them;

an updated and illustrated key of identification; and comments on the morphological diversity of the group. With that, we hope to lay the taxonomical and morphological bases for future studies in this group, focusing on its diversity, ecology and phylogenetic relationships.

Key words: Galling thrips, Morphology, Neotropics, New species, Taxonomy

Introduction

Out of the great diversity of Thysanoptera species found in the Neotropics, a remarkable genus is *Holopothrips* (Phlaeothripidae), for its species richness and association with galls. Proposed in 1914 based on two Panamanian species collected from galls, *Holopothrips* currently comprises 36 species, of which at least 10 have been described from galls. Few species are also known to feed and breed inside abandoned galls of other insects (Bournier 1993; Zamora *et al.* 2015), whereas other are frequently found coexisting inside galls of other *Holopothrips* species. Besides the biological and ecological relevance, some *Holopothrips* species have also been reported producing extensive damage in cultivated plants. *Holopothrips ananasi* was described as a pest of pineapple in Rio de Janeiro (Costa Lima 1935b), and *H. fulvus* was recently studied damaging cashew in Northeastern Brazil (Lima *et al.* 2017). *Holopothrips tabebuia* is also known to induce serious damages in the leaves of Trumpet trees in Caribbean region (Cabrera & Segarra 2008) and one of the new species described here, *Holopothrips infestans* **sp. nov**. is reported as a pest of feijoa in South Brazil (Hickel & Ducroquet 1993).

Currently a combination of morphological characters is used to diagnose a *Holopothrips* species: presence of a third pair of wing-retaining setae on abdominal tergites II–VII, presence of anterior discal setae on metanotum, and males with multiple and complex pore plates (Mound & Marullo 1996); visible and well-developed female spermatheca (Zamora *et al.* 2015). However, all of these traits are variable within the genus, with some species lacking one of the required diagnostic features, but still being considered a species of *Holopothrips*. At the same time, a high level of homoplasy is observed as well in several other morphological characters such as colouration, body size and chaetotaxy. Thus, despite some of this variation being useful for species identification, this also makes harder to define relationships between species based on morphology alone.

To add to the existing difficulties, the current state of species diversity of the genus *Holopothrips* is severely underestimated. Just in the collection of Universidade Federal do Rio Grande do Sul (UFRGS - Brazil), over 1000 specimens are registered as *Holopothrips*, and

running these specimens through the unique identification key available (Mound & Marullo 1996) does not yield reliable identifications. Thus, here we start to address some of these difficulties in the study of the genus *Holopothrips*, by describing 24 new species, including photos and information on the galls of many taxa. We also explore and discuss on the morphological diversity of the group, providing an updated and illustrated identification key for the genus.

Finally, our objective here is more than simply describing new species. We aim to provide a more reliable foundation for studying this remarkable diversity and encourage studies on diversification and ecological patterns of gall-induction of these thrips. Most species described here are based in material collected in several parts from Brazil in the last 10 years. However, the area sampled here covers less than half of the Brazilian territory, and judging by the scattered *Holopothrips* material deposited in Thysanoptera collections, the species presented here may be only a small part of the diversity of this genus. When considering only the specimens deposited at UFRGS, about 15 undescribed species are still in the shelves, all based on very few individuals, or represented only by poorly preserved series of specimens with no host-plant data.

Material and Methods

Material revised and depositaries

Holotypes for all newly described species will be deposited at Universidade Federal do Rio Grande do Sul (UFRGS - Brazil) or at the British Museum of Natural History (BMNH - England), and paratypes for some of them will be deposited in further collections.

Type specimens for several previously described species of *Holopothrips* were studied, and these species are denoted with an asterisk (*). For species that types were not examined, information and illustrations from original descriptions and literature (Mound & Marullo 1996) or specimens previously identified by comparison with types were used.

The species *H. affinis*, *H. elongatus*, *H. ferrisi* and *H. seini* were not included in the identification key provided in this work, due to lack of access to type specimens and/or information in the literature.

Specimens from the following collections were studied for this work: Australian National Insect Collection (ANIC - Australia), British Museum of Natural History (BMNH - England), Smithsonian Natural Museum of Natural History, which is held at United States Department of Agriculture (USDA, Beltsville, USA), Senckenberg Museum (SMF - Germany)

and Universidade Federal do Rio Grande do Sul (UFRGS - Brazil).

Collection codes for all *Holopothrips* specimens from UFRGS that were studied in this work are provided in Supplementary File 1.

Mounting, identification and descriptions

All species described in this work were mounted in microscopic slides, most of them clarified with NaOH for 12–24 hours and preserved in Canada Balsam. Due to this procedure, colouration described might be lighter than in live specimens. Some specimens were pressured during mounting, which make the measures listed slightly different from fresh specimens.

All newly described species were run in the identification key provided by Mound & Marullo (1996), then compared with original descriptions and type specimens, whenever available, to confirm its identity.

Nomenclature and abbreviations

Most morphological terms follow Mound & Marullo (1996), and Bhatti (1998) for some head and thorax structures. Differently from Mound & Marullo, we used the term "Pore plates" instead of "Glandular areas".

The following abbreviations are used: po - postocular setae; am - pronotal anteromarginal setae; aa - pronotal anteroangular setae; ml - pronotal midlateral setae; ep - pronotal epimeral setae; pa - pronotal posteroangular setae; WR - abdominal wing retaining setae. Setae organized in a row or group will be named from the innermost pair towards the most external or apical pair as S1, S2, S3... Sn.

Taxonomy

Holopothrips Hood, 1914

Holopothrips Hood, 1914:49 (type species: *Holopothrips signatus* Hood, 1914, by original designation).

Phrasterothrips Priesner, 1921:210 (type species: *Phrasterothrips conducans* Priesner, 1921, by monotypy). Synonymised by Mound & Marullo, 1996:289.

Diploacanthothrips Moulton, 1933:239 (type species: *Diploacanthothrips fuscus* Moulton, 1933, by monotypy). Synonymised with *Phrasterothrips*, by Priesner, 1949:127.

Homorothrips Hood, 1954:52 (type species: *Homorothrips erianthi* Hood, 1954, by monotypy).

Synonymised by Mound & Marullo, 1996:289.

Anoplothrips Hood, 1954:53 (type species: *Anoplothrips jaboticabae* Hood, 1954, by monotypy). Synonymised by Mound & Marullo, 1996:289.

Caraibothrips Bournier, 1993:234. (type species: *Caraibothrips inquilinus* Bournier, 1993, by monotypy). Synonymised by Mound & Marullo, 1996:289.

Type species: *Holopothrips signatus* Hood, 1914: 50.

Natural History

Many members of *Holopothrips* are known to induce alterations in leaf structure for sheltering and feeding. Although most of these changes are relatively simple, they show considerable cell hypertrophy and tissue hyperplasia, and might be considered as true galls (Jorge *et al.* 2016). Most of these structures develop as folded or twisted leaves (Figs 1, 2, 9, 12–14), but galls formed by hard and thickened tissues are reported for few species, such as *H. molzi* in *Myrcia guianensis* (Fig. 3). Field observations suggest that some galls start after feeding activity by a single adult (e. g. *H. claritibialis* and *H. striatus*), and alterations in leaf lamina became clear after 6 days (Cavalleri & Kaminski 2007; Jorge *et al.* 2016). However, the species *H. chaconi* and *H. inquilinus* are known to be successors or invaders of galls of other insects (Bournier 1993; Zamora *et al.* 2015), and some of the species described here were found living inside other *Holopothrips* galls.

The species of *Holopothrips* are associated with a remarkable diversity of plants. Most hosts are dicotyledons, and Bignoniaceae, Melastomataceae and especially Myrtaceae seem to support a large diversity of these thrips. However, *H. ananasi* and *H. tillandsiae* are known to be associated with Bromeliaceae, whereas *H. erianthi* and *H. graminis* were described from Southeastern Brazil from grasses, although there is no indication that these species use Poaceae as host. Curiously, few *Holopothrips* members seem to have the ability of inducing galls in more than one plant species. This is true for *H. claritibialis*, which induces similar alterations on leaf tissues of two closely related *Mollinedia* species (Monimiaceae) in South Brazil (Cavalleri & Kaminski 2007), and *H. tabebuia* inducing galls in *Tabebuia heterophylla* and *T. aurea* in Puerto Rico (Cabrera & Segarra 2008). However, the data presented here suggest that most species uses only one plant species as host.

Due to the galling behaviour of most species, the traditional beating technique is usually ineffective for collecting these insects. Large populations of these thrips are rarely found outside

galls, but isolated individuals are frequently collected on non-host shrubs and grasses, as well in the leaf-litter. Given the large number of species and their intraspecific variation, description of new species should be based on specimens of both sexes, including immature whenever possible, together with a precise recognition of the host-plant. However, the identification of these plants might also be problematic in many cases, especially within diverse groups with several similar species.

The current knowledge of habits, host plants and distribution of *Holopothrips* species is summarized in table 1.

Morphological variation

Colouration: The majority of *Holopothrips* species are uniformly brown, although the shade of brown is variable from very dark, almost black (Figs 26, 189, 196) to light or yellowish brown (Figs 107, 224), with some specimens of *H. varicolor* **sp. nov.** being almost yellow. Twelve species of *Holopothrips* have the abdomen strikingly bicoloured: four of them have the body mainly brown with only abdominal segments II–III yellow (Fig. 220), or abdominal segments II–V in *H. hilaris*; and the remaining eight have the body mainly yellow, with only the head, abdominal segment X, and sometimes segments VIII–IX brown (Figs 32, 51, 85, 95).

The more frequent pattern of colouration for the legs is having all femora concolourous with the body, mid and hind tibiae concolourous as well but lighter near apex (from just the tip to apical third or half), fore tibiae and all tarsi yellow or clearly lighter than fore femora (Figs 16, 39, 130, 137, 181, 186). However, exceptions are not uncommon, such as the fore tibiae being brown in several dark-bodied species (Figs 26, 76, 189, 270), or all tibiae being almost white in *H. claritibialis* (Fig. 55), or the brown species *H. pennatus* having all legs fully yellow (Fig. 209). An uncommon variation is the presence of yellow hind femora but brown hind tibiae in *H. hilaris* and *H. signatus* (Fig. 220), although in the latter individuals with brown hind femora have been observed (Hood 1914).

Antenna also presents some variation: usually segments I–II are concolourous with head, III–VI lighter or bicoloured, due to being shaded on apical half, and VII–VIII shaded or brown (Figs 16–17, 26, 186). Some species have the antenna yellow on segments III–VIII (Figs 209, 224), and some bicoloured species may have segment III brown basally (Figs 120, 208, 219).

The fore wings may be hyaline (Figs 26, 76, 130, 157) or shaded yellow or light brown (Figs 64, 70, 137, 239, 246). The basal area, especially around the sub-basal setae, is shaded in

several species (Figs 45, 189, 220). A median dark line on fore wing is usually absent, or only weakly indicated.

Head: Several characteristics are variable and of identification interest. Firstly, the ratio between head length and width, which ranges from head slightly wider than long right behind eyes in *H. clarisetis* **sp. nov.** (Fig. 61), and some individuals of *H. inconspicuus* **sp. nov.**, *H. mariae*, *H. singularis* **sp. nov.** and *H. varicolor* **sp. nov.** (Figs 109, 240, 275), to over 1.8 times as long as wide in *H. oaxacensis* and *H. permagnus* (Hood 1938; Johansen 1986) (Fig. 210). However, the majority of *Holopothrips* species lie in between these extremes, having heads between 1.1–1.4 times as long as wide. However, the proportions of head may be influenced by pressure during the mounting process, so specimens that were not flattened by pressure should be used for the analysis of this character.

Head sculpture is usually formed by weak transverse lines, but in *H. ananasi* it is markedly reticulate, and in *H. singularis* **sp. nov.** the sculpture is irregularly reticulate (Figs 22, 240). Few species bear minute teeth in the angles of dorsolateral sculpture (Figs 225, 234), giving the area a punctuate appearance.

Compound eyes are frequently large, bulbous, sometimes bean-shaped (Figs 33, 86, 96, 102, 221), being this a characteristic commonly associated to *Holopothrips*. Still, some species have not so enlarged eyes, or somewhat reduced in comparison to the eyes of other *Holopothrips* species (Figs 46, 61, 190).

There is one pair of postocular setae in all *Holopothrips* species, although in *H. fulvus* and *H. singularis* **sp. nov.** they seem to be reduced to the size of discal setae (Fig. 86), or fully absent (Fig. 240). A third major seta or even a secondary pair of large setae may be present inner to po in some specimens (Fig. 138); it is possible that this extra po is actually one of the postocellar pairs. The tip of po setae is as variable as the pronotal setae, less commonly acute (e. g. *H. porrosati*, *H. stannardi*) or blunt (e. g. *H. atlanticus* **sp. nov.**, *H. magnus* **sp. nov.**, *H. orites*), with expanded or capitate tips being more frequent (e. g. *H. claritibialis*, *H. maiae* **sp. nov.**, *H. tenuis*). The length of po can range from barely differentiated from discal setae (Figs 52, 233) to longer than the dorsal length of the eye (Figs 158, 197), being usually in between these extremes, about as long as the dorsal width of an eye.

The maxillary stylets vary in position within the head, the most common combination being retraction until postocular setae and about one third of head width apart or less (Figs 33, 96, 99, 113). Few species have the maxillary stylets retracted to the posterior margin of eyes

and closer to each other medially, almost touching in *H. ananasi*, *H. cardosoi* **sp. nov.** or *H. conducans* (Figs 22, 46, 68). Other species have the maxillary stylets less retracted into the head, sometimes barely leaving the mouth cone (Fig. 109) or, in species with a longer head, reaching halfway to po base (Figs 158, 167, 190). Stylets less retracted into the head tend to be more separated from each other, having a V shape (Figs 40, 77, 131, 225) in contrast to the usual parallel disposition (Figs 73, 86, 240, 275).

Mouth cone can be somewhat rounded at tip, and in this case the labial palps tend to be reduced to what looks like a basal plate, barely projecting from the labium (Figs 185, 241). In contrast, there are several *Holopothrips* species with the mouth cone longer and pointed, sometimes extending beyond the posterior margin of fore coxae, with labial palps usually being longer and with visible segmentation (Figs 114, 171, 276).

Antenna: The main antennal character used for species identification is the number of sense cones on segments III–IV. Three sense cones in each seems to be the most common pattern within the genus, but reductions in the number of sense cones occur in a variety of species (Mound & Marullo 1996). Species such as *H. carolinae*, *H. graminis*, *H. longisetus* **sp. nov**. bear only two sense cones in antennal segments III–IV. There are also cases where the number of sense cones is variable within the same species, such as in *H. jaboticabae* (1–2 cones on III and 2–3 on IV), *H. fulvus* (usually three sense cones on both segments, but specimens with one sense cone absent were observed) (Lima *et al*. 2017) or *H. mariae* (usually with two sense cones on each segment, but individuals with three sense cones on III have been registered) (Mound & Marullo 1996). This variation seems to be present as well in *H. clarisetis* **sp. nov.**, with the observed females bearing two sense cones on IV and the single available male bearing three sense cones.

Prothorax: Pronotal sculpture is usually weakened or absent medially, being present only near posterior margins and, sometimes, anterior margins. In *H. reticulatus* **sp. nov.** the pronotum is fully reticulate, and in *H. singularis* **sp. nov.** the sculpture is absent only in a small median portion of pronotum.

All five pairs of major pronotal setae are usually present, although reductions in size are not uncommon. Several species (Figs 99, 102, 175, 190, 225) have the am setae reduced, not different from discal setae, or with variable length between different individuals of the same species (Figs 158, 160). In some other species (Figs 96, 146, 265) the aa setae are minute, which

might be associated with ml arising closer to anterior margin. Length of pronotal setae in general also varies greatly, with some species having these setae except ep very short (Figs 167, 271) and others having elongate setae, with ep and pa longer than 100 µm (Figs 150, 158).

The epimera usually bears one pair of major setae, but a second minute seta is present internally to the major pair. In some species this secondary pair is fully developed, thus the epimeral region bears two pairs of major setae (Figs 27, 68, 158, 167, 190, 197).

Tip of pronotal setae is also variable, more frequently expanded or capitate (Figs 22, 257, 260), sometimes blunt (Figs 27, 167, 190), and some species may have some setae acute (e. g. *H. stannardi*). Not all setae have the same type of apex, with smaller setae (usually am and/or aa) frequently having acute or blunt apex in contrast to the capitate tips of longer setae.

Mesonotum: The mesonotal sculpture ranges from well-defined equiangular reticles (Figs 34, 57, 100, 227) to elongate or irregular reticles (Figs 22, 214) to mostly transverse lines (Figs 191, 205). While most *Holopothrips* species do not have internal markings within the mesonotal sculpture, several species bear them, sometimes weaker and restricted to few reticles (Fig. 126), in others well defined and filling all reticles (Figs 83, 214, 235). Sometimes the median sculpture converges towards the posteromedian suture of mesonotum, with the sculpture becoming elongate or almost striate.

Metathorax: Similar to the mesonotum, the metanotum bears variable sculpture, especially on median and posterior areas. Laterally the sculpture tends to be formed by elongate reticles or striate, independent of the median pattern. The most common pattern medially seems to be longitudinally elongate reticles, sometimes weakly defined and without internal markings (Figs 19, 47, 63), in others well defined, with internal markings (Figs 133, 235, 245) or without them (Figs 188, 279). Few species, such as *H. hambletoni* or *H. punctatus* **sp. nov.**, have the metanotum covered by equiangular reticles, usually without internal markings or with faint ones (Figs 100, 231). In some species the metanotal sculpture is striate, either through the whole sculptured area (Figs 74, 195, 198, 206, 258) or on anterior half, with elongate to equiangular reticulation covering the posterior half (Figs 91, 127, 215, 267). Although more uncommon, striate sculpture can also bear weaker lines in between the striae, which could also be considered internal markings (Fig. 145).

Anteriorly to the major median setae of metanotum, all *Holopothrips* bear at least one or two smaller setae. While most species have one or two pairs of these setae, *H. bicolor* **sp.**

nov. usually bears more than five pairs of setae, frequently asymmetrically placed (Fig. 38). This trait is not exclusive to the genus, being found in a variety of Phlaeothripidae species (called the "group c" of metanotal setae in Bhatti (1998), which also mentions several genera unrelated to *Holopothrips* that bear these setae).

Ventrally, most *Holopothrips* have well defined metapleural sutures, although in *H. carolinae*, *H. hilaris*, *H. tillandsiae* and *H. tupi* they seem to be reduced, and in *H. johanseni* **sp. nov.**, *H. longisetus* **sp. nov.**, *H. pictus* and *H. signatus* no metapleural suture is observed (Fig. 142). In at least *H. inconspicuus* **sp. nov.** and *H. singularis* **sp. nov.** the metapleural suture seems to be variable within the species, being present in some individuals and not visible in others.

Abdomen: The presence of a third pair of wing retaining setae (WR) on tergites II–VII is usually mentioned as one of the diagnostic features of the genus, being indeed found in most species (Figs 18, 60, 218). However, species such as *H. inconspicuus* **sp. nov.**, *H. jaboticabae*, *H. tillandsiae* and *H. varicolor* **sp. nov.** frequently lack this third WR in several tergites, and in the species *H. clarisetis* **sp. nov.** and *H. infestans* **sp. nov.** the third WR is mostly absent from all tergites. While usually smaller than the other two WR pairs, the third pair may be well-developed and sigmoid, or small and weakly curved, sometimes easily confused with lateral setae. Some other Phlaeothripidae genera (e.g. *Euoplothrips* Hood, *Mesothrips* Zimmerman, *Pristothrips* Hood) may have three or more pairs of wing-retaining setae, usually multiple pairs on abdominal tergites II–IV, but these seem to be related to the large bodies of the species that bear them.

The shape of pelta is highly variable: some are sharply triangular (Fig. 177), others still triangular but with irregular (Figs 78, 127, 192) or curved (Figs 162, 188, 199, 259) margins, and few species have the pelta with a median constriction (Figs 117, 123). *Holopothrips ananasi* and *H. kaminskii* **sp. nov.** are unique in having large lateral wings basally, and in the latter it is also associated with a constriction, giving this species a bell-shaped pelta (Figs 23, 147). Sculpture is always present, usually formed by reticles covering the whole pelta (Figs 117, 211, 278), but sometimes it might be weaker or absent near posterior area (Figs 228, 238, 242), margins (Figs 127, 170) or medially (Fig. 162). The reticulation may be almost equiangular (Figs 23, 36, 250) or elongate medially (Figs 28, 199, 206), and internal markings may be present (Figs 259, 273) or not.

Pore plates: In *Holopothrips* they are frequently present in more than one sternite, usually VII–VIII or sometimes VI–VIII (Figs 59, 101, 128, 179, 244), with *H. brevicapitatum* **sp. nov.** having plates in sternites IV–VIII (Fig. 42).

On sternite VIII the usual pattern is the presence of three pore plates, two anteroangular plates and a transverse band posterior to discal setae, usually reaching the laterals of sternite (Figs 31, 128, 179). Median interruptions in the posterior plate are not uncommon, and in some species such interruption may be large enough to separate this plate into two lateral bands (Fig. 89). In other cases, the two anteroangular plates may be absent (Figs 48, 201), and the remaining posterior plate may be reduced to a small median band (Figs 21, 66, 72, 128). In few species the posterior plate of sternite VIII might extend laterally towards the tergite, from barely reaching the spiracle to almost circumventing the segment (Fig. 129). Several *Holopothrips* species also have the pore plates with a clear reticulate pattern (Figs 35, 75, 179, 244), contrasting to the usual punctuate appearance of the pore plates of other Phlaeothripinae species.

Intraspecific variation of pore plates has been observed in some species, such as presence of median interruptions in the posterior plate or differences in the area occupied by the pore plates, in some specimens of *H. claritibialis* (Cavalleri & Kaminski 2007), or presence of connections between the anteroangular plates and the posterior plate in few specimens (Fig. 194).

Few *Holopothrips* species are known to have males lacking pore plates. In this work, we observed the absence of pore plates in *H. graminis*, *H. inconspicuus* **sp. nov.**, *H. kaminskii* **sp. nov.**, *H. longisetus* **sp. nov.**, *H. molzi* and *H. tillandsiae*. Mound & Marullo (1996) also mentions in the key that males of *H. seini* and *H. urinator* do not have pore plates.

Spermatheca: Visible in all observed species of *Holopothrips* even after maceration, possibly being more sclerotized than in other Thysanoptera species. It seems to be a useful diagnostic character for the group, as the spermatheca is rarely seen in other phlaeothripids. Some species have the spermatheca swollen medially (Figs 24, 43, 67), while in others it is curled and not enlarged (Figs 20, 30, 49, 263). Swollen spermathecas vary from only slightly enlarged medially (Figs 88, 204) to greatly swollen or almost round medially (Figs 135, 154, 281). Curled spermathecas vary in thickness, from very thin (Figs 98, 193, 200) to greatly thickened (Fig. 163). While usually small and restricted to abdominal segment IX, in *H. tillandsiae* the spermatheca is very elongate, with some curls reaching abdominal segment VI (Zamora *et al.* 2015).

Fore legs: Unarmed in all species, but the hamus is robust or greatly enlarged in three species: *H. brevicapitatum* **sp. nov.**, *H. longihamus* **sp. nov**. and *H. longisetus* **sp. nov.** (Figs 151, 159). The fore femora in some species may be robust, but never greatly swollen (Figs 40, 64, 150, 166, 246, 274–275).

Fore wings: Always macropterous and with margins parallel. There is variation in the shape of the tip of the sub-basal setae, which seems to agree with the shape of tip seen in other major body setae. With the exception of *H. carolinae*, all species bear duplicated cilia on fore wings, and the number is highly variable between species (from 4–5 cilia in *H. mariae* specimens to 16–27 in *H. nigrum* **sp. nov.**), within species, and between the right and left fore wings of the same individual (Cavalleri & Kaminski 2007).

Key to *Holopothrips* species

(Excluding *H. affinis* (Bagnall), *H. elongatus* Moulton, *H. ferrisi* Moulton and *H. seini* (Watson)).

1. Abdomen sharply bicoloured, with at least segments II–III clear yellow and at least tube brown (Figs 51, 95, 120, 219, 220) 2
- Abdomen uniformly coloured, yellowish, light brown or dark brown, sometimes anterior segments slightly lighter but not sharply different from subsequent segments (Figs 39, 107, 112, 189, 209, 224)..... 13

2. Head and thorax brown, at least abdominal segment II yellow (Fig. 220)..... 3
- Thorax yellow, only head and final abdominal segments brown (Figs 32, 51, 120) 6

3. Abdominal segments II–V yellow; hind femora yellow .....*hilaris*
- Abdominal segments IV–V brown; hind femora usually brown 4

4. Postocular setae with acute to blunt apex, shorter than 50 m; hind femora sometimes yellow (Figs 220–223).....*signatus*
- Postocular setae with capitate apex, longer than 50 m; hind femora always brown..... 5

5. Postocellar setae length subequal or slightly longer than the diameter of an ocellus; metanotal sculpture with equiangular reticulation between the median major setae; abdominal segments I–II clear yellow and III–VII darker ..... *balteatus*

- Postocellar setae shorter than the diameter of an ocellus; metanotum sculptured with longitudinally elongate reticles between the median major setae; abdominal segments I–III clear yellow (Figs 216–218) ..... *pictus*

6. Abdominal segment VIII mostly yellow, in some females the posterior margin might be light brown (Figs 51, 85, 95) 7

- Abdominal segment VIII mostly brown, sometimes lighter near anteromedian margin (Figs 32, 120, 208, 219) 9

7. Abdominal segment IX clear yellow; head mostly brown, yellow only near posterior margin; antennal segments III–IV with two sense cones each; fore wings without duplicated cilia (Figs 51–52) ..... *carolinae*

- Abdominal segment IX brown; head brown anteriorly and medially, and yellow laterally and near posterior margin; antennal segments III–IV usually with three sense cones each; fore wings with duplicated cilia 8

8. Head length and width subequal with curved cheeks; postocular setae reduced or absent; fore wing clavus shaded light brown; female spermatheca enlarged medially; male with pore plates only on sternite VIII (Figs 85–89) ..... *fulvus*

- Head clearly longer than wide with straight cheeks; postocular setae well-developed; fore wing clavus yellowish; female spermatheca not enlarged; male with pore plates on sternites VII–VIII (Figs 95–98) ..... *graziae* **sp. nov.**

9. Head sharply bicoloured, brown anteriorly and medially, yellow elsewhere; fore wing with a brown longitudinal strip on basal half, clavus shaded brown; epimera with two pairs of major setae (Figs 120–121) ..... *inquilinus*

- Head uniformly brown, sometimes slightly lighter on posterior margin, but never strongly bicoloured; fore wing pale with clavus yellow; epimera with one pair of major setae 10

10. Postocular setae short, about as long as the diameter of an ocellus or smaller; female spermatheca enlarged medially; male with pore plates on sternites VI–VIII (Figs 32–38) .....*bicolor* **sp. nov.**

- Postocular setae well-developed, usually longer than the diameter of an ocellus; female spermatheca S-shaped, thin or thickened but never enlarged medially; male never with pore plates on sternite VI 11

11. Head light brown; pronotum clear yellow; antennal segment III clear yellow; metanotal sculpture with longitudinally elongated reticles, almost forming a striate pattern anteriorly (Figs 260–263) ..... *tabebuia*

- Head dark brown, slightly lighter near posterior margin; pronotum slightly shaded brown anteriorly; antennal segment III dark brown on basal half, yellow on apical half; metanotal sculpture reticulate, equiangular to slightly elongate, but never looking striate 12

12. Abdominal segment VIII fully brown; postocular setae with capitate apex; labial palps well-developed, longer than wide, projecting from the margin of mouth cone; pronotal aa setae capitate; male with pore plates on sternites VII–VIII, on VIII with two anteroangular plates and one transversal band, which extends toward tergite VIII (Fig. 208) .....*paulus*

- Abdominal segment VIII light yellow on anterior half and brown on posterior half; postocular setae with acute apex; labial palps reduced, similar to a papilla; pronotal am and aa setae acute to blunt; male with a single transverse pore plate on sternite VIII, not extending toward tergite VIII (Fig. 219) ..... *porrosati*

13. Pronotum with two pairs of long setae on epimeral region 14

- Pronotum with one pair of long setae on epimeral region; sometimes with a second pair, but it is either much shorter or present in only one side 25

14. Maxillary stylets not retracted to postocular setae level, V-shaped (Figs 158, 167, 190).. 15

- Maxillary stylets retracted at least to postocular setae level, parallel-sided (Figs 17, 46, 68, 197) 19

15. Antennal segments III–IV with two sense cones each, IV sometimes with a third, smaller sense cone (about half to less than two thirds of the length of the other sense cones); male

sternites without pore plates 16
- Antennal segments III–IV with three sense cones each, IV sometimes with a fourth, smaller sense cone (about half to less than two thirds of the length of the other sense cones); male with pore plate at least on sternite VIII 17

16. Major pronotal setae except for epimerals very short, not reaching 30 µm long; po setae very short, about as long as the diameter of an ocellus; sculpture on metanotum reaching close to the posterior margin of metanotal craspedum; fore leg hamus not enlarged (Figs 186–188) .....*molzi*
- Major pronotal setae (except am in few specimens) elongate, 50 µm or more long; po setae longer than the dorsal length of the eye; sculpture on metanotum sharply tapering, waning before the posterior margin of metanotal craspedum; fore leg hamus thickened, almost reaching beyond the lateral of tarsus (Figs 157–165) .....*longisetus* **sp. nov.**

17. Body brown to light brown, fore tibiae yellow, sometimes shaded light brown basally; postocular setae shorter than the dorsal length of an eye, at most 70 µm long; tergite II with short transverse lines of sculpture covering the whole structure, forming a striate pattern; male with a single pore plate on sternite VIII, a thin transverse band posterior to discal setae (Figs 166–173).....*magnus* **sp. nov.**
- Body dark brown, fore tibia usually also brown; postocular setae about as long as the dorsal length of an eye, more than 80 µm long; tergite II with sculpture formed by irregular elongate reticles medially; male with three pore plates on sternite VIII, two anteroangular bands and a transverse band posterior to discal setae..... 18

18. Pronotal am and coxal setae well-developed, more than 18 µm long, comparable to aa or longer; lateral margins of pelta not irregular and without lateral wings; male pore plates on sternite VIII, with regular margins (Figs 26–31)..... *atlanticus* **sp. nov.**
- Pronotal am and coxal setae thin and short, less than 15 µm long, shorter than aa in size; pelta with very irregular lateral margins and lateral wings; male pore plates with irregular margins occurring on sternites VII–VIII (Figs 189–195)..... *nigrisetis* **sp. nov.**

19. Fore wings with basal area darker than apical half, sometimes only around the bases of the three sub-basal setae (Figs. 45, 54)..... 20

- Basal area of fore wings not clearly darker than the rest of the fore wing (Figs 16, 70)..... 23

20. Head and metanotal sculpture weak to absent medially; mouth cone not reaching posterior margin of fore coxae; metapleural sutures either very small or absent; third pair of WR absent on tergites V–VI, frequently absent in at least one side on III–IV and VII; female spermatheca not enlarged medially, but long, extending all the way to abdominal segment VII; male without pore plates (Figs 268–269) ..... *tillandsiae*
- Head and metanotum with well-defined sculpture; mouth cone reaching posterior margin of fore coxae; metapleural suture present; third pair of WR present in tergites II–VII; female spermatheca restricted to segment IX; male with pore plates at least on sternite VIII 21

21. Body light brown, head and posterior segments of abdomen are the darkest parts of body; female spermatheca enlarged medially; male sternite VIII with two small anteroangular pore plates and one transversal plate posterior to discal setae, with anterior projections toward the anterior plate; epimeral suture usually complete; chitinous islet might be present anterior to prosternal ferna; pelta without campaniform sensilla or with small setae instead (Figs 53–54) .....*chaconi*
- Body brown to dark brown; female spermatheca not enlarged; male sternite VIII with a single pore plate posterior to discal setae; epimeral suture usually incomplete; without chitinous islet anterior to prosternal ferna; pelta usually with paired campaniform sensilla..... 22

22. Metanotal sculpture longitudinally striate; pelta with anterior margin acute, sculpture bearing internal markings; male with a single pore plate on sternite VIII (Figs 196–201) .....*nigrum* **sp. nov.**
- Metanotal sculpture formed by weak and slightly elongate reticles; pelta with anterior margin straight to slightly curved, sculpture without internal markings; male with pore plates on sternites VII–VIII (Figs 45–50) ..... *cardosoi* **sp. nov.**

23. Head with clearly reticulate sculpture on dorsal surface; mesonotal sculpture with internal markings; metanotal sculpture formed by clearly defined equiangular reticles medially; female spermatheca enlarged medially; male sternites VII–VIII with pore plates, on VIII with two small anteroangular plates and one transverse pore plate posterior to discal setae (Figs 22–25) .....*ananasi*

- Head with transverse lines of sculpture on head, sometimes enclosing elongate irregular reticles; mesonotal sculpture without internal markings; metanotal sculpture formed by weak slightly elongate reticles medially; female spermatheca not enlarged medially; male with only one small median pore plate posterior to discal setae on sternite VIII 24

24. Median reticles on pelta longitudinally elongate and with weak internal markings; tergite II with irregular transversely elongated reticles; fore wing shaded light brown; basantra absent; inducing galls in *Myrcia splendens* (Figs 68–72)..... *conducans*
- Median reticles on pelta small and closely equiangular, without internal markings; tergite II with sculpture transversely striate; fore wing pale to yellowish; basantra faintly indicated; inducing galls in *Myrcia selloi* (Figs 16–21).....*acrioris* **sp. nov.**

25. Body mostly brown, with inner apical half of all femora yellow; head slightly wider than long, maxillary stylets retracted to posterior margin of eyes and close medially (Fig. 61); abdominal tergites II–VII without a third pair of WR, sometimes a straight setae close to the WR on V–VII; female spermatheca enlarged medially, male with faint spot-like pore plates on sternite VIII (Figs 61–67) .....*clarisetis* **sp. nov.**
- Not this combination of characters..... 26

26. Antennal segment IV with two sense cones, sometimes bearing a third, smaller sense cone (about half to less than two thirds of the length of the other sense cones); antennal segment III usually with two, sometimes with three sense cones 27
- Antennal segment IV with three sense cones, sometimes bearing a fourth, smaller sense cone (about half to less than two thirds of the length of the other sense cones); antennal segment III always with three sense cones 31

27. Head much longer than wide, over 400 µm long; antennal segment III with three sense cones, VI with two; epimeral sutures complete or almost complete [fore tibia mostly brown; female spermatheca not enlarged medially; male sternites VII–VIII with three pore plates each, two anterolateral and one transverse band posterior to discal setae] (Figs 210–215) *permagnus*
- Head shorter, 300 µm or less long; antennal segments III–IV with two sense cones each; epimeral sutures incomplete 28

28. Maxillary stylets V-shaped, not reaching the postocular setae, half or more of head width apart (Figs 131, 182); sometimes a second epimeral setae developed, but either only in one side or much smaller than the major ep setae 29
- Maxillary stylets parallel, a third or less of head width apart; epimeral region always with only one pair of major setae..... 30

29. Body brown; mesonotal sculpture with faint internal markings on median reticles; metanotal sculpture sometimes with very faint internal markings; anterior margin of pelta rounded; abdominal sternite VIII with the discal setae in a single regular row; male sternites VI–VIII with pore plates, on VIII two anterolateral plates and one transverse band posterior to discal setae (Figs 181–185)..... *mariae*
- Body light brown to yellowish brown; mesonotal sculpture without internal markings; metanotal sculpture always bearing well defined internal markings; anterior margin of pelta straight; abdominal sternite VIII with the discal setae irregularly placed, sometimes forming two rows; male sternite VIII without or with faint indications of an irregular transverse pore plate, posterior to discal setae (Figs 130–136) ..... *irregularis* **sp. nov.**

30. Pronotal am and aa setae reduced to the size of discal setae, with ml setae positioned closer to the anterior margin; metanotal sculpture without internal markings (Figs 90–94) .... *graminis*
- Pronotal am setae reduced, but aa well-developed, about 50 µm long; metanotal sculpture with internal markings ..... *urinator*

31. Dorsolateral sculpture of head with minute teeth on angles (Figs 225, 234) 32
- Dorsolateral sculpture of head without any teeth..... 34

32. Epimeral suture forking and extending around the basal pore of pa setae (Fig. 226); mesonotal sculpture without internal markings; metanotal sculpture with equiangular reticulation, not bearing internal markings; female spermatheca enlarged medially; male sternites VI–VIII with pore plates with punctuate texture, on VIII posterior band extends towards tergite VIII (Figs 224–231)..... *punctatus* **sp. nov.**
- Epimeral suture not reaching pa setae; mesonotal sculpture with internal markings; metanotal sculpture with longitudinally elongate reticulation, bearing internal markings; female spermatheca not enlarged medially; male pore plates with reticulate texture, not extending

towards tergite on VIII 33

33. Fore tibia light brown basally, lighter near apex; head with transversely elongate reticulation, postocular setae small but slightly longer and more robust than other head setae; sculpture covering the whole pronotum, reticulate anteriorly and transverse lines posteriorly; metanotal sculpture with clear internal markings in all reticles; male pore plates on sternites VI–VIII (Figs 232–238)..... *reticulatus* **sp. nov.**
- Fore tibia clear yellow; head with small irregular reticulation, almost equiangular medially, postocular setae absent or similar in appearance to other head setae; sculpture on pronotum weaker to almost absent medially; metanotal sculpture with internal markings weak or absent on median reticles; male pore plates on sternites V–VIII (Figs 239–245) .... *singularis* **sp. nov.**

34. Metanotal sculpture thoroughly formed by equiangular to very slightly elongate reticles, without internal markings, sometimes becoming elongate or almost striate on lateral limits (Figs 57, 100, 106)..... 35
- Metanotal sculpture either striate (Figs 145, 206), or with clearly elongate reticles usually bearing internal markings (Figs 249, 273), or with a somewhat irregular pattern (Fig. 123); if with somewhat equiangular reticles posteriorly, then with sculpture elongate or almost striate anteriorly (Fig. 127)..... 38

35. Metanotal reticulation weakly defined and slightly elongate; third pair of WR absent on tergites II–VII [male with a single small median pore plate on sternite VIII] (Figs 112–119) ..... *infestans* **sp. nov.**
- Metanotal reticulation well defined and mostly equiangular, at least medially; third pair of WR present on tergites II–VII 36

36. All legs fully yellow; labial palps not projected from mouth cone, similar to a papilla (Fig. 209) ..... *pennatus*
- At least femora brown; labial palps projected from mouth cone 37

37. Fore wing clavus shaded; prosternum with chitinous islet above ferna; tergite IX setae S1 acute; male with pore plates on sternites VII–VIII (Figs 55–60) ..... *claritibialis*
- Fore wing clavus pale; prosternum without chitinous islet; tergite IX setae S1 capitate; male

with pore plates on sternites VI–VIII (Figs 99–101)..... *hambletoni*

38. Maxillary stylets at least half of head width apart or more, usually v-shaped and not reaching postocular setae (Figs 77, 109, 150)..... 39
- Maxillary stylets about a third of head width apart or less, usually parallel-sided and retracted to at least the postocular setae (Figs 73, 175, 253)..... 45

39. Pronotal ep and pa setae short, less than 80 µm long; third pair of WR absent at least on abdominal tergite II, frequently reduced or lacking in further tergites 40
- Pronotal ep and pa setae long, more than 90 µm long; third pair of WR present on abdominal tergites II–VII 42

40. Head clearly longer than wide; abdominal tergite IX setae S1 and S2 acute; female spermatheca not enlarged medially (Figs 76–81).....*curiosus* **sp. nov.**
- Head length and width subequal, or slightly wider than long; abdominal tergite IX setae S1 and S2 capitate; female spermatheca enlarged medially 41

41. Meso- and metanotal sculpture clearly defined medially; pelta with anterior margin acute, sculpture covering the whole structure and with faint internal markings in some reticles (Figs 122–123)..... *jaboticabae*
- Meso- and metanotal sculpture weak or absent medially; pelta with anterior margin round or straight, sculpture weak on posterior region and without internal markings (Figs 107–111) ..... *inconspicuus* **sp. nov.**

42. Fore tarsal hamus enlarged, extending beyond the lateral margin of fore tarsus (Fig. 151); metanotal sculpture irregular, but not thoroughly finely striate (Fig. 156); female spermatheca enlarged medially (Figs 43, 154)..... 43
- Fore tarsal hamus not enlarged; metanotal sculpture thoroughly striate; female spermatheca not enlarged (Fig. 148) 44

43. Pronotal aa setae long, more than 40 µm long; pelta with small lateral wings and 4 or 5 campaniform sensilla; male with faintly indicated pore plates on sternites VII–VIII (Figs 149–156).....*longihamus* **sp. nov.**

- Pronotal aa setae short, less than 25 µm long; pelta without lateral wings and with two or less campaniform sensilla; male with well-defined pore plates on sternites IV–VIII (Figs 39–44) ..... *brevicapitatum* **sp. nov.**

44. Mesonotal sculpture without internal markings; pelta triangular with anterior margin acute; male with pore plates on sternite VIII (Fig. 207) ..... *omercooperi*
- Mesonotal sculpture with internal markings; pelta strongly bell-shaped with anterior margin rounded; male without pore plates (Figs 143–148) ..... *kaminskii* **sp. nov.**

45. Body dark brown, with fore tibia and major body setae brown as well; head length more than 1.7 times longer than head width; antennal segment VIII constricted at base; pronotal am setae minute; metanotal sculpture striate anteriorly and reticulate posteriorly; male pore plates on tergites VII–VIII ..... *oaxacensis*
- Not this combination of characters; head less than 1.7 times longer than wide 46

46. Mesonotal sculpture with internal markings, sometimes very faint and/or restricted to only a few anterior or median reticles (Fig. 126) 47
- Mesonotal sculpture without internal markings 51

47. Metanotal sculpture finely striate thoroughly (Fig. 206) [large-bodied species with head more than 1.5 times as long as width behind eyes, fore wings pale with shaded clavus, postocular setae with blunt apex, female spermatheca enlarged medially] (Figs 202–206) ..... *orites*
- Metanotal sculpture not finely striate (Fig. 139), or striate anteriorly but forming reticles on posterior half (Figs 127, 267) 48

48. Head more than 1.5 times as long as width behind eyes; pelta with anterior margin acute, median reticles thin and longitudinally elongate with internal markings (Figs 127, 267); males with pore plates on sternites VII–VIII 49
- Head less than 1.4 times as long as width behind eyes; pelta with anterior margin straight, median reticles not particularly thin (Figs 139, 273); males with pore plates either on sternites VI–VIII or only on VIII 50

49. Fore wings and clavus shaded; prosternal basantra present, chitinous islet above ferna

absent; abdominal tergite IX setae S1 and S2 capitate (Figs 124–129) ..... *inversus*
- Fore wings and clavus pale; prosternal basantra absent, chitinous islet above ferna present; abdominal tergite IX setae S1 weakly capitate but S2 acute (Figs 264–267) ..... *tenuis*

50. Body brown to dark brown, fore tibia also brown; metapleural sutures present; female spermatheca not enlarged medially; male with pore plates only on sternite VIII (Figs 270–273) ..... *tupi*
- Body brown on females, lighter on males, fore tibia yellow; metapleural sutures absent; female spermatheca enlarged medially; male with pore plates on sternites VI–VIII (Figs 137–142) ..... *johanseni* **sp. nov.**

51. Head more than 1.5 times as long as width behind eyes; pelta with anterior margin acute, sculpture with thin elongate reticles with internal markings medially [large dark brown species with metanotum finely striate, female spermatheca not enlarged, male with pore plates on sternites VII–VIII] (Figs 255–259)..... *striatus*
- Head less than 1.4 times as long as width behind eyes; pelta without thin elongate reticles medially, and without internal markings 52

52. Body light brown to almost yellow; basantra present; metanotal sculpture with small irregular reticles medially, forming a somewhat concentric pattern, almost striate on posterior half (Fig. 279); third pair of WR absent on tergites II–III, frequently absent or present only in one side in further tergites; male with pore plates on abdominal sternites V–VIII (Figs 274–281)..... *varicolor* **sp. nov.**
- Body brown; basantra absent; metanotal sculpture usually striate anteriorly; third pair of WR present at least on abdominal tergites III–VII; male without pore plate on abdominal sternite V 53

53. Fore wings and clavus pale; pelta sharply triangular, with lateral margins straight and anterior margin acute (Fig. 177); third pair of WR absent on abdominal tergite II [male with pore plates on sternites VII–VIII] (Figs 174–180) ..... *maiae* **sp. nov.**
- Fore wings and clavus shaded; pelta not so sharply triangular; third pair of WR present on tergite II 54

54. Postocular and pronotal setae with acute to blunt apexes [male pore plates with punctuate texture and occurring only on sternite VIII] (Figs 252–254) ..... *stannardi*
- Postocular and pronotal setae capitate 55

55. Metanotal sculpture with longitudinal lines enclosing thin elongate reticles with internal markings (Fig. 249); pelta elongate with broad lateral wings; female spermatheca enlarged medially (Figs 246–251)..... *spermathecus* **sp. nov.**
- Metanotal sculpture striate (Fig. 74); pelta not forming conspicuous lateral wings; female spermatheca not enlarged medially (Figs 73–75)..... *erianthi*

***Holopothrips acrioris* sp. nov.**

(Figs 16–21)

Diagnostic features. Body uniformly brown; two pairs of long setae on epimeral region; metanotal sculpture formed by slightly elongate and weakly defined reticles, without internal markings; pelta without elongate reticles with internal markings; sternite II with transversely striate sculpture; males with a single transverse pore plate posterior to discal setae; female spermatheca not enlarged.

Macropterous female: Body (Fig. 16) uniformly brown, fore tibia brownish yellow and all tarsi yellow, tergite X dark brown with extreme base and apex lighter. Antennal segment I–II concolourous with head, II yellow on extreme apex; III–IV yellow, V–VI yellow on basal half and shaded brown on apical half, VII–VIII brown. Fore wings pale to very weakly shaded, without median dark line, clavus shaded; major body setae yellow.

Head (Fig. 17) about 1.2 times as long as width behind eyes, dorsal surface with transverse lines of sculpture, cheeks slightly curved. Eyes well-developed, dorsal length about 0.4 of head length; po with acute to blunt apex, about as long as the dorsal width of the eye. Maxillary stylets parallel, reaching close to posterior margin of eye and less than 0.2 of head width apart. Mouth cone with pointed tip, barely reaching the posterior margin of fore coxae. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 17) trapezoidal, very faint reticulate sculpture medially and weak transverse lines near margins; epimeral sutures incomplete. Six major pairs of pronotal setae, two pairs of epimeral setae; am and aa small with acute to blunt tips, ml, ep and pa well-developed and with blunt tips; basantra faintly indicated; prosternal ferna well-developed, not

touching medially. Mesonotum with irregular reticulation medially, which becomes elongated laterally; internal markings on sculpture absent. Metanotum (Fig. 19) with faint irregular reticles medially, elongated laterally, internal markings on sculpture absent; one or two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 14 to 17 duplicated cilia.

Pelta (Fig. 18) triangular with somewhat irregular margins, anterior margin acute ending in a straight tip, no lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta; almost equiangular reticles medially, slightly elongated reticles laterally, almost striate on posterior margin, internal markings on sculpture absent. Tergite II (Fig. 18) with well-defined transversal lines, enclosing some small reticles medially; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1 with blunt to slightly capitate apex, S2 blunt and S3 finely acute. Tube about 0.85 of head length and about 2.3 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 20) S-shaped, not thickened or swollen medially.

Measurements (female holotype in microns): Length about 2390; head length 232, width behind eyes 202, po length 52, eye dorsal length 84; median length of pronotum 150, width across ep 315, am 17, aa 20, ml 50, ep 100, pa 65; width of mesonotum 340; fore wing length 900; tergite IX setae S1 170, S2 187, S3 145; tergite X length 217, basal width 97, apical width 45; length(width) of antennal segments III–VIII 75(35), 65(35), 62(30), 57(27), 55(25), 30(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plates (Fig. 21) with punctuate texture present on sternite VIII, a small transverse pore plate posterior to discal setae.

Measurements (male paratype in microns): Length about 2212; head length 235, width behind eyes 185, po length 69, eye dorsal length 82; median length of pronotum 122, width across ep 287, am 12, aa 21, ml 50, ep 92, pa 50; width of mesonotum 302; fore wing length 830; tergite IX setae S1 165, S2 172, S3 130; tergite X length 187, basal width 85, apical width 42; length(width) of antennal segments III–VIII 64(32), 60(32), 60(30), 50(25), 45(22), 30(12), respectively.

Larvae: body pale with rings of red internal pigmentation on prothorax, metathorax and abdominal segments III–IV and VII; abdominal segments IX–X light brown.

Material studied. Holotype female, Brazil, Rio Grande do Sul, Santana da Boa Vista, in *Myrcia selloi* gall, 23.ii.2013 (Cavalleri, A.), at UFRGS. Slide code UFRGS 3216.

Paratypes: 12 males, 24 females and 1 larva collected with holotype, at UFRGS.

Non-type specimens: 21 males and 30 females, Brazil, Rio Grande do Sul, Santo Antônio das Missões, in *Myrcia selloi* gall, 03.ii.2013 (Cavalleri, A.), at UFRGS.

Etymology. Junction of *acri* (acute) and *oris* (mouth), indicating the pointed mouth cone.

Comments. This species is very similar to *H. conducans*, being differentiated only by the lack of elongate reticles with internal markings on pelta, and having the sculpture on abdominal tergite II almost striate, in contrast to the irregular reticulation in *H. conducans*. Some other minute variations between both species were observed in coxal setae length, appearance of metanotal sculpture and width of male pore plates. It is very similar to *H. infestans* **sp. nov.** as well, but *H. acrioris* has two pairs of epimeral setae (Fig. 17), third pair of WR on abdominal tergites II–VII, and pelta differently shaped (Fig. 18). *Holopothrips acrioris* has been collected inducing terminal rosette galls in *Myrcia selloi* (Myrtaceae) (Fig. 8) in Southern Brazil.

***Holopothrips affinis* (Bagnall, 1924)**

Phrasterothrips affinis Bagnall, 1924:633.

This Brazilian species was not observed in this work. In its original description, *H. affinis* is considered close to *H. omercooperi*, being differentiated mostly by having shorter head, longer postocular setae and reduced am setae, besides few other minute differences (Bagnall 1924). Mound & Marullo (1996) differentiates these two species by the occurrence of male pore plates, which are present on sternites VI–VIII in *H. affinis* but only in sternite VIII in *H. omercooperi*.

******Holopothrips ananasi* **Costa Lima, 1935**

(Figs 22–25)

Holopothrips ananasi Costa Lima, 1935:43.

Diagnostic features. Body uniformly brown; head long with well-defined reticulate sculpture, maxillary stylets retracted to compound eyes and touching medially; two pairs of long setae on epimeral region; metanotal sculpture formed by well-defined equiangular reticles; pelta with long lateral wings; males with pore plates on sternites VII–VIII, a transverse band posterior to discal setae on VII and three plates on VIII; female spermatheca enlarged medially.

Comments. Originally described as a pest in pineapple, based on two collections in Southeastern Brazil from damaged leaves of the plant. The head of this species is unusual in being longer than wide, bearing small and well defined equiangular reticulation dorsally (Fig. 22) and having maxillary stylets extending anteriorly to the posterior margin of eyes and

touching medially (Fig. 22). Larvae are yellow but with extensive red internal pigmentation.

Material studied. 1 male and 1 female paratypes; Brazil, Rio de Janeiro, Deodoro, in *Ananas sativus*, 15.vii.1933 (Silva, A.), at NMNH; Cotype, 1 male, Brazil, code 1203, at BMNH.

***Holopothrips atlanticus* sp. nov.**

(Figs 26–31)

Diagnostic features. Body uniformly dark brown; maxillary stylets v-shaped; two pairs of long setae on epimeral region; metanotal sculpture longitudinally striate; males with three pore plates on sternite VIII only; female spermatheca not enlarged.

Macropterous male: Body (Fig. 26) uniformly dark brown, all tarsi a lighter shade of brown, tergite X almost black, with apex lighter. Antennal segment I concolourous with head, II dark brown basally and yellow on apex, III–V yellow, with V slightly shaded light brown on apical half, VI yellow on basal half and shaded light brown on apical half, VII brown with basal fourth yellow, VIII brown. Fore wings pale but lightly shaded brown near base, without median dark line, clavus shaded; major body setae dark brown.

Head (Fig. 27) about 1.4 times as long as width behind eyes, dorsal surface with transverse lines of sculpture; cheeks straight to very slightly curved, with short and stout lateral setae, few minute teeth sometimes present on dorsal sculpture near posterior margin of eyes. Eyes large, dorsal length about 0.4 of head length; po with blunt apex, subequal or longer than dorsal length of the eye. Maxillary stylets V-shaped, reaching close to po level and about half of head width apart. Mouth cone with pointed tip, reaching ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 27) trapezoidal, few transverse lines of sculpture near posterior margin, very faint lines of sculpture indicated elsewhere; epimeral sutures usually incomplete, but complete in some specimens. Six pairs of well-developed pronotal setae, two pairs on epimera; all pairs with blunt to weakly expanded tips. Basantra faintly indicated; prosternal ferna well-developed, almost or touching medially. Mesonotum with small irregular reticles medially, elongate reticles or transverse lines laterally and anteriorly; internal markings on sculpture absent. Metanotum (Fig. 29) with longitudinal lines forming a striate pattern, bearing faint internal markings; one pair of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 15 to 22 duplicated cilia.

Pelta (Fig. 28) triangular, anterior margin acute ending in a straight tip, no lateral wings; one pair of campaniform sensilla present. Sculpture covering the whole pelta; with

longitudinally elongated and narrow reticles, exhibiting internal markings medially, wider irregular reticles laterally. Tergite II with irregular reticles medially, elongate laterally and posteriorly; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with acute apexes. Tube about 0.7–0.9 of head length and about 2.3–2.6 times as long as greatest width near base, apical width about 0.5 of basal width. Sternite VIII (Fig. 31) with two anteroangular pore plates and one transversal band posterior to discal setae, with reticulate texture.

Measurements (male holotype in microns): Length about 2488; head length 300, width behind eyes 205, po length 107, eye dorsal length 117; median length of pronotum 140, width across ep 272, am 19, aa 27, ml 62, ep 100, pa 82; width of mesonotum 292; fore wing length 1020; tergite IX setae S1 227, S2 240, S3 237; tergite X length 221, basal width 95, apical width 47; length(width) of antennal segments III–VIII 77(35), 70(36), 70(32), 65(25), 62(22), 37(12), respectively.

Macropterous female: Similar to male in both colouration and structure, but slightly larger; spermatheca (Fig. 30) S-shaped but not swollen or thickened.

Measurements (female paratype in microns): Length about 2962; head length 341, width behind eyes 240, po length 137, eye dorsal length 125; median length of pronotum 157, width across ep 332, am 51, aa 17, ml 100, ep 150, pa 112; width of mesonotum 362; fore wing length 1270; tergite IX setae S1 275, S2 325, S3 265; tergite X length 305, basal width 117, apical width 55; length(width) of antennal segments III–VIII 95(44), 85(42), 85(37), 77(30), 70(24), 45(12), respectively.

Material studied. Holotype male, Brazil, Rio de Janeiro, Paraty, in *Myrcia brasiliensis* gall, 29.xii.2010 (Cavalleri, A.), at UFRGS. Slide code UFRGS 0975.

Paratypes: 2 males, 1 female collected with holotype, at UFRGS.

Etymology. Named after the Atlantic Rainforest, the vegetational area from which this species has been collected.

Comments. The striate metanotal sculpture of this species is uncommon in being formed by thick short lines thorough (Fig. 29), while other *Holopothrips* with striate metanotum usually have thin long lines or are striate anteriorly and reticulate posteriorly. *Holopothrips atlanticus* shares some similarities with *H. omercooperi*, but is differentiated by having two setae on epimeral region (Fig. 27), fore tibia brown (Fig. 26), and median reticles on pelta being thin and longitudinally elongate with internal markings (Fig. 28). This species also has some similarities with *H. magnus* **sp. nov.**, but *H. atlanticus* has a much darker body (Fig. 26), longer pronotal

setae (Fig. 27), and males bear three pore plates on sternite VIII (Fig. 31). *Holopothrips atlanticus* may be related to some other large, dark-bodied species with two pairs of epimeral setae of the genus, such as *H. cardosoi* **sp. nov.** and *H. nigrum* **sp. nov.** (both species with maxillary stylets parallel instead of V-shaped and one single pore plate on sternite VIII instead of three), or *H. nigrisetis* **sp. nov.** (which is differentiated by the minute am and coxal setae, and whose males have pore plates on sternite VII besides of VIII).

***Holopothrips balteatus* Hood, 1955**

Holopothrips balteatus Hood, 1955:141.

This species, originally described from Southern Brazil, was not observed in this work. It is one of four *Holopothrips* species with the body mostly brown but having few abdominal segments pale, with only the pelta and abdominal segment II being yellow in *H. balteatus*. The key in Mound & Marullo (1996) differentiates this species from *H. pictus* by the size of postocellar setae and metanotal reticulation, and this step has been repeated in the key presented in the current work.

****Holopothrips bicolor* sp. nov.**

(Figs 32–38)

Diagnostic features. Body mostly yellow with head and abdominal segments VII–X fully brown; dorsolateral surface of head with minute teeth on sculpture; one pair of long setae on epimeral region; metanotal sculpture formed by equiangular reticles; males with pore plates on sternites VI–VIII; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 32) bicoloured, mostly light yellow, with head and abdominal segments VII–X dark brown. Antennal segments I–II concolourous with head, III yellow with base light brown, IV–VI yellow, VII yellow basally and light brown apically, VIII light brown. Fore wings pale, without median dark line, clavus light yellow; major body setae light yellow.

Head (Fig. 33) about 1.25 times as long as width behind eyes, dorsal surface with transverse lines of sculpture enclosing some transversely elongated reticles; cheeks curved, bearing several minute teeth on sculpture dorsolaterally. Eyes large, slightly kidney-shaped, dorsal length about 0.5 of head length; po with acute to slightly expanded apex, subequal or shorter than the diameter of an ocellus. Maxillary stylets parallel, reaching po level and about a third of head width apart. Mouth cone with rounded tip, not reaching the posterior margin of

fore coxae. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 33) rectangular to slightly trapezoidal, faint reticulate sculpture covering its surface, better defined near margins; epimeral sutures incomplete and short. Five pairs of well-developed pronotal setae, one pair on epimera; all pairs with capitate tips. Basantra absent; prosternal ferna well-developed, almost touching medially, anterior margins weakly produced. Mesonotum (Fig. 34) with equiangular reticulation medially, elongate laterally and anteriorly; internal markings on sculpture absent. Metanotum (Fig. 38) with equiangular reticles, slightly elongate near laterals, internal markings on sculpture absent; six to eleven anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 5 to 8 duplicated cilia.

Pelta (Fig. 36) triangular to arcuate, anterior margin rounded to straight, no lateral wings but with weak projections near base; one pair of campaniform sensilla present. Sculpture present anteromedially but weaker or absent posteriorly; almost equiangular reticles medially, elongated reticles laterally, internal markings on sculpture present in some specimens. Tergite II apparently smooth medially but with lines on lateral thirds; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1 and S2 with capitate apexes, S3 finely acute. Tube about 0.7 of head length and about 2.3 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 37) swollen medially.

Measurements (female holotype in microns): Length about 2587; head length 271, width behind eyes 220, po length 17, eye dorsal length 137; median length of pronotum 162, width across ep 305, am 40, aa 42, ml 37, ep 80, pa 54; width of mesonotum 315; fore wing length 950; tergite IX setae S1 127, S2 145, S3 137; tergite X length 200, basal width 91, apical width 45; length(width) of antennal segments III–VIII 72(25), 62(27), 65(27), 57(22), 52(19), 37(11), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plates (Fig. 35) with reticulate texture present on sternites VI–VIII: VI–VII with two anteroangular plates and two lateral plates posterior to discal setae, VIII with two anteroangular plates and a median transverse band posterior to discal setae.

Measurements (male paratype in microns): Length about 2113; head length 242, width behind eyes 192, po length 19, eye dorsal length 125; median length of pronotum 142, width across ep 250, am 26, aa 39, ml 42, ep 75, pa 47; width of mesonotum 272; fore wing length

820; tergite IX setae S1 110, S2 127, S3 125; tergite X length 172, basal width 74, apical width 40; length(width) of antennal segments III–VIII 80(24), 65(25), 62(25), 62(22), 50(15), 30(9), respectively.

Material studied. Holotype female, Brazil, Rio Grande do Sul, Santana do Livramento, in *Myrcia palustris*, 5.ii.2013 (Cavalleri, A.), at UFRGS. Slide code UFRGS 3771.

Paratypes: 9 males and 11 females collected with holotype, at UFRGS.

Etymology. Species named in reference of its striking bicoloured pattern.

Comments. *Holopothrips bicolor* is one of the species in the genus with a striking bicoloured body (Fig. 32) and bears almost equiangular reticulation in the metanotum, without any internal markings (Fig. 38), like the brown-coloured species *H. claritibialis* Cavalleri & Kaminski, *H. hambletoni* Hood and *H. pennatus* Moulton. It is also among the few species with multiple minute teeth on the dorsolateral sculpture of head. This species shares with *H. fulvus* having postocular setae minute and head with large eyes and curved cheeks, but is readily differentiated by its fully brown head (Fig. 33), brown abdominal segment VIII and male pore plates occurring on abdominal sternites VI–VIII (Fig. 35). *Holopothrips bicolor* may be related to the other seven bicoloured species of the genus whose body is mostly yellow, being differentiated by having the head and abdominal segment VIII fully brown, postocular setae about as long as the diameter of an ocellus and female spermatheca enlarged. A male and a female were studied from leaves of *Myrcia guianensis* collected in the city of Camaçari, Bahia state, Brazil, and are believed to belong to the same species.

***Holopothrips brevicapitatum* sp. nov.**

(Figs 39–44)

Diagnostic features. Body uniformly brown; maxillary stylets v-shaped; one pair of long pronotal setae on epimeral region; metanotal sculpture irregularly striate; male with pore plates on sternites IV–VIII; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 39) uniformly dark brown, with fore tibia and all tarsi yellow, tergite X dark brown with apical half and extreme base lighter. Antennal segment I–II concolourous with head, II lighter on extreme apex, III yellow, IV yellow slightly shaded brown on apical half, V–VI yellow on basal half and light brown on apical half, VII light brown with extreme base lighter, VIII light brown. Fore wings weakly shaded, without median dark line, clavus shaded; major body setae yellowish brown.

Head (Fig. 40) about 1.15 times as long as width behind eyes, dorsal surface with

transverse lines of sculpture, cheeks straight to slightly curved. Eyes well-developed, dorsal length about 0.4 of head length; po with blunt apex, slightly shorter than the dorsal length of the eye. Maxillary stylets V-shaped, not reaching po and more than half of head width apart. Mouth cone with rounded tip, not reaching ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 40) trapezoidal, surface smooth medially, few transverse lines present near posterior margins; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; am reduced or absent, aa small and with blunt tip, ml, ep and pa well-developed and with slightly expanded tips. Basantra absent; prosternal ferna well-developed, not touching medially. Mesonotum with faint transverse lines, sometimes enclosing few irregular reticles; internal markings on sculpture absent. Metanotum (Fig. 41) with longitudinal short lines forming a somewhat striate pattern, internal markings on sculpture absent; two or three anterior discal setae and one pair of median major setae present. Fore tarsal hamus slightly enlarged, sometimes projecting beyond lateral of tarsus. Fore wings with 6 to 11 duplicated cilia.

Pelta (Fig. 44) triangular, anterior margin straight, no lateral wings; paired campaniform sensilla present, but at least one specimen without them was observed. Sculpture covering the whole pelta; irregular reticles anteromedially, elongated irregular reticles posteriorly, internal markings on sculpture absent. Tergite II with faint reticulation anteriorly, weaker or absent medially and posteriorly; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.8 of head length and about 2.0 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 43) swollen medially.

Measurements (female holotype in microns): Length about 2034; head length 227, width behind eyes 202, po length 90, eye dorsal length 102; median length of pronotum 135, width across ep 265, am 24, aa 14, ml 80, ep 107, pa 102; width of mesonotum 287; fore wing length 890; tergite IX setae S1 220, S2 247, S3 205; tergite X length 192, basal width 90, apical width 45; length(width) of antennal segments III–VIII 65(35), 50(34), 55(32), 52(27), 52(25), 37(10), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plates (Fig. 42) with punctuate texture present on sternites IV–VIII: IV–V with two small anteroangular plates, and two reduced lateral plates posterior to discal setae; VI–VII with two anteroangular plates, and a transverse band posterior to discal setae, sometimes

interrupted medially; VIII with two anteroangular plates, and a transverse band posterior to discal setae, not interrupted.

Measurements (male paratype in microns): Length about 2014; head length 222, width behind eyes 190, po length 72, eye dorsal length 99; median length of pronotum 145, width across ep 267, am 26, aa 11, ml 62, ep 102, pa 97; width of mesonotum 282; fore wing length 920; tergite IX setae S1 200, S2 225, S3 222; tergite X length 167, basal width 84, apical width 42; length(width) of antennal segments III–VIII 65(32), 55(32), 62(31), 57(30), 50(22), 37(12), respectively.

Material studied. Holotype female, Brazil, Minas Gerais, Serra do Cipó, 1600 m, in *Miconia* sp. gall, 10.iv.2011 (Kaminski, L.A.), at UFRGS. Slide code UFRGS 1058.

Paratypes: 5 males and 25 females collected with holotype, at UFRGS.

Etymology. Combination of Latin words *brevis* (small) and *capitatum* (head), in reference to the short head of the species.

Comments. *Holopothrips brevicapitatum* is unique within the genus for males having pore plates on sternites IV–VIII (Fig. 42), while most *Holopothrips* species have pore plates restricted to sternites VI–VIII, and only *H. signatus*, *H. singularis* **sp. nov.**, *H. varicolor* **sp. nov.** and specimens of possibly *H. pictus* have pore plates on sternite V, but never on IV. Other noteworthy trait of this species is the fore tarsal hamus thin but apparently elongate, appearing to extend beyond the lateral margin of fore tarsus in some specimens. *Holopothrips brevicapitatum* have some similarities with *H. affinis* and *H. omercooperi* such as the V-shaped stylets and striate metanotum, but is quickly differentiated by the shorter head and male pore plates. *Holopothrips brevicapitatum* was found inducing rolled galls in *Miconia* young leaves (Fig. 14) in Southeastern Brazil.

***Holopothrips cardosoi* sp. nov.**

(Figs 45–50)

Diagnostic features. Body uniformly brown; maxillary stylets parallel, almost touching medially, and retracted beyond posterior margin of eyes; two pairs of long pronotal setae on epimeral region; metanotal sculpture with weakly defined elongate reticles, without internal markings; male with pore plates on sternites VII–VIII, a single transverse plate extending to lateral limits on each sternite; female spermatheca not enlarged.

Macropterous female: Body (Fig. 45) uniformly brown, fore tibia yellow on apical half and shaded brown on basal half, fore tarsi yellow, mid and hind tarsi brownish yellow, tergite

X dark brown but lighter apically. Antennal segment I concolourous with head, II brown but lighter apically, III yellow and shaded light brown on apical half, IV–VI yellow basally and brown apically, VII–VIII brown. Fore wings slightly shaded with area around sub-basal setae light brown, without median dark line, clavus brown; major body setae yellow to light brown.

Head (Fig. 46) about 1.2 times as long as width behind eyes, dorsal surface with transverse lines of sculpture, forming a few irregular transversely elongated reticles, cheeks straight. Eyes well-developed but not as enlarged as in some *Holopothrips* species, dorsal length about 0.36 of head length; po with weakly expanded apex, about as long as the dorsal length of the eye. Maxillary stylets parallel, reaching the posterior margin of eyes and very close or touching each other medially. Mouth cone with pointed tip, reaching the posterior margin of fore coxae. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 46) trapezoidal, few lines of reticulate sculpture faintly indicated medially, almost striate near posterior margin; epimeral sutures incomplete and short. Six major pairs of pronotal setae, two pairs on epimeral region; am reduced, aa, ml, ep and pa well-developed and with blunt to slightly expanded tips. Basantra faintly indicated; prosternal ferna well-developed, close medially but not touching. Mesonotum with irregular reticulation medially, which becomes elongated laterally; internal markings on sculpture absent. Metanotum (Fig. 47) with longitudinally elongated reticles medially, longitudinal lines laterally, internal markings on sculpture absent; one pair of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 18 to 23 duplicated cilia.

Pelta (Fig. 50) triangular, anterior margin straight, with weak lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta; small irregular reticles medially, larger and slightly elongated reticles laterally and posteriorly, internal markings on sculpture absent. Tergite II with short transverse lines forming a striate pattern, sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1 with acute to slightly expanded apex, S2 and S3 finely acute. Tube about 0.8–0.9 of head length and about 2.2 times as long as greatest width near base. Spermatheca (Fig. 49) curled, weakly thickened but not swollen medially.

Measurements (female holotype in microns): Length about 2745; head length 282, width behind eyes 225, po length 92, eye dorsal length 75; median length of pronotum 167, width across ep 355, aa 60, ml 107, ep 130, pa 137; width of mesonotum 350; fore wing length 1100;

tergite IX setae S1 235, S2 255, S3 252; tergite X length 250, basal width 112, apical width 50; length(width) of antennal segments III–VIII 75(37), 67(36), 67(32), 60(27), 60(22), 35(11), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Sternites VII–VIII (Fig. 48) each with a transversal pore plate with reticulate aspect placed posteriorly to discal setae.

Measurements (male paratype in microns): Length about 2330; head length 247, width behind eyes 207, po length 85, eye dorsal length 75; median length of pronotum 157, width across ep 332, am 12, aa 50, ml 70, ep 112, pa 117; width of mesonotum 325; fore wing length 1010; tergite IX setae S1 200, S2 215, S3 222; tergite X length 202, basal width 102, apical width 46; length(width) of antennal segments III–VIII 65(32), 57(31), 60(30), 57(25), 60(20), 35(12), respectively.

Material studied. Holotype female, Brazil, Minas Gerais, Uberlândia, in *Myrcia* sp. gall, 1.vi.2016 (Cardoso, J.C.F.), at UFRGS. Slide code UFRGS 5065.

Paratypes: 2 males and 18 females collected with holotype, at UFRGS.

Non-type specimens: 4 females collected with holotype, at UFRGS.

Etymology. Named after J. Cardoso, the collector of the type specimens.

Comments. The head of *H. cardosoi* is characteristic in being longer than wide and having maxillary stylets very close medially, touching each other in some specimens (Fig. 46), a trait that is shared with *H. ananasi*. However, *H. cardosoi* lacks the characteristic sculpture formed by small equiangular reticles that *H. ananasi* has in the head and metanotum, and has the antennal segments shorter and more robust. Another remarkable trait of this species is the lack of anteroangular pore plates in males, bearing only the posterior transverse band on sternites VII–VIII (Fig. 48). *Holopothrips cardosoi* may be related to some other large, dark-bodied species with two pairs of epimeral setae of the genus, such as *H. atlanticus* **sp. nov.** and *H. nigrisetis* **sp. nov.** (both with V-shaped maxillary stylets instead of parallel, and three pore plates on sternite VIII instead of one), and *H. nigrum* **sp. nov.** (which has closely striate metanotal sculpture instead of reticles). This species induces terminal rosette galls in an undetermined *Myrcia* species (Fig. 5), very similar in structure with that one induced by *H. conducans* in *M. splendens* (Fig. 6).

******Holopothrips carolinae* **Mound & Marullo, 1996**

(Figs 51–52)

Holopothrips carolinae Mound & Marullo, 1996:295.

Diagnostic features. Body mostly yellow, with head brown with posterior margin yellow and abdominal segment X brown; one pair of long setae on epimeral region; metanotal sculpture reticulate; fore wings without duplicated cilia; pelta sculpture reticulate, weaker or absent posteriorly; female spermatheca not enlarged.

Comments. This bicoloured species is known only from the female holotype collected from Costa Rica in *Pentaclethra* (Fabaceae). It is unique in the absence of duplicated cilia in fore wings, and in having only segment X of the abdomen brown in colour (Fig. 51), whereas all other bicoloured species of *Holopothrips* have at least abdominal segments IX and X brown. Antennal segments III & IV bear only two sensorial cones each.

Material studied. Female holotype, Costa Rica, La Selva, in *Pentaclethra* canopy fogging, 5.x.1992, code LAM 2410 (BMNH).

******Holopothrips chaconi* **Zamora, Hanson & Mound, 2015**

(Figs 53–54)

Holopothrips chaconi Zamora, Hanson & Mound, 2015:1038.

Diagnostic features. Body uniformly brown; maxillary stylets parallel; pronotal am and aa setae very small, two pairs of long setae on epimeral region; metanotal sculpture formed by slightly elongate reticles, some with faint internal markings; pelta apparently without campaniform sensilla, or with short stout setae instead of sensilla; males with pore plates on sternites VII–VIII; female spermatheca enlarged medially.

Comments. This light brown species was recently described from Costa Rica, breeding in abandoned cecidomyiid galls in *Piper* spp. leaves. Males have irregular transverse pore plates on sternites VII–VIII, usually complete medially on VIII but broader laterally, always interrupted medially on VII. Larvae are pale yellow and lack red internal pigmentation.

Material studied. Paratypes: 1 male, Costa Rica, San José Province, Zurquí de Moravia, in *Piper bredenmey* gall, 8.xi.2013 (Zamora, S.); 1 female, same locality, in *Piper lanosibrae* gall, 7.viii.2013 (Zamora, S.); both at BMNH.

****Holopothrips clarisetis*** **sp. nov.**

(Figs 61–67)

Diagnostic features. Body uniformly brown; head slightly wider than long; maxillary stylets parallel, close medially and retracted beyond posterior margin of eyes; one pair of long pronotal

setae on epimeral region; metanotal sculpture formed by elongate reticles, without internal markings; male with small median pore plate only on sternite VIII, interrupted medially; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 64) uniformly brown, with apical internal half of all femora lighter, fore femora light brown, fore tarsi brownish yellow, mid and hind tarsi light brown, tergite X dark brown basally and lighter on apical half. Antennal segment I–II light brown, II lighter on apical half, III yellow shaded light brown on apical half, IV very light brown, V–VIII light brown. Fore wings shaded, slightly darker near base, without median dark line, clavus shaded brown; major body setae yellow.

Head (Fig. 61) about 0.8 times as long as width behind eyes, dorsal surface with transverse lines of sculpture, weaker medially, cheeks curved. Eyes well-developed but not as enlarged as in some *Holopothrips* species, dorsal length about 0.4 of head length; po with capitate apex, shorter than the dorsal length of the eye. Maxillary stylets parallel, reaching eyes, very close medially. Mouth cone with pointed tip, reaching the posterior margin of fore coxae. Antennae 8-segmented, III with 2 sense cones and IV with 2 or 3 sense cones.

Pronotum (Fig. 61) wide and trapezoidal, surface smooth, with few transverse lines near posterior margin; epimeral sutures incomplete. Five major pairs of pronotal setae, one pair on epimeral region; am reduced, aa, ml, ep and pa well-developed and with capitate tips. Basantra absent; prosternal ferna well-developed, touching medially. Mesonotum (Fig. 62) reticulate, almost equiangular medially and elongate laterally; internal markings on sculpture absent. Metanotum (Fig. 63) with faint longitudinally elongated reticles, internal markings on sculpture absent; four to six anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 7 to 9 duplicated cilia.

Pelta (Fig. 65) triangular, anterior margin straight, with weak lateral wings in some specimens; paired campaniform sensilla present. Sculpture covering the whole pelta; irregular reticles surrounded by elongated ones medially, transversely elongated irregular reticles anteriorly, internal markings on sculpture absent. Tergite II with slightly elongated reticulation, which becomes closer to striate and less defined on further tergites. Third pair of wing retaining setae mostly absent, but sometimes a small and not curved lateral setae is close to the wing retaining pairs. Tergite IX setae S1, S2 and S3 with capitate apexes. Tube about 0.85 of head length and about 1.8 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 67) swollen medially.

Measurements (female holotype in microns): Length about 1906; head length 162, width

behind eyes 200, po length 37, eye dorsal length 62; median length of pronotum 127, width across ep 270, am 6, aa 35, ml 35, ep 62, pa 35; width of mesonotum 287; fore wing length 720; tergite IX setae S1 82, S2 89, S3 87; tergite X length 140, basal width 75, apical width 37; length(width) of antennal segments III–VIII 60(26), 52(29), 52(29), 55(27), 47(27), 27(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plate (Fig. 66) with punctuate texture and present on sternite VIII, faint irregular median spots posterior to discal setae.

Measurements (male paratype in microns): Length about 1659; head length 147, width behind eyes 182, po length 29, eye dorsal length 62; median length of pronotum 112, width across ep 247, am 5, aa 27, ml 32, ep 57, pa 32; width of mesonotum 250; fore wing length 680; tergite IX setae S1 87, S2 87, S3 82; tergite X length 117, basal width 67, apical width 32; length(width) of antennal segments III–VIII 57(25), 45(27), 50(27), 47(25), 45(22), 25(10), respectively.

Material studied. Holotype female, Brazil, Rio Grande do Sul, Jaquirana, in unidentified Myrtaceae, 28.i.2013 (Cavalleri, A.), at UFRGS. Slide code UFRGS 4115.

Paratypes: 1 male, 1 female collected with holotype. Slide codes UFRGS 4116 and 4117, respectively.

Etymology. Species named after its light-coloured major body setae.

Comments. *Holopothrips clarisetis* has some uncommon characters, such as the slightly wider than long head with long maxillary stylets (Fig. 61), reaching the posterior margin of eyes, and absence of the third pair of WR in all tergites. The metanotal sculpture is formed by weak slightly elongate reticles (Fig. 63), similar to *Holopothrips conducans* (Priesner). *Holopothrips infestans* **sp. nov.** shares with this species the lack of a third WR and a similar metanotal sculpture, but the shape of the head, pelta and female spermatheca are different between these two species. *Holopothrips clarisetis* was studied inducing galls in an unidentified Myrtaceae in South Brazil, where the terminal leaves became twisted and red pigmented (Fig. 10).

******Holopothrips claritibialis* **Cavalleri & Kaminski, 2007**

(Figs 55–60)

Holopothrips claritibialis Cavalleri & Kaminski, 2007:63.

Diagnostic features. Body uniformly brown, with all tibiae yellow; maxillary stylets parallel; one pair of long setae on epimeral region; chitinous islets present anterior to ferna; mesonotal

and metanotal sculpture formed by broad reticles; pelta with broad reticulation, weaker or absent near anterior and posterior margins; males with two anteroangular and one posterior transversal pore plates on sternites VII–VIII; female spermatheca enlarged medially.

Comments. Known only from Southern Brazil, this brown species is unusual in having all tibiae extensively yellow (Fig. 55). The prosternum also bears a pair of chitinous islets (Fig. 58) close to ferna (also exhibited by some specimens of *H. chaconi*, *H. graminis*, *H. tenuis* and *H. singularis* **sp. nov.**) This species shares some similarities with other *Holopothrips* with equiangular metanotal sculpture, such as *H. hambletoni*, *H. pennatus* and *H. punctatus* **sp. nov.**, but the tibiae colouration sets *H. claritibialis* apart. Larvae are largely pale, with no red internal pigmentation. It was described damaging leaves of *Mollinedia schottiana* (Cavalleri & Kaminski 2007), but has been studied inducing malformations on *Mollinedia elegans* leaves as well. This damage includes yellowing, cell necrosis and irregular depressions on the underside of leaves.

Material studied. 2 male and 2 female paratypes; Brazil, Rio Grande do Sul, Maquiné, in *Mollinedia schottiana* leaves, 3.xi.2006 (Cavalleri, A.), at UFRGS. Slide codes UFRGS 0827, UFRGS 0829, UFRGS 0832 and UFRGS 0846.

******Holopothrips conducans* **(Priesner, 1921)**

(Figs 68–72)

Phrasterothrips conducans Priesner, 1921:210.

Phrasterothrips brasiliensis Bagnall, 1924:632.

Diploacanthothrips fuscus Moulton, 1933:240.

Diagnostic features. Body uniformly brown; maxillary stylets parallel, touching medially in some specimens, retracted to posterior margin of compound eyes; two pairs of long setae on epimeral region; metanotal sculpture formed by slightly elongate and weakly defined reticles, sometimes with faint internal markings; pelta fully reticulate, bearing few internal markings in some reticles; abdominal tergite II irregularly reticulate; males with a single median transverse pore plate posterior to discal setae; female spermatheca not enlarged.

Comments. This thrips was originally described in the genus *Phrasterothrips* from specimens collected in Paraguay with no host information. The two synonyms recognised for this species were described from leaf-galls in Brazil. We studied specimens labelled as "cotypes" from SFM and compared with specimens from several parts of Brazil. Individuals considered belonging to the same species have been studied also from Nicaragua (see Mound & Marullo 1996).

Although we observed some variation in body length, shape of tip of major setae and pelta sculpture, here we consider all of them to belong to the same species. *Holopothrips conducans* is very similar to *H. acrioris* **sp. nov.**, having only small differences in sculpture, but these species induce galls in different species of *Myrcia*. *Holopothrips infestans* **sp. nov.** also resembles *H. conducans*, but lacks the second pair of ep and has the pelta with a different shape.

Field observations indicate that these thrips induce leaf-galls on *Myrcia splendens*, forming a convoluted terminal structure which is usually inhabited by dozens of individuals (Fig. 6) (Costa Lima 1935a). Not rarely, individuals of other *Holopothrips* species are also collected inside *M. splendens* galls, including two records of *H. longisetus* **sp. nov.**, specimens identified as *H. erianthi*, and three individuals of a still undescribed species.

Material studied. 2 male and 3 female cotypes; Paraguay, at SMF (Germany). Slide with code SMF T 7468.

Non-type specimens: 2 males and 2 females, Nicaragua, Rio San Juan, in *Eugenia* sp. gall, vii.1994 (Rueda, R.), at BMNH.

***Holopothrips curiosus* sp. nov.**

(Figs 76–81)

Diagnostic features. Body uniformly brown, including fore tibiae; maxillary stylets v-shaped; one pair of long pronotal setae on epimeral region; metanotal sculpture with elongate reticles looking almost striate, with internal markings; reticulation on pelta without internal markings; male with three pore plates on sternites VII–VIII, posterior plate on VII interrupted medially; female spermatheca not enlarged.

Macropterous female: Body (Fig. 76) uniformly brown, with fore tarsi lighter, tergite X darker basally and concolourous with body on apex. Antennal segments I–II concolourous with head, II lighter on extreme apex, III yellow shaded brown on apical third, IV–VI yellow basally and brown apically, VII–VIII brown. Fore wings pale but weakly shaded near base, without median dark line, clavus shaded; major body setae light brown.

Head (Fig. 77) about 1.5 times as long as width behind eyes, dorsal surface with transverse lines of sculpture, cheeks slightly curved. Eyes well-developed, dorsal length about 0.39 of head length; po with blunt to slightly expanded apex, almost as long as the dorsal width of the eye. Maxillary stylets V-shaped, reaching halfway to po level and about half of head width apart. Mouth cone with rounded tip, not reaching ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 77) rectangular to weakly trapezoidal, surface smooth medially, with few transverse lines of sculpture near posterior margin; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; all pairs well-developed, am with blunt tip, aa, ml, ep and pa with capitate tips. Basantra absent; prosternal ferna well-developed, not touching medially. Mesonotum (Fig. 81) with irregular reticulation medially, which becomes elongated near margins, in some specimens looks closer to transverse lines; internal markings on sculpture absent. Metanotum (Fig. 81) with longitudinal lines, sometimes forming a striate pattern, sometimes enclosing thin and elongated reticles, internal markings on sculpture present; one pair of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 7 to 12 duplicated cilia.

Pelta (Fig. 78) triangular with very irregular margins, anterior margin acute, no lateral wings but with weak projections near base; paired campaniform sensilla present. Sculpture covering the whole pelta; irregular elongated reticles medially, larger laterally, short transverse lines near posterior margin, internal markings on sculpture absent. Tergite II with transverse lines of sculpture enclosing elongated reticles; sculpture less defined on further tergites. Tergites III–VII with three pairs of wing retaining setae, sometimes absent on IV–V. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.7 of head length and about 2.2 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca S-shaped, not thickened or swollen medially (Fig. 79).

Measurements (female holotype in microns): Length about 1916; head length 225, width behind eyes 169, eye dorsal length 86; median length of pronotum 105, width across ep 207, am 15, aa 7, ml 25, ep 55, pa 49; width of mesonotum 225; fore wing length 730; tergite IX setae S1 182, S2 177, S3 170; tergite X length 150, basal width 72, apical width 37; length(width) of antennal segments III–VIII 65(25), 54(27), 57(27), 52(25), 52(22), 30(10), respectively.

Macropterous male: Similar to female in both colouration, size and structure. Pore plates (Fig. 80) with reticulate texture and present on sternites VII–VIII, two anteroangular plates and one transverse band posterior to discal setae, this band interrupted medially on VII.

Measurements (male paratype in microns): Length about 2014; head length 252, width behind eyes 172, po length 60, eye dorsal length 97; median length of pronotum 119, width across ep 210, am 22, aa 12, ml 30, ep 70, pa 59; width of mesonotum 240; fore wing length 790; tergite IX setae S1 165, S2 175, S3 172; tergite X length 167, basal width 75, apical width 40; length(width) of antennal segments III–VIII 67(25), 51(29), 57(27), 55(24), 55(20), 35(10),

respectively.

Larvae: Body mainly yellow but with rings of red internal pigmentation on thorax and abdomen.

Material studied. Holotype female, Brazil, Rio Grande do Sul, São Francisco de Paula, in *Siphoneugena reitzii* gall, 1.xii.2012 (Cavalleri, A.), at UFRGS. Slide code UFRGS 3436.

Paratypes: 2 males, 1 female and 4 larvae collected with holotype, at UFRGS.

Etymology. Named after the species having a curious combination of several uncommon traits within the genus.

Comments. *Holopothrips curiosus* is a relatively small-sized species with head longer than wide. It is uncommon in having the body fully brown, including fore tibia and all tarsi (Fig. 76), which tend to be yellow in most *Holopothrips* species. The sculpture on abdominal tergite II apparently bears few and weakly defined striae inside some reticles. The galls induced by this thrips appear as rolled or folded leaf margins, with necrotic spots along the surface (Fig. 1).

***Holopothrips elongatus* Moulton, 1929**

Holopothrips elongatus Moulton, 1929:14.

This Mexican species was not observed in this work. Mound & Marullo (1996) compares this species to *H. tenuis*, differentiating *H. elongatus* from it by the longer head (two times longer than wide) and ml setae.

***Holopothrips erianthi* (Hood, 1954)**

(Figs 73–75)

Homorothrips erianthi Hood, 1954:52.

Diagnostic features. Body uniformly brown; head slightly longer than wide, maxillary stylets parallel, retracted to posterior margin of eyes; one pair of long setae on epimeral region; mesonotal sculpture without internal markings; metanotal sculpture striate thoroughly; pelta with irregular reticles covering the whole structure, without internal markings; males with two anteroangular pore plates on sternites VI–VIII, and a widely interrupted posterior transverse plate on VIII.

Comments. Originally described in the monotypic genus *Homorothrips*, based on individuals collected from a species of grass in Southeastern Brazil. In the UFRGS collection there are several specimens from different areas of Brazil, from a variety of plants (including *Myrcia splendens*, the apparent host plant of *H. conducans* galls), which are believed to belong to this

species. No type specimens could be observed in this work.

Material studied: 2 non-type specimens; Brazil, Minas Gerais (?), in *Lithraea brasiliensis*, at ANIC. Slide with code "9Mg57-2".

***Holopothrips ferrisi* Moulton, 1929**

(Figs 82–84)

Holopothrips ferrisi Moulton, 1929:13.

Diagnostic features. Body uniformly brown; head long with maxillary stylets parallel, very close together medially; one pair of long setae on epimeral region; mesonotal and metanotal sculpture with internal markings; metanotum with elongate reticles, looking almost striate anteriorly; pelta with anterior margin forming an angular curve, reticulation covering the whole structure; males with pore plates on sternites VII–VIII, two anteroangular plates and two laterals on VII, two anteroangulars and one posterior transverse band on VIII, this transverse band extending towards tergite VIII.

Comments. This Mexican species was originally described from females collected from *Coccoloba* sp.. A male specimen identified as *H. ferrisi* by comparison with types was studied here, having some unusual traits such as the long head and long maxillary stylets, which almost touch each other medially (Fig. 82). This species is similar to *H. oaxacensis*, which in its original description was differentiated from *H. ferrisi* mostly by differences in body size.

Material studied: 1 male non-type specimen; Mexico, Chiapas, 30.v.2014 (Infante, F.), at ANIC.

***Holopothrips fulvus* Morgan, 1929**

(Figs 85–89)

Holopothrips fulvus Morgan 1929:6.

Holopothrips anacardii Hood, 1942:581.

Diagnostic features. Body mostly yellow with head bicoloured and abdominal segments IX–X brown; head cheeks rounded, po setae reduced or absent, maxillary stylets parallel; one pair of long setae on epimeral region; metanotal sculpture formed by broad reticles, without internal markings; pelta with broad reticles, without internal markings; males with three pore plates on sternite VIII; female spermatheca weakly swollen medially.

Comments. Another species with a striking bicoloured body, *H. fulvus* was described from Bahia, Brazil, on cotton, and recorded posteriorly (as the synonymized species *H. anacardii*)

damaging *Anacardium occidentale* (Anacardiaceae) and *Caryocar villosum* (Caryocaraceae) (Mound & Marullo 1996; Lima *et al*. 2017). We studied some type specimens of the synonymy *H. anacardii* in this work. A detailed and illustrated redescription of this species is provided by Lima *et al*. (2017).

Material studied. 1 male paratype (*H. anacardii*); Brazil, Bahia, in *Anacardium occidentale* leaves, (Bondar, G.), at NMNH. Slide with code "691".

Non-type specimen: 2 female topotypes (*H. anacardii*); Brazil, Bahia (Bondar, G.), at BMNH and NMNH. Slides with codes "1292" and "Bondar, 691".

******Holopothrips graminis* **Hood, 1955**

(Figs 90–94)

Holopothrips graminis Hood, 1955:149.

Diagnostic features. Body uniformly brown; maxillary stylets parallel; one pair of long setae on epimeral region; minute chitinous islets present anterior to ferna; metanotal sculpture formed by very thin reticles anteriorly, looking almost striate, and elongate posteriorly; pelta with small lateral wings basally, reticulation weaker or absent near anterior and posterior margins, without internal markings; female spermatheca not enlarged.

Comments. The original description of the species placed *H. graminis* tentatively within the genus *Holopothrips*, due to this species not having the enlarged bean-shaped eyes common to the genus, but several other species recognized as *Holopothrips* also lack such enlarged eyes. The type specimens of this species were collected probably together with the type series of *H. erianthi*, as both descriptions have the same collection data. However, both species are readily differentiated by the number of sense cones on antennal segments III–IV (2 in *H. graminis*, 3 in *H. erianthi*), tip of pronotal setae (acute to blunt in *H. graminis*, capitate in *H. erianthi*) and metanotal sculpture (Fig. 91) (elongate reticles in *H. graminis*, striate in *H. erianthi*).

Material studied. 1 female paratype; Brazil, São Paulo, Piracicaba, in *Erianthus asper*, 3.viii.1950 (Souza Dias, D.P.), at NMNH. Slide with code "Hood No. 1282".

Holopothrips graziae **sp. nov.**

(Figs 95–98)

Diagnostic features. Body mostly yellow, with head and abdominal segment VIII bicoloured, abdominal segments IX–X fully brown; head clearly longer than wide, with maxillary stylets parallel; one pair of long pronotal setae on epimeral region; metanotal sculpture with

equiangular reticulation; male with three pore plates on sternites VII–VIII; female spermatheca not enlarged.

Macropterous female: Body (Fig. 95) bicoloured, mostly yellowish white with anteriomedian region of head, abdominal segments IX–X and posterior area of segment VIII brown. Antennal segment I concolourous with apical half of head, II lighter brown, III brown basally and white apically, IV–VI white, VII–VIII shaded light brown. Fore wings hyaline, median dark line faintly indicated, clavus pale; major body setae yellowish white.

Head (Fig. 96) about 1.5 times longer than width behind eyes, dorsal surface with faintly indicated transverse lines of sculpture, cheeks straight. Eyes well-developed, bean-shaped, dorsal length about 0.47 of head length; po with capitate apex, slightly shorter than the dorsal width of the eye. Maxillary stylets parallel, reaching slightly anterior to po and about a fifth of head width apart. Mouth cone with rounded tip, not reaching the anterior margin of ferna. Antennae 8-segmented, III and IV with 3 sense cones each.

Pronotum (Fig. 96) trapezoidal to rectangular, surface smooth; epimeral sutures incomplete and short. Three major pairs of pronotal setae, one pair on epimeral region; am small or reduced with acute tip, one pair of capitate setae on anteroangular area (which may be the actual aa or an anteriorly placed ml) ep and pa well-developed and capitate. Basantra absent; prosternal ferna well-developed, close medially but not touching. Mesonotum with irregular reticulation medially, which become transversely elongate reticles anteriorly and laterally; internal markings on sculpture absent. Metanotum with equiangular reticles, longitudinally elongated on extreme lateral, internal markings on sculpture absent; one pair of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with five to seven duplicated cilia.

Pelta triangular, anterior margin straight to rounded, without lateral wings; paired campaniform sensilla present. Sculpture weak but covering the whole pelta, formed by small elongate reticles medially, larger near margins, internal markings absent. Tergite II apparently smooth medially. Third pair of wing-retaining setae present on tergites II–VII. Tergite IX setae S1 with capitate apex, S2 blunt to capitate, S3 finely acute. Tube about 0.6 of head length and about 2.4 times as long as greatest width near base, apical width about 0.56 of basal width. Spermatheca (Fig. 98) S-shaped and thin.

Measurements (female holotype in microns): Length about 2804, head length 325, width behind compound eyes 215, po length 69, eye dorsal length 151; median length of pronotum 152, width across ep 312, am 9, major setae on anterior angle 87, ep 97, pa 80; width of

mesonotum 302; fore wing length 1020; tergite IX setae S1 162, S2 175, S3 135; tergite X length 207, basal width 85, apical width 47; length(width) of antennal segments III–VIII 92(29), 75(27), 77(27), 70(24), 57(20), 37(10), respectively.

Macropterous male: Similar to female in both colouration and structure, but smaller and with abdominal segment VIII clear yellow. Pore plates (Fig. 97) with punctuate texture and present on sternites VII–VIII, two anteroangular plates and one transverse plate posterior to discal setae.

Measurements (male paratype in microns): Length about 2192, head length 285, width behind compound eyes 180, po length 40, eye dorsal length 135; median length of pronotum 137, width across ep 252, am minute, major setae on anterior angle 52, ep 81, pa 60; width of mesonotum 250; fore wing length 840; tergite IX setae S1 150, S2 157, S3 147; tergite X length 167, basal width 70, apical width 40; length(width) of antennal segments III–VIII 87(25), 72(25), 72(25), 62(22), 57(20), 32(10), respectively.

Material studied. Holotype female, Peru, Madre de Dios, Rio Tambopata reserve, 30 km SW of Pto. Maldonato, 290 m (12°50'S 69°20'W), fogging from ground on primary flood plain, 27.x.1983 (Stork, N. col.), at BMNH.

Paratypes: 2 males and 1 female collected with holotype, at BMNH.

Etymology. Species named after Dr. Jocélia Grazia.

Comments. Yet another strikingly bicoloured species within the genus, *H. graziae* is notable for its elongate bicoloured head (Fig. 96). While *H. carolinae, H. fulvus* and *H. inquilinus* also have bicoloured heads, none of them has the head more than 1.25 times as long as width behind eyes. Furthermore, *H. carolinae* has abdominal segments VIII–IX yellow (IX is brown in *H. graziae*), *H. fulvus* lacks a major pair of po and has curved cheeks, and *H. inquilinus* has two pairs of epimeral setae, while *H. graziae* has only one pair (Fig. 96).

This species has been mentioned by the code "sp. n. Peru" in Mound & Marullo (1996). The four specimens from BMNH we studied were labeled as "*Holopothrips incaicus* Paratype", but no article describing a species with this name has ever been published; thus, we decided on creating a description based on the four specimens we observed.

******Holopothrips hambletoni* **Hood, 1938**

(Figs 99–101)

Holopothrips hambletoni Hood, 1938:235.

Holopothrips certus Moulton 1938:379.

Diagnostic features. Body uniformly brown; maxillary stylets parallel; one pair of long setae on epimeral region; mesonotal and metanotal sculptures formed by broad reticles without internal markings; males with three broad pore plates on sternites VI–VIII, the posterior plate on VI interrupted medially, and the posterior plate on VIII extending towards the tergite.

Comments. Described from some specimens collected in a plant without identification in Southeastern Brazil, *H. hambletoni* is one of the few uniformly brown *Holopothrips* species with somewhat equiangular reticles on metanotum, without internal markings (Fig. 100). This trait is shared with *H. ananasi* (whose reticles are smaller and present on the head as well), *H. claritibialis*, *H. pennatus* (both having all tibiae clear yellow, while *H. hambletoni* has the mid and hind tibiae bicoloured or brown), *H. punctatus* **sp. nov.** (who bears minute teeth of sculpture laterally on head and has a lighter body colour) and *H. tillandsiae* (who bears two pairs of ep setae and males lack any pore plates).

Material studied. 1 male paratype; Brazil, São Paulo, from unidentified plant, ix.1935, (Hambleton, E.J.), at NMNH. Slide with note "No. 10, his letter of June 9, 1936".

******Holopothrips hilaris* **Hood, 1938**

(Figs 102–106)

Holopothrips hilaris Hood, 1938:233.

Diagnostic features. Body mostly brown, with abdominal segments I–V yellow; maxillary stylets parallel; one pair of long setae on epimeral region; basantra present; metanotal sculpture formed by thin and elongate reticles anteriorly, and broad reticles posteriorly, with internal markings; males with three pore plates on sternites VII–VIII; female spermatheca not enlarged.

Comments. Another species described from Southeastern Brazil, *H. hilaris* is unique within the genus for having the body mostly brown, but pelta (Fig. 105) and abdominal segments II–V clear yellow; and is one of two species of *Holopothrips* with specimens having hind femora yellow but hind tibiae brown. The other species with this unusual colour pattern for the hind legs, *H. signatus*, has only abdominal segments II–III yellow. The host plant of this species is unknown, with the type series being collected from an unidentified herb.

Material studied. 1 female paratype, Brazil, São Paulo, on leaves of an herb, ix.1935 (Hambleton, E.J.), at NMNH. Slide with note "No. 9, his letter of June 9, 1936".

***Holopothrips inconspicuus* sp. nov.**

(Figs 107–111)

Diagnostic features. Body uniformly brown; head length and width subequal, with maxillary stylets v-shaped; one pair of long pronotal setae on epimeral region; metanotal sculpture very weakly defined to absent anteromedially; third pair of abdominal WR mostly absent; male without pore plates; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 107) uniformly light brown to almost yellow, with fore tibia and fore tarsi slightly lighter, tergite X slightly darker on basal half. Antennal segment I–II light brown, III–V yellow slightly shaded brown on apical half, VI light brown with extreme base yellow, VII–VIII light brown. Fore wings weakly shaded, almost hyaline on tip, without median dark line, clavus shaded; major body setae yellow.

Head (Fig. 109) length and width behind eyes subequal, dorsal surface with very faint transverse lines of sculpture on posterior margin, smooth medially; cheeks straight to very weakly curved. Eyes well-developed, dorsal length about 0.4 of head length; po with capitate apex, slightly shorter than the dorsal width of the eye. Maxillary stylets V-shaped, not reaching po level and more than half of head width apart. Mouth cone mostly round, with a small pointed tip, not reaching the posterior margin of fore coxae. Antennae 8-segmented, III and IV with 3 sense cones each.

Pronotum (Fig. 109) trapezoidal with faint transverse lines of sculpture near posterior margin, surface smooth elsewhere; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; am reduced and with acute tip, aa, ml, ep and pa well-developed and with capitate tips. Basantra apparently faintly indicated in some observed specimens; prosternal ferna well-developed, close medially, sometimes touching each other. Mesonotum (Fig. 108) apparently smooth medially, with very faint lines of sculpture laterally and anteriorly; internal markings on sculpture absent. Metanotum (Fig. 108) with very faint or absent sculpture medially, longitudinal lines laterally, internal markings on sculpture absent; one to four anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 4 to 6 duplicated cilia.

Pelta (Fig. 110) arcuated to almost bell-shaped, anterior margin rounded to straight, with lateral wings; paired campaniform sensilla present, but sometimes with a small seta in place of a sensilla. Sculpture present anteriorly but weaker medially and posteriorly; irregular elongated reticles, internal markings on sculpture absent. Tergite II with weak irregular reticles anteriorly, transversal lines laterally, faint or absent medially and posteriorly; sculpture less defined on further tergites. Third pair of wing retaining setae mostly absent, being observed only on tergite VII and sometimes on tergites V–VI. Tergite IX setae S1 and S2 with expanded apexes, S3

finely acute. Tube about 0.75 of head length and about 1.8 times as long as greatest width near base, apical width about 0.45 of basal width. Spermatheca (Fig. 111) swollen medially.

Measurements (female holotype in microns): Length about 1639; head length 175, width behind eyes 187, po length 45, eye dorsal length 65; median length of pronotum 117, width across ep 240, am 7, aa 26, ml 40, ep 75, pa 50; width of mesonotum 230; fore wing length 590; tergite IX setae S1 115, S2 112, S3 137; tergite X length 132, basal width 72, apical width 35; length(width) of antennal segments III–VIII 60(27), 50(27), 47(27), 47(25), 45(20), 25(10), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller; sternites without pore plates.

Measurements (male paratype in microns): Length about 1442; head length 157, width behind eyes 165, po length 30, eye dorsal length 62; median length of pronotum 110, width across ep 220, am 9, aa 17, ml 32, ep 62, pa 49; width of mesonotum 220; fore wing length 560; tergite IX setae S1 100, S2 102, S3 140; tergite X length 117, basal width 70, apical width 30; length(width) of antennal segments III–VIII 52(25), 39(27), 50(25), 47(22), 42(20), 26(10), respectively.

Material studied. Holotype female, Brazil, São Paulo, Bertioga, in *Myrcia multiflora* gall, 23.11.2005 (Maia, V.C.), at UFRGS. Slide code UFRGS 1147.

Paratypes: 7 males and 9 females collected with holotype, at UFRGS. Brazil, Espírito Santo, Santa Teresa, 4 males and 6 females in *Inga* sp., 04.iv.2009 (Maia, V.C.), at UFRGS.

Etymology. Species named after its weakened/inconspicuous sculpture on head, meso- and metanotum.

Comments. Despite the absence of a third pair of WR in most abdominal tergites, this species has the usual sense cone formula of the genus, anterior discal setae on metanotum and female spermatheca visible (Fig. 111). One of the defining traits of this species is having the sculpture on head, meso- and metanotum weakened to absent medially (Figs 108–109), while most *Holopothrips* species have the sculpture at least in meso- and metanotum well defined. Another remarkable trait is the lack of pore plates on males, a character shared with only other seven species of the genus. *Holopothrips inconspicuus* is similar in some aspects to *H. jaboticabae* such as the short head, pelta with a slight constriction and third pair of WR frequently lacking, but *H. jaboticabae* has only two sense cones and well-defined metanotal sculpture. According to Maia *et al.* (2008), *H. inconspicuus* induces leaf-rolled galls in *Myrcia multiflora*.

***Holopothrips infestans* sp. nov.**

(Figs 112–119)

Diagnostic features. Body uniformly brown; maxillary stylets parallel; one pair of long pronotal setae on epimeral region; metanotal sculpture with weakly defined reticles, without internal markings; pelta somewhat constricted medially and with broad basal wings; third pair of abdominal WR mostly absent; male with single median pore plate on sternite VIII; female spermatheca not enlarged.

Macropterous female: Body (Fig. 112) uniformly brown, with fore tibia and fore tarsi yellow, tergite X dark brown on basal half and lighter on apical half. Antennal segment I concolourous with head, II brown on basal half and yellow on apical half, III–IV yellow, V–VI yellow shaded light brown on apical half, VII light brown with base yellow, VIII light brown. Fore wings weakly shaded, without median dark line, clavus shaded; major body setae brownish yellow.

Head (Fig. 113) length and width behind eyes subequal, sometimes very slightly longer, dorsal surface with transverse lines of sculpture, cheeks slightly curved. Eyes well-developed, dorsal length about 0.4 of head length; po with slightly expanded to capitate apex, slightly shorter than the dorsal width of the eye. Maxillary stylets parallel, reaching po level and about a fourth of head width apart. Mouth cone (Fig. 114) with pointed tip, reaching the posterior margin of fore coxae. Antennae 8-segmented, III and IV with 3 sense cones each.

Pronotum (Fig. 113) trapezoidal, surface smooth medially, with few lines enclosing irregular elongate reticles near posterior margin; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; am small or reduced with acute tip, aa, ml, ep and pa well-developed and with slightly expanded to capitate tips. Basantra absent; prosternal ferna well-developed, close medially but not touching, anterior margins weakly produced. Mesonotum (Fig. 115) with reticulation medially, some almost equiangular reticles surrounded by elongated reticles or transverse lines; internal markings on sculpture absent. Metanotum (Fig. 116) with faint irregular reticles, longitudinally elongated laterally, internal markings on sculpture absent; two to five anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 10 to 14 duplicated cilia.

Pelta (Fig. 117) weakly bell-shaped, anterior margin rounded or with a projection ending in a straight margin, with wide lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta, sometimes weaker medially; almost equiangular reticles medially, elongated near anterior and posterior margins, internal markings on sculpture absent. Tergite II

(Fig. 117) with small irregular reticles medially and elongated anterolaterally; sculpture less defined on further tergites. Third pair of wing retaining setae mostly absent, but sometimes a small and not curved lateral setae is close to the wing retaining pairs. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.85 of head length and about 2.0 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 119) S-shaped, slightly thickened medially but not swollen.

Measurements (female holotype in microns): Length about 2548, head length 240, width behind eyes 212, po length 62, eye dorsal length 97; median length of pronotum 157, width across ep 312, am 12, aa 46, ml 85, ep 107, pa 95; width of mesonotum 350; fore wing length 1020; tergite IX setae S1 192, S2 250, S3 237; tergite X length 205, basal width 100, apical width 45; length(width) of antennal segments III–VIII 72(30), 65(32), 65(29), 69(27), 62(25), 30(14), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plate (Fig. 118) with reticulate texture and present on sternite VIII, a thin transverse band posterior to discal setae.

Measurements (male paratype in microns): Length about 2153; head length 212, width behind eyes 197, po length 57, eye dorsal length 87; median length of pronotum 147, width across ep 275, am 7, aa 25, ml 60, ep 97, pa 86; width of mesonotum 287; fore wing length 840; tergite IX setae S1 250, S2 265, S3 262; tergite X length 170, basal width 87, apical width 42; length(width) of antennal segments III–VIII 70(30), 60(30), 65(27), 65(25), 60(22), 36(14), respectively.

Larvae: Body largely yellow but with conspicuous rings of red internal pigmentation on thorax and abdomen.

Material studied. Holotype female, Brazil, Rio Grande do Sul, São Francisco de Paula, in *Acca sellowiana* leaves, 28.ix.2013 (Cavalleri, A.), at UFRGS. Slide code UFRGS 3209.

Paratypes: 4 males and 3 females collected with holotype, at UFRGS. Brazil, Rio Grande do Sul, São Francisco de Paula (FLONA), 1 male, 2 females and 5 larvae in *Acca sellowiana* galls, 17.i.2014 (Cavalleri, A.), at UFRGS.

Non-type specimens: 3 males and 3 females, Brazil, Santa Catarina, Videira, in *Acca sellowiana*, 18.xii.1989 (Hickel, E. R.); 2 males, Brazil, Rio Grande do Sul, São Francisco de Paula, in *Acca sellowiana* leaves, 13.x.2006 (Cavalleri, A.); same locality, 1 male and 1 female, in *Acca sellowiana* galls, 1.i.2007 (Cavalleri, A.); same locality, 4 males and 3 females, in *Acca sellowiana*, 30.xii.2007 (Cavalleri, A.); 1 male and 1 female, Brazil, Rio Grande do Sul,

Jaquirana, in *Acca* sp., 28.i.2013 (Cavalleri, A.); all at UFRGS.

Etymology. Named in reference to the damage this species causes to leaves of *Acca sellowiana* (Fig. 11).

Comments. This species lacks the third pair of WR in most specimens, similarly to *H. clarisetis* **sp. nov.** and *H. inconspicuus* **sp. nov.** but fits the other diagnostic characters of the genus. It can be differentiated from these two species for having the head slightly longer than wide (Fig. 113) and female spermatheca not enlarged medially (Fig. 119). *Holopothrips infestans* is structurally very similar to *H. acrioris* **sp. nov.** and *H. conducans*, sharing with them the pattern of metanotal sculpture (Fig. 116) and the reduced pore plates of males (Fig. 118), but differs from both species in having only one pair of epimeral setae (Fig. 113) and pelta with a weak constriction near base (Fig. 117). Apparently, *H. infestans* feeds only on *Acca sellowiana*, where induces characteristic galls by rolling the leaf margins (Fig. 11). This thrips is referred as a pest of feijoa by Hickel & Ducroquet (1993) in Santa Catarina state, South Brazil, mentioned as '*Phrasterothrips* sp.' by these authors.

******Holopothrips inquilinus* **(Bournier, 1993)**

(Figs 120–121)

Caraibothrips inquilinus Bournier, 1993:236.

Diagnostic features. Body mostly yellow, with head bicoloured and abdominal segments VIII–X fully brown; maxillary stylets parallel; two pairs of long setae on epimeral region; metanotal sculpture formed by weakly defined reticulation, without internal markings; males with three pore plates on sternites VII–VIII.

Comments. Originally described in *Caraibothrips*, this species is frequently misidentified as *H. tabebuia* due to its sharply bicoloured body (Fig. 120). However, *H. inquilinus* can be differentiated by the presence of two pairs of long epimeral setae on pronotum (Fig. 121) and the weakly reticulate sculpture on metanotum. Sternites VII–VIII of the male bear one posterior and two anterolateral pore plates. This thrips was described from Guadeloupe breeding inside empty cecidomyiid galls on leaves of *Inga* (Fabaceae), and is also reported to Panama (Goldarazena *et al*. 2012).

Material studied. 1 female paratype; Guadeloupe, Duclos, inside old Cecidomyiidae gall, 4.vii.1985 (Etienne, M.J.), at BMNH.

******Holopothrips inversus* **Hood, 1955**

(Figs 124–129)

Holopothrips inversus Hood, 1955:146.

Diagnostic features. Body uniformly brown; maxillary stylets parallel; one pair of long setae on epimeral region; basantra weakly developed; metanotal sculpture formed by elongate reticles, looking almost striate anteriorly, and few equiangular reticles posteriorly, with internal markings; pelta with anterior margin forming a pointed tip, sculpture with few thin reticles medially, weaker or absent near lateral and anterior margins; males with three broad pore plates on sternites VII–VIII, the posterior plate on VIII extending towards tergite.

Comments. This is yet another *Holopothrips* species described from Southeastern Brazil, without the identification of its host plant. It has an unusually long head, about 1.6 times longer than wide (Fig. 124). Mesonotum bears internal markings in the lateral reticles (Fig. 126); the metanotal sculpture is formed by very elongate reticles with internal markings anteriorly, almost forming a striate pattern, which becomes almost equiangular posteriorly (Fig. 127). This species is comparable to some other *Holopothrips* with elongate heads, such as *H. claritibialis, H. hambletoni* (whose metanotal sculpture is mostly equiangular) *H. orites, H. permagnus* (species with much larger bodies) or *H. oaxacensis* (which has minute am setae and maxillary stylets closer together in the head).

Material studied. 1 male paratype; Brazil, São Paulo, Itanhaém, 17.vi.1948 (Hood, J.D. and Lane, J.), at NMNH. Slide with code "Hood No. 1637".

***Holopothrips irregularis* sp. nov.**

(Figs 130–136)

Diagnostic features. Body light brown; maxillary stylets v-shaped and not retracted to base of po; usually one pair of long pronotal setae on epimeral region, sometimes a second but shorter setae present in one side; metanotal sculpture with elongate reticles, forming a concentric pattern posteriorly, with internal markings; discal setae on sternite VIII irregularly placed, not organized in a single row; male with faintly indicated irregular pore plates on sternite VIII only; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 130) uniformly light brown, with fore tibia and fore tarsi yellow, mid and hind tarsi brownish yellow, tergite X brown on basal half and lighter on apical half. Antennal segment I concolourous with head, II brown with apical third yellow, III–V yellow, VI yellow shaded light brown on apical half, VII very light brown with base yellow, VIII very light brown. Fore wings pale, without median dark line, clavus yellowish; major body

setae light yellow.

Head (Fig. 131) length and width behind eyes subequal to slightly longer, dorsal surface with transverse lines of sculpture, cheeks straight. Eyes well-developed, somewhat bulbous, dorsal length about 0.4 of head length; po with blunt to weakly capitate apex, about as long as the dorsal width of the eye. Maxillary stylets V-shaped, reaching halfway to po level and more than half of head width apart. Mouth cone with rounded tip, not reaching ferna. Antennae 8-segmented, III and IV with 2 sense cones each.

Pronotum (Fig. 132) trapezoidal, weak transverse lines of sculpture near posterior margin, in some specimens very faint reticulation is visible on anterior third; epimeral sutures incomplete. Five major pairs of pronotal setae, one pair on epimeral region, sometimes a second well-developed ep setae present; am and aa short with acute to blunt tips, ml, ep and pa well-developed and with slightly expanded to weakly capitate tips. Basantra absent; prosternal ferna well-developed, in some specimens might look fused medially. Mesonotum (Fig. 132) with irregular reticulation medially, elongated laterally and anteriorly, almost striate posteriorly; internal markings on sculpture absent. Metanotum (Fig. 133) with longitudinally elongated reticles, forming a concentric pattern posteriorly, internal markings on sculpture present; one or two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus slightly thickened, but not greatly enlarged or extending beyond lateral margin of tarsus. Fore wings with 5 to 7 duplicated cilia.

Pelta (Fig. 134) triangular with irregular margins, anterior margin acute ending in a straight tip, with weak lateral wings; paired campaniform sensilla present. Sculpture faint but covering the whole pelta, sometimes weaker near margins; almost equiangular reticles medially, transversally elongated reticles posteriorly, internal markings on sculpture absent. Tergite II with transversely elongated reticles anterolaterally, irregular reticles anteromedially and laterally, sculpture weaker or absent medially; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae, sometimes might be absent on II. Tergite IX setae S1 with acute to blunt apex, S2 acute and S3 finely acute. Tube about 0.9 of head length and about 1.7–2.0 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 135) swollen medially.

Measurements (female holotype in microns): Length about 2005; head length 202, width behind eyes 195, po length 45, eye dorsal length 87; median length of pronotum 140, width across ep 265, am 27, aa 12, ml 50, ep 92, pa 82; width of mesonotum 270; fore wing length 900; tergite IX setae S1 237, S2 262, S3 217; tergite X length 205, basal width 102, apical width

50; length(width) of antennal segments III–VIII 55(32), 45(32), 52(31), 50(30), 57(27), 40(15), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plate (Fig. 136) apparently present on sternite VIII, which has very faint irregular spots with punctuate texture posterior to discal setae.

Measurements (male paratype in microns): Length about 1758; head length 195, width behind eyes 170, po length 50, eye dorsal length 82; median length of pronotum 130, width across ep 245, am 22, aa 20, ml 35, ep 92, pa 76; width of mesonotum 250; fore wing length 820; tergite IX setae S1 210, S2 227, S3 175; tergite X length 175, basal width 95, apical width 42; length(width) of antennal segments III–VIII 55(31), 40(30), 50(31), 42(27), 52(22), 40(14), respectively.

Material studied. Holotype female, Brazil, Minas Gerais, São Tomé das Letras, in *Eugenia* sp. gall, 12.vi.2012 (Maia, V.C.), at UFRGS. Slide code UFRGS 4618.

Paratypes: 4 males and 25 females collected with holotype, at UFRGS.

Etymology. Named in reference to the irregular reticles in the metanotum.

Comments. *Holopothrips irregularis* has the metanotal sculpture forming a somewhat concentric pattern of elongate reticles posteriorly (Fig. 133), which is uncommon among other *Holopothrips* species. Moreover, this species has the antenna mostly yellow on segments III–VIII, with VII–VIII being only weakly shaded; two sense cones on antennal segments III–IV, and female spermatheca greatly enlarged medially (Fig. 135). This species shares some similarities with *H. mariae*, especially the metanotal sculpture; however, *H. irregularis* differs in size, colouration, and having no internal markings on the mesonotal sculpture. Males of *H. mariae* have well defined pore plates on abdominal sternites VI–VIII, while in *H. irregularis* there are only faint indications of irregular spots posterior to discal setae on sternite VIII (Fig. 136).

***Holopothrips jaboticabae* (Hood, 1954)**

(Figs 122–123)

Anoplothrips jaboticabae Hood, 1954:54.

Diagnostic features. Body uniformly brown; maxillary stylets v-shaped; one pair of long setae on epimeral region; metanotal sculpture formed by irregular and elongate reticles, with few internal markings; pelta with weak constriction medially and lateral wings basally, few internal markings on sculpture; female spermatheca enlarged medially.

Comments. Originally described in the monotypic genus *Anoplothrips* from female specimens collected from "jaboticaba", a popular name used for at least nine different species, of which *Plinia cauliflora* (Myrtaceae) is the most common (Mattos 1983). *Holopothrips jaboticabae* is one of the few species of the genus that commonly lack the third pair of wing-retaining setae in some tergites, with the specimen observed in this study having them only on tergites IV–VII. Some other unusual features are the slightly enlarged fore femora; am, aa and ml usually small or reduced (Fig. 122); and the pelta being constricted medially, giving it a weak bell-like shape (Fig. 123).

Material studied. 1 female non-type; Brazil, São Paulo, in *Myrcia* sp., ix.1956, at NMNH.

***Holopothrips johanseni* sp. nov.**

(Figs 137–142)

Diagnostic features. Body uniformly brown; second pair of shorter postocular setae sometimes present; maxillary stylets parallel; one pair of long pronotal setae on epimeral region; metanotal sculpture with thin elongate reticles, looking almost striate; metapleural sutures absent; reticulation on pelta not reaching posterior margin and without internal markings; male with three pore plates on sternites VI–VIII, posterior plate interrupted medially on VI–VII; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 137) uniformly brown, with fore tibiae, apex of mid and hind tibiae and all tarsi yellow. Antennal segments I–II concolourous with head, II yellow on extreme apex, III–VI yellow, VII yellow basally and lightly shaded brown apically, VIII very light brown. Fore wings shaded, median dark line present, clavus shaded; major body setae light brown.

Head (Fig. 138) about 1.3 times longer than width behind eyes, dorsal surface with transverse lines of sculpture, sometimes enclosing few elongate reticles; cheeks slightly curved. Eyes well-developed, dorsal length about 0.4 of head length; two pairs of postocular setae present: internal pair shorter and with acute apexes; external pair longer and with capitate apexes, slightly shorter than the dorsal width of the compound eye. Maxillary stylets parallel, reaching po level and about a fourth to a third of head width apart. Mouth cone with rounded tip, not reaching the anterior margin of ferna. Antennae 8-segmented, III and IV with 3 sense cones each.

Pronotum (Fig. 138) trapezoidal, surface smooth medially, but with transversely elongate reticles near posterior margin and reticulation faintly indicated anteriorly; epimeral

sutures incomplete. Five major pairs of pronotal setae, one pair on epimeral region; all pairs well-developed and with expanded to capitate tips. Basantra absent; prosternal ferna well-developed, close medially and touching in at least one observed specimen. Mesonotum (Fig. 139) with small irregular reticulation medially, elongate laterally; internal markings on sculpture present. Metanotum (Fig. 139) with strongly marked longitudinal lines, enclosing some irregular elongate reticles; internal markings faintly present in some anterior and median reticles. Three or four anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with four to six duplicated cilia.

Pelta (Fig. 139) triangular, anterior margin straight, without lateral wings; paired campaniform sensilla present. Sculpture covering the median area of pelta, weaker or absent near posterior margin and anterior region; few equiangular reticles medially, surrounded by elongate reticles; internal markings on sculpture absent. Tergite II apparently smooth medially, faint lines of sculpture laterally. Third pair of WR setae present on tergites II–VII. Tergite IX setae S1 with expanded to capitate apexes, S2 blunt to slightly expanded, S3 finely acute. Tube about 0.7 of head length and about 2.4 times as long as greatest width near base, apical width about half of basal width. Spermatheca (Fig. 141) swollen medially.

Measurements (female holotype in microns): Length about 2212, head length 247, width behind compound eyes 181, po length 57, eye dorsal length 107; median length of pronotum 117, width across ep 260, am 50, aa 39, ml 62, ep 97, pa 85; width of mesonotum 287; fore wing length 900; tergite IX setae S1 135, S2 162, S3 150; tergite X length 200, basal width 82, apical width 42; length(width) of antennal segments III–VIII: 67(30), 55(29), 60(27), 55(22), 45(20), 35(12), respectively.

Macropterous male: Similar to female in structure, but slightly smaller; observed specimens seemed lighter than holotype. Pore plates (Fig. 140) with punctuate texture and present on sternites VI–VIII: two anteroangular plates and one transverse band posterior to discal setae; the posterior band is interrupted medially on VI–VII.

Measurements (male paratype in microns): Length about 1906, head length 215, width behind compound eyes 167, po length 47, eye dorsal length 95; median length of pronotum 105, width across ep 237, am 40, aa 32, ml 55, ep 87, pa 72; width of mesonotum 260; fore wing length 790; tergite IX setae S1 117, S2 135, S3 157; tergite X length 162, basal width 75, apical width 40; length(width) of antennal segments III–VIII 60(25), 45(27), 52(25), 52(20), 45(20), 30(10), respectively.

Material studied. Holotype female, Costa Rica, Braulio Carrillo National Park, in *Drymonia*

sp. twisted leaves, 13.iv.1992, at BMNH. Code LAM 2241.

Paratypes: 2 males and 1 female collected with holotype, at BMNH.

Etymology. Species named after Dr. Roberto Johansen, for his contributions to the studies of neotropical Thysanoptera.

Comments. This species is unusual in having a second pair of postocular setae, internally to the usual major pair (Fig. 138); it is possible that these setae are actually one of the postocellar pair, dislocated from the usual position. Another difference in relation to other *Holopothrips* species is the lack of metapleural sutures (Fig. 142). The two males studied had the body notably paler in relation to the two females observed - if this is sexual dimorphism or the males were just teneral adults remains unknown. *Holopothrips johanseni* has some similarities with *H. reticulatus* **sp. nov.**, but the latter differs in the two characters mentioned above, plus having internal markings in the sculpture on pelta and female spermatheca not enlarged.

This species has been mentioned by the code "sp. n. CR2" in Mound & Marullo (1996). The four specimens from BMNH we studied were labeled as "*Holopothrips centraliamericanus* Paratype", but no article describing a species with this name has ever been published; thus, we decided on creating a description based on the four specimens we had access to.

***Holopothrips kaminskii* sp. nov.**

(Figs 143–148)

Diagnostic features. Body uniformly brown; maxillary stylets v-shaped; one pair of long pronotal setae on epimeral region; metanotal sculpture longitudinally striate; pelta clearly bell-shaped; male without pore plates; female spermatheca not enlarged.

Macropterous female: Body (Fig. 143) brown, with anterior half of abdomen slightly lighter, all tarsi yellow to light brown, tergite X brown basally and lighter on apical half. Antennal segment I concolourous with head, II yellow with extreme base brown, III–IV light yellow, V–VI yellow shaded light brown, VII yellowish to very light brown, VIII yellow lightly shaded with brown. Fore wings pale, without median dark line, clavus pale; major body setae yellow to very light brown.

Head (Fig. 146) about 1.2–1.3 times as long as width behind eyes, dorsal surface with weak transverse lines of sculpture, cheeks straight to very slightly curved. Eyes well-developed, dorsal length about 0.4 of head length; po with expanded apex, about as long as the dorsal length of the eye, sometimes a third well-developed setae present. Maxillary stylets V-shaped, reaching close to po level, about a third to a half of head width apart. Mouth cone with rounded

tip, not reaching the posterior margin of fore coxae. Antennae 8-segmented, III with 2–3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 146) trapezoidal, with few transverse lines near posterior margin, and faint indication of reticulation anteriorly; epimeral sutures incomplete, sometimes almost reaching the posterior margin of pronotum. Four or five major pairs of pronotal setae, one pair on epimeral region; am and aa reduced, sometimes absent; ml variable, either short with acute tip or long with capitate tip, ep and pa well-developed and with capitate tips. Basantra absent; prosternal ferna well-developed, not close medially. Mesonotum (Fig. 144) with irregular reticles medially; internal markings on sculpture present, but faint and restricted to few reticles. Metanotum (Fig. 145) with long longitudinal lines forming a striate pattern, few internal markings on sculpture present anteromedially; one or two anterior discal setae and one pair or median major setae present. Fore tarsal hamus not enlarged. Fore wings with 11 to 14 duplicated cilia.

Pelta (Fig. 147) bell-shaped, anterior margin rounded, with very long lateral wings; paired campaniform sensilla present and one pair of short setae medially to the sensilla. Sculpture covering the whole pelta but might be weaker laterally; almost equiangular reticles medially, surrounded by elongated irregular reticles laterally, transverse striation near posterior margin, internal markings on sculpture absent. Tergite II with well-defined irregular reticles medially, transverse lines laterally; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.75 of head length and about 2.0 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 148) S-shaped, slightly thickened but not swollen medially.

Measurements (female holotype in microns): Length about 2390; head length 260, width behind eyes 205, po length 87, eye dorsal length 95; median length of pronotum 162, width across ep 290, am 35, ml 50, ep 112, pa 102; width of mesonotum 317; fore wing length 980; tergite IX setae S1 305, S2 270, S3 212; tergite X length 197, basal width 97, apical width 50; length(width) of antennal segments III–VIII 72(32), 54(32), 62(32), 57(27), 50(25), 36(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller; sternites without pore plates.

Measurements (male paratype in microns): Length about 1777; head length 232, width behind eyes 197, po length 80, eye dorsal length 90; median length of pronotum 135, width

across ep 275, am 7, ml 50, ep 95, pa 90; width of mesonotum 300; fore wing length 900; tergite IX setae S1 237, S2 237, S3 235; tergite X length 172, basal width 82, apical width 46; length(width) of antennal segments III–VIII 65(27), 52(27), 57(30), 52(27), 45(25), 32(11), respectively.

Larvae: Body largely yellow but with conspicuous rings of red internal pigmentation on thorax and abdomen.

Material studied. Holotype female, Brazil, Bahia, Lençóis, in *Vochysia* cf. *obovata* gall, 6.ii.2007 (Kaminski, L.A.), at UFRGS. Slide code UFRGS 0990.

Paratypes: 1 male and 4 females collected with holotype, at UFRGS.

Non-type specimens: 2 females collected with holotype, at UFRGS.

Etymology. Named after Lucas Kaminski, for his frequent help with collecting thrips specimens.

Comments. This species is unique within the genus in having a clearly bell-shaped pelta, with well-defined median constriction and long lateral wings (Fig. 147).. *Holopothrips kaminskii* shares a few similarities with *H. affinis* and *H. omercooperi*, in the V-shaped maxillary stylets, head longer than wide and striate metanotum, but is readily differentiated from both by the pelta shape and lack of male pore plates. This thrips was found inducing galls on leaves of *Vochysia* cf. *obovata*, which become folded along the midvein (Figs 12–13).

***Holopothrips longihamus* sp. nov.**

(Figs 149–156)

Diagnostic features. Body uniformly brown; maxillary stylets v-shaped; one pair of long pronotal setae on epimeral region; fore leg hamus greatly enlarged; metanotal sculpture with irregular and very elongate reticles, looking almost striate, without internal markings; pelta usually with four or five campaniform sensilla; male with weak and irregular pore plates, posterior to discal setae, on sternites VII–VIII; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 149) brown, with apex of fore femora, fore and mid tibiae, and all tarsi yellow, tergite X concolourous with body but lighter apically. Antennal segment I concolourous with head, II yellowish on apical half, III–IV yellow, V–VI yellow on basal half and shaded brown on apical half, VII yellow on basal half and brown on apical half, VIII brown (Fig. 151). Fore wing light yellow, without median dark line, clavus shaded; major body setae yellow.

Head (Fig. 150) about 1.25 times as long as width behind eyes, but variation was

observed among specimens from 1.15 to 1.37 times; dorsal surface with transverse lines of sculpture, cheeks straight. Eyes well-developed, dorsal length about 0.4 of head length; po with slightly expanded to capitate apex, about as long as the dorsal length of the eye. Maxillary stylets V-shaped and low on head, about a third to a half of head width apart. Mouth cone with pointed tip, almost reaching the posterior margin of fore coxae. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 150) trapezoidal, surface mostly smooth, faint lines of sculpture present near anterior and posterior margins; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; am reduced or absent, aa, ml, ep and pa well-developed and with slightly expanded tips. Basantra absent; prosternal ferna well-developed, almost touching medially. Mesonotum (Fig. 152) with very faint reticulation medially, sometimes not visible or absent, elongate reticles or transverse lines laterally; internal markings on sculpture absent. Metanotum (Fig. 156) with few elongated reticles medially, irregular longitudinal lines laterally forming a striate pattern, internal markings on sculpture absent; one to three pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus greatly enlarged, pointing sideways and extending beyond lateral margin of tarsus (Fig. 151). Fore wings with 3 to 7 duplicated cilia.

Pelta (Fig. 153) triangular with somewhat irregular margins, anterior margin acute ending in a straight tip, with lateral wings; multiple campaniform sensilla present, usually 4–5. Sculpture present anteromedially but weaker or absent laterally and posteriorly; irregular reticles surrounded by elongated ones medially, weak irregular lines laterally, internal markings on sculpture absent. Tergite II with irregular reticulation, weaker posteriorly and elongate laterally; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.7–0.9 of head length and about 2 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 154) swollen medially.

Measurements (female holotype in microns): Length about 2133; head length 230, width behind eyes 187, po length 85, eye dorsal length 95; median length of pronotum 162, width across ep 270, am 30, aa 57, ml 110, ep 125, pa 129; width of mesonotum 262; fore wing length 960; tergite IX setae S1 205, S2 250, S3 212; tergite X length 192, basal width 86, apical width 45; length(width) of antennal segments III–VIII 57(32), 47(35), 52(35), 47(32), 47(26), 37(15), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly

smaller. Pore plates (Fig. 155) with punctuate texture and present on sternites VII–VIII: VII with irregular faint spots posterior to discal setae, VIII with an irregular transverse band posterior to discal setae.

Measurements (male paratype in microns): Length about 1955; head length 216, width behind eyes 157, po length 75, eye dorsal length 82; median length of pronotum 155, width across ep 227, aa 45, ml 87, ep 100, pa 107; width of mesonotum 237; fore wing length 860; tergite IX setae S1 167, S2 195, S3 172; tergite X length 150, basal width 75, apical width 40; length(width) of antennal segments III–VIII 50(32), 40(32), 45(32), 42(27), 42(22), 32(10), respectively.

Larvae: body pale without red internal pigmentation, abdominal segments IX–X light brown.

Material studied. Holotype female, Brazil, São Paulo, Paranapiacaba, in leaf galls of cf. *Miconia* sp., 21.x.2006 (Kaminski, L.A.), at UFRGS. Slide code UFRGS 0962.

Paratypes: 15 males, 34 females and 3 larvae collected with holotype, at UFRGS.

Non-type specimens: 1 male, 6 females and 1 larva collected with holotype, at UFRGS.

Etymology. Named in reference to the greatly enlarged fore tarsal hamus this species bears.

Comments. *Holopothrips longihamus* is one of the three species within the genus with an enlarged fore tarsal hamus, and the only one where the hamus is both thickened and elongate, extending beyond the lateral margin of tarsus (Fig. 151). Another curious trait is the frequent presence of at least four or five campaniform sensilla irregularly placed in the pelta (Fig. 153), contrasting to the usual symmetrical pair seen in other *Holopothrips*. This species also has elongate pronotal setae, with ep and pa easily surpassing 100 µm long, and somewhat stout fore femora (Fig. 150). *Holopothrips longihamus* induces marginal rolled-leaf galls in an undetermined Melastomataceae tree.

***Holopothrips longisetus* sp. nov.**

(Figs 157–165)

Diagnostic features. Body uniformly brown; maxillary stylets v-shaped; two pairs of long pronotal setae on epimeral region; fore leg hamus thickened; metanotal sculpture with irregular slightly elongate reticles, not reaching close to posterior margin of metanotal craspedum; pelta with anterior margin acute and reticulation weaker to absent medially; male without pore plates; female spermatheca thickened, but not enlarged medially.

Macropterous female: Body (Fig. 157) brown, with head and basal half of tergite X

slightly darker, fore tibia slightly lighter than fore femora. Antennal segment I concolourous with head, II brown at base and yellow at apex, III–IV yellow, V yellow weakly shaded with brown on apical half, VI light brown with basal fourth yellow, VII–VIII light brown. Fore wings pale, without median dark line; major body setae brownish yellow.

Head (Fig. 158) about 1.4 times as long as width behind eyes, dorsal surface with transverse lines of sculpture, cheeks slightly curved. Eyes well-developed, somewhat bulbous, dorsal length about 0.35 of head length; po with acute to slightly capitate apex, longer than eyes, sometimes a second well-developed seta is present internally to po pair. Maxillary stylets V-shaped, reaching halfway to po and about 0.4 of head width apart. Mouth cone with pointed tip, reaching close to posterior margin of ferna. Antennae 8-segmented, III and IV with 2 sense cones each.

Pronotum (Fig. 158) trapezoidal, with weak equiangular reticulation medially; epimeral sutures incomplete and short. Six major pairs of pronotal setae, two pairs on epimeral region; am variable in size from half of aa length (Fig. 160) to subequal (Fig. 158), with acute to slightly capitate tip; aa, ml, ep and pa well-developed and with blunt to weakly capitate tips. Basantra absent; prosternal ferna well-developed, close medially but not touching. Mesonotum (Fig. 161) reticulate, equiangular medially and transversely elongated near anterior margin; internal markings on sculpture absent. Metanotum (Fig. 165) with irregular reticles medially, longitudinally elongated laterally, faint internal markings on sculpture present medially; one pair of anterior discal setae and one pair of median major setae present. Fore tarsal hamus thickened and almost extending beyond lateral margin of tarsus (Fig. 159). Fore wings with 9 to 11 duplicated cilia.

Pelta (Fig. 162) triangular, anterior margin acute, no lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta but weaker medially; almost equiangular reticles medially, surrounded by elongated reticles, internal markings on sculpture absent. Tergite II with well-defined transverse lines forming irregular reticulation; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae, but in some specimens might be present only in one side or absent in some tergites. Tergite IX setae much longer than tube, S1, S2 and S3 finely acute. Tube about 0.85 of head length and about 2.0 times as long as greatest width near base, apical width about 0.55 of basal width. Spermatheca (Fig. 163) curled and thickened, but not swollen medially.

Measurements (female holotype in microns): Length about 2350; head length 255, width behind eyes 187, po length 147, eye dorsal length 90; median length of pronotum 165, width

across ep 282, am 70, aa 85, ml 135, ep 130, pa 127; width of mesonotum 302; fore wing length 980; tergite IX setae S1 437, S2 462, S3 350; tergite X length 215, basal width 100, apical width 57; length(width) of antennal segments III–VIII 67(35), 57(32), 66(35), 62(30), 65(25), 34(15), respectively.

Macropterous male: Similar to female in colouration and structure, but slightly smaller; sternites (Fig. 164) without pore plates; S3 on tergite IX reduced or absent.

Measurements (male paratype in microns): Length about 2044; head length 225, width behind eyes 165, po length 125, eye dorsal length 77; median length of pronotum 147, width across ep 250, am 84, aa 57, ml 107, ep 107, pa 105; width of mesonotum 267; fore wing length 800; tergite IX setae S1 350, S2 325; tergite X length 177, basal width 85, apical width 45; length(width) of antennal segments III–VIII 57(31), 50(30), 60(30), 55(27), 52(22), 40(12), respectively.

Larvae: Body largely yellow, but with conspicuous rings of red internal pigmentation on thorax and most of abdominal segments.

Material studied. Holotype female, Brazil, Goiás, Goiânia, in *Myrcia splendens* galls, 20.ix.2014 (Cavalleri, A.), at UFRGS. Slide code UFRGS 4391.

Paratypes: 22 males, 72 females and 22 larvae collected with holotype, at UFRGS.

Non-type specimens: 2 males and 7 females collected with holotype; 10 females, Brazil, Mato Grosso, Chapada dos Guimarães, in *Myrcia splendens* galls, 18.i.2012 (Maia, V.C.); all at UFRGS.

Etymology. Species named after its very long major body setae.

Comments. *Holopothrips longisetus* has some of the defining characters of the genus, like the third pair of WR (although sometimes absent or present in only one side in some specimens), the anterior discal setae on metanotum and the visible female spermatheca (Fig. 163). However, there are only two sense cones on antennal segments III–IV, and males have no pore plates (Fig. 164), both characters that have been observed already in few other species within the genus. This thrips was studied inducing leaf galls on *M. splendens*, characterized by marginal leaf fold or curl, on one or both sides (Fig. 7).

***Holopothrips magnus* sp. nov.**

(Figs 166–173)

Diagnostic features. Body uniformly brown; maxillary stylets v-shaped; most major pronotal setae rather short, only the two pairs of epimeral setae elongate; basantra present; metanotal

sculpture with thin elongate reticles, looking almost striate, with internal markings; pelta with thin reticles filled with internal markings medially; male with one single median pore plate on sternite VIII; female spermatheca not enlarged.

Macropterous female: Body (Fig. 166) uniformly light brown, with fore tibia lighter and all tarsi yellow, tergite X dark brown but lighter on extreme base and apex. Antennal segments I–II concolourous with head, III–V yellow, VI yellow weakly shaded with light brown on apical half, VII yellow on basal half and light brown on apical half, VIII light brown. Fore wings pale, without median dark line; major body setae brownish yellow.

Head (Fig. 167) about 1.3 times as long as width behind eyes, dorsal surface with transverse lines of sculpture enclosing elongate reticles, cheeks straight. Eyes large, dorsal length about 0.4 of head length; po with blunt apex, slightly longer than the diameter of an ocellus. Maxillary stylets V-shaped, reaching halfway to posterior margin of eyes and more than half of head width apart. Mouth cone somewhat round, with a small pointed tip, reaching the posterior margin of basantra. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 167) trapezoidal, with weak transverse striation near posterior margin, smooth medially; epimeral sutures incomplete and short. Six major pairs of pronotal setae, two pairs on epimeral region; am and pa reduced and with acute tips, aa and ml short, ep well-developed, all with blunt tips. Basantra (Fig. 171) present and well defined, slightly wider than long or subequal; prosternal ferna well-developed, not touching medially, anterior margins weakly produced. Mesonotum (Fig. 168) with irregular reticles, sometimes lateral limits of reticles fainter; internal markings on sculpture absent. Metanotum (Fig. 169) with short longitudinal lines forming a striate pattern, sometimes enclosing elongate irregular reticles medially, internal markings on sculpture present; one pair of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 12 to 20 duplicated cilia.

Pelta (Fig. 170) triangular to arcuate, anterior margin straight, with lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta but weaker or absent laterally; thin longitudinally elongated reticles medially with internal markings, weak irregular reticles laterally. Tergite II with short transverse lines, looking almost striate; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.9 of head length and about 2.4 times as long as greatest width near base, apical width about 0.45 of basal width. Spermatheca (Fig. 172) curled

but not thickened or swollen medially.

Measurements (female holotype in microns): Length about 2982; head length 282, width behind eyes 220, po length 42, eye dorsal length 117; median length of pronotum 165, width across ep 330, am 9, aa 22, ml 32, ep 87, pa 15; width of mesonotum 362; fore wing length 850 (approximate); tergite IX setae S1 225, S2 247, S3 225; tergite X length 262, basal width 111, apical width 50; length(width) of antennal segments III–VIII 82(35), 72(35), 70(35), 65(27), 60(22), 32(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but smaller. Pore plate (Fig. 173) with punctuate texture on sternite VIII, a thin median band posterior to discal setae.

Measurements (male paratype in microns): Length about 2449; head length 247, width behind eyes 192, po length 67, eye dorsal length 100; median length of pronotum 135, width across ep 270, am 5, aa 20, ml 30, ep 82, pa 5; width of mesonotum 302; fore wing length 900 (approximate); tergite IX setae S1 182, S2 212, S3 212; tergite X length 217, basal width 92, apical width 42; length(width) of antennal segments III–VIII 72(32), 62(32), 62(30), 55(25), 55(22), 30(12), respectively.

Material studied. Holotype female, Brazil, Rio de Janeiro, Cabo Frio, in *Smilax rufescens* gall, 30.xi.2011 (Carvalho-Fernandes, S.P.), at UFRGS. Slide code UFRGS 4824.

Paratype: 1 male collected with holotype, at UFRGS. Slide code UFRGS 4825.

Etymology. Species named after its large and robust body.

Comments. This species has some uncommon traits within the genus, such as the pronotal setae having blunt apexes and being rather small, with pa being almost as small as the minute am (Fig. 167); and presence of a clearly defined basantra (Fig. 171). *Holopothrips magnus* shares some similarities with *H. atlanticus* **sp. nov.** and *H. omercooperi*, but is easily differentiated by having a much lighter body colour, shorter pronotal setae, and male with a single median pore plate on sternite VIII (Fig. 173), similar to the pore plate seen in *H. conducans*.

***Holopothrips maiae* sp. nov.**

(Figs 174–180)

Diagnostic features. Body uniformly brown; maxillary stylets halfway between parallel and v-shaped, about 1/3 of head width apart at maxillary bridge level; one pair of long pronotal setae on epimeral region; metanotal sculpture striate thoroughly; pelta sharply triangular, with straight margins and without internal markings on sculpture; male with three reticulate pore

plates on sternites VII–VIII, posterior plate on VII with a large median interruption; female spermatheca not enlarged.

Macropterous female: Body (Fig. 174) uniformly brown, with fore tibia lighter, all tarsi yellow, tergite X dark brown on basal half and lighter on apical half. Antennal segment I concolourous with head, II brown on basal half and yellow on apical half, III yellow lightly shaded light brown on apical half, IV light brown with base yellowish, V–VIII brown. Fore wings pale, without median dark line; major body setae yellow.

Head (Fig. 175) about 1.1 times as long as width behind eyes, dorsal surface with weak transverse lines of sculpture, cheeks curved. Eyes well-developed, dorsal length about 0.4 of head length; po with capitate apex, about as long as the dorsal width of the eye. Maxillary stylets loosely parallel to slightly V-shaped, reaching po level and about a third of head width apart. Mouth cone pointed, reaching close to anterior margin of ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 175) trapezoidal, surface smooth medially, transverse lines of sculpture present near posterior margin; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; am reduced, aa, ml, ep and pa well-developed and with capitate tips. Basantra absent; prosternal ferna well-developed, almost touching medially, anterior margins weakly produced in at least one specimen. Mesonotum (Fig. 176) with irregular reticulation medially, surrounded by elongate reticulation or transverse lines; internal markings on sculpture absent. Metanotum (Fig. 180) with short longitudinal lines forming striations, enclosing a few elongated reticles medially, faint internal markings on sculpture present medially; one or two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 9 to 12 duplicated cilia.

Pelta (Fig. 177) sharply triangular, anterior margin acute, with small lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta; longitudinally elongated reticles medially, larger irregular reticles laterally, internal markings on sculpture absent. Tergite II with transversely elongate irregular reticles; sculpture less defined on further tergites. Tergites III–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.8 of head length and about 2.3 times as long as greatest width near base, apical width about 0.55 of basal width. Spermatheca (Fig. 178) S-shaped, slightly thickened but not swollen medially.

Measurements (female holotype in microns): Length about 2390; head length 230, width behind eyes 205, po length 59, eye dorsal length 100; median length of pronotum 132, width

across ep 275, am 6, aa 42, ml 52, ep 95, pa 107; width of mesonotum 287; fore wing length 950; tergite IX setae S1 202, S2 217, S3 175; tergite X length 190, basal width 85, apical width 47; length(width) of antennal segments III–VIII 65(34), 55(32), 60(30), 55(30), 55(25), 35(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plates (Fig. 179) with reticulate texture and present on sternites VII–VIII: two anteroangular plates and one transverse band posterior to discal setae, this band interrupted medially on VII.

Measurements (male paratype in microns): Length about 2153; head length 210, width behind eyes 192, po length 50, eye dorsal length 85; median length of pronotum 120, width across ep 270, am 12, aa 37, ml 70, ep 97, pa 107; width of mesonotum 262; fore wing length 900; tergite IX setae S1 200, S2 200, S3 195; tergite X length 175, basal width 80, apical width 45; length(width) of antennal segments III–VIII 60(32), 50(32), 55(30), 50(27), 52(21), 37(12), respectively.

Larvae: body pale, with dark red pigmentation on prothorax, metathorax and abdominal segments III–IV and VI–VII; antennal segments and abdominal segments IX–X lightly shaded brown.

Pupa: body pale but filled with granules of red pigmentation thoroughly.

Material studied. Holotype female, Brazil, Minas Gerais, Itamonte, Brejo da Lapa, in *Marlierea* sp. gall (lateral gem), 15.iii.2012 (Maia, V.C.), at UFRGS. Slide code UFRGS 4693.

Paratypes: 12 males, 10 females and 11 larvae collected with holotype, at UFRGS.

Non-type specimen: 1 female collected with holotype, at UFRGS.

Etymology. Named after Valeria Maia, for her work with plant galls and constant collection of galling thrips for study.

Comments. One of the unusual traits of this species is the pelta sharply triangular, with straight lateral margins and small lateral wings (Fig. 177), while most *Holopothrips* species have the lateral margins of pelta slightly curved or irregular, and lack basal wings. Classifying the position of the maxillary stylets (Fig. 175) of *H. maiae* is difficult: while it is about one third of head width apart like in other species of *Holopothrips* with parallel stylets, the shape of the stylets seems to be closer to a V-shape, thus this species might represent an intermediate state between both. *Holopothrips maiae* shares some similarities with *H. erianthi*, but males lack pore plates on sternite VI and fore wings are thoroughly pale. It is also very similar to *H. spermathecus* **sp. nov.**, but differs from it on the metanotal sculpture, female spermatheca not

being enlarged (Fig. 178), and on the absence of a third pair of WR on abdominal tergite II.

******Holopothrips mariae* **Mound & Marullo, 1996**

(Figs 181–185)

Holopothrips mariae Mound & Marullo, 1996:298.

Diagnostic features. Body uniformly brown; maxillary stylets v-shaped; usually one pair of long setae on epimeral region, sometimes a second smaller seta present; basantra present; metanotal sculpture formed by elongate reticulation, with very faint internal markings in some reticles; setal pairs S1–S3 on tergite IX with acute apex; males with pore plates on segments VI–VIII; female spermatheca enlarged medially.

Comments. This is a small-bodied member of the genus (observed specimens less than 1900 µm long), with short head and antennae and V-shaped maxillary stylets in the head (Fig. 182). According to Mound & Marullo (1996), the length of am setae on pronotum is highly variable, as well as the presence of a second pair of long setae on epimera. Most type specimens have only two sense cones on antennal segments III–IV, but at least one specimen with a third sense cone on antennal segment III was recorded. Males have a slender transversal pore plate on sternites VI–VIII, with VIII also having paired anterolateral pore plates. It was described from specimens collected by fogging in Amazonian floodplain forest in Peru.

Material studied. 1 male and 1 female paratypes; Peru, Madre de Dios, Rio Tambopata Reserve, 30 km S.W. of Pto. Maldonato, 290 m (12°50'S 69°20'W), fogging from ground on primary floodplain, 27.x.1983 (Stork, N.), at BMNH.

******Holopothrips molzi* **Lindner, Mendonça Jr. & Cavalleri, 2016**

(Figs 186–188)

Holopothrips molzi Lindner, Mendonça & Cavalleri, 2016:141.

Diagnostic features. Body uniformly brown; antennal segments III–IV with two sense cones each; maxillary stylets v-shaped; pronotal setae mostly small, except for the two long pairs on epimeral region; metanotal sculpture formed by slightly elongate reticles, without internal markings; males without pore plates; female spermatheca not enlarged.

Comments. This brown species was recently described from Southern Brazil inducing marginal leaf fold galls on *Myrcia guianensis*. It is remarkable for being one of eight species of *Holopothrips* whose males lack pore plates. *Holopothrips molzi* resembles *H. conducans* in having pronotum with two pairs of long setae on epimera and metanotum bearing longitudinally

elongate reticulation (Fig. 188). However, the am setae on *H. molzi* are always minute and males do not have sternal pore plates. Larvae are mainly white with red internal pigmentation forming rings around the thorax and abdomen. The galls induced by *H. molzi* (Fig. 3) are usually invaded by the phytophagous *Myrciathrips variabilis*, which also feeds and breeds inside the gall (Lindner *et al.* 2016).

Material studied. 2 male and 2 female paratypes; Brazil, Rio Grande do Sul, São Francisco de Paula, Pró-Mata, in *Myrcia guianensis* gall, 17.ii.2014 (Cavalleri, A.), at UFRGS. Slide codes UFRGS 3687, UFRGS 3688, UFRGS 3718 and UFRGS 3719.

***Holopothrips nigrisetis* sp. nov.**

(Figs 189–195)

Diagnostic features. Body uniformly dark brown; maxillary stylets v-shaped; two pairs of long pronotal setae on epimeral region; metanotal sculpture striate thoroughly; pelta with irregular and slightly curved margins; male with three pore plates with irregular margins on sternites VII–VIII; female spermatheca not enlarged.

Macropterous female: Body (Fig. 189) uniformly brown, with tarsi brown but slightly lighter than tibiae, tergite X dark brown with apex lighter. Antennal segment I–II concolourous with head, II lighter on extreme apex, III yellow, IV–V yellow weakly shaded brown on apical half, VI yellowish brown with base paler, VII–VIII light brown. Fore wings pale with basal half weakly shaded and extreme base light brown, median dark line present on hind wings but weakly indicated or absent on fore wings, clavus shaded; major body setae dark brown.

Head (Fig. 190) about 1.5 times as long as width behind eyes, dorsal surface with transverse lines of sculpture, cheeks straight. Eyes well-developed, dorsal length about 0.3 of head length; po with blunt to slightly capitate apex, almost as long as the dorsal length of the eye. Maxillary stylets V-shaped, reaching halfway to po level and about half of head width apart. Mouth cone with pointed tip, reaching close to anterior margin of ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 190) trapezoidal, surface smooth medially, transverse lines of sculpture near posterior margin; epimeral sutures incomplete. Six major pairs of pronotal setae, two pairs on epimeral region; am reduced, all other setae well-developed; aa with blunt tip, ml, ep and pa with blunt to slightly capitate tips. Basantra absent; prosternal ferna well-developed, close medially but not touching. Mesonotum (Fig. 191) with short transverse lines enclosing elongated reticles; internal markings on sculpture absent. Metanotum (Fig. 195) with long lines

forming a striate pattern, sometimes enclosing thin longitudinally elongated reticles, internal markings on sculpture present; one or two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 10 to 16 duplicated cilia.

Pelta (Fig. 192) triangular with very irregular margins, anterior margin straight to almost acute, with lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta, sometimes weaker near anterior margin; thin longitudinally elongated reticles medially, elongated irregular reticles laterally, internal markings on sculpture present medially. Tergite II with irregular transversely elongate reticles medially; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with acute apexes. Tube about 0.8 of head length and about 2.3–2.6 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 193) thickened medially but not swollen.

Measurements (female holotype in microns): Length about 2864; head length 305, width behind eyes 207, po length 85, eye dorsal length 97; median length of pronotum 152, width across ep 317, am 10, aa 32, ml 55, ep 92, pa 92; width of mesonotum 345; fore wing length 1060; tergite IX setae S1 252, S2 287, S3 255; tergite X length 265, basal width 109, apical width 55; length(width) of antennal segments III–VIII 87(39), 75(37), 75(35), 67(32), 67(27), 47(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plates (Fig. 194) with reticulate texture and irregular margins present on sternites VII–VIII: VII with one transverse band posterior to discal setae, VIII with two anteroangular plates, and one transverse band posterior to discal setae.

Measurements (male paratype in microns): Length about 2567; head length 287, width behind eyes 187, po length 80, eye dorsal length 97; median length of pronotum 140, width across ep 292, am 10, aa 31, ml 57, ep 100, pa 85; width of mesonotum 325; fore wing length 1000; tergite IX setae S1 225, S2 255, S3 257; tergite X length 230, basal width 99, apical width 47; length(width) of antennal segments III–VIII 80(35), 65(32), 69(35), 65(30), 65(22), 40(10), respectively.

Material studied. Holotype female, Brazil, Espírito Santo, Santa Teresa, in *Myrcia* sp. gall, 3.iv.2009 (Maia, V.C.), at UFRGS. Slide code UFRGS 1174.

Paratypes: 3 males and 5 females collected with holotype, at UFRGS.

Etymology. Species named after its dark-coloured major body setae.

Comments. One of the unusual traits of this species is the pelta with very irregular lateral

margins, which are frequently eroded and curved (Fig. 192). The limits of male pore plates are also irregular, with the anteroangular plates in sternite VIII frequently being linked to the posterior plate near lateral margins (Fig. 194). In sternite VII of some specimens it is unclear if the anteroangular plates are absent or reduced to small spots linked to the posterior plate. *Holopothrips nigrisetis* may be related to some other large, dark-bodied species with two pairs of epimeral setae of the genus, such as *H. atlanticus* **sp. nov.** (which has pronotal am and coxal setae well-developed and longer than aa setae, and pore plates only on sternite VIII), *H. cardosoi* **sp. nov.** and *H. nigrum* **sp. nov.** (both species with parallel maxillary stylets instead of V-shaped, and males with a single pore plate on sternite VIII). Maia *et al.* (2014) observed this thrips inducing galls in the leaves of an undetermined *Myrcia* species.

***Holopothrips nigrum* sp. nov.**

(Figs 196–201)

Diagnostic features. Body uniformly dark brown; maxillary stylets parallel; two pairs of long pronotal setae on epimeral region; metanotal sculpture striate thoroughly; pelta with anterior margin pointed and internal markings; male with a single transverse pore plate on sternite VIII; female spermatheca not enlarged.

Macropterous female: Body (Fig. 196) uniformly dark brown, fore tibia, apexes of mid and hind tibia and mid and hind tarsi lighter brown, fore tarsi yellow, tube dark brown with apical third lighter. Antennal segments I–II concolourous with head, II lighter on extreme apex; III–VI yellow on basal half and brown on apical half, gradually getting darker, VII brown with extreme base yellow, VIII brown. Fore wings pale, darker near base, without median dark line, clavus shaded; major body setae dark brown.

Head (Fig. 197) about 1.5 times as long as width behind eyes, dorsal surface with weak transverse lines of sculpture; cheeks straight to slightly curved, some specimens bearing minute teeth on sculpture dorsolaterally. Eyes well-developed, dorsal length about 0.34 of head length; po with acute to blunt apex, longer than the dorsal length of the eye. Maxillary stylets parallel, reaching po level and less than 0.2 of head width apart. Mouth cone with sharply pointed tip, reaching beyond the posterior margin of fore coxae. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 197) trapezoidal, faint reticulate sculpture medially and striate on anterior and posterior margins; epimeral sutures usually incomplete, ranging from short to almost reaching posterior margin of pronotum; in at least two observed specimens the epimeral

suture is complete in one side. Six major pairs of pronotal setae, two pairs on epimeral region; all pairs well-developed and with blunt tips, aa, ml and pa sometimes with slightly expanded tips. Basantra absent; prosternal ferna well-developed, touching medially. Mesonotum (Fig. 198) with short transverse lines forming small irregular reticles, with its lateral limits faint; internal markings on sculpture absent. Metanotum (Fig. 198) with longitudinal short lines forming a striate pattern, faint internal markings on sculpture present near anterior margin; one or two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 16 to 27 duplicated cilia.

Pelta (Fig. 199) triangular with lateral margins slightly curved, anterior margin acute, no lateral wings; paired campaniform sensilla present. Sculpture covering the whole pelta; very thin longitudinally elongated reticles medially, elongated reticles laterally, posteromedian area almost striate, internal markings on sculpture present. Tergite II with well-defined transverse striation, sometimes with weak internal markings; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1, S2 and S3 with finely acute apexes. Tube about 0.85 of head length and about 2.6 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 200) S-shaped but not thickened or swollen medially.

Measurements (female holotype in microns): Length about 3436; head length 367, width behind eyes 244, po length 135, eye dorsal length 122; median length of pronotum 182, width across ep 347, am 56, aa 62, ml 100, ep 160, pa 140; width of mesonotum 397; fore wing length 1530; tergite IX setae S1 270, S2 325, S3 255; tergite X length 325, basal width 122, apical width 57; length(width) of antennal segments III–VIII 102(41), 95(40), 97(37), 85(30), 75(27), 51(14), respectively.

Macropterous male: Similar to female in both colouration and structure, but slightly smaller. Pore plate (Fig. 201) with reticulate texture and present on sternite VIII, a single transverse band posterior to discal setae.

Measurements (male paratype in microns): Length about 3308; head length 350, width behind eyes 235, po length 132, eye dorsal length 120; median length of pronotum 175, width across ep 352, am 42, aa 76, ml 117, ep 147, pa 130; width of mesonotum 400; fore wing length 1500; tergite IX setae S1 282, S2 300, S3 312; tergite X length 297, basal width 107, apical width 55; length(width) of antennal segments III–VIII 102(40), 92(37), 92(35), 87(27), 72(25), 50(15), respectively.

Material studied. Holotype female, Brazil, Minas Gerais, Monte Verde, in *Acca sellowiana*

leaf gall, 10.x.2009 (Kaminski, L.A.), at UFRGS. Slide code UFRGS 1191.

Paratypes: 6 males and 2 females collected with holotype, at UFRGS.

Non-type specimens: 8 males and 8 females, Brazil, Minas Gerais, Serra do Cipó, in Myrtaceae, 23.iv.2013 and 31.viii.2013 (Toma, T.), at UFRGS.

Etymology. Named in reference to the dark body colour of the species.

Comments. *Holopothrips nigrum* may be related to some other large, dark-bodied species with two pairs of epimeral setae of the genus, such as *H. atlanticus* **sp. nov.** and *H. nigrisetis* **sp. nov.** (both species with V-shaped maxillary stylets and males with three pore plates on sternite VIII, instead of parallel stylets and a single plate on VIII), or *H. cardosoi* **sp. nov.** (whose metanotal sculpture is reticulate instead of striate, and males have pore plates on sternite VII besides of VIII).

***Holopothrips oaxacensis* Johansen, 1986**

Holopothrips oaxacensis Johansen 1986:80.

This Mexican species was not studied in this work. It was described from specimens collected in *Serjania racemosa* leaves, but without any indication of it being the species' host plant. *Holopothrips oaxacensis* has the body dark brown, including fore tibiae, very long head (about 1.8 times longer than wide), tergite IX setae S2 shorter than S1 and S3, and males have pore plates on sternites VII–VIII.

***Holopothrips omercooperi* (Bagnall, 1924)**

(Fig. 207)

Phrasterothrips omercooperi Bagnall, 1924:633.

Diagnostic features. Body uniformly brown with fore tibiae yellow; maxillary stylets probably wide apart and low on head; one pair of long setae on epimeral region; mesonotal sculpture without internal markings; metanotal sculpture striate; males with three pore plates on sternite VIII only; female spermatheca not enlarged.

Comments. Described from Brazil, this species is very similar to *H. affinis*, with few differences in body size and occurrence of male pore plates (only on sternite VIII in *H. omercooperi*, and in sternites VI–VIII in *H. affinis*). It has also some similarities with *H. kaminskii* **sp. nov.**, but the new species has a unique bell-shaped pelta and males lack any pore plates.

Material studied. 1 female paratype and 1 male "type"; Brazil (Omer-Cooper, J.), at BMNH.

Slides with code “No. 79, Bagnall Coll.”.

******Holopothrips orites* **Hood, 1942**

(Figs 202–206)

Holopothrips orites Hood, 1942:579.

Diagnostic features. Body uniformly brown; head clearly longer than wide, with maxillary stylets parallel, not retracted to base of po setae; one pair of long setae on epimeral region; mesonotal sculpture with internal markings; metanotal sculpture very closely striate thoroughly; pelta with elongate thin reticles medially, bearing internal markings; female spermatheca enlarged medially.

Comments. This Peruvian species is one of the largest members of the genus, being about 3.5 millimeters long. It has some similarities with *H. striatus*, but the latter lacks internal markings in the mesonotal sculpture, the metanotum is not as finely striate, and females do not have the spermatheca enlarged medially.

Material studied. 2 female paratypes; Peru, Huanuco, vicinity of Shishmay, 3000 m, on flowers, 15–21.ix.1937 (Woytkowski, F.), at BMNH and NMNH. Slides with code “Hood No. 1448”.

******Holopothrips paulus* **Mound & Marullo, 1996**

(Fig. 208)

Holopothrips paulus Mound & Marullo, 1996:299.

Diagnostic features. Body mostly yellow, with head and abdominal segments VIII–X fully brown; maxillary stylets parallel; labial palps reduced; one pair of long setae on epimeral region; metanotal sculpture formed by equiangular to slightly elongate reticles; males with three pore plates on sternites VII–VIII, the posterior plate on VIII extending towards tergite; female spermatheca not enlarged.

Comments. This sharply bicoloured species is a very characteristic member of the genus. The antennal segments I–II, basal third of III and apical half of VII are dark brown. Males have pore plates on sternites VII–VIII, with paired anteroangular plates and one transversal area on VIII, which curiously extends toward tergite VIII as in *H. inversus* and *H. tabebuia*. It was described from one female and two males collected in dead twigs in Costa Rica. It is possibly close to other bicoloured *Holopothrips* from Central America, such as *H. inquilinus*, *H. porrosati* and *H. tabebuia*.

Material studied. Female holotype and 1 male paratype; Costa Rica, Zurquí, 15 km NE of San José, in dead *Rubus fruticosus* stems, 7.ix.1991, at BMNH. Slides with code "LAM 2115".

******Holopothrips pennatus* **Moulton, 1938**

(Fig. 209)

Holopothrips pennatus Moulton, 1938:379.

Holopothrips arachnionis Hood, 1955:139.

Diagnostic features. Body uniformly brown, with all legs fully yellow, clavus and basal area of fore wings shaded brown; maxillary stylets probably parallel; one pair of long setae on epimeral region; metanotal sculpture formed by equiangular reticulation without internal markings; female spermatheca enlarged medially.

Comments. This species, described from Southeastern Brazil from an unidentified Apocynaceae, is unique for its combination of uniformly brown body and legs clear yellow (Fig. 209), while the other brown *Holopothrips* species have at least the femora brown. It shares with *H. ananasi*, *H. claritibialis*, *H. hambletoni*, *H. punctatus* **sp. nov.**, *H. tillandsiae* and a few bicoloured species the metanotal sculpture formed by equiangular reticles, but is easily differentiated from all of them by the unusual leg colouration.

Material studied. 1 female paratype; Brazil, Minas Gerais, on woody Apocymaceae, 1.v.1933 (Hambleton, E.J.), at BMNH. Slide with code "No. 5227".

******Holopothrips permagnus* **Hood, 1938**

(Figs 210–215)

Holopothrips permagnus Hood, 1938:236.

Diagnostic features. Body uniformly brown; head much longer than wide, about 400 µm long, maxillary stylets parallel; one pair of long setae on epimeral region; mesonotal sculpture with internal markings; metanotal sculpture striate anteriorly and with elongate reticles posteriorly, with internal markings; pelta with lateral wings basally, reticulation without internal markings; males with pore plates on sternites VII–VIII, two anteroangular plates and a transverse posterior band on VIII; female spermatheca not enlarged.

Comments. Described from Peru, collected from an unidentified plant. *Holopothrips permagnus* is one of the largest species of the genus, characterized by its dark brown colour, including all tibiae, very long head (observed specimen with head over 1.8 times longer than wide - Fig. 210). Pronotal am and aa setae are very reduced, while ml is long and dislocated

closer to the anterior margin of pronotum (Fig. 212). This species is comparable to other species with elongate head, such as *H. claritibialis, H. hambletoni* (whose metanotal reticulation is equiangular and lack internal markings), *H. inversus* (a much smaller species), *H. orites* (whose metanotal sculpture is finely striate thoroughly) and *H. oaxacensis* (which was recorded only from Mexico).

Material studied. 1 female paratype; Peru, Cajamarca, vicinity of Celendin, 1–3.vi.1936 (Woytkowski, F.), at NMNH. Slide with code "Hood No. 1187".

***Holopothrips pictus* Hood, 1942**

(Figs 216–218)

Holopothrips pictus Hood, 1942: 584.

Diagnostic features. Body mostly brown, with abdominal segments II–III yellow; head with postocular setae well-developed, with capitate apex; maxillary stylets parallel; one pair of long setae on epimeral region; metanotal sculpture formed by longitudinally elongate reticles, bearing internal markings; pelta with reticulation bearing internal markings; males with pore plates on sternites VI–VIII; female spermatheca enlarged medially.

Comments. Originally described from Southeastern Brazil, this is one of four species of *Holopothrips* with mostly brown body but few abdominal segments pale. In *H. pictus* only segments II–III are yellow (Fig. 218), and the hind femora is uniformly brown. This species is similar to *H. balteatus*, being differentiated only by having the postocellar setae shorter than the diameter of an ocellus, having metanotal reticles more elongate and the third abdominal segment yellow. A series of two males and five females, collected from Southern Brazil together with the type series of *H. punctatus* **sp. nov.**, are very similar to *H. pictus* and believed to belong to this species.

Material studied. 1 female non-type; Brazil, Santa Catarina, Seara, Nova Teutônia, 300–500 m, on litter, vii.1957 (Plaumann, F.), at NMNH.

****Holopothrips porrosati* Mound & Marullo, 1996**

(Fig. 219)

Holopothrips porrosati Mound & Marullo, 1996:301.

Diagnostic features. Body mostly yellow, with head and abdominal segments IX–X fully brown and segment VIII bicoloured; antennal segment VIII with broad base, looking almost fused to VII in some specimens; maxillary stylets parallel; one pair of long setae on epimeral

region; metanotal sculpture formed by equiangular reticles medially, which become elongate laterally and posteriorly; males with a single transverse pore plate posterior to discal setae on sternite VIII; female spermatheca not enlarged.

Comments. This species is very similar to another Costa Rican species, *H. paulus*, from which differs in having abdominal segment VIII bicoloured and males with a single pore plate on sternite VIII. It is known only from the type series collected on the leaves of *Philodendron* (Araceae) in Costa Rica. Apparently, *H. porrosati* induces translucent spots on leaves where the eggs are laid (Mound & Marullo 1996). This pattern is very similar with that one observed in *H. claritibialis* on *Mollinedia* spp. in Brazil.

Material studied. 1 male and 2 female paratypes; Costa Rica, Porrosati, 30 km N of San Jose, in *Philodendron* sp. leaves, 18.xi.1992, at BMNH. Slides with code "LAM 2383".

***Holopothrips punctatus* sp. nov.**

(Figs 224–231)

Diagnostic features. Body uniformly light brown; head with sharply straight margins, maxillary stylets v-shaped, and minute teeth on sculpture dorsolaterally; one pair of long pronotal setae on epimeral region; metanotal sculpture with equiangular reticles, without internal markings; sculpture on pelta weak to absent near posterior margin; male with pore plates on sternites VI–VIII, posterior plate on VIII extending slightly towards tergite; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 224) light brown, with head and tergite X slightly darker, fore tibia and all tarsi yellow, mid tibia yellow on apical half and hind tibia yellow on apex. Antennal segment I concolourous with head, II light brown basally and yellow apically, III–VIII clear yellow. Fore wings pale but very light brown on area around sub-basal setae, without median dark line, clavus shaded; major body setae yellow.

Head (Fig. 225) about 1.3 times as long as width behind eyes, dorsal surface with transverse lines of sculpture, sometimes enclosing elongated reticles; cheeks straight, bearing several minute teeth on sculpture dorsolaterally. Eyes large, dorsal length about 0.4 of head length; po with weakly capitate apex, about as long as the dorsal width of the eye. Maxillary stylets V-shaped, not reaching po level and more than half of head width apart. Mouth cone with rounded tip, not reaching ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 225) trapezoidal, with weak lines of sculpture near posterior margin but

smooth medially; epimeral sutures incomplete and short, in some specimens apparently bifurcating around pa setae (Fig. 226). Five major pairs of pronotal setae, one pair on epimeral region; am small, aa, ml, ep and pa well-developed and with weakly capitate tips. Basantra absent; prosternal ferna well-developed, close medially but not touching, anterior margins weakly produced in some specimens. Mesonotum (Fig. 227) with equiangular reticulation medially, which becomes transversely elongated anterolaterally; internal markings on sculpture absent. Metanotum (Fig. 231) with equiangular reticles, slightly elongated near margins, internal markings on sculpture absent; one or two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 4 to 8 duplicated cilia.

Pelta (Fig. 228) triangular, wider basally than long medially, anterior margin straight to slightly curved, no lateral wings but with weak projections near base; paired campaniform sensilla present. Sculpture present medially but weaker or absent posteriorly and near margins; elongated reticles surrounded by irregular ones medially, weak irregular lines laterally, internal markings on sculpture absent. Tergite II without visible sculpture; tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1 with blunt to slightly expanded apex, S2 and S3 finely acute. Tube about 0.8 of head length and about 2.5 times as long as greatest width near base, apical width about 0.6 of basal width. Spermatheca (Fig. 229) swollen medially.

Measurements (female holotype in microns): Length about 2646; head length 287, width behind eyes 224, po length 77, eye dorsal length 107; median length of pronotum 140, width across ep 305, am 17, aa 40, ml 62, ep 105, pa 80; width of mesonotum 325; fore wing length 980; tergite IX setae S1 225, S2 235, S3 187; tergite X length 242, basal width 87, apical width 54; length(width) of antennal segments III–VIII 82(30), 62(30), 72(27), 70(25), 72(25), 27(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but smaller. Pore plates (Fig. 230) with punctuated texture and present on sternites VI–VIII: VIII with a transversal band posterior to discal setae and two anteroangular plates, VII with only the transverse band, VI with irregular spots posterior to discal setae. Posterior plate on VIII extending towards tergite, slightly past spiracles.

Measurements (male paratype in microns): Length about 2093; head length 237, width across cheeks 182, po length 60, eye dorsal length 97; median length of pronotum 120, width across ep 255, am 15, aa 37, ml 55, ep 80, pa 57; width of mesonotum 277; fore wing length 830; tergite IX setae S1 182, S2 205, S3 197; tergite X length 195, basal width 79, apical width

45; length(width) of antennal segments III–VIII 77(27), 60(25), 65(25), 62(22), 62(21), 40(10), respectively.

Material studied. Holotype female, Brazil, Rio Grande do Sul, Antônio Prado, Gruta Natural, in *Mollinedia* leaf galls, 18.ii.2010 (Cavalleri, A.), at UFRGS. Slide with code UFRGS 1083.

Paratypes: 2 males and 17 females collected with holotype, at UFRGS.

Etymology. Species named after the distinct punctuate appearance of the dorsolateral area of its head, due to the presence of minute teeth in the sculpture.

Comments. This species also has the curious trait of the posterior pore plate on sternite VIII extending towards the tergite, which is found in few other species, such as *H. hambletoni* or *H. paulus*. *Holopothrips punctatus* is very similar in appearance and structure to *H. hambletoni*, but *H. punctatus* differs by having the maxillary stylets wider apart (Fig. 225), minute teeth on dorsolateral sculpture of head, and the posterior pore plate on sternite VIII extending barely past the spiracle, while in *H. hambletoni* it extends for about a third of the tergite width. *Holopothrips pennatus* also shares some similarities with this species, but is differentiated by having all legs fully yellow (except for coxae). *Holopothrips punctatus* was found co-existing with *H. claritibialis* on *Mollinedia* leaves in South Brazil.

***Holopothrips reticulatus* sp. nov.**

(Figs 232–238)

Diagnostic features. Body uniformly brown; head with maxillary stylets weakly v-shaped, postocular setae reduced, and minute teeth on sculpture dorsolaterally; pronotum surface reticulate, with one pair of long setae on epimeral region; metanotal sculpture with longitudinally elongate reticles, with internal markings; sculpture on pelta weak to absent near posterior margin, with few internal markings; male with reticulate pore plates on sternites VI–VIII; female spermatheca not enlarged.

Macropterous female: Body (Fig. 232) uniformly brown, with apical half of fore tibia lighter, all tarsi light yellow, tergite X slightly darker on basal area. Antennal segment I–II concolourous with head, II lighter on extreme apex, III–VI yellow, VII–VIII weakly shaded with light brown. Fore wings pale but shaded brown near base, without median dark line, clavus shaded; major body setae light brown.

Head (Fig. 233) about 1.2 times as long as width behind eyes, dorsal surface with transverse lines of sculpture; cheeks straight to weakly curved, bearing several minute teeth on sculpture dorsolaterally (Fig. 234). Eyes large, slightly kidney-shaped, dorsal length about 0.5

of head length; po with acute to slightly capitate apex, about as long or shorter than the diameter of an ocellus. Maxillary stylets distantly parallel to weakly V-shaped, reaching po level, about half of head width apart. Mouth cone with rounded tip, not reaching ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional smaller sense cone.

Pronotum (Fig. 233) trapezoidal, with irregular reticulate sculpture covering its surface; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; all pairs well-developed and with capitate tips. Basantra apparently weakly indicated in some specimens; prosternal ferna well-developed, almost touching medially, anterior margins weakly produced. Mesonotum (Fig. 235) with equiangular reticulation medially, elongated laterally; internal markings on sculpture present. Metanotum (Fig. 235) with longitudinally elongated reticles, internal markings on sculpture present; one or two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 5 to 8 duplicated cilia.

Pelta (Fig. 238) triangular, anterior margin straight, no lateral wings but with weak projections near base; paired campaniform sensilla present. Sculpture covering the whole pelta but weaker posteriorly; almost equiangular to irregular reticles medially, elongated laterally, internal markings on sculpture present. Tergite II with reticulation restricted to lateral thirds, smooth medially; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1 and S2 with slightly expanded apexes, S3 finely acute and shorter. Tube about 0.7 of head length and about 2.0–2.3 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 237) curled but not thickened or swollen medially.

Measurements (female holotype in microns): Length about 1995; head length 237, width behind eyes 200, po length 17, eye dorsal length 120; median length of pronotum 132, width across ep 250, am 22, aa 34, ml 39, ep 79, pa 30; width of mesonotum 275; fore wing length 800; tergite IX setae S1 122, S2 130, S3 95; tergite X length 185, basal width 77, apical width 40; length(width) of antennal segments III–VIII 71(27), 62(27), 65(25), 57(25), 45(17), 22(10), respectively.

Macropterous male: Similar to female in both colouration and structure, but smaller. Pore plates (Fig. 236) with reticulate texture and present on sternites VI–VIII: two anterolateral plates and two lateral plates posterior to discal setae on VI–VII, two anterolateral plates and one transverse band posterior to discal setae on VIII.

Measurements (male paratype in microns): Length about 1442; head length 200, width

behind eyes 155, po length 15, eye dorsal length 95; median length of pronotum 97, width across ep 185, am 12, aa 25, ml 35, ep 55, pa 20; width of mesonotum 207; fore wing length 570; tergite IX setae S1 77, S2 97, S3 100; tergite X length 122, basal width 57, apical width 35; length(width) of antennal segments III–VIII 60(22), 49(22), 55(22), 47(20), 42(17), 30(10), respectively.

Material studied. Holotype female, Brazil, Pará, Itaituba, in *Myrciaria dubia*, 14.x.2013 (Cavalleri, A.), at UFRGS. Slide code UFRGS 3622.

Paratypes: 10 males and 19 females collected with holotype, at UFRGS.

Non-type specimens: 1 male and 1 female collected with holotype, at UFRGS.

Etymology. Species named after its remarkable reticulate sculpture present over the pronotal surface.

Comments. *Holopothrips reticulatus* bears unusual well-defined reticulation over the pronotum, which is usually weak or absent medially in other *Holopothrips* species. This species shares some similarities with *H. mariae*, but differs in having three sense cones on antennal segments III–IV, fore wings pale with shaded basal area, pelta with internal markings on sculpture (Fig. 238), female spermatheca not enlarged (Fig. 237). It also shares some similarities with *H. johanseni* **sp. nov.**, but *H. reticulatus* differs from them in having a single pair of reduced postocular setae, metapleural sutures present, pelta sculpture with internal markings (Fig. 238), female spermatheca not enlarged (Fig. 237).

***Holopothrips seini* (Watson, 1927)**

Liothrips seini Watson 1927:59.

Originally described in the genus *Liothrips* from Dominican Republic. This species was not examined in this work, but the body setae of *H. seini* are described as mostly short and inconspicuous, with ep being the only elongate pronotal setae, and ml is apparently absent.

****Holopothrips signatus* Hood, 1914**

(Figs 220–223)

Holopothrips signatus Hood, 1914:50.

Diagnostic features. Body mostly brown, with abdominal segments II–III yellow, hind femora frequently yellow as well; maxillary stylets parallel; one pair of long setae on epimeral region; metanotal sculpture formed by elongate reticles bearing internal markings; pelta reticulate and without internal markings; males with pore plates on sternites V–VIII; female spermatheca

enlarged medially.

Comments. The type species of the genus, described from Panama in *Hura crepitans* galls, together with *H. tenuis.* It is one of four *Holopothrips* species with body mostly brown, but few abdominal segments pale. In *H. signatus* only segments II–III are yellow, and the hind femora is clear yellow in contrast to the brown tibia (Fig. 220). However, this seems to be a variable characteristic, as the original description noted that some specimens had the hind femora almost as brown as the body, and at least one of the individuals studied in this work had the hind femora largely shaded brown. Males have pore plates in sternites V–VIII, two anteroangular plates and two lateral plates posterior to discal setae; however, the posterior plate in sternite VIII may be a complete band or interrupted medially (Fig. 223).

Material studied. 1 male and 1 female paratypes; Panama, Taboga Island, under surface of *Hura crepitans* leaves, 18.x.1913 (Zetek, J.), at BMNH. 1 male topotype, same collection data, at NMNH.

***Holopothrips singularis* sp. nov.**

(Figs 239–245)

Diagnostic features. Body uniformly brown, fore wings shaded brown; head with maxillary stylets parallel, minute teeth on sculpture dorsolaterally, and po setae absent; one pair of long setae on epimeral region; metanotal sculpture with longitudinally elongate reticles, with weak internal markings; sculpture on pelta weak to absent near posterior margin; male with reticulate pore plates on sternites V–VIII; female spermatheca not enlarged.

Macropterous male: Body (Fig. 239) uniformly brown, with fore tibia, apical third of mid and hind tibiae and all tarsi yellow, tergite X light brown, lighter on apex. Antennal segment I–II concolourous with head, II lighter on extreme apex, III–VI clear yellow, VII–VIII yellow slightly shaded light brown. Fore wings shaded but lighter on tip, median dark line faintly indicated, clavus shaded; major body setae light brown.

Head (Fig. 240) length subequal to width behind eyes, dorsal surface with clear reticulation; cheeks curved, bearing several minute teeth on sculpture dorsolaterally. Eyes large, slightly kidney-shaped, dorsal length about 0.5 of head length; major po setae absent, but some small discal setae are present posterior to eyes. Maxillary stylets parallel, reaching posterior margin of eyes and about a third of head width apart. Mouth cone (Fig. 241) with rounded tip, close to but not reaching ferna. Antennae 8 segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 240) rectangular, clear irregularly reticulate sculpture on its surface; epimeral sutures incomplete and short. Five major pairs of pronotal setae, one pair on epimeral region; am reduced and with acute to blunt tip, aa, ml, ep and pa well-developed and with capitate tips. Basantra (Fig. 241) weakly indicated; prosternal ferna well-developed, close medially but not touching; a chitinous islet seen above ferna in one specimen, absent in the others. Mesonotum (Fig. 245) with equiangular reticulation; faint internal markings on sculpture present. Metanotum (Fig. 245) with longitudinally elongated reticles, internal markings on sculpture present on lateral reticles; two or three pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 6 to 8 duplicated cilia.

Pelta (Fig. 242) triangular, anterior margin straight, with weak lateral wings; paired campaniform sensilla present. Sculpture present medially but weaker or absent posteriorly and near margins; slightly elongated reticles medially, longer irregular reticles laterally, internal markings on sculpture observed in one specimen, but absent in others. Tergite II with irregular reticles on lateral thirds, sculpture weaker or absent medially; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1 with blunt to slightly capitate apex, S2 and S3 acute. Tube about 0.7–0.85 of head length and about 2.3 times as long as greatest width near base, apical width about 0.5 of basal width. Sternites V–VIII (Fig. 244) with pore plates with reticulate texture: V–VII with two anterolateral plates and two lateral plates posterior to discal setae, VIII with two anterolateral plates and a transverse band posterior to discal setae.

Measurements (male holotype in microns): Length about 1718; head length 197, width behind eyes 187, eye dorsal length 100; median length of pronotum 102, width across ep 235, am 14, aa 22, ml 25, ep 57, pa 35; width of mesonotum 245; fore wing length 690; tergite IX setae S1 65, S2 100, S3 85; tergite X length 145, basal width 62, apical width 35; length(width) of antennal segments III–VIII 60(25), 52(25), 55(25), 50(20), 42(17), 30(9), respectively.

Macropterous female: Similar to male in colour and structure, but slightly larger; spermatheca (Fig. 243) curled, slightly thickened medially but not swollen.

Measurements (female paratype in microns): Length about 1916; head length 200, width behind eyes 220, eye dorsal length 110; median length of pronotum 114, width across ep 255, am 16, aa 37, ml 25, ep 72, pa 35; width of mesonotum 285; fore wing length 800; tergite IX setae S1 77, S2 135, S3 100; tergite X length 170, basal width 75, apical width 40; length(width) of antennal segments III–VIII 67(27), 55(27), 60(30), 55(24), 47(20), 30(10), respectively.

Material studied. Holotype male, Brazil, Rio de Janeiro, Paraty, Trindade beach, in a gall of an unidentified Myrtaceae, 29.xii.2010 (Cavalleri, A.), at UFRGS. Slide code UFRGS 1200.

Paratypes: 1 male, 1 female collected with holotype, at UFRGS.

Etymology. Species named after its unique combination of characters, which makes it easy to recognize among other *Holopothrips* species.

Comments. This is a highly distinct species with several remarkable traits, such as the head clearly reticulate with minute teeth on the dorsolateral sculpture (Fig. 240), absence of a defined postocular setae and male pore plates present on sternites V–VIII (Fig. 244). Some of these traits are shared with *H. reticulatus* **sp. nov.**, which is differentiated from *H. singularis* by having the head reticulation longitudinally elongate and no male pore plates on sternite V.

***Holopothrips spermathecus* sp. nov.**

(Figs 246–251)

Diagnostic features. Body uniformly brown; head with maxillary stylets parallel; one pair of long setae on epimeral region; metanotal sculpture with elongate and narrow reticles, with weak internal markings; pelta elongate and with lateral basal wings, anterior margin round; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 246) uniformly brown, with fore tibia and all tarsi brownish yellow, basal half of tergite X darker. Antennal segment I concolourous with head, II brown on basal two thirds and yellow near apex, III–IV clear yellow, V yellow weakly shaded light brown on apical half, VI yellow on basal half and light brown on apical half, VII–VIII light brown. Fore wings shaded light brown with base slightly darker, median dark line present on hind wings but not on fore wings, clavus shaded; major body setae light brown.

Head (Fig. 247) length subequal to width behind eyes, dorsal surface with weak transverse lines of sculpture, sometimes enclosing elongated reticles, cheeks straight. Eyes well-developed, dorsal length about 0.4 of head length; po with slightly expanded apex, shorter than the dorsal width of the eye. Maxillary stylets parallel, reaching po level and less than a fifth of head width apart. Mouth cone with sharply pointed tip, reaching the posterior margin of fore coxae. Antennae 8-segmented, III and IV with 3 sense cones each.

Pronotum (Fig. 247) trapezoidal, striate on posterior margin and with weak lines of sculpture near margins, but smooth medially; epimeral sutures incomplete, but reaching close to posterior margin of pronotum. Five major pairs of pronotal setae, one pair on epimeral region; am with acute to weakly capitate tip, aa, ml, ep and pa well-developed and with weakly capitate

tips. Basantra absent; prosternal ferna well-developed, close or touching medially. Mesonotum (Fig. 248) with irregular reticulation medially, which becomes elongate anterolaterally; internal markings on sculpture absent. Metanotum (Fig. 249) with longitudinally elongate irregular reticles, almost forming a striate pattern, internal markings on sculpture present; two pairs of anterior discal setae and one pair of median major setae present. Fore tarsal hamus not enlarged. Fore wings with 8 to 10 duplicated cilia.

Pelta (Fig. 250) triangular to weakly bell-shaped, anterior margin rounded, with lateral wings, slightly longer than wide right above basal wings; paired campaniform sensilla present. Sculpture covering the whole pelta; almost equiangular reticles medially, elongated reticles laterally, internal markings on sculpture absent. Tergite II with irregular reticles medially, transversally elongated laterally; sculpture less defined on further tergites. Tergites II–VII with three pairs of wing retaining setae. Tergite IX setae S1 with acute apex, S2 acute to slightly blunt, S3 acute. Tube about 0.8 of head length and about 1.9 times as long as greatest width near base. Spermatheca (Fig. 251) swollen medially.

Measurements (female holotype in microns): Length about 2034; head length 200, width behind eyes 192, po length 50, eye dorsal length 77; median length of pronotum 127, width across ep 250, am 30, aa 24, ml 50, ep 75, pa 57; width of mesonotum 267; fore wing length 780; tergite IX setae S1 140, S2 142, S3 160; tergite X length 157, basal width 87, apical width 40; length(width) of antennal segments III–VIII 67(30), 55(30), 60(30), 55(25), 52(20), 30(12), respectively.

Larvae: Body mainly yellow, but with red internal pigmentation on thorax and abdomen.

Material studied. Holotype female, Brazil, Minas Gerais, Belo Horizonte, in *Myrciaria floribunda* leaf gall, x.2012 (Portugal, A.S.), at UFRGS. Slide code UFRGS 3130.

Paratype: 1 female and 2 larvae collected with holotype, at UFRGS.

Etymology. Species named after its swollen spermatheca, which separates *H. spermathecus* from other similar-looking species.

Comments. *Holopothrips spermathecus* is very similar to species such as *H. erianthi*, *H. maiae* **sp. nov.** and *H. stannardi*, with the main traits used to differentiate it being the metanotal sculpture not closely striate (Fig. 249) and enlarged female spermatheca (Fig. 251). Moreover, *H. spermathecus* differs from *H. erianthi* in having the am setae reduced and head shorter (Fig. 247); from *H. maiae* **sp. nov.** by the maxillary stylets being closer medially (Fig. 247) and base of fore wings being shaded; and from *H. stannardi* by having pronotal setae capitate and fernal

plates touching medially. According to Santana (2014), *H. spermathecus* induces leaf-folded galls in *Myrciaria floribunda* (Fig. 2). Specimens identified as *H. erianthi* were also collected from these galls.

******Holopothrips stannardi* **Mound & Marullo, 1996**

(Figs 252–254)

Mixothrips craigheadi Stannard, 1968:138. (Gynaecoid form)

Holopothrips stannardi Mound & Marullo, 1996:302.

Diagnostic features. Body uniformly brown; maxillary stylets parallel; pronotal setae with acute to blunt tips, one pair on epimeral region; metanotal sculpture formed by short longitudinal lines, sometimes enclosing thin reticles; pelta without elongate reticles bearing internal markings; males with three pore plates on sternite VIII only; female spermatheca thickened but not enlarged medially.

Comments. This species has body uniformly dark brown and wings slightly shaded. Males have sternite VIII bearing a narrow transverse pore plates and two additional oval anterolateral plates. It shares some similarities with *H. erianthi*, *H. maiae* and *H. spermathecus*, but differs for having po and all major pronotal setae acute to blunt, in contrast to the capitate setae of the other species. This thrips has the most northern distribution of the genus and is known only from leaf-rolled galls of *Eugenia axillaris* in Florida. It was collected together with *Mixothrips craigheadi* inside the galls and it is not clear which species is the gall inducer.

Material studied. 1 male 2 female paratypes; United States, Florida, Everglades National Park, in *Eugenia axillaris* leaves, 18.ix.1960 (Craighead, F.C.), at BMNH and NMNH. Slides with code "6110784".

******Holopothrips striatus* **Jorge, Cavalleri, Bedetti & Isaías, 2016**

(Figs 255–259)

Holopothrips striatus Jorge, Cavalleri, Bedetti & Isaias, 2016:175.

Diagnostic features. Body uniformly dark brown; maxillary stylets not retracted to po level; one pair of long setae on epimeral region; metanotal sculpture thoroughly striate; pelta anterior margin forming an acute tip, sculpture with thin reticles medially, bearing internal markings; males with pore plates on sternites VII–VIII, two anteroangular plates and a transverse posterior band, which is largely interrupted medially on VII; female spermatheca not enlarged.

Comments. This dark brown species is known only from the type series collected in leaf-rolled

galls of *Myrcia retorta* (Fig. 4) in Southern Brazil (Jorge *et al.* 2016). The head is about 1.4 times as long as wide and the maxillary stylets are wide apart and retracted to basal third of head length (Fig. 256). The anteromarginal setae are very short and the metanotum is characteristic in having longitudinally striate sculpture (Fig. 258). Larvae are largely white, but with bright transverse bands of red internal pigmentation on thorax and abdomen. The general body structure of *H. striatus* resembles the Peruvian species *H. orites*, but is differentiated from it by the overall smaller body size, absence of internal markings on mesonotal sculpture, and female spermatheca not being swollen medially. Other dark-bodied *Holopothrips* species, such as *H. atlanticus*, *H. nigrum* and *H. nigrisetis* also have some similarities, but *H. striatus* is distinct from these species in lacking the second pair of major ep setae (Fig. 257).

Material studied. 2 male 2 female paratypes; Brazil, Rio Grande do Sul, São Francisco de Paula, Pró-Mata, in *Myrcia retorta* gall, 17.ii.2014 (Cavalleri, A. col.), at UFRGS. 1 female non-type, Rio Grande do Sul state, Cambará do Sul, Aparados da Serra, in *Myrcia guianensis* gall, 27.i.2013 (Cavalleri, A.), at UFRGS. Slides with codes UFRGS 2476, UFRGS 3449, UFRGS 3450, UFRGS 3455, UFRGS 3456.

***Holopothrips tabebuia* Cabrera & Segarra, 2008**

(Figs 260–263)

Holopothrips tabebuia Cabrera & Segarra, 2008:232.

Diagnostic features. Body mostly yellow, with head and pterothorax light brown, abdominal segments VIII–X dark brown; maxillary stylets parallel; one pair of long setae on epimeral region; metanotal sculpture formed by longitudinally elongate reticles, looking almost striate anteriorly; males with pore plates on sternites VII–VIII, two anteroangular plates and one posterior transverse band; female spermatheca s-shaped and not enlarged.

Comments. This species resembles *H. inquilinus* in general appearance, but *H. tabebuia* has pronotum with only one pair of long epimeral setae instead of two pairs (Fig. 260), and its metanotum is sculptured with longitudinal and narrow reticles (Fig. 261). The transversal pore plate on sternite VIII is prolonged onto the tergite as in *H. inversus* and *H. paulus*. Larvae are pale and without red internal pigmentation. Recently introduced in Florida, *H. tabebuia* is a common species in the Northern Caribbean, where is possibly originated (Cabrera & Segarra 2008). It has been observed inducing leaf-curling galls in a few *Tabebuia* (Bignoniaceae) species (Fig. 15), and in some cases, causing the death of young plants (Malumphy & Reid 2017).

Material studied. 1 male non-type; United States, Florida, Dade, Hialeah, 7925 NW 2nd Ct., in *Tabebuia* sp., 20.ii.2002 (Davis, L.), slide with code "E2002-0692"; 1 female non-type; United States, Florida, Dade, Miami, 7061 SW 129th Ave., in *Tabebuia* sp., 4.iii.2002 (Putland, E.), slide with code "E2002-0691"; both at NMNH.

******Holopothrips tenuis* **Hood, 1914**

(Figs 264–267)

Holopothrips tenuis Hood, 1914:52.

Diagnostic features. Body uniformly brown; head clearly longer than wide, with maxillary stylets parallel; pronotal aa setae reduced and ml closer to anterior margin, one pair of long setae on epimeral region; metanotal sculpture striate anteriorly and reticulate posteriorly, bearing internal markings; pelta with thin elongate reticles medially; males with pore plates on sternites VII–VIII; female spermatheca very thin, not enlarged medially.

Comments. Described from *Hura crepitans* galls in Panama, together with the type species of the genus, *H. signatus*. *Holopothrips tenuis* is a medium to large-bodied species, with head longer than wide (but not as long as *H. orites* or *H. permagnus*), large eyes. Males have pore plates on sternites VII–VIII, in the usual pattern of two anteroangular plates and one posterior transverse band.

Material studied. 1 male 2 female paratypes; Panama, Taboga Island, under surface of *Hura crepitans* leaves, 18.x.1913 (Zetek, J.), at BMNH and NMNH.

******Holopothrips tillandsiae* **Mound & Marullo, 1996**

(Figs 268–269)

Holopothrips tillandsiae Mound & Marullo, 1996:303.

Diagnostic features. Body uniformly brown; maxillary stylets parallel; two pairs of long setae on epimeral region; metanotal sculpture formed by weakly defined reticles, without internal markings; males without pore plates; female spermatheca not enlarged medially, but elongate and extending to abdominal segment VI.

Comments. This brown species is a remarkable member of the genus. The head is as wide as long (Fig. 269) and some specimens exhibit a second pair of postocular setae about 0.5 times as long as the major pair. Pronotal setae are well-developed and capitate, including am and aa. Moreover, males of *H. tillandsiae* lack sternal pore plates and the female spermatheca is curiously long, extending forward into the sixth abdominal segment. It is known only from

specimens collected on *Tillandsia compressa* (Bromeliaceae) in Costa Rica.

Material studied. 1 male and 1 female paratypes; Costa Rica, San José, in *Tillandsia compressa*, 16.iii.1937 (Neverman), at BMNH.

******Holopothrips tupi* **Hood, 1955**

(Figs 270–273)

Holopothrips tupi Hood, 1955:143.

Diagnostic features. Body uniformly dark brown, including fore tibiae; maxillary stylets parallel, po setae somewhat short; one pair of long setae on epimeral region; metanotal sculpture formed elongate reticles, with internal markings; pelta with slightly elongate reticles bearing internal markings; males with three pore plates on sternite VIII only; female spermatheca not enlarged.

Comments. Described from Southeastern Brazil, but without any identification on the host plant. *Holopothrips tupi* shares some similarities with *H. signatus*, but the latter is a bicoloured species with po setae longer. The pronotal setae of *H. tupi* is dark and stout, somewhat short when compared to the setae of other *Holopothrips* species. The reticles on pelta bear internal markings, but are not elongate and thin like in some other species with this characteristic (Fig. 273). Females have an s-shaped spermatheca (Fig. 272).

Material studied. 2 female paratypes; Brazil, São Paulo, Serra da Cantareira, Franco da Rocha, leaves of unidentified shrub or tree, 11.vi.1948 (Hood, J.D., Lane, F. and Filho, L.T.), at BMNH and NMNH. Slides with code "Hood No. 1609".

Holopothrips urinator **De Santis, 1957**

Holopothrips urinator De Santis, 1957:1.

This species, described from a single female from Argentina, was not studied in this work. It is one of the few *Holopothrips* species that have only two sense cones on antennal segments III–IV, and the metanotal sculpture is formed by elongate reticles with internal markings (Mound & Marullo 1996).

****Holopothrips varicolor*** **sp. nov.**

(Figs 274–281)

Diagnostic features. Body uniformly light brown; head with maxillary stylets parallel; one pair of long setae on epimeral region; metanotal sculpture with irregular reticles forming a

concentric pattern anteromedially, without internal markings; male with anteroangular pore plates on sternites V–VIII, and a posterior transverse plate on VIII; female spermatheca enlarged medially.

Macropterous female: Body (Fig. 274) light brown to brownish yellow; all femora light brown basally and paler on apical or inner half, all tarsi yellow, tergite X darker than body on basal half and light brown on apical half. Antennal segment I concolourous with head, II light brown on basal half and yellow on apical half, III–IV yellow, V yellow slightly shaded light brown on apical half, VI yellow on basal half and shaded light brown on apical half, VII very light brown and lighter near base, VIII very light brown. Fore wings lightly tinted with yellow, weakly shaded near base, without median dark line, clavus shaded; major body setae yellow.

Head (Fig. 275) length and width behind eyes subequal, sometimes slightly wider than long; dorsal surface with weak transverse lines of sculpture, cheeks slightly curved. Eyes well-developed, dorsal length about 0.4 of head length; po with capitate apex, shorter than dorsal width of the eye. Maxillary stylets parallel, reaching posterior margin of eyes and about 0.2 of head width apart. Mouth cone (Fig. 276) with pointed tip, almost reaching ferna. Antennae 8-segmented, III with 3 sense cones and IV with 3 sense cones + 1 additional small sense cone.

Pronotum (Fig. 275) rectangular to weakly trapezoidal, with few transverse lines of sculpture near posterior margin, surface smooth elsewhere; epimeral sutures incomplete. Five major pairs of pronotal setae, one pair on epimeral region; am small or reduced and with weakly capitate tip, aa, ml, ep and pa well-developed and with capitate tips. Basantra (Fig. 276) faintly indicated, wider than long; prosternal ferna well-developed, close medially but not touching, anterior margins produced. Mesonotum (Fig. 277) with transverse lines enclosing a few irregular elongated reticles, almost equiangular posteriorly; internal markings on sculpture absent. Metanotum (Fig. 279) with irregular reticles, forming a somewhat concentric pattern anteromedially, longitudinally elongate laterally and posteriorly, internal markings on sculpture absent; two to four anterior discal setae and one pair of median major setae present. Fore tarsal hamus slightly thickened at base but not enlarged. Fore wings with 7 to 10 duplicated cilia.

Pelta (Fig. 278) triangular with somewhat irregular margins, anterior margin straight, with weak projections near base, sometimes looking like basal wings; paired campaniform sensilla present. Sculpture covering the whole pelta; small irregular reticles medially, surrounded by elongated ones laterally, internal markings on sculpture absent, but faint markings were seen in one specimen. Tergite II with very faint irregular reticles; sculpture less defined on further tergites. Tergites V–VII with third pair of wing retaining setae, sometimes

only on one side; setae sometimes present on tergite IV as well. Tergite IX setae S1 and S2 with slightly capitate apexes, S3 finely acute. Tube about 0.85 of head length and about 1.9 times as long as greatest width near base, apical width about 0.5 of basal width. Spermatheca (Fig. 281) swollen medially.

Measurements (female holotype in microns): Length about 2271; head length 185, width behind eyes 190, po length 36, eye dorsal length 75; median length of pronotum 142, width across ep 262, am 12, aa 35, ml 37, ep 67, pa 50; width of mesonotum 295; fore wing length 740; tergite IX setae S1 125, S2 125, S3 162; tergite X length 157, basal width 84, apical width 45; length(width) of antennal segments III–VIII 62(30), 54(29), 57(27), 56(25), 52(22), 30(12), respectively.

Macropterous male: Similar to female in both colouration and structure, but smaller. Pore plates (Fig. 280) with reticulate texture and present on sternites V–VIII: V–VII with two anteroangular plates, smaller on V; VIII with two anteroangular plates and a thin band posterior to discal setae.

Measurements (male paratype in microns): Length about 1797; head length 157, width behind eyes 175, po length 24, eye dorsal length 67; median length of pronotum 112, width across ep 225, am 19, aa 30, ml 30, ep 47, pa 40; width of mesonotum 237; fore wing length 650; tergite IX setae S2 105, S3 150; tergite X length 132, basal width 72, apical width 37; length(width) of antennal segments III–VIII 55(27), 46(27), 51(25), 49(22), 47(20), 26(11), respectively.

Material studied. Holotype female, Brazil, Rio de Janeiro, Arraial do Cabo, in *Neomitranthes obscura* rolled leaf, 28.xi.2011 (Carvalho-Fernandes, S.P.), at UFRGS. Slide code UFRGS 4793.

Paratypes: 12 males and 10 females collected with holotype, at UFRGS. Brazil, Rio de Janeiro, Araruama, collected in *Neomitranthes obscura* rolled leaves, 3 females on 30.xi.2011 and 1 female on 26.iii.2012 (Carvalho-Fernandes, S.P.), at UFRGS.

Non-type specimens: 1 male and 2 females collected with holotype; 2 females, Brazil, Rio de Janeiro, Araruama, *Neomitranthes obscura* rolled leaves, 26.iii.2012 (Carvalho-Fernandes, S.P.); all at UFRGS.

Etymology. Species named after the variation in body colour observed between specimens, from light brown to almost yellow.

Comments. *Holopothrips varicolor* is remarkable for its light-coloured body (Fig. 274), with some specimens looking almost yellow in transmitted light, and for the somewhat concentric

pattern formed by the anteromedian reticles in the metanotum (Fig. 279). Other interesting traits are the lack of discal setae on pronotum, the presence of a weakly indicated prosternal basantra (Fig. 276), absence of the third WR on abdominal tergites II–III and females with enlarged spermatheca (Fig. 281). This species shares some similarities to *H. maiae* **sp. nov.** and *H. spermathecus* **sp. nov.** in the shape of head and position of maxillary stylets, but differs in the metanotal sculpture (Fig. 279). The metanotal sculpture of *H. varicolor* differs from species with mostly equiangular reticulation in the metanotum, such as *H. hambletoni* or *H. pennatus*, for being formed by smaller reticles with not as well-defined contours. This thrips is known to induce leaf galls on *Neomithrantes obscura* (Fig. 9) (Carvalho-Fernandes *et al.* 2016).

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References

Bagnall, R.S. (1924) Brief descriptions of new Thysanoptera XIV. *Annals and Magazine of Natural History*, 14(9), 625–640.

Bhatti, J.S. (1998) *New perspectives in the structure and taxonomy of Tubulifera*. Scientia Publishing, New Delhi, 205 pp.

Bournier, A. (1993) Thysanoptères de Martinique et de Guadeloupe. *Journal of Pure and Applied Zoology*, 3(3), 227–240.

Cabrera I. & Segarra A. (2008) A new gall-inducing species of *Holopothrips* (Thysanoptera: Phlaeothripinae) from *Tabebuia* trumpet trees in the Caribbean region. *Florida Entomologist*, 91(2), 232–236.

Carvalho-Fernandes, S.P., Ascendino, S., Maia, V.C. & Couri, M.S. (2016) Diversity of insect galls associated with coastal shrub vegetation in Rio de Janeiro, Brazil. *Anais da Academia Brasileira de Ciências*, 88(3), 1407–1418.

Cavalleri, A. & Kaminski, L.A. (2007) A new *Holopothrips* species (Thysanoptera: Phlaeothripidae) damaging *Mollinedia* (Monimiaceae) leaves in Southern Brazil.

Zootaxa, 1625, 61–68.

Costa Lima, A.M. (1935a) Tisanopterocecidias do Brasil. *O Campo*, 6: 25–29.

Costa Lima, A.M. (1935b) Um novo tisanoptero praga do abacaxi. *O Campo*, 6, 43–45.

Goldarazena, A., Gattesco, F., Atencio, R. & Korytowski, C. (2012) An updated checklist of the Thysanoptera of Panama with comments on host associations. *Check List*, 8(6), 1232–1247.

Hickel E.R & Ducroquet, J.H.J. (1993) Pragas da goiabeira serrana: tripes (*Phrasterothrips* sp. e *Liothrips* sp.) (Thysanoptera: Phlaeothripidae). *Anais da Sociedade Entomológica do Brasil*, 22, 381–384.

Hood, J.D. (1914) Two new Thysanoptera from Panama. *Insecutor inscitiae menstruus*, 2, 49–53.

Hood, J.D. (1938) Studies in Neotropical Thysanoptera VII. *Revista de Entomologia*, 9(1–2), 218–247.

Johansen, R.M. (1986) Nuevos thrips tubuliferos (Insecta: Thysanoptera), de Mexico, XIII. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Serie Zoología*, 56, 73–100.

Jorge, N.C., Cavalleri, A., Bedetti, C.S. & Isaias, R.M. (2016) A new leaf-galling *Holopothrips* (Thysanoptera: Phlaeothripidae) and the structural alterations on *Myrcia retorta* (Myrtaceae). *Zootaxa*, 4200(1), 174–180.

Lima, M.G.A., Dias-Pini, N.S., Lima, E.F.B., Maciel, G.P.S. & Vidal-Neto, F.C. (2017) Identification and pest status of *Holopothrips fulvus* (Thysanoptera: Phlaeothripidae) on dwarf-cashew crops in Northeastern Brazil. *Revista Brasileira de Entomologia*, 61(4), 271–274.
http://dx.doi.org/10.1016/j.rbe.2017.07.007

Lindner, M.F., Mendonça Jr., M.S. & Cavalleri, A. (2016) *Holopothrips molzi* **sp.n.** (Thysanoptera, Phlaeothripidae): natural history and interactions in Myrtaceae galls. *Zootaxa*, 4114(2), 139–148.
http://dx.doi.org/10.11646/zootaxa.4114.2.3

Maia, V.C., Magenta, M.A.G. & Martins, S.E. (2008) Ocorrência e caracterização de galhas de insetos em áreas de restinga de Bertioga (São Paulo, Brasil). *Biota Neotropica*, 8(1), 167–197.

Maia, V.C., Cardoso, L.J.T. & Braga, J.M.A. (2014) Insect galls from Atlantic Forest areas of Santa Teresa, Espírito Santo, Brazil: characterization and occurrence. *Boletim do Museu*

de Biologia Mello Leitão, 33, 47–129.

Malumphy, C. & Reid, S. (2017) White cedar thrips *Holopothrips tabebuia* - UKOT plant pest fact sheet. Fera Science Ltd., Sand Hutton, York, UK, 5pp. Available from: http://www.nonnativespecies.org/home/index.cfm (Dec. 28, 2017)

Mattos, J.L.R. (1983) *Fruteiras nativas do Brasil: jaboticabeiras*. Nobel, Porto Alegre, Rio Grande do Sul, Brasil, 92 pp.

Mound, L.A. (2013) Homologies and Host-Plant Specificity: Recurrent Problems in the Study of Thrips. *Florida Entomologist*, 96(2), 318–322.

Mound, L.A. & Marullo, R. (1996) The thrips of Central and South America: an introduction (Insecta: Thysanoptera). *Memoirs on Entomology, International, 6*, 1–488.

Retana-Salazar, A.P. & Nishida, K. (2007) First gall-inducing thrips on *Elaphoglossum* ferns: A new genus and species of thrips, *Jersonithrips galligenus* from Costa Rica (Insecta, Thysanoptera, Phlaeothripidae). *Senckenbergiana biologica*, 87(2), 143–148.

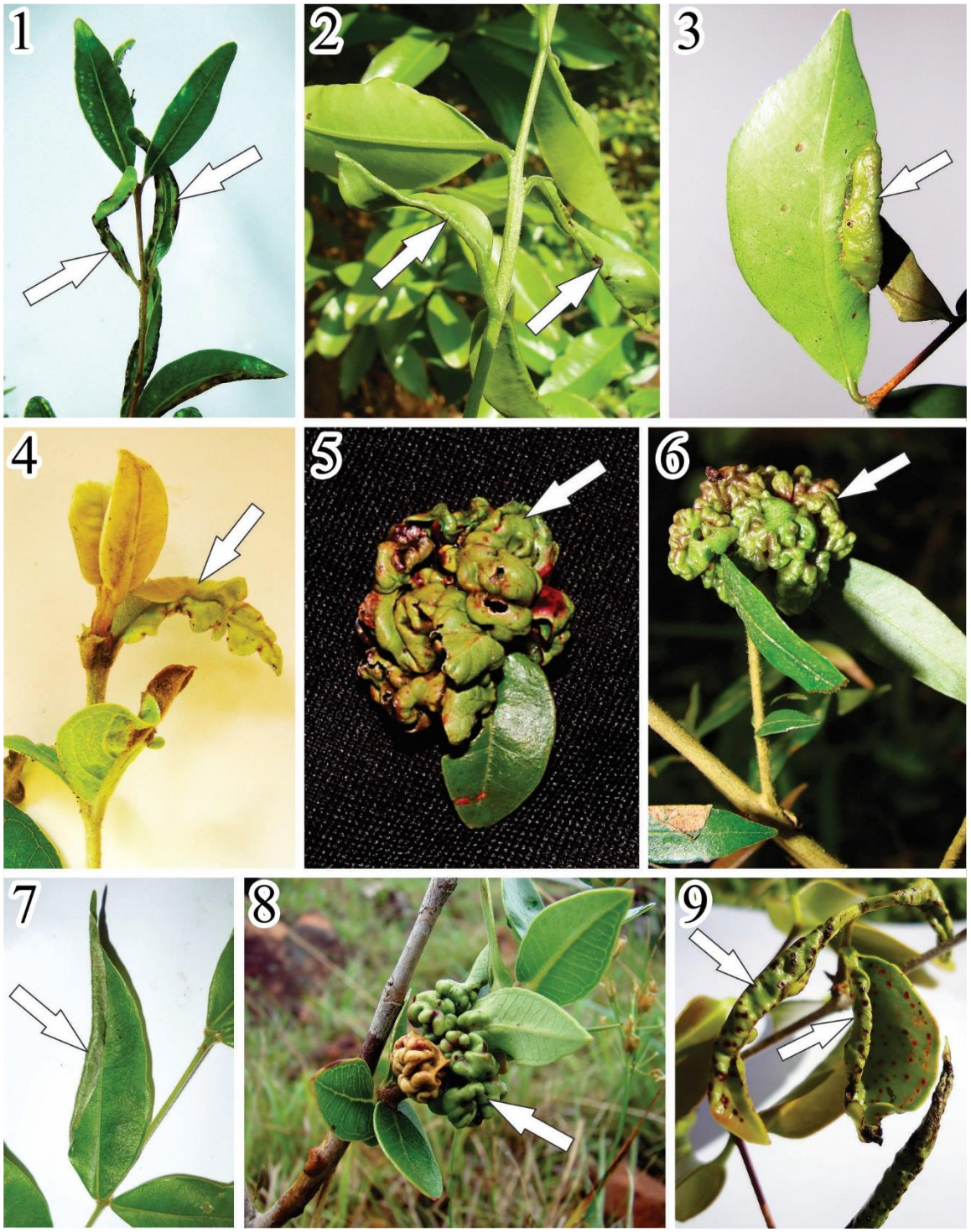
Retana-Salazar, A.P. & Soto-Rodríguez, G.A. (2008) A new genus and species of gall-inducing thrips (Thysanoptera: Tubulifera) from the neotropical region. *Brenesia*, 69, 59–64.

Santana, A.P. (2014) *Galhas do Parque Estadual Serra Verde: Produção de Conhecimento e Estratégias de Interpretação Ambiental*. Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil, 114pp. [Dissertation]

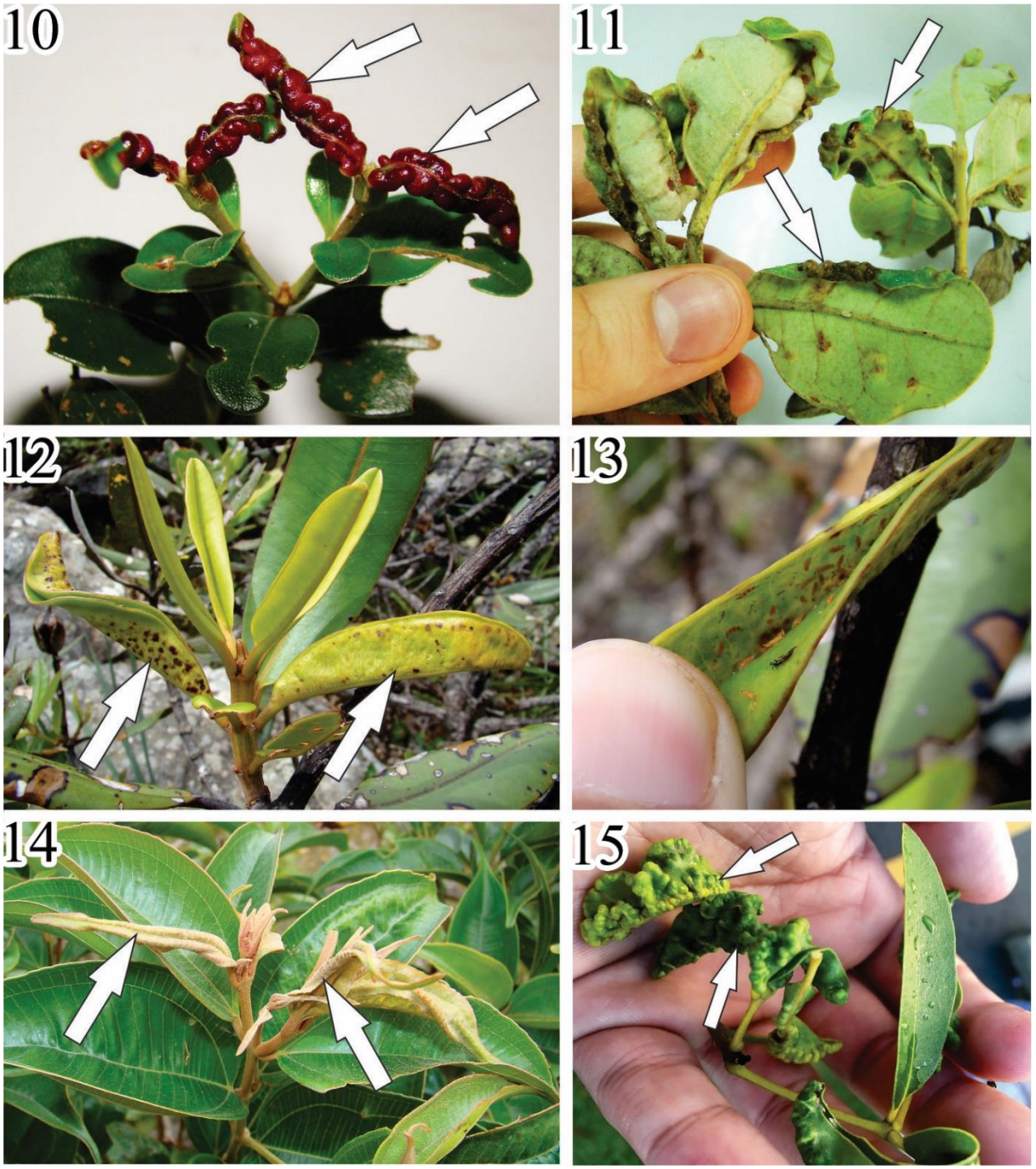
Soto-Rodríguez, G.A., Nishida, K. & Retana-Salazar, A.P. (2012) A new genus of gall-dwelling thrips from Costa Rica (Thysanoptera: Phlaeothripidae: Phlaeothripinae). *Revista Mexicana de Biodiversidad*, 83, 605–610.

ThripsWiki (2018) Thrips Wiki: providing information on the World's thrips. Available from http://thrips.info/wiki/Main_Page (Accessed February 21st, 2018).

Zamora, S., Hanson, P. & Mound, L.A. (2015) On the biology of *Holopothrips chaconi* **sp.n.** (Thysanoptera, Phlaeothripinae) from leaf-vein galls on *Piper* species in Costa Rica. *Revista Biologia Tropical*, 63(4), 1035–1042.

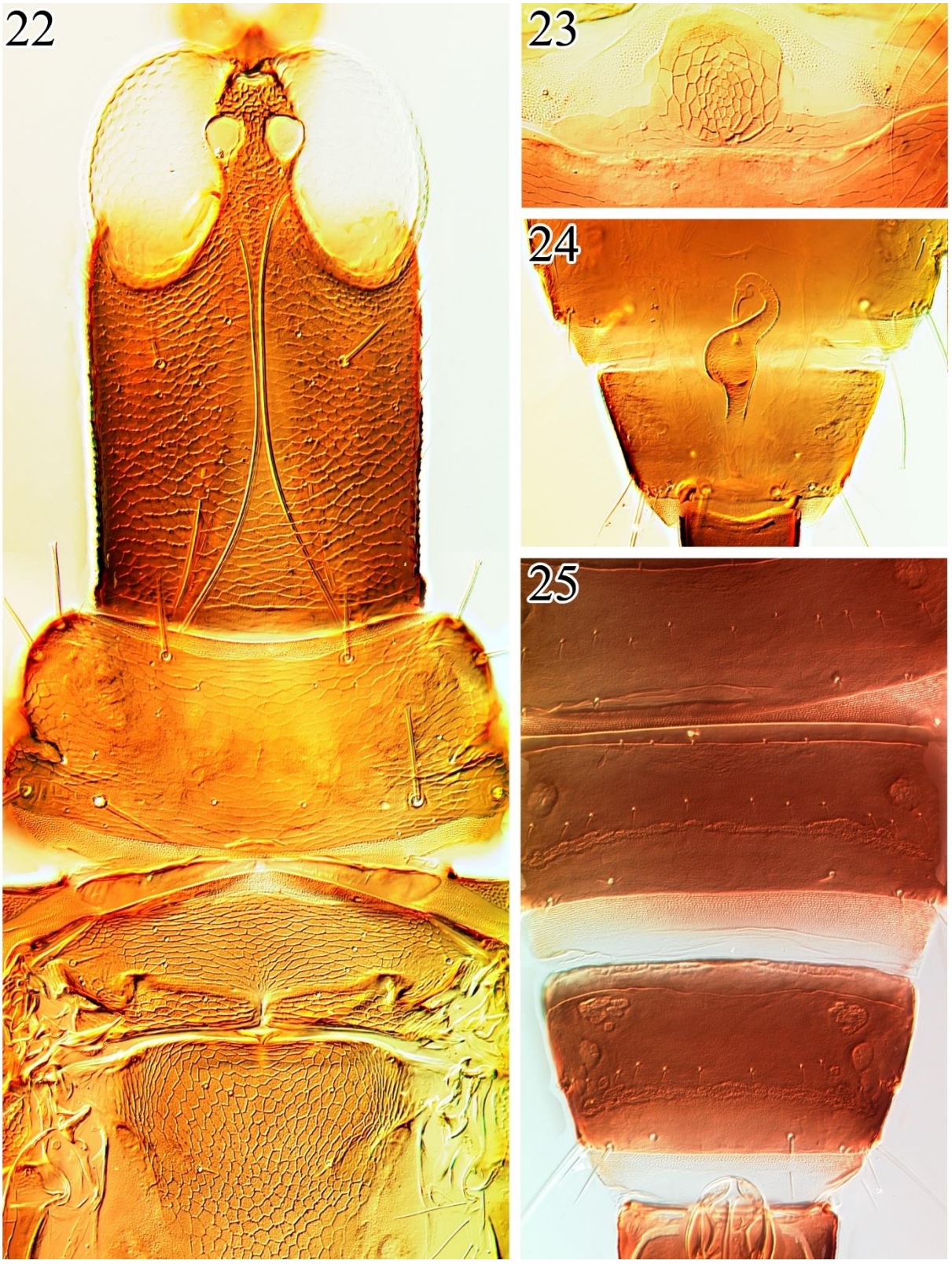


FIGURES 1–6. Leaf-galls induced by *Holopothrips* (white arrows). (1) galls on *Siphoneugena reitzii* (by *H. curiosus*); (2) galls on *Myrciaria floribunda* (by *H. spermathecus*) (Photo: André Santana); (3) gall on *Myrcia guianensis* (by *H. molzi*); (4) gall on *Myrcia retorta* (by *H. striatus*); (5) gall on *Myrcia* sp. (by *H. cardosoi*) (Photo: João C. Cardoso); (6) gall on *Myrcia splendens* (by *H. conducans*); (7) gall on *Myrcia splendens* (by *H. longisetus*); (8) gall on *Myrcia selloi* (by *H. acrioris*); (9) galls on *Neomitranthes obscura* (by *H. varicolor*) (Photo: Sheila Carvalho-Fernandes).

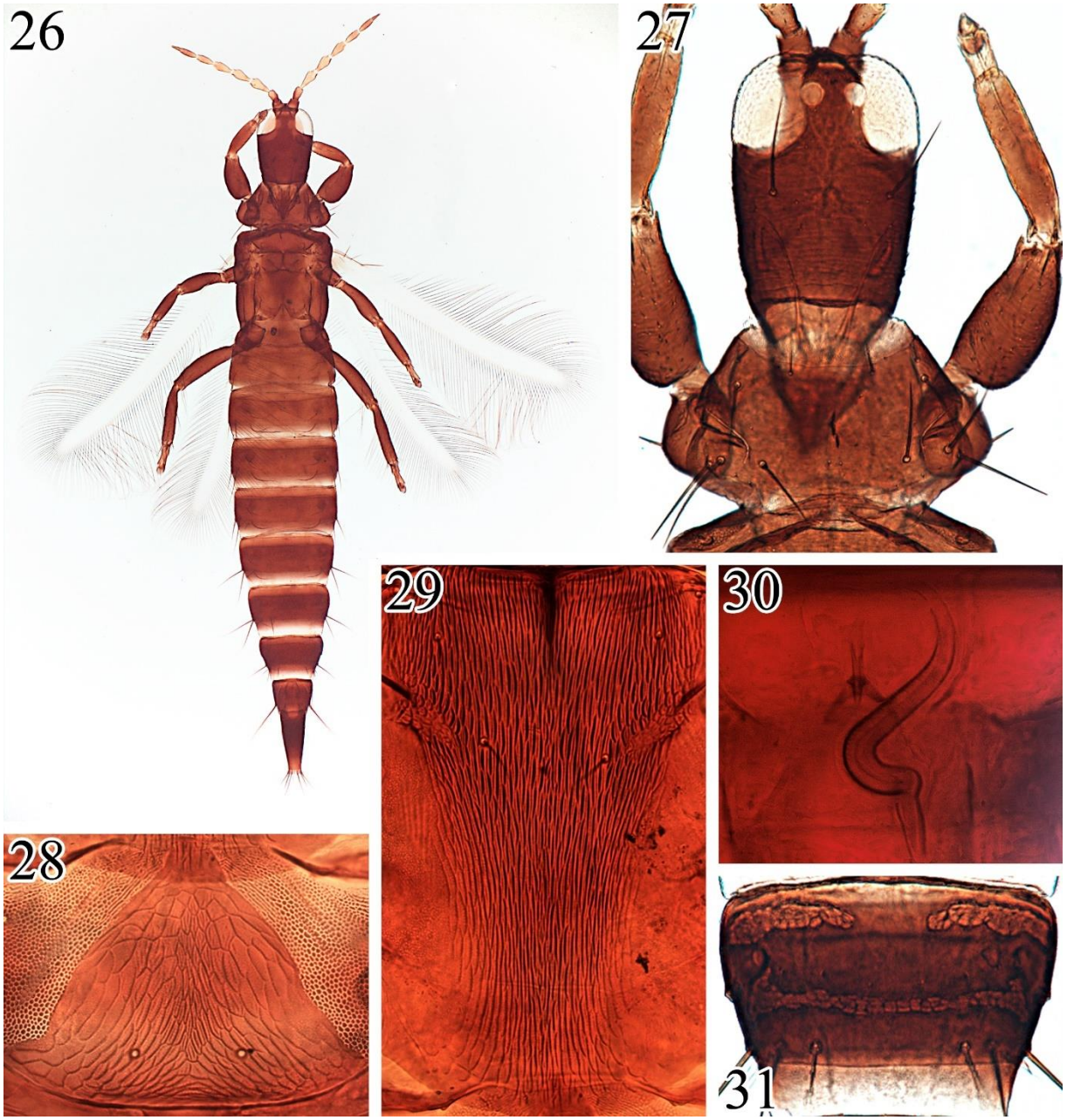


FIGURES 10–15. Leaf-galls induced by *Holopothrips* (white arrows). (10) galls on Myrtaceae (by *H. clarisetis*); (11) galls on *Acca sellowiana* (by *H. infestans*); 12–13. galls on *Vochysia* cf. *obovata* (by *H. kaminskii*) (Photos: Lucas A. Kaminski): (12) general view; (13) opened gall; (14) galls on *Miconia* sp. (by *H. brevicapitatum*); (15) galls on *Tabebuia heterophylla* (by *H. tabebuia*) (Photo: Irma Cabrera).

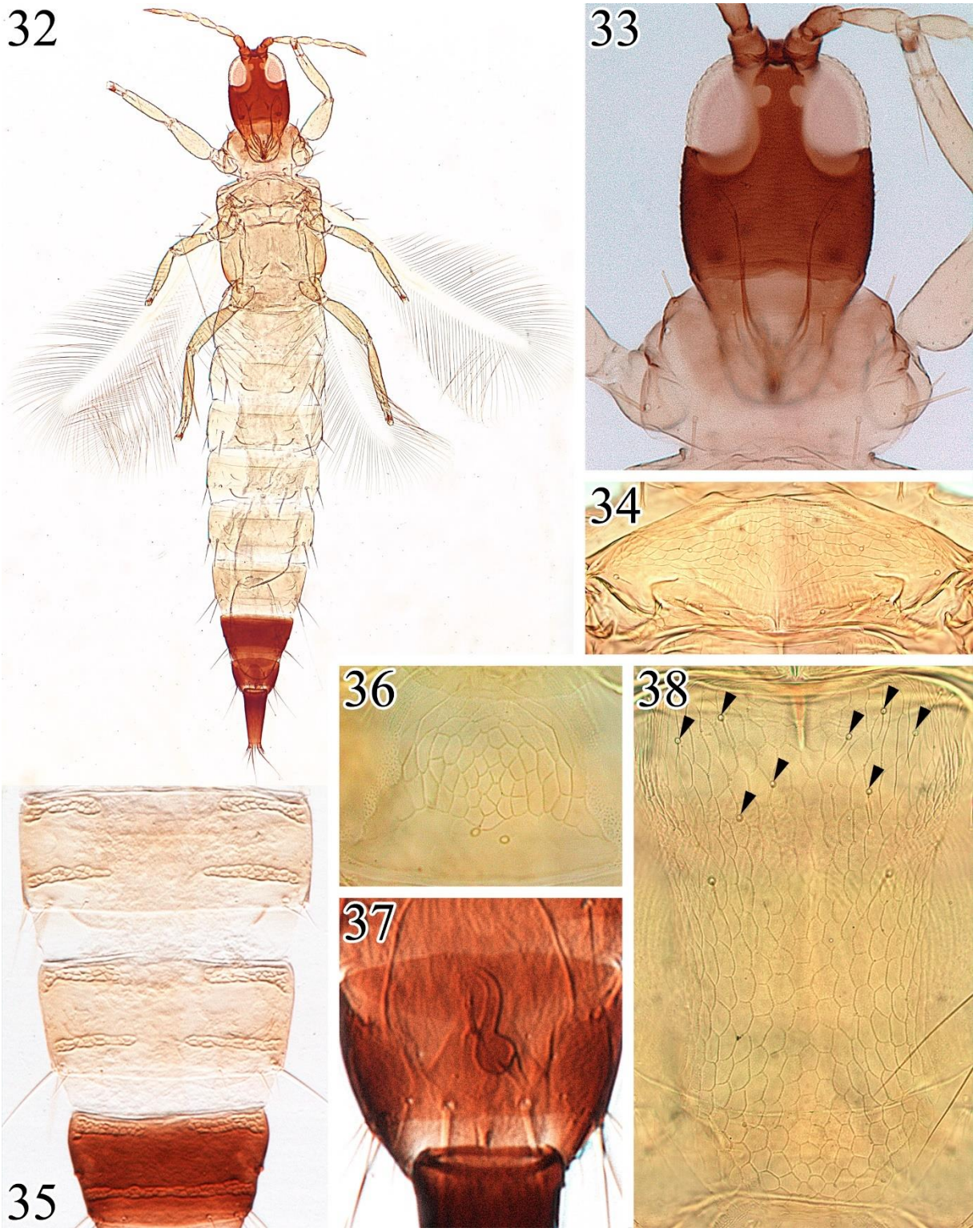
FIGURES 16–21. *Holopothrips acrioris* **sp. nov.** holotype and paratypes. (16) body; (17) head and pronotum; (18) pelta and abdominal tergite II; (19) metanotal sculpture; (20) spermatheca; (21) pore plate on abdominal sternite VIII.



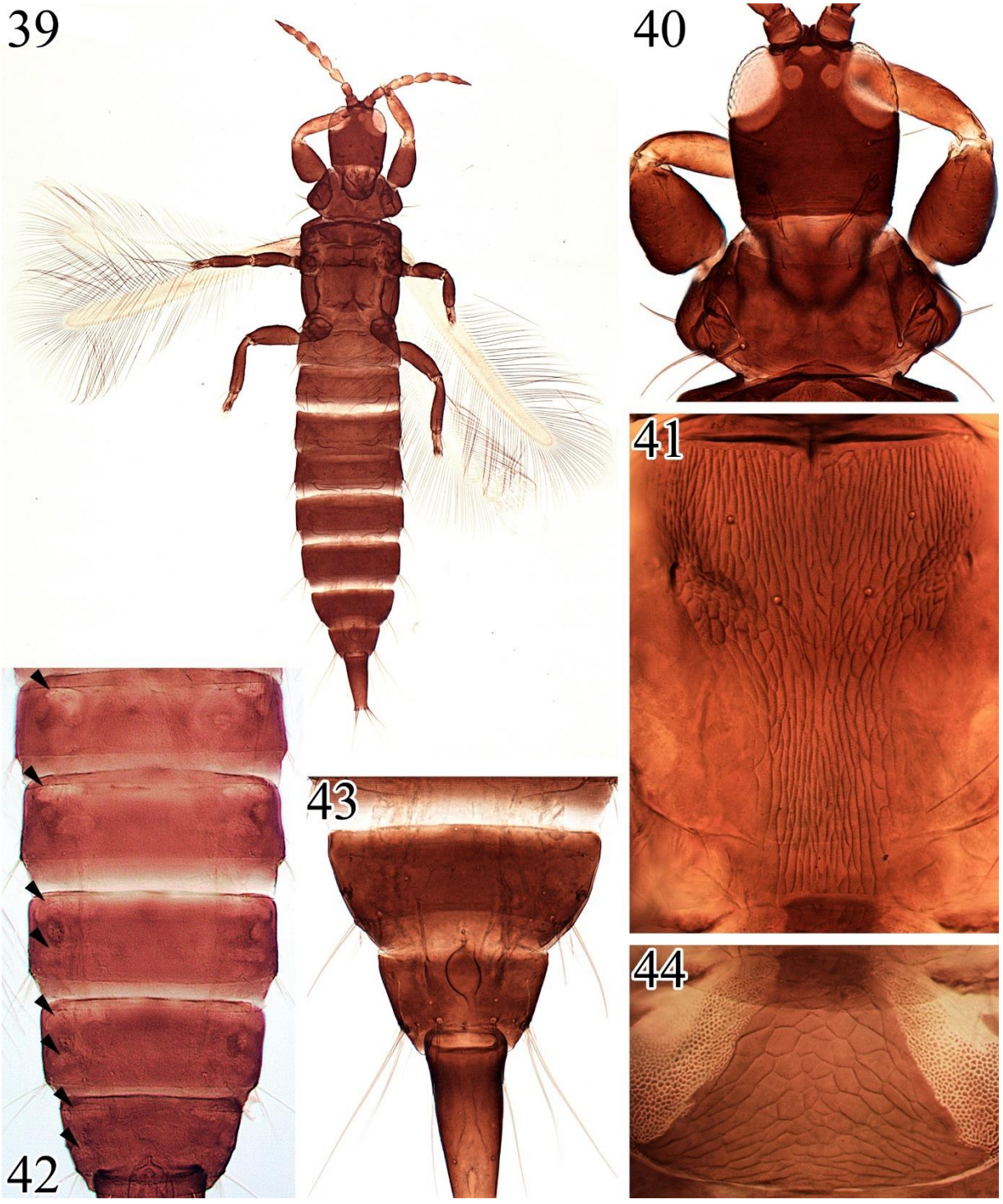
FIGURES 22–25. *Holopothrips ananasi* paratypes. (22) head, pronotum, mesonotum and anterior half of metanotum; (23) pelta; (24) spermatheca; (25) pore plates on abdominal sternites VII–VIII.



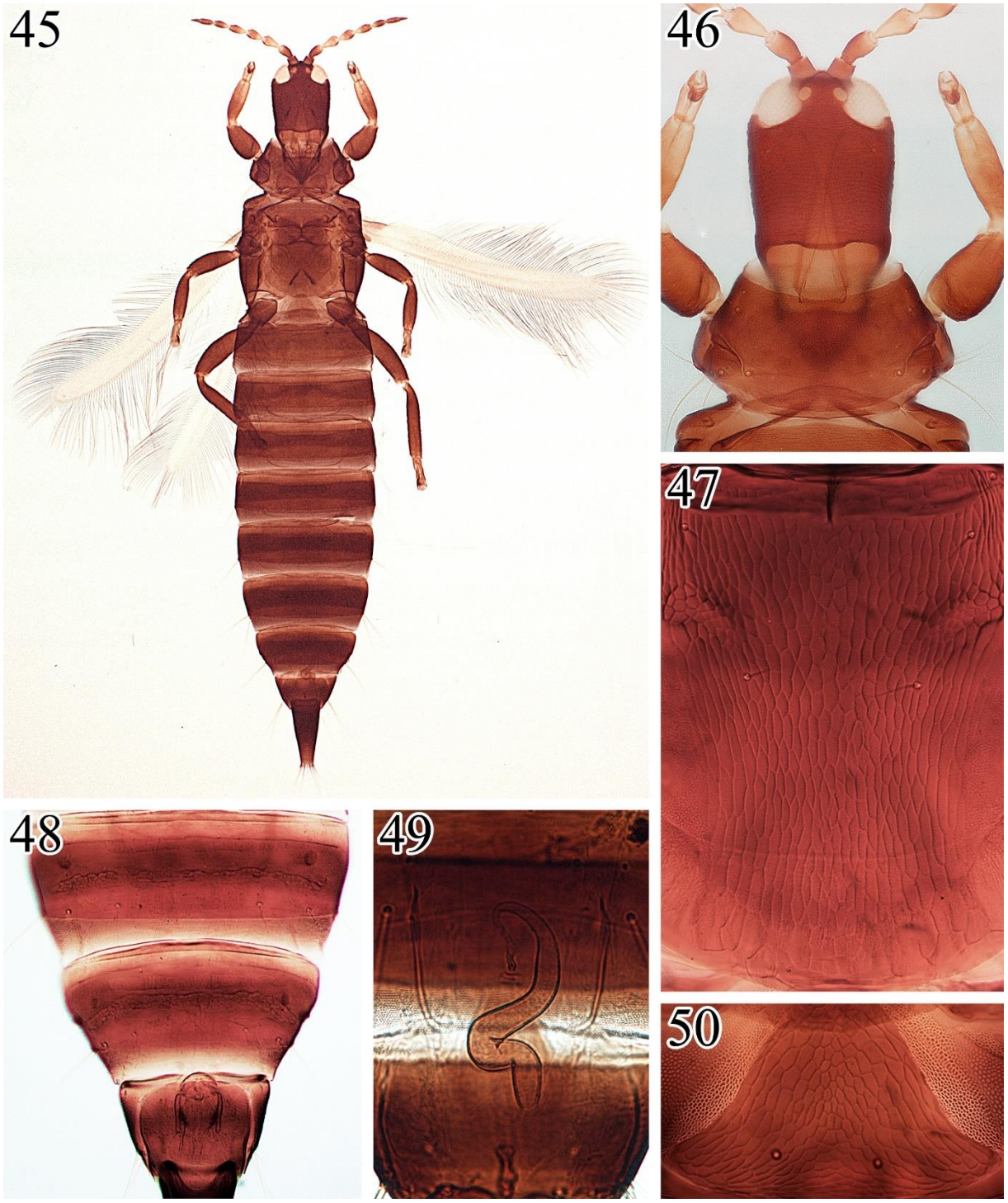
FIGURES 26–31. *Holopothrips atlanticus* **sp. nov.** holotype and paratypes. (26) body; (27) head and pronotum; (28) pelta; (29) metanotum; (30) spermatheca; (31) pore plates on abdominal sternite VIII.



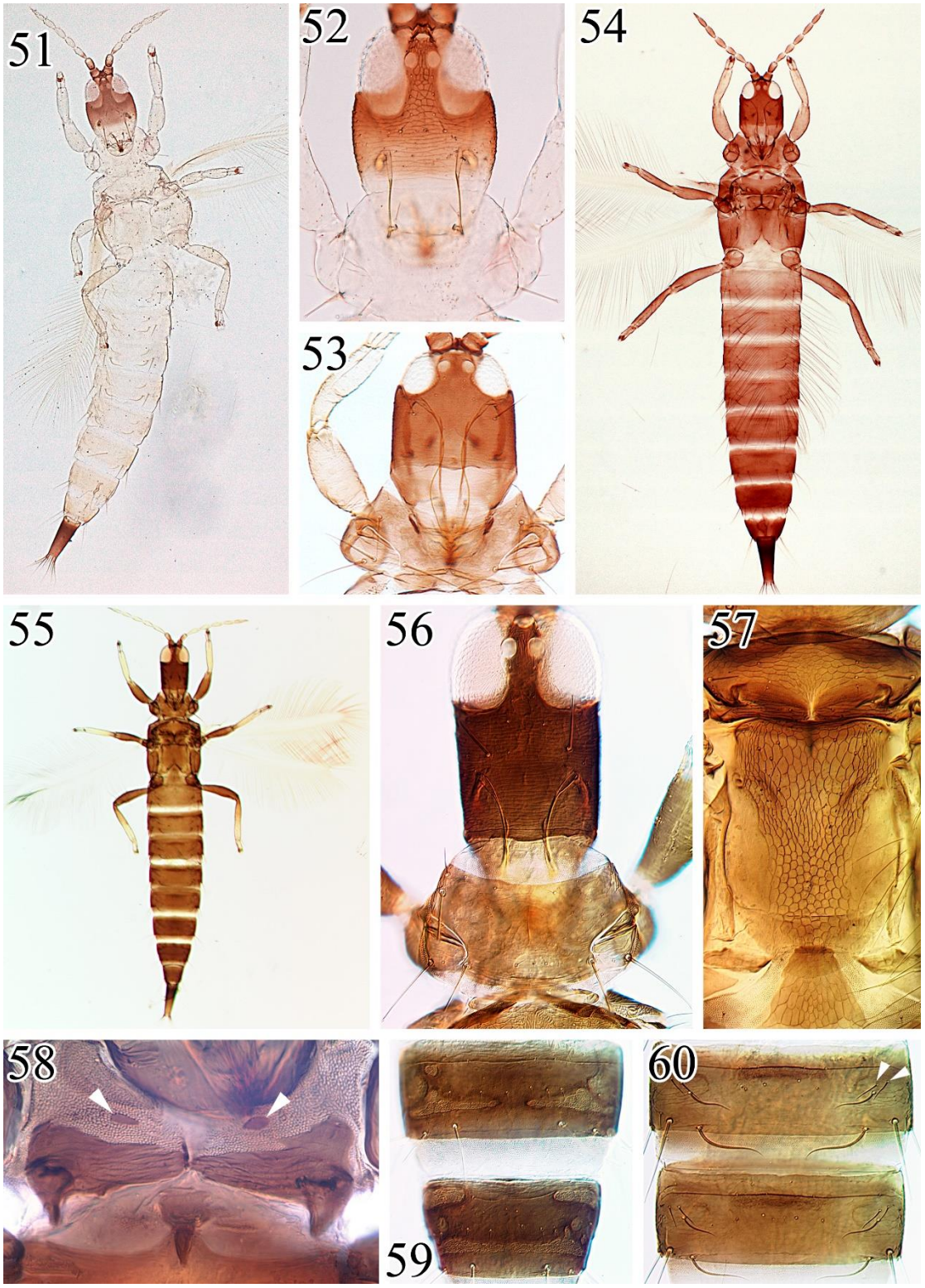
FIGURES 32–38. *Holopothrips bicolor* **sp. nov.** holotype and paratypes. (32) body; (33) head and pronotum; (34) mesonotum; (35) pore plates on sternites VI–VIII; (36) pelta; (37) spermatheca; (38) metanotum, showing the anterior discal setae (black arrows).



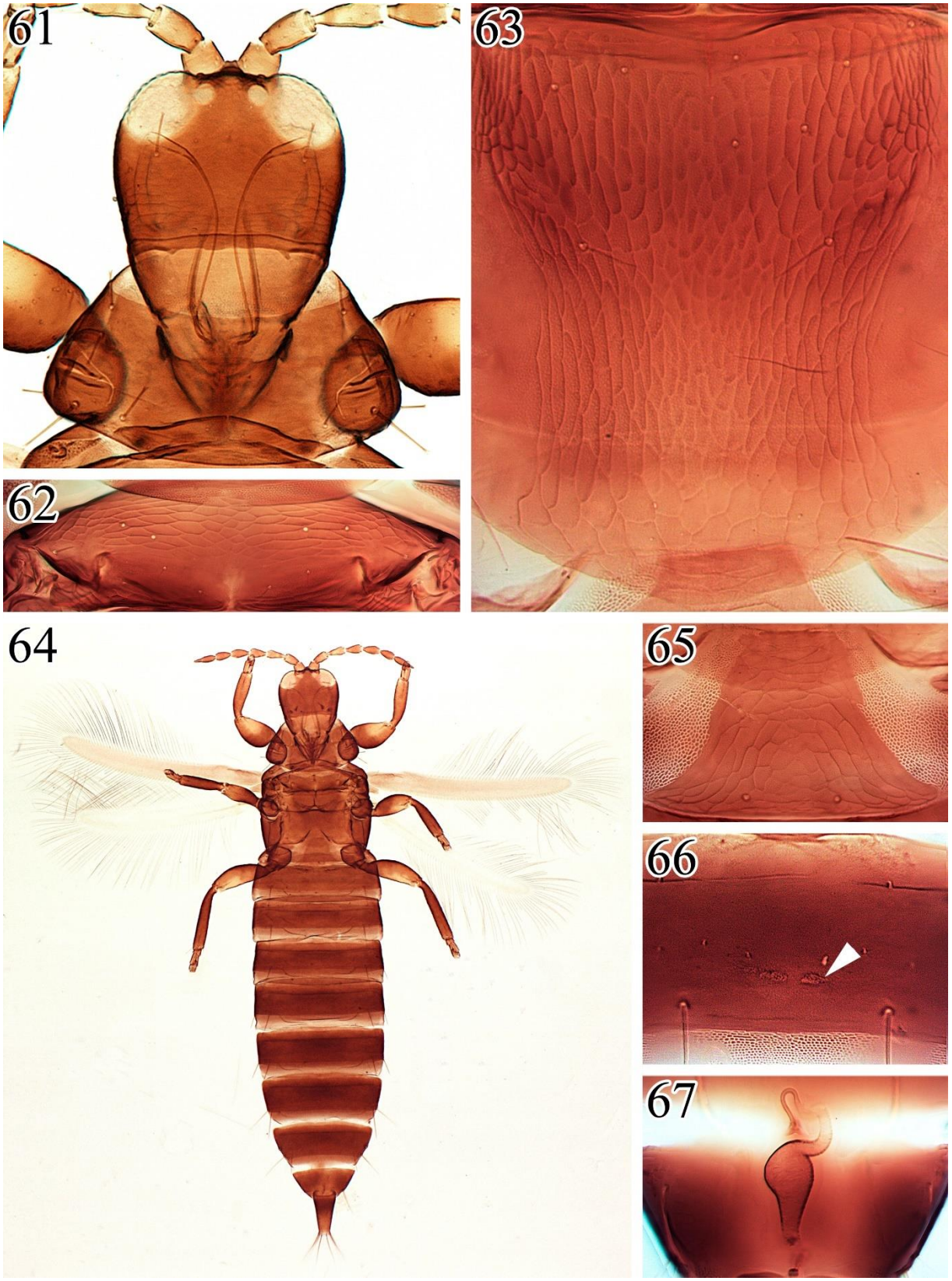
FIGURES 39–44. *Holopothrips brevicapitatum* **sp. nov.** holotype and paratypes. (39) body; (40) head and pronotum; (41) metanotal sculpture; (42) pore plates on abdominal sternites IV–VIII (black arrows); (43) spermatheca; (44) pelta.



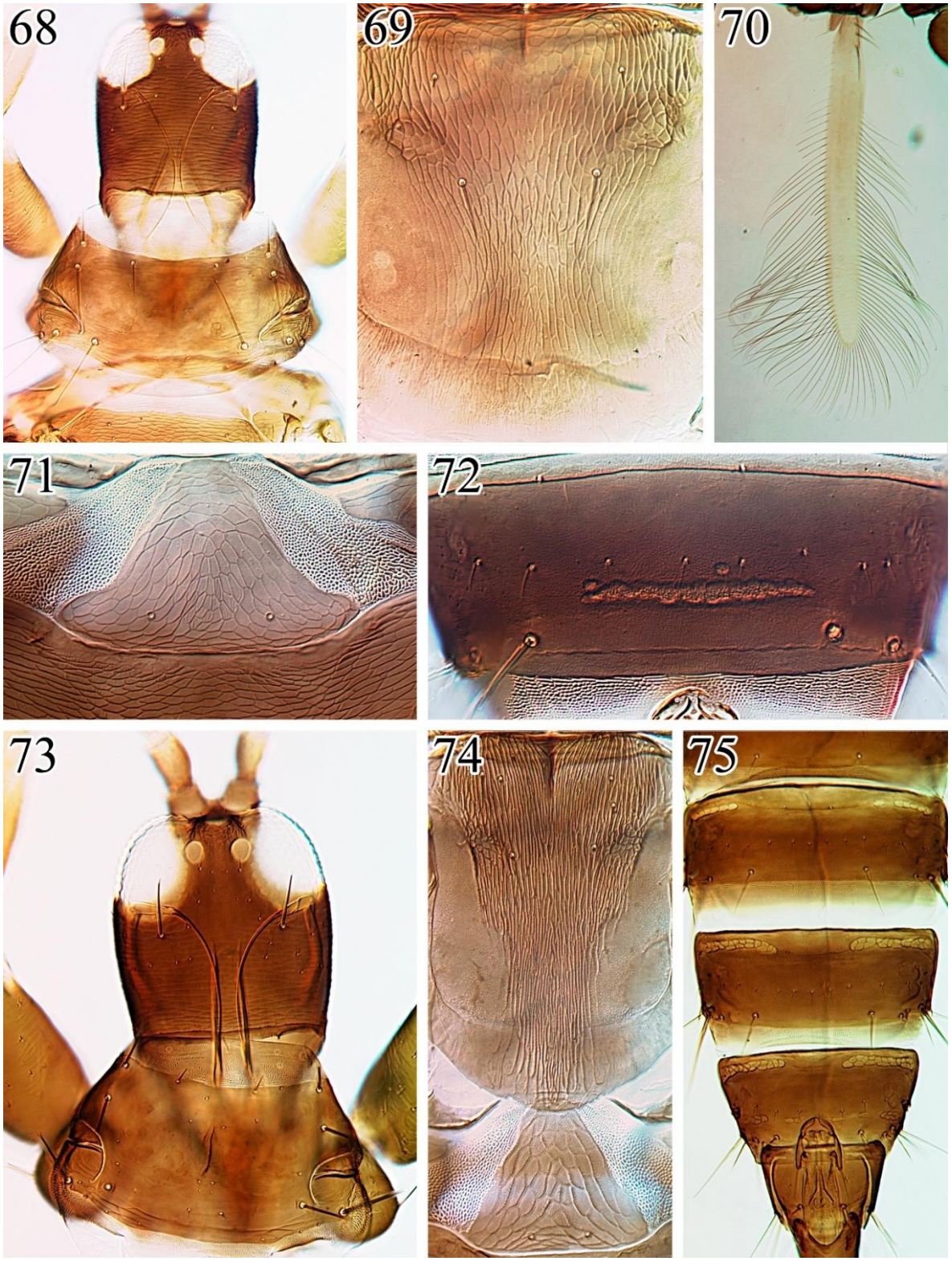
FIGURES 45–50. *Holopothrips cardosoi* **sp. nov.** holotype and paratypes. (45) body; (46) head and pronotum; (47) metanotal sculpture; (48) pore plates on abdominal sternites VII–VIII; (49) spermatheca; (50) pelta.



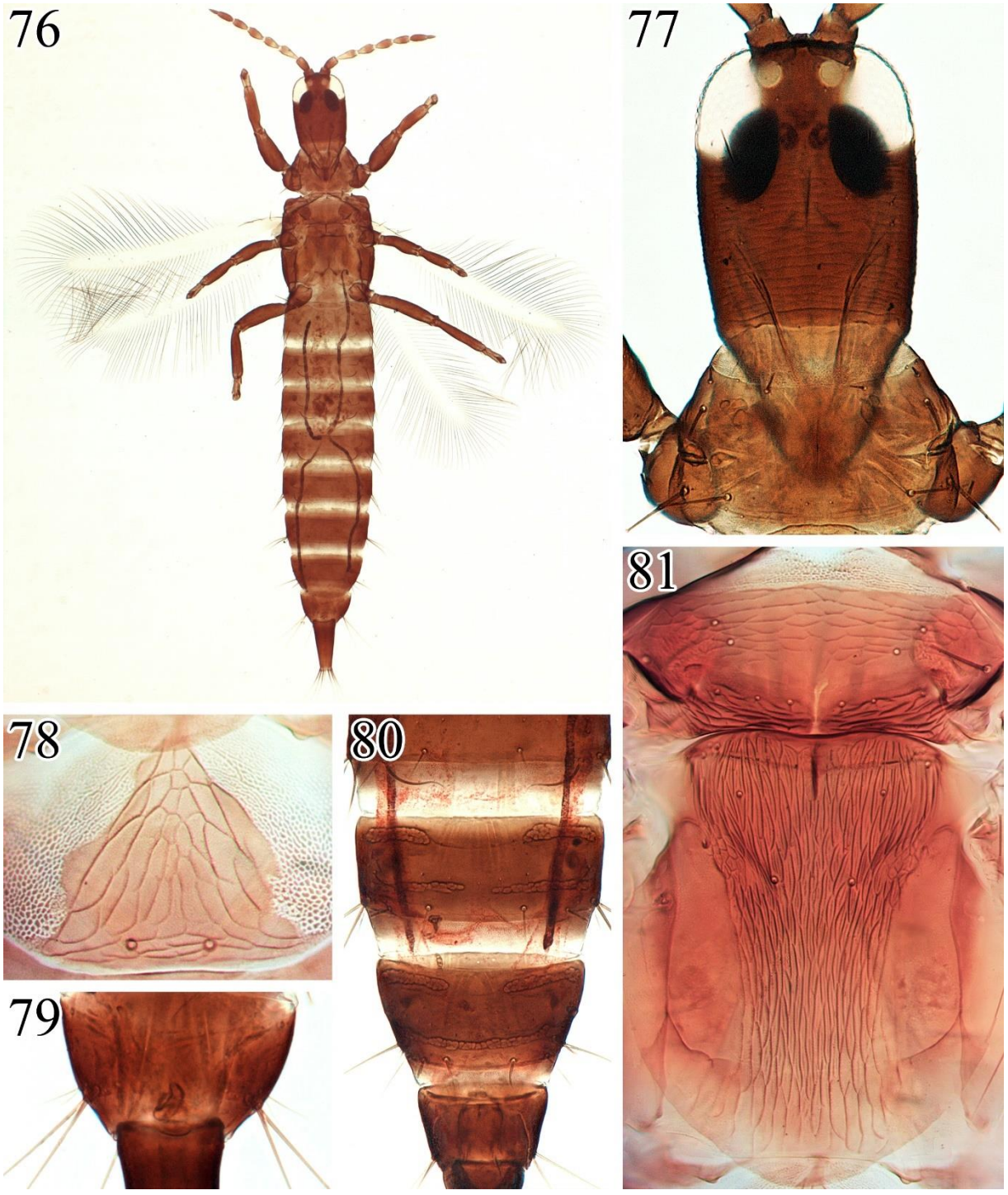
FIGURES 51–60. *Holopothrips carolinae, H. chaconi and H. claritibialis*. 51–52. *Holopothrips carolinae*, female holotype: (51) body; (52) head and pronotum; 53–54. *Holopothrips chaconi*, paratypes: (53) male paratype, head and pronotum; (54) female paratype, body; 55–60. *Holopothrips claritibialis*: (55) body; (56) head and pronotum; (57) mesonotum, metanotum and pelta; (58) prosternum, showing chitinous islets (white arrows); (59) pore plates on abdominal sternites VII–VIII; (60) abdominal tergites III–IV, showing the third and a fourth wing-retaining seta (white arrows).



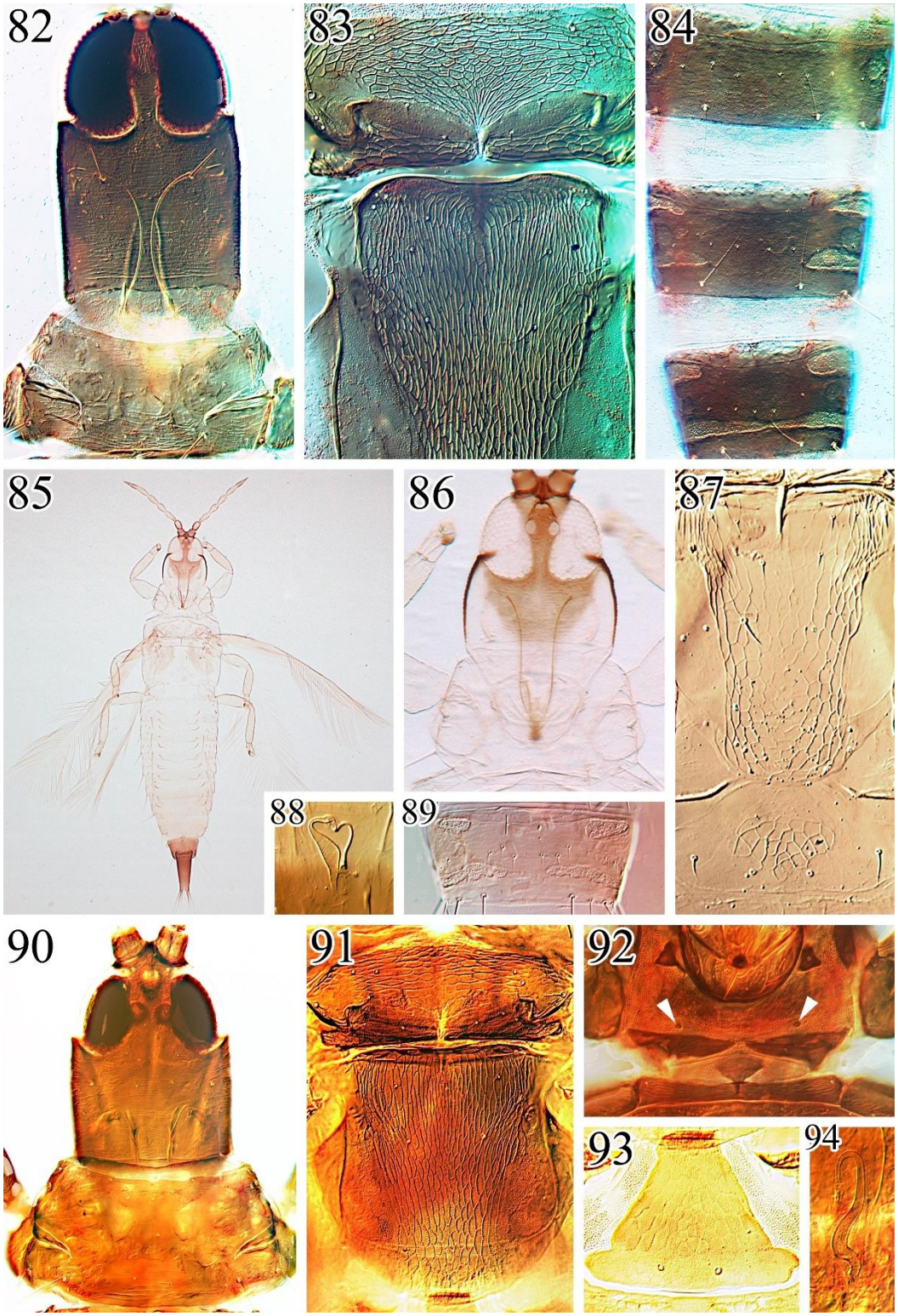
FIGURES 61–67. *Holopothrips clarisetis* **sp. nov.** holotype and paratypes. (61) head and pronotum; (62) mesonotum; (63) metanotum; (64) body; (65) pelta; (66) pore plate on abdominal sternite VIII (white arrow); (67) spermatheca.



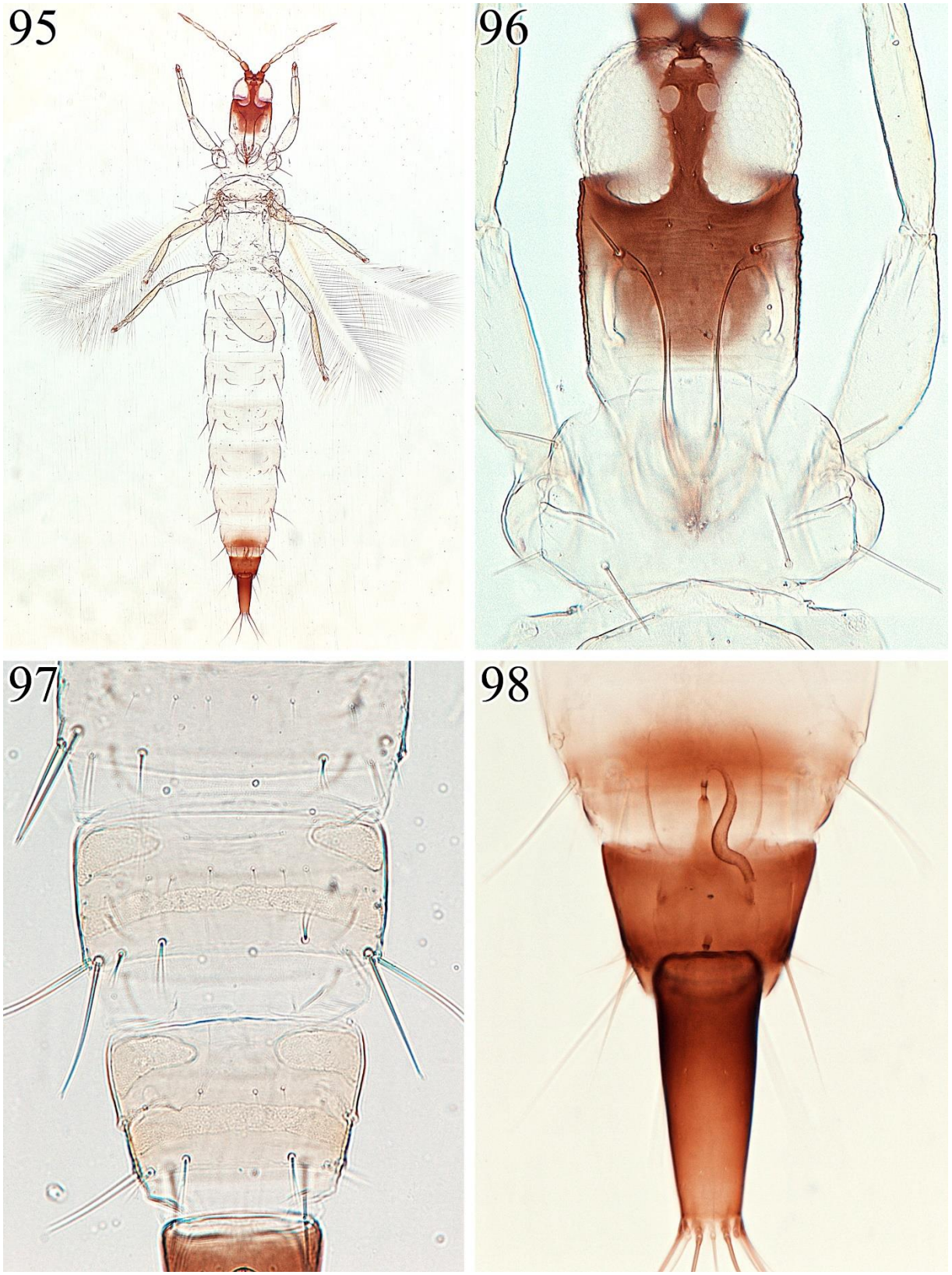
FIGURES 68–75. *Holopothrips conducans* and *H. erianthi*. 68–72 *Holopothrips conducans*: (68) head and pronotum; (69) metanotal sculpture; (70) shaded fore wing; (71) pelta; (72) pore plate on abdominal sternite VIII; 73–75 *Holopothrips erianthi*: (73) head and pronotum; (74) metanotum and pelta; (75) pore plates on abdominal sternites VI–VIII.



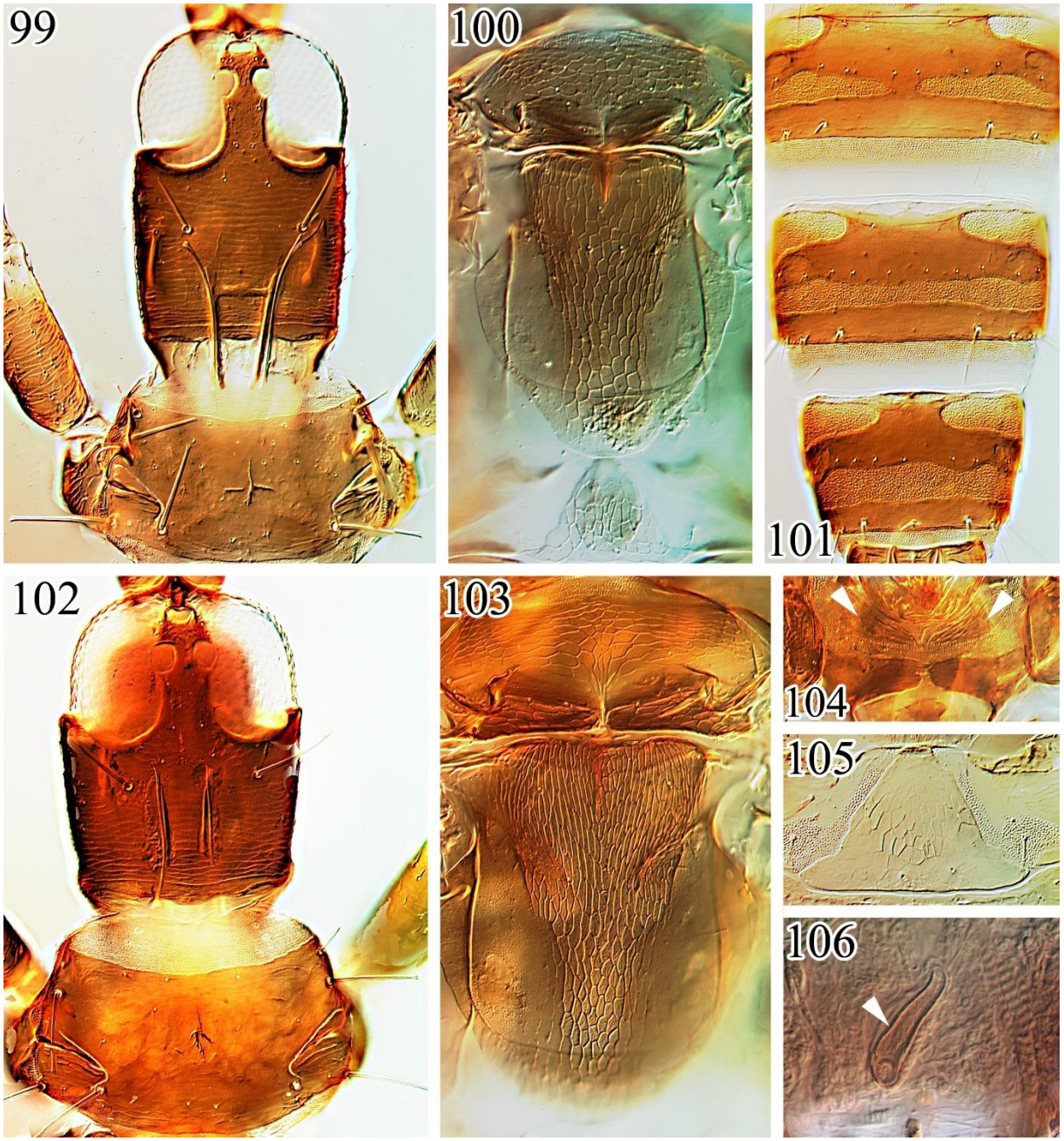
FIGURES 76–81. *Holopothrips curiosus* **sp. nov.** holotype and male paratype. (76) body; (77) head and pronotum; (78) pelta; (79) spermatheca; (80) pore plates on abdominal sternites VII–VIII; (81) mesonotum and metanotum.



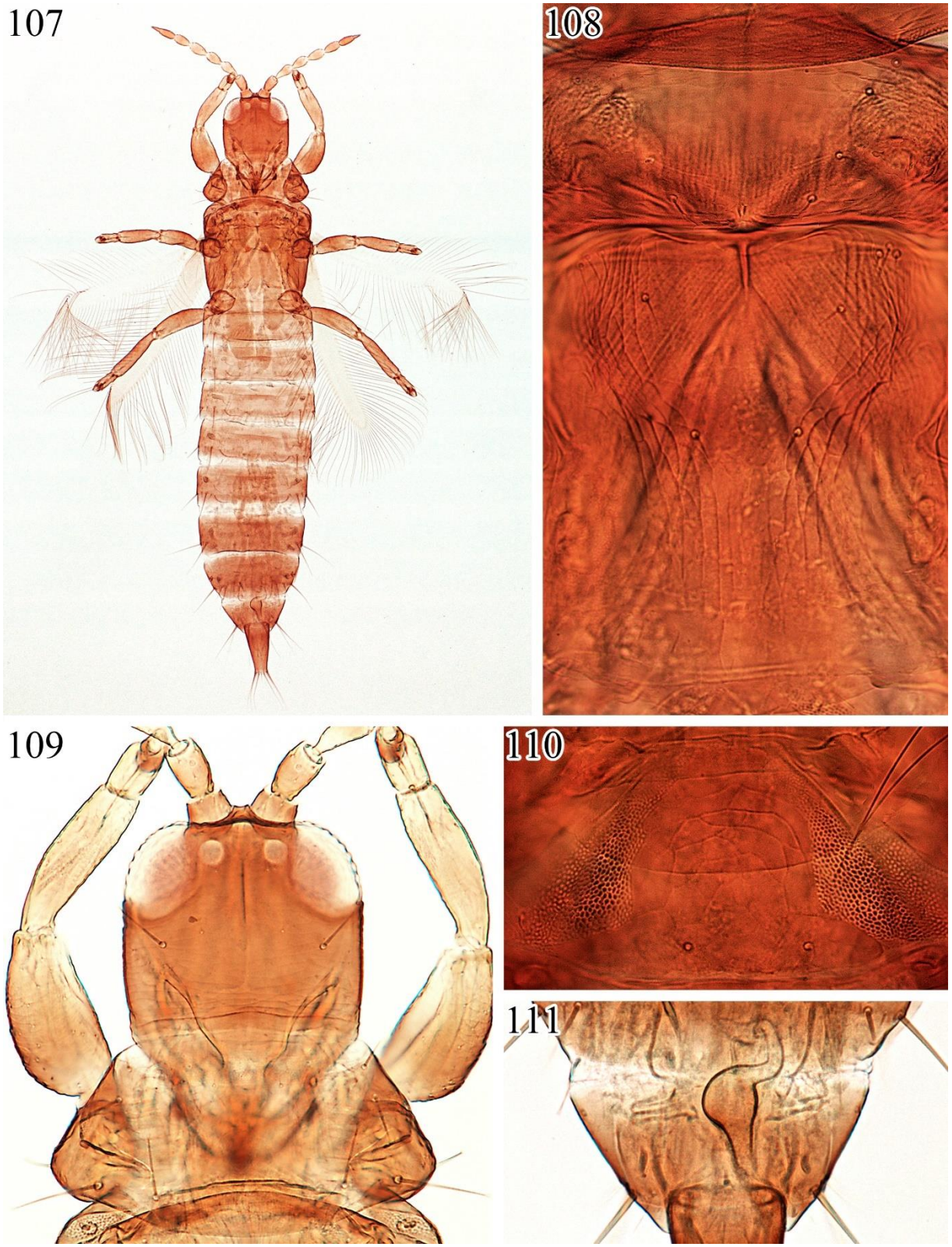
FIGURES 82–94. *Holopothrips ferrisi*, *H. fulvus* and *H. graminis*. 82–84. *Holopothrips ferrisi*: (82) head and pronotum; (83) mesonotum and part of metanotum; (84) pore plates on abdominal sternites VII–VIII; 85–89. *Holopothrips fulvus*, *H. anacardii* synonymy paratype and topotypes: (85) body; (86) head and pronotum; (87) metanotum and pelta; (88) spermatheca; (89) pore plates on abdominal sternite VIII; 90–94. *Holopothrips graminis* paratype: (90) head and pronotum; (91) mesonotum and metanotum; (92) prosternum showing chitinous islets (white arrows); (93) pelta; (94) spermatheca.



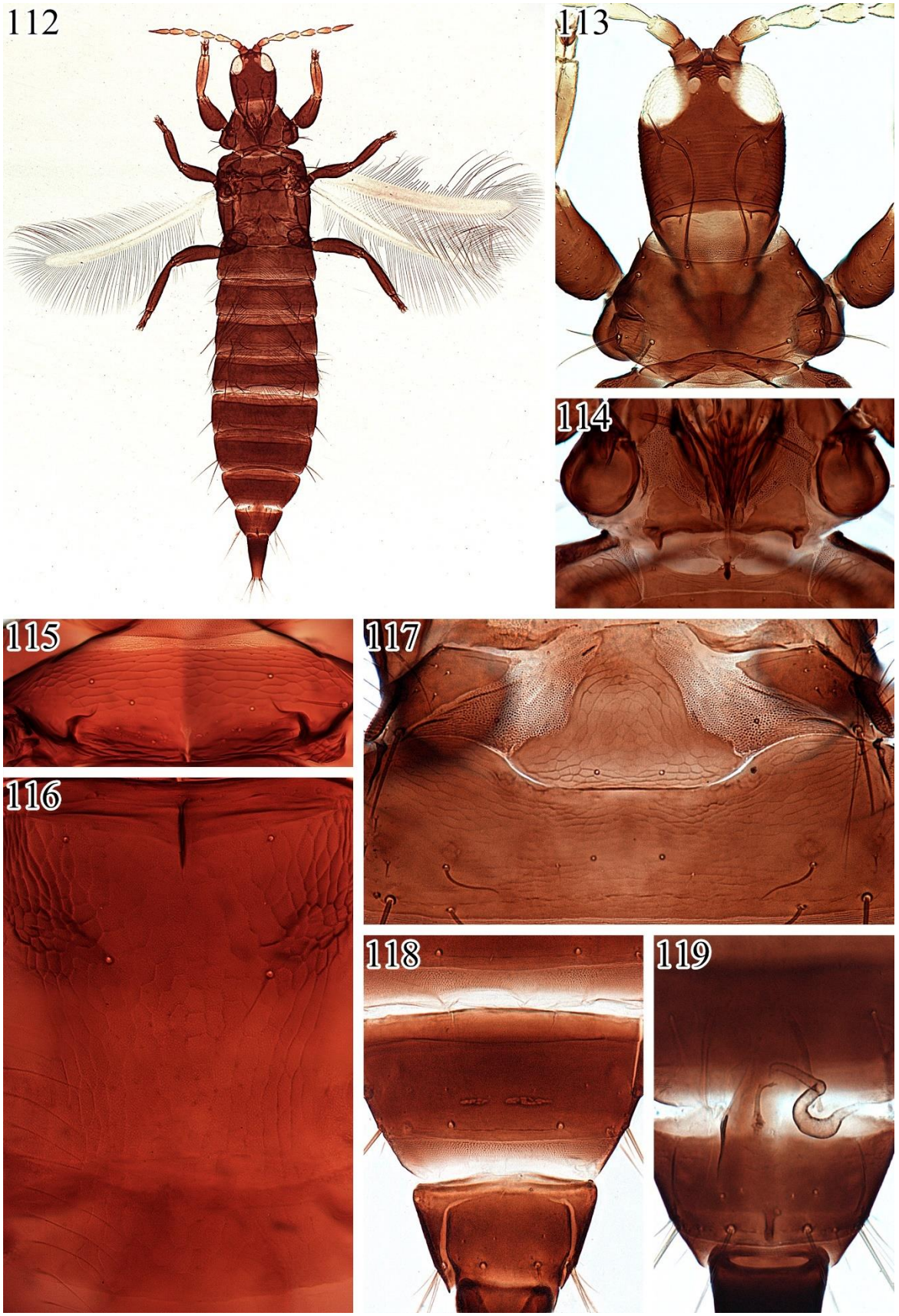
FIGURES 95–98. *Holopothrips graziae* **sp. nov.** holotype and paratype. (95) body; (96) head and pronotum; (97) pore plates on abdominal sternites VII–VIII; (98) spermatheca.



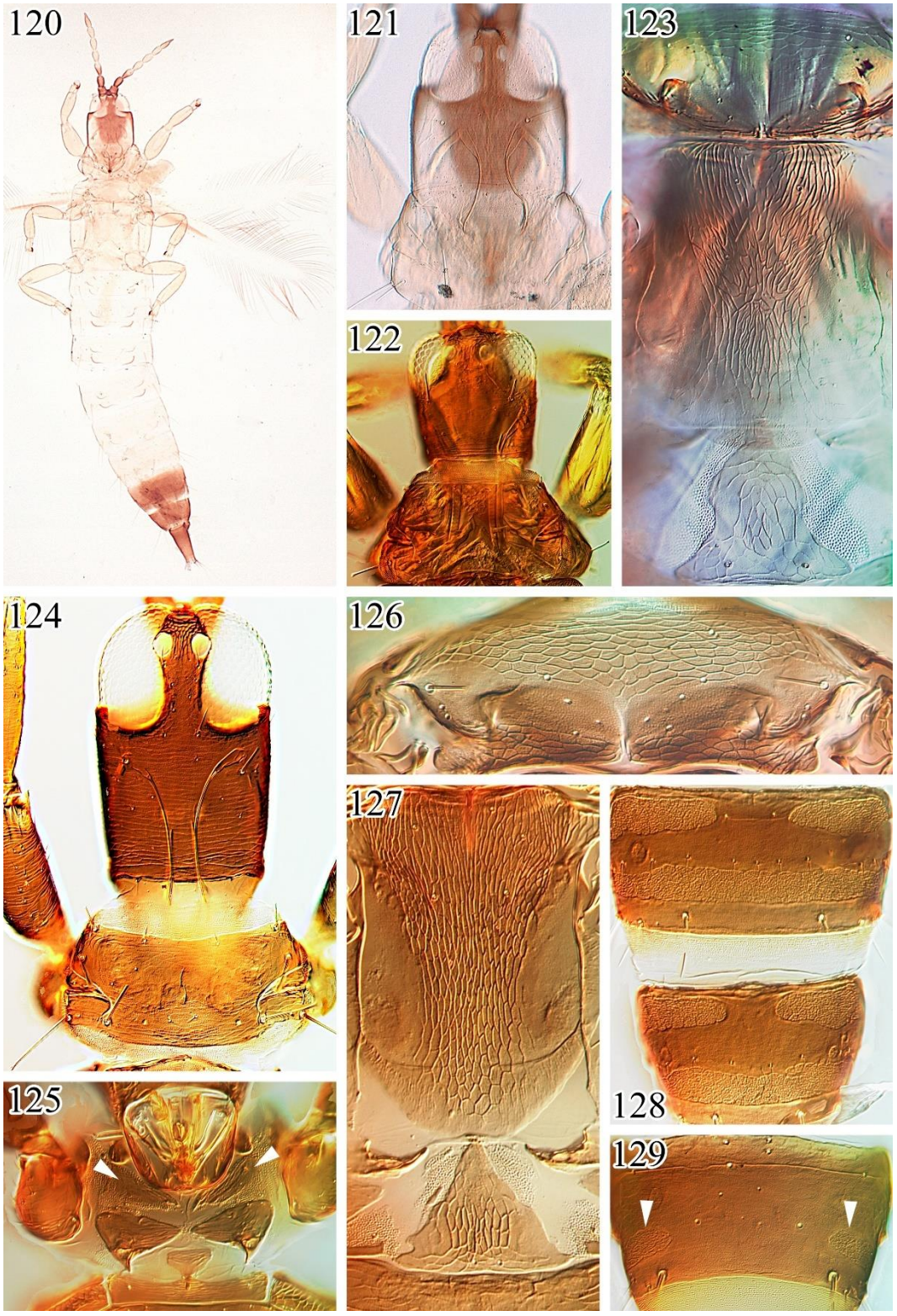
FIGURES 99–106. *Holopothrips hambletoni* and *H. hilaris*. 99–101. *Holopothrips hambletoni* paratype: (99) head and pronotum; (100) mesonotum, metanotum and pelta; (101) pore plates on abdominal sternites VI–VIII; 102–106. *Holopothrips hilaris* paratype: (102) head and pronotum; (103) mesonotum and metanotum; (104) prosternum showing basantra (white arrows); (105) pelta; (106) spermatheca (white arrow).



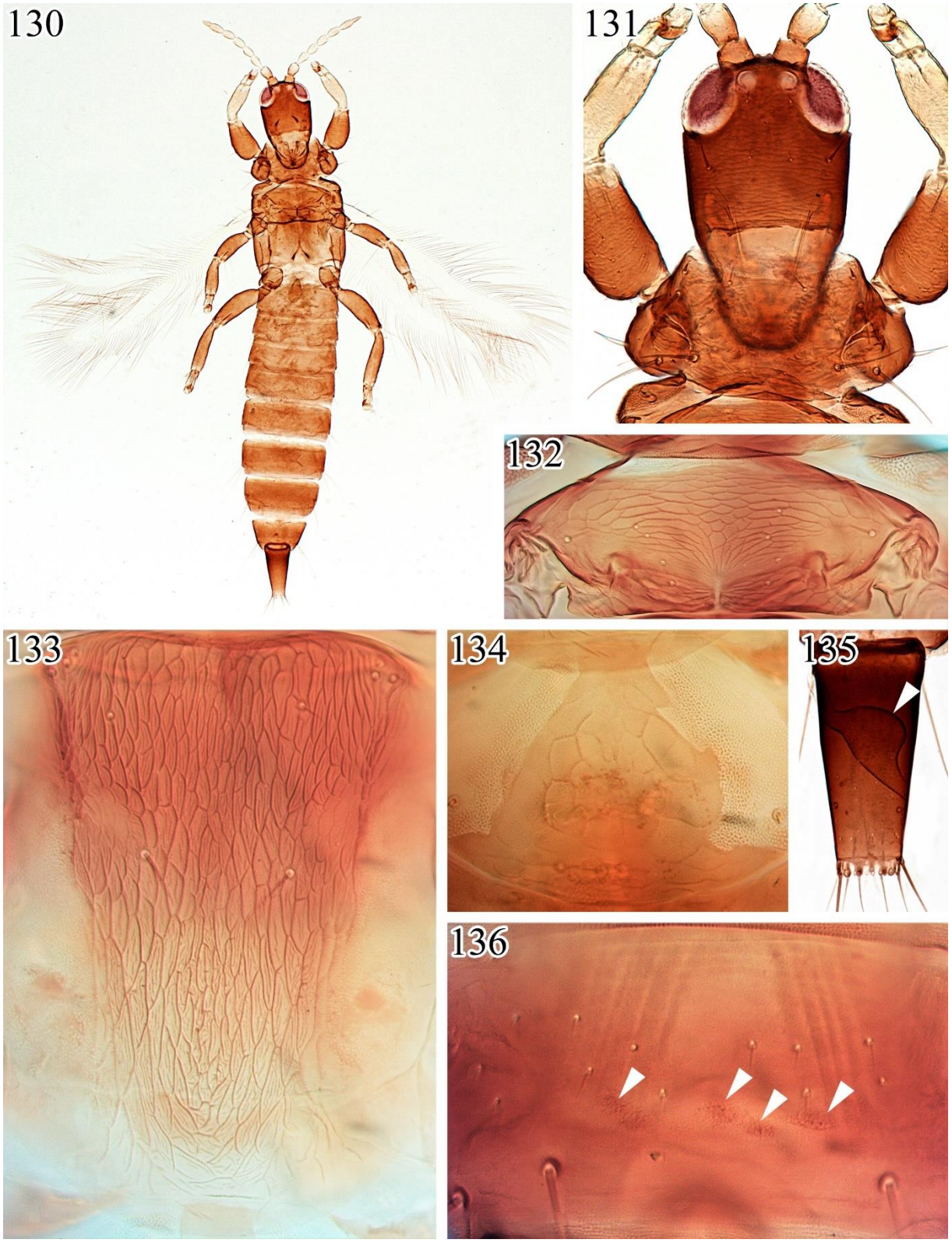
FIGURES 107–111. *Holopothrips inconspicuus* **sp. nov.** holotype and paratypes. (107) body; (108) mesonotum and metanotum; (109) head and pronotum; (110) pelta; (111) spermatheca.



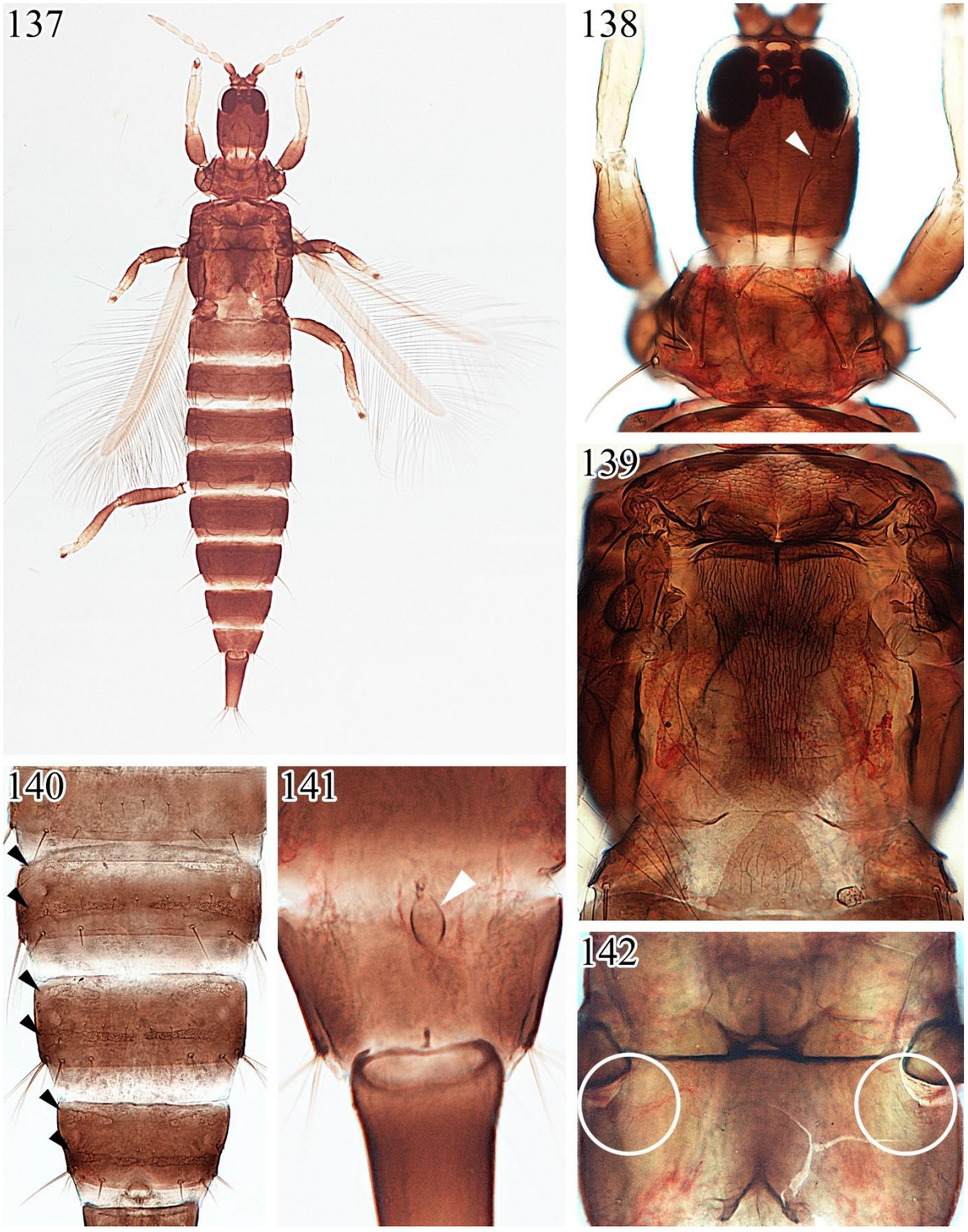
FIGURES 112–119. *Holopothrips infestans* **sp. nov.** holotype and paratypes. (112) body; (113) head and pronotum; (114) prosternum; (115) mesonotum; (116) metanotum; (117) pelta and abdominal tergite II; (118) pore plate on abdominal sternite VIII; (119) spermatheca.



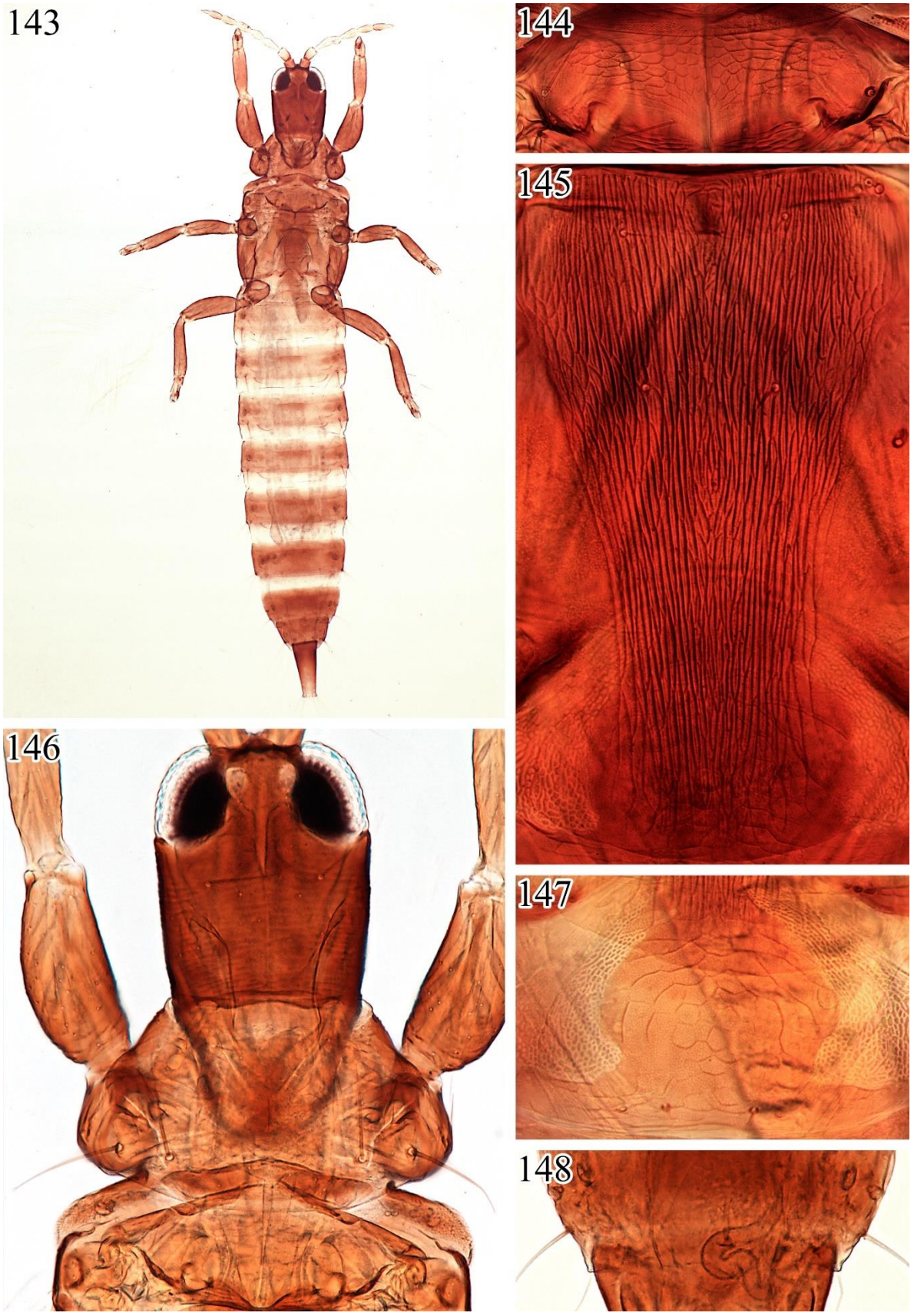
FIGURES 120–129. *Holopothrips inquilinus, H. inversus* and *H. jaboticabae*. 120–121. *Holopothrips inquilinus* paratype: (120) body; (121) head and pronotum; 122–123. *Holopothrips jaboticabae*: (122) head and pronotum; (123) mesonotum, metanotum and pelta; 124–129. *Holopothrips inversus* paratype: (124) head and pronotum; (125) prosternum, showing basantra (white arrows); (126) mesonotum; (127) metanotum and pelta; (128) pore plates on abdominal sternites VII–VIII; (129) pore plates extending towards abdominal tergite VIII (white arrows).



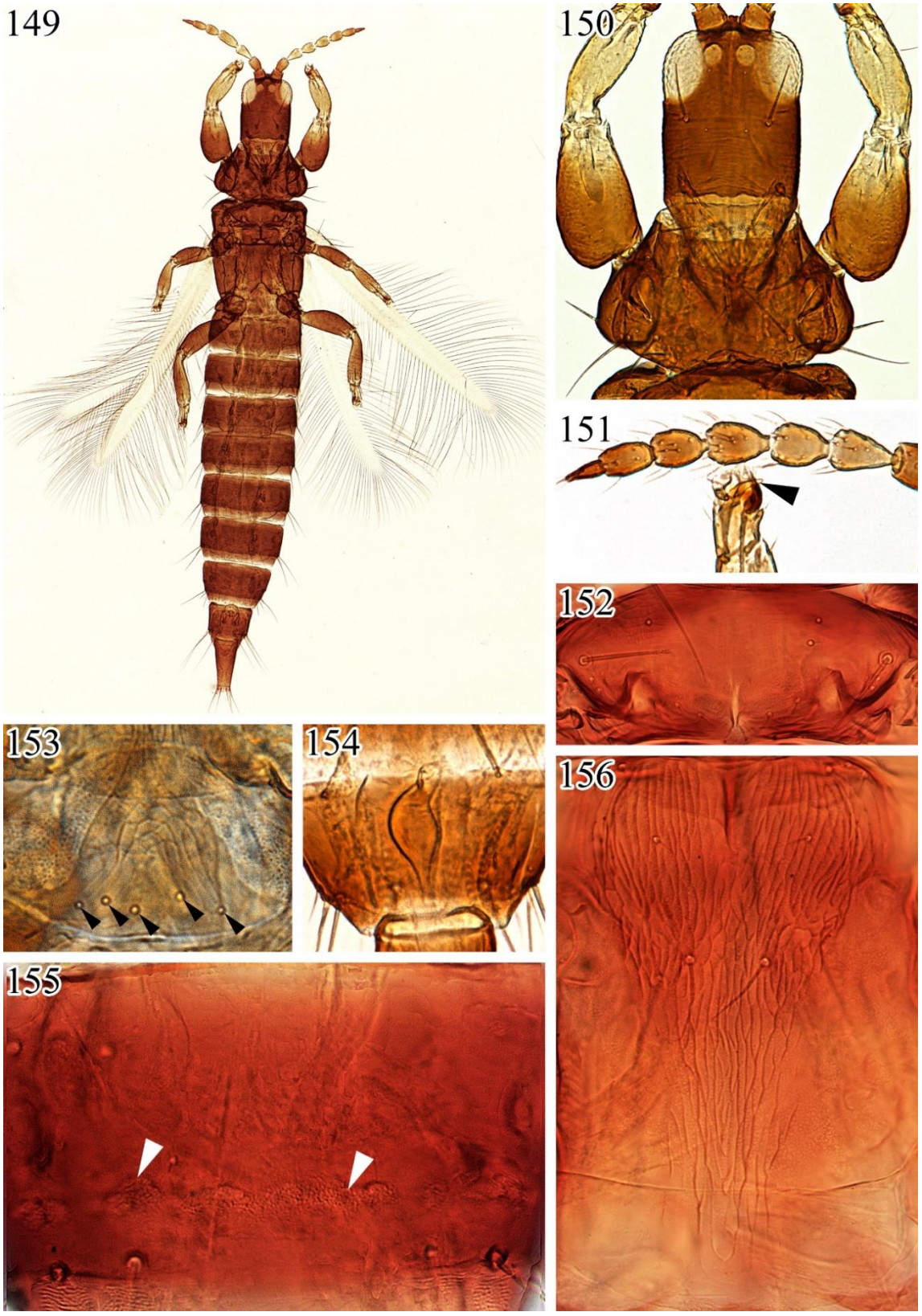
FIGURES 130–136. *Holopothrips irregularis* **sp. nov.** holotype and paratypes. (130) body; (131) head and pronotum; (132) mesonotum; (133) metanotum; (134) pelta; (135) spermatheca; (136) male abdominal sternite VIII, showing faint spots, which may be pore plates (white arrows).



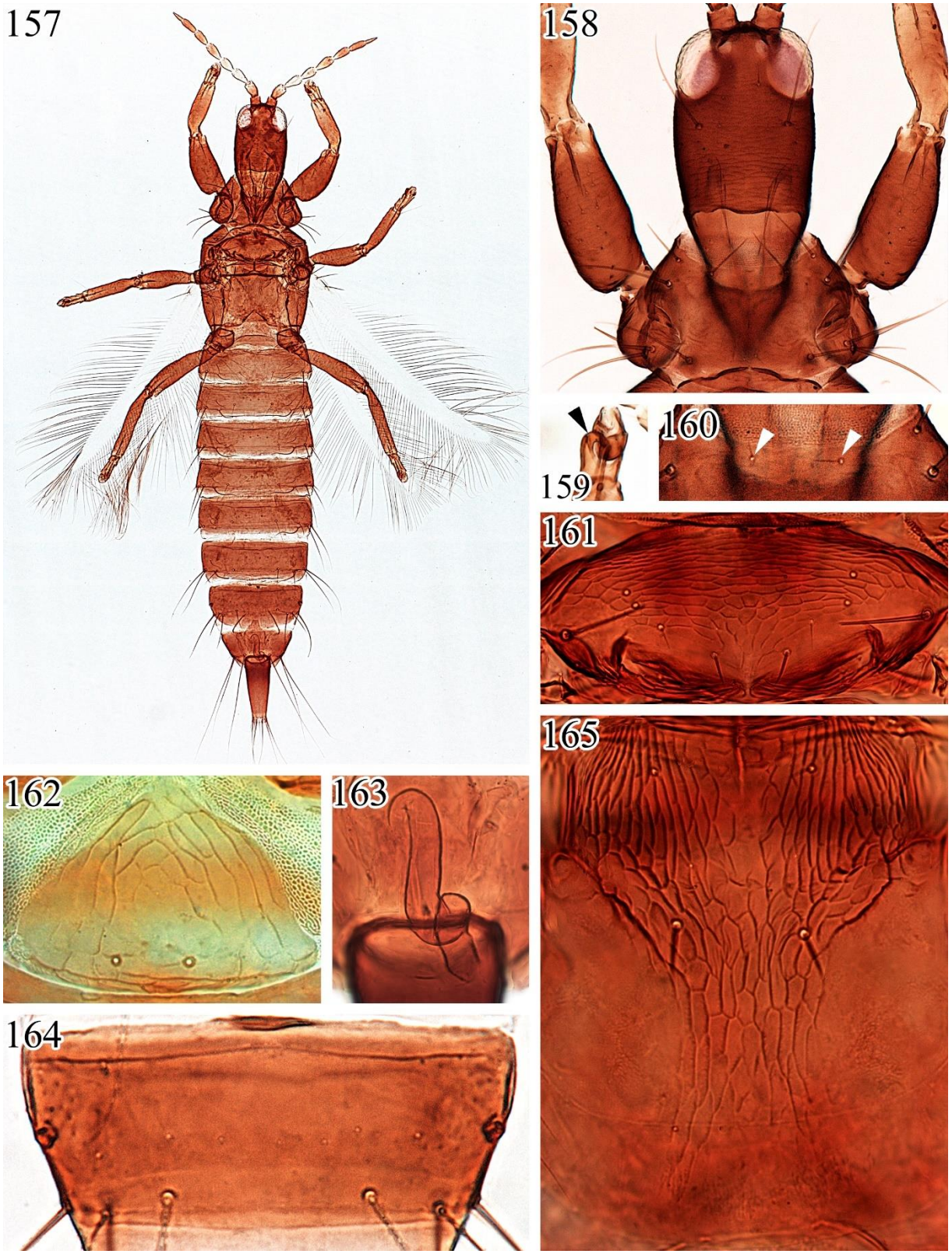
FIGURES 137–142. *Holopothrips johanseni* **sp. nov.** holotype and paratypes. (137) body; (138) head and pronotum, showing the secondary postocular setae (white arrow); (139) mesonotum, metanotum and pelta; (140) pore plates on abdominal sternites VI–VIII (black arrows); (141) spermatheca (white arrow); (142) mesosternum and metasternum, showing the absence of metapleural sutures (white circles).



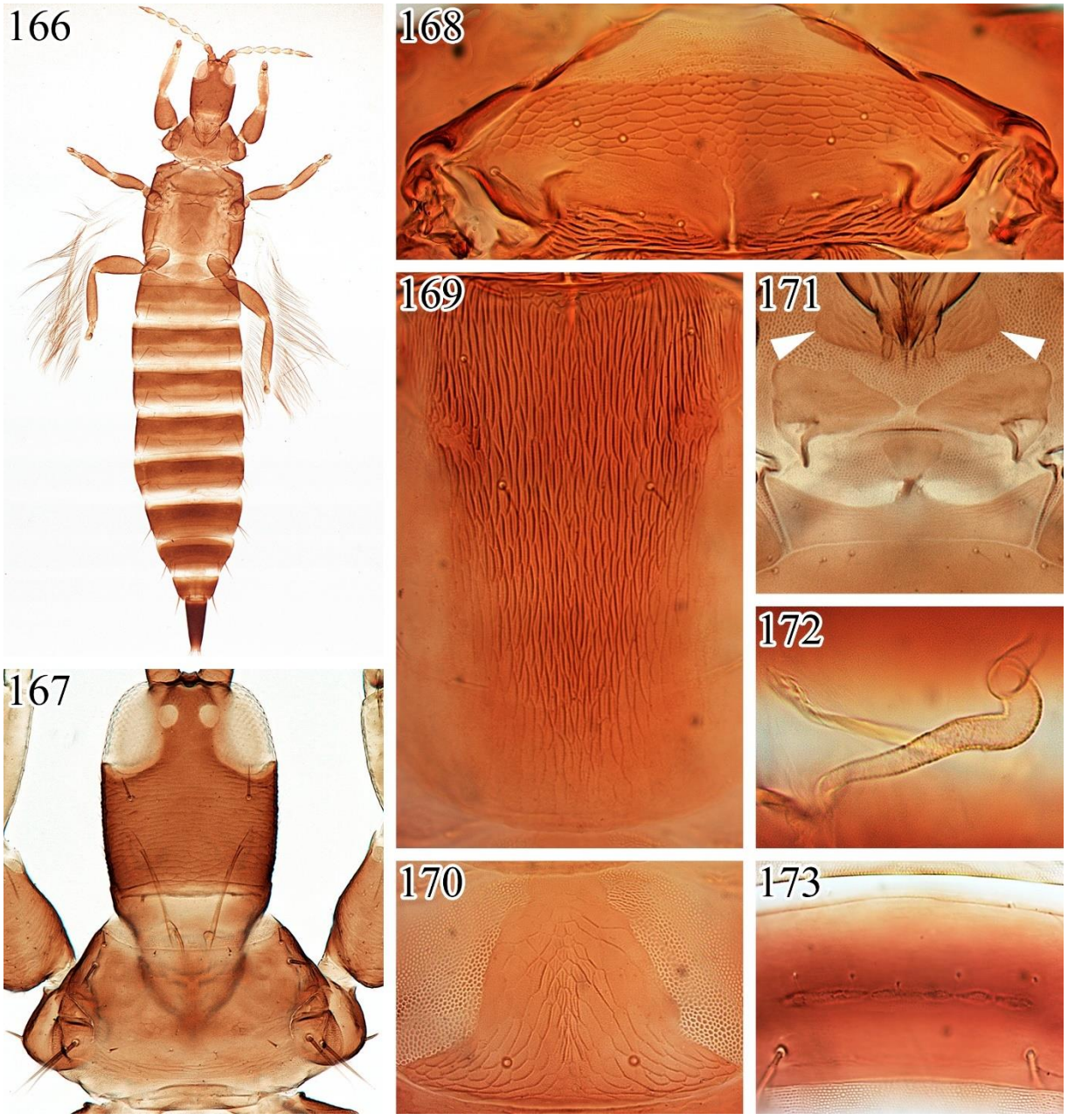
FIGURES 143–148. *Holopothrips kaminskii* **sp. nov.** holotype and paratypes. (143) body (wings not showing due to edition of photo); (144) mesonotum; (145) metanotum; (146) head and pronotum; (147) pelta; (148) spermatheca.



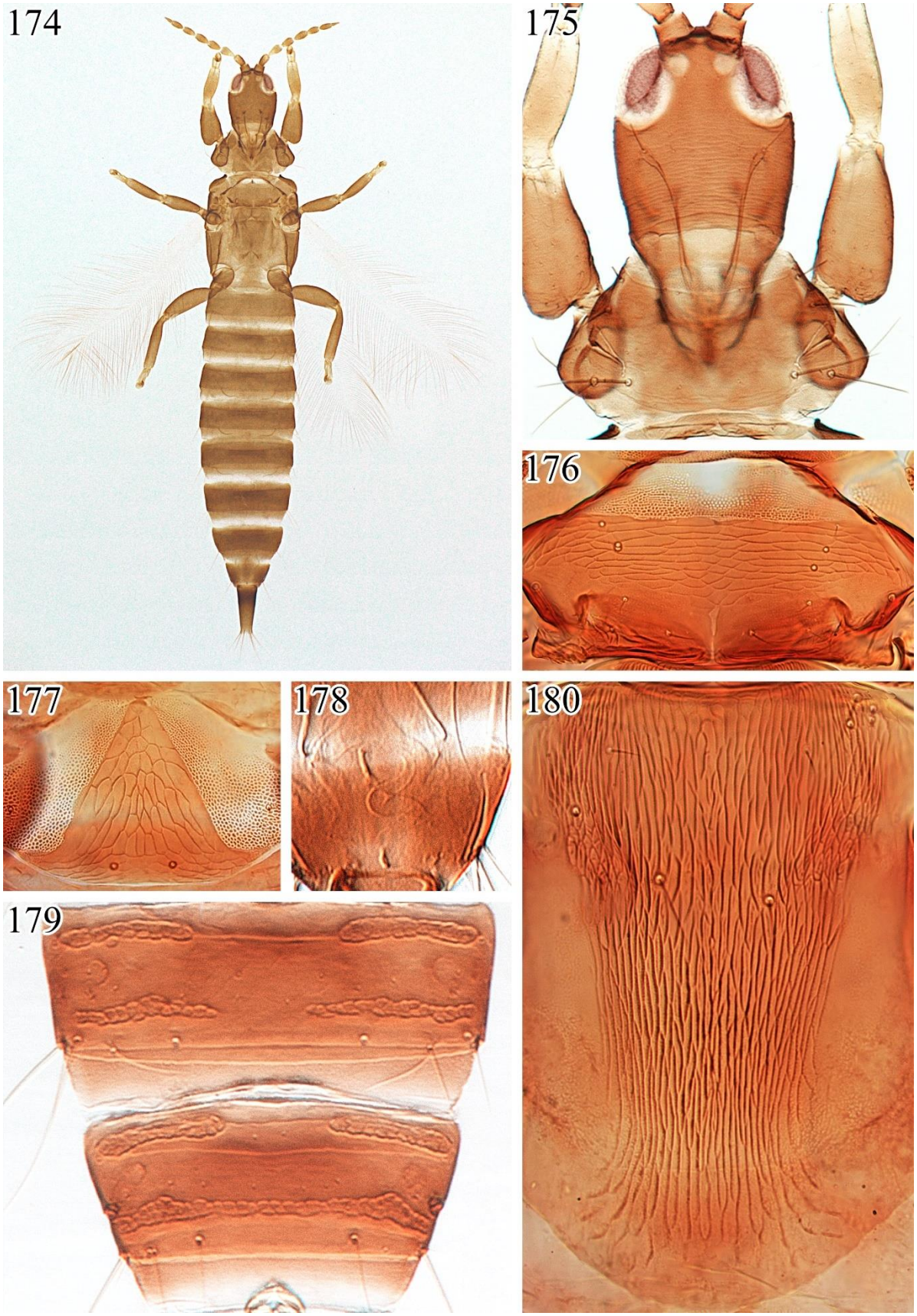
FIGURES 149–156. *Holopothrips longihamus* **sp. nov.** holotype and paratypes. (149) body; (150) head and pronotum; (151) antenna and fore tarsus, showing the enlarged hamus (black arrow); (152) mesonotum; (153) pelta, showing the multiple campaniform sensilla (black arrows); (154) spermatheca; (155) male sternite VIII, showing weak spots, which may be the pore plates (white arrows); (156) metanotum.



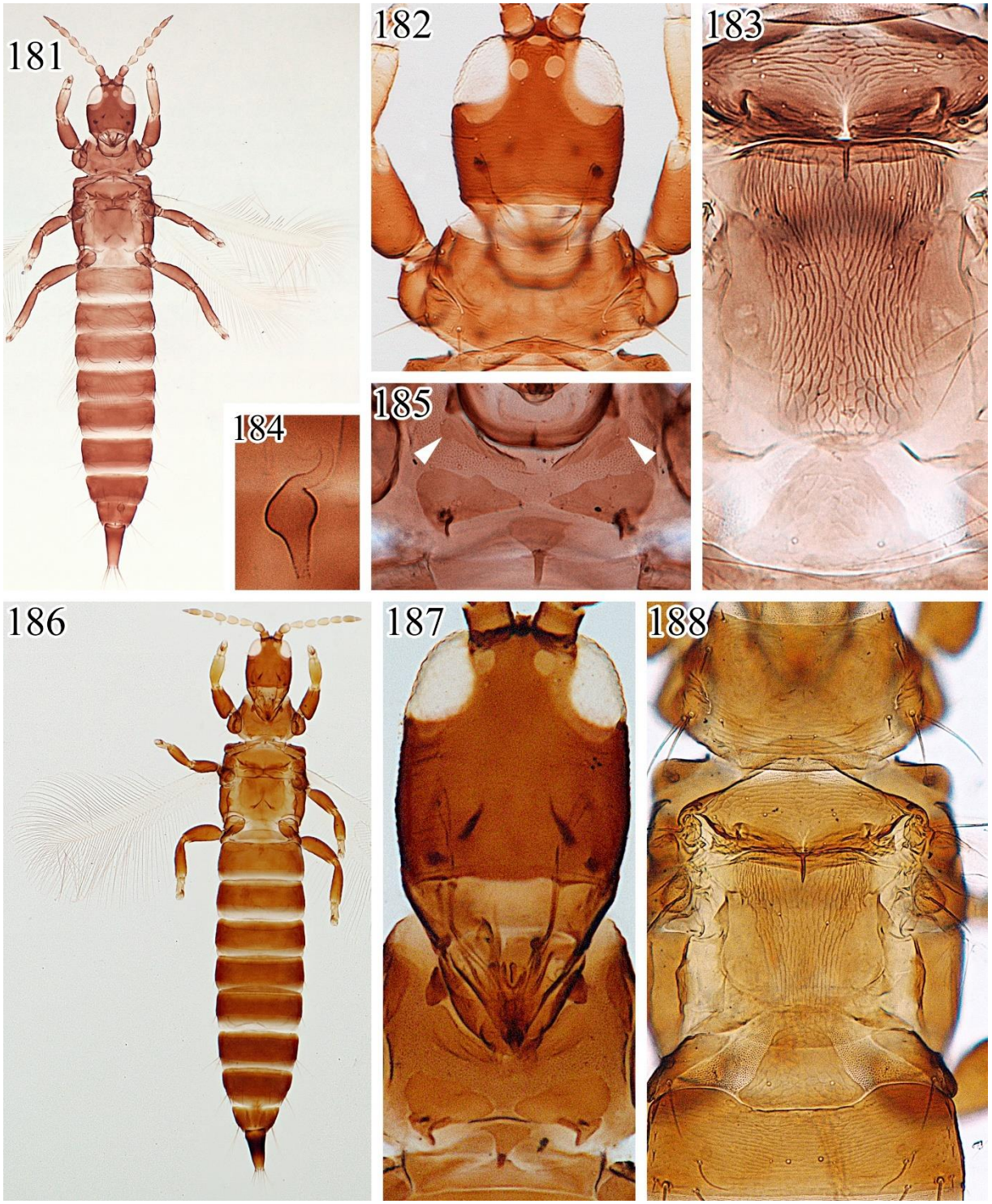
FIGURES 157–165. *Holopothrips longisetus* **sp. nov.** holotype and paratypes. (157) body; (158) head and pronotum, with long pronotal setae, including am; (159) fore tarsus, showing robust hamus (black arrow); (160) detail of pronotum, showing shorter am setae (white arrows); (161) mesonotum; (162) pelta; (163) spermatheca; (164) male abdominal sternite VIII, showing absence of pore plate; (165) metanotum.



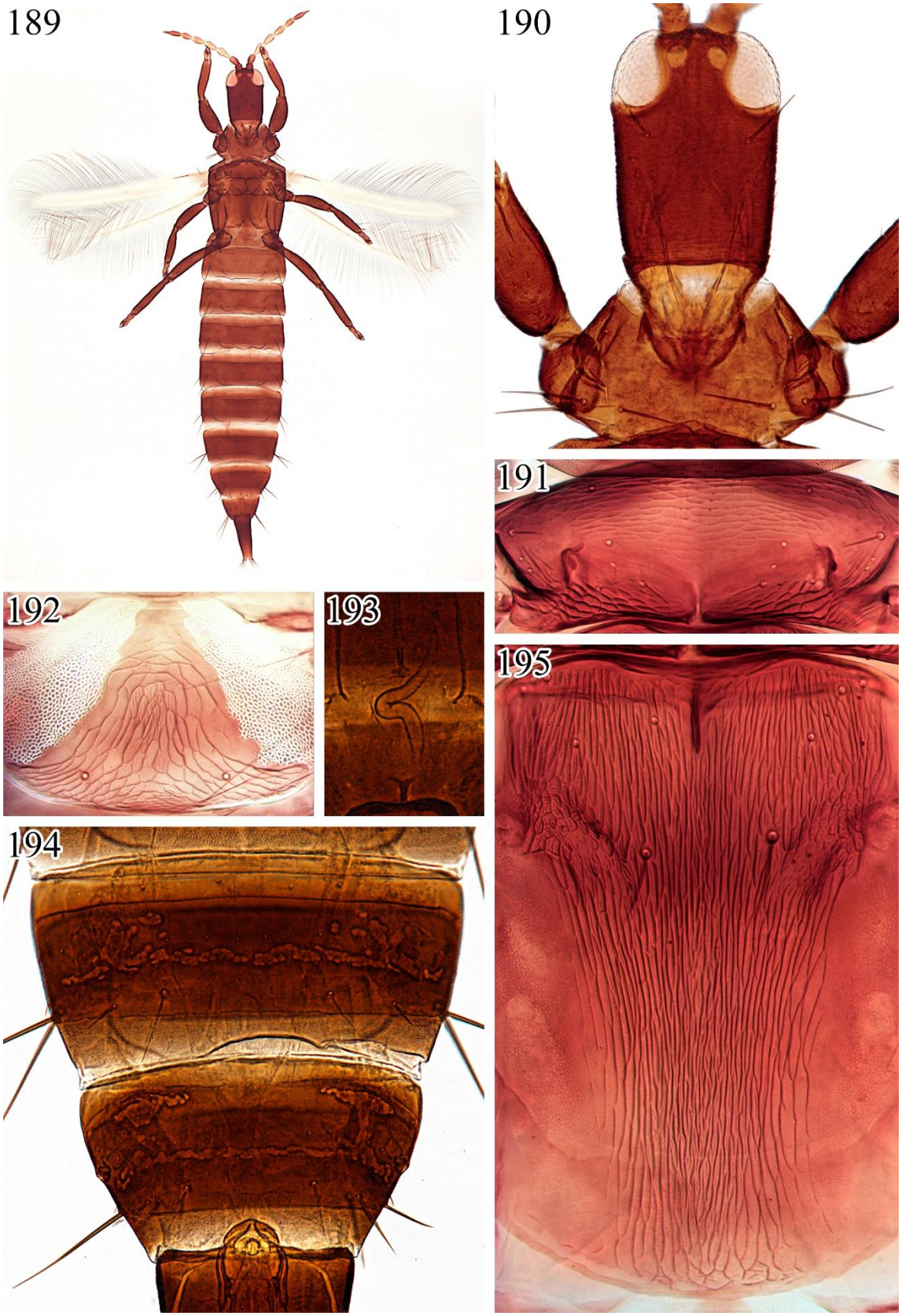
FIGURES 166–173. *Holopothrips magnus* **sp. nov.** holotype and paratype. (166) body; (167) head and pronotum; (168) mesonotum; (169) metanotum; (170) pelta; (171) prosternum, showing basantra (white arrows); (172) spermatheca; (173) pore plate on abdominal sternite VIII.



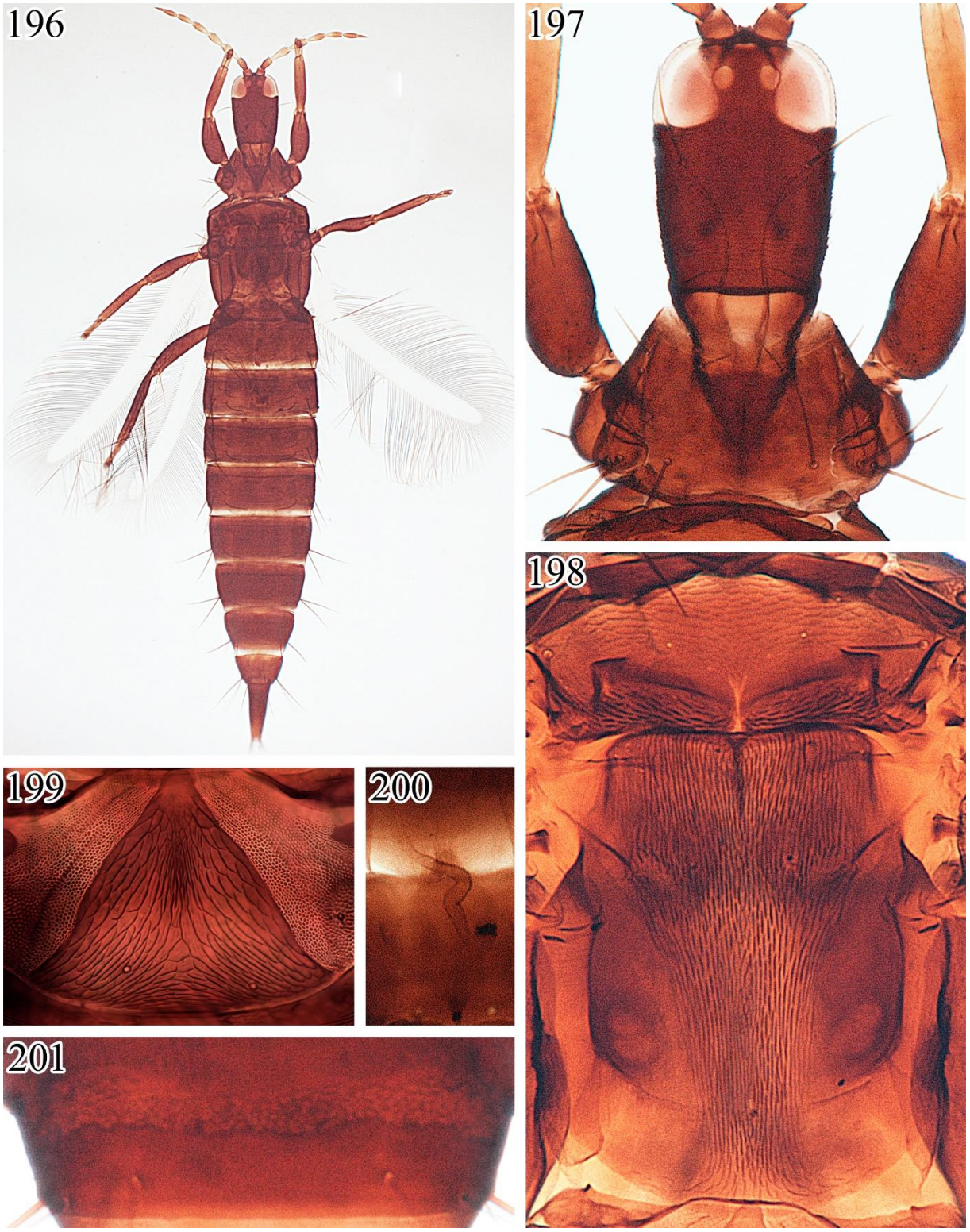
FIGURES 174–180. *Holopothrips maiae* **sp. nov.** holotype and paratypes. (174) body; (175) head and pronotum; (176) mesonotum; (177) pelta; (178) spermatheca; (179) pore plates on abdominal sternites VII–VIII; (180) metanotum.



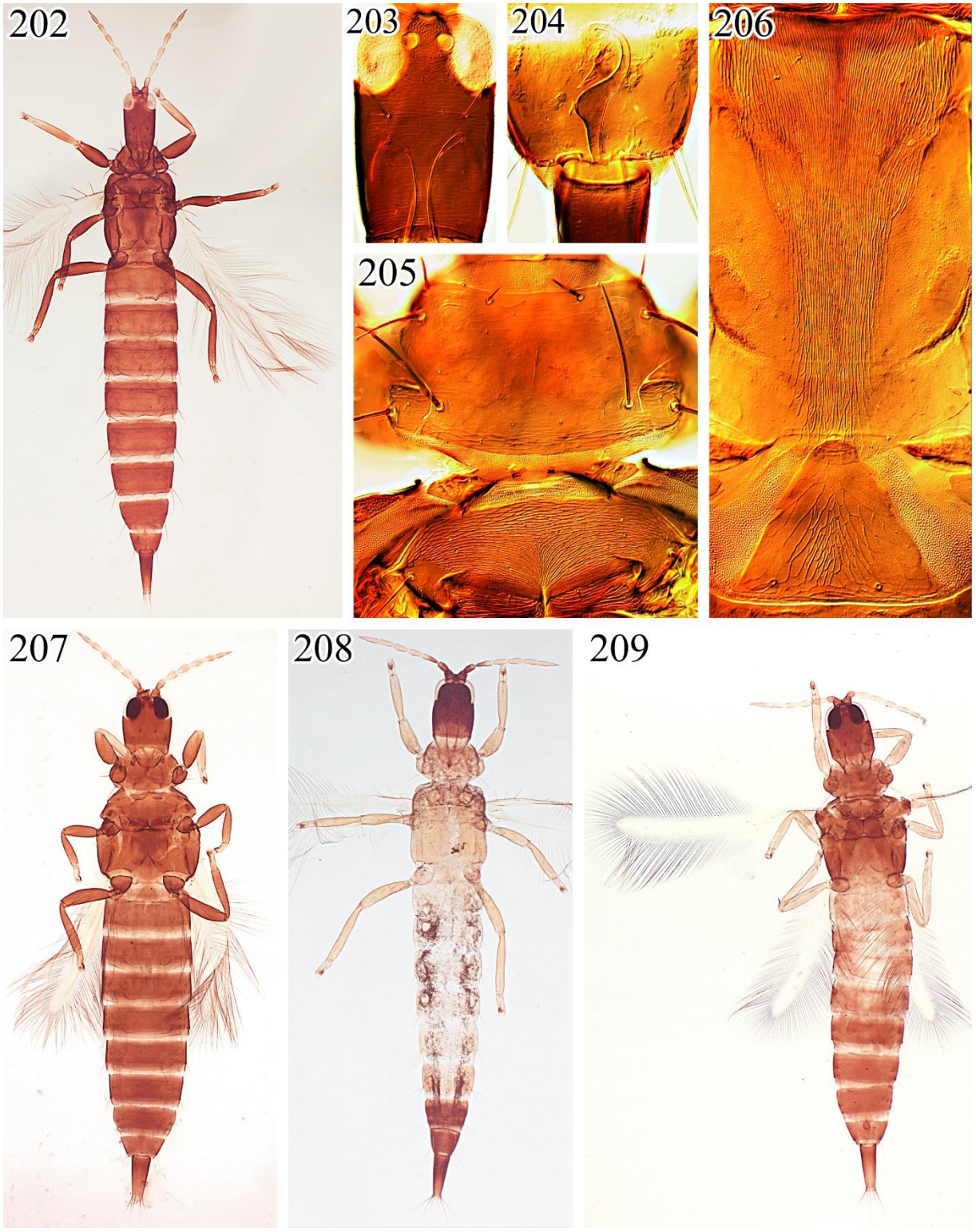
FIGURES 181–188. *Holopothrips mariae* and *H. molzi*. 181–185. *Holopothrips mariae* paratypes: (181) body; (182) head and pronotum; (183) mesonotum, metanotum and pelta; (184) spermatheca; (185) prosternum, showing basantra (white arrows); 186–188. *Holopothrips molzi* paratypes: (186) body; (187) head and prosternum; (188) pronotum, mesonotum, metanotum, pelta and abdominal tergite II.



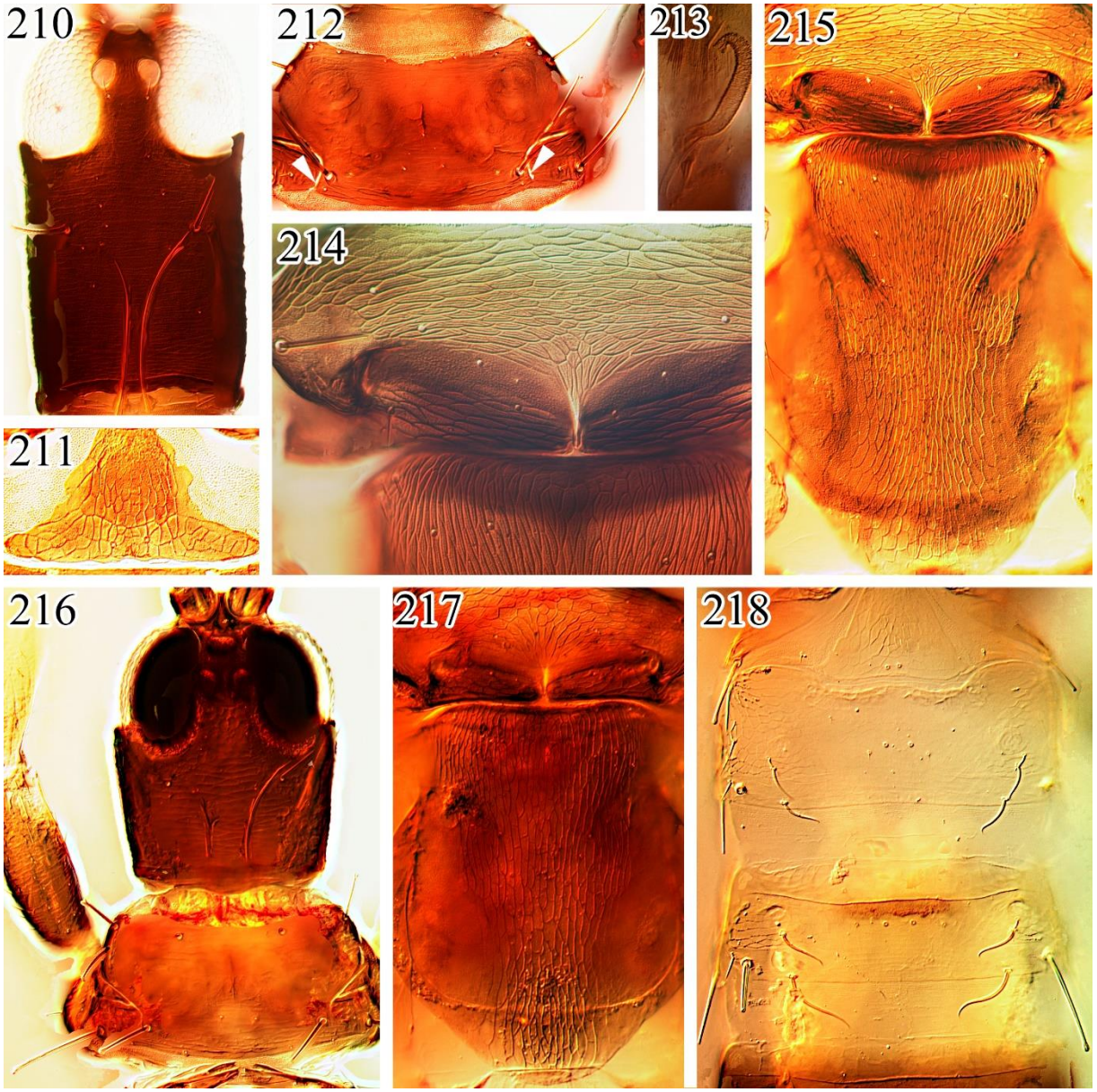
FIGURES 189–195. *Holopothrips nigrisetis* **sp. nov.** paratypes. (189) body; (190) head and pronotum; (191) mesonotum; (192) pelta; (193) spermatheca; (194) pore plates on abdominal sternites VII–VIII; (195) metanotum.



FIGURES 196–201. *Holopothrips nigrum* **sp. nov.** holotype and paratypes. (196) body; (197) head and pronotum; (198) mesonotum and metanotum; (199) pelta; (200) spermatheca; (201) pore plate on abdominal sternite VIII.

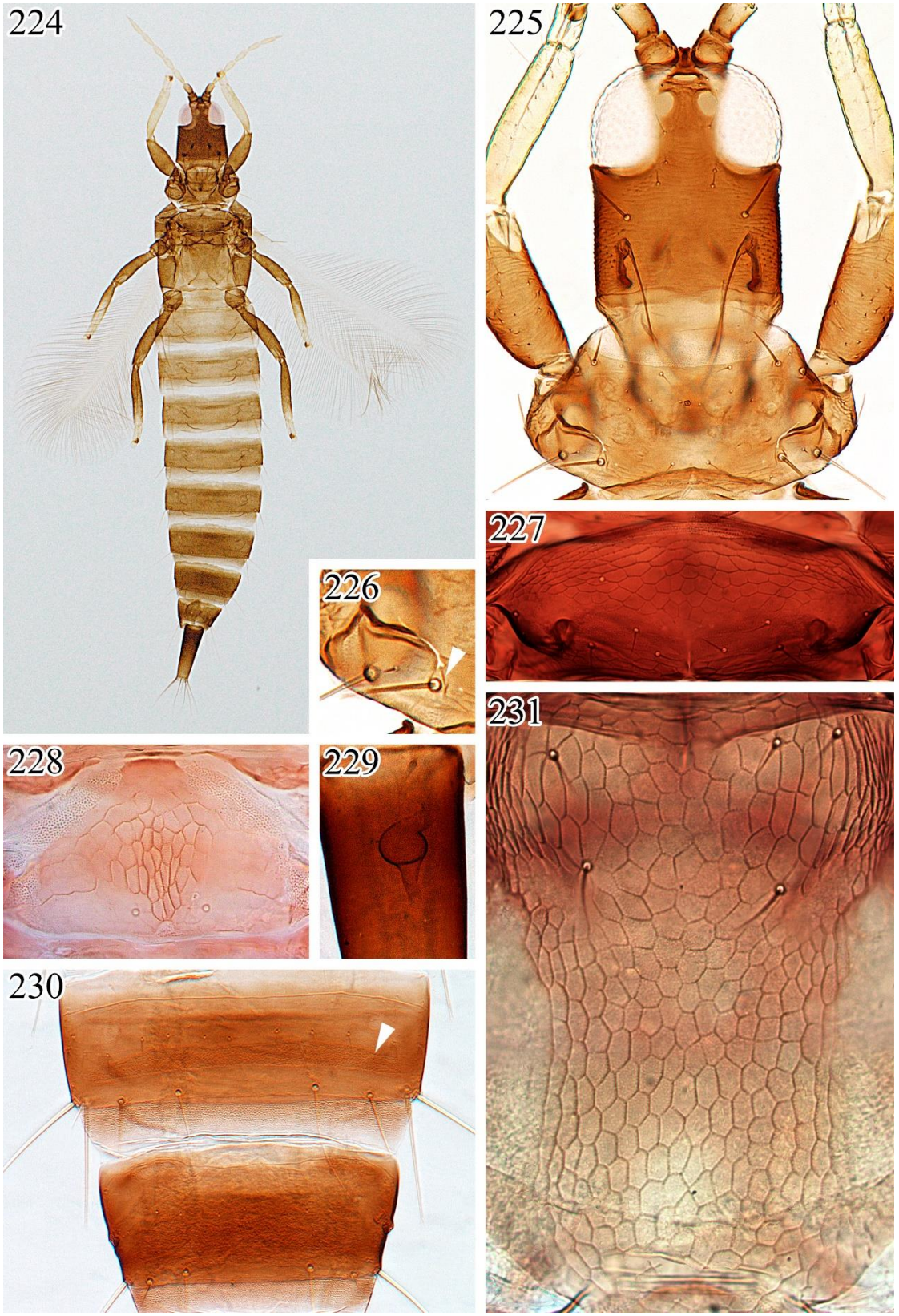


FIGURES 202–209. *Holopothrips omercooperi, H. orites, H. paulus* and *H. pennatus*. 202–206. *Holopothrips orites* paratypes: (202) body; (203) head; (204) spermatheca; (205) pronotum and mesonotum; (206) metanotum and pelta; (207) *Holopothrips omercooperi* paratype, body; (208) *Holopothrips paulus* paratype, body; (209) *Holopothrips pennatus* paratype, body.

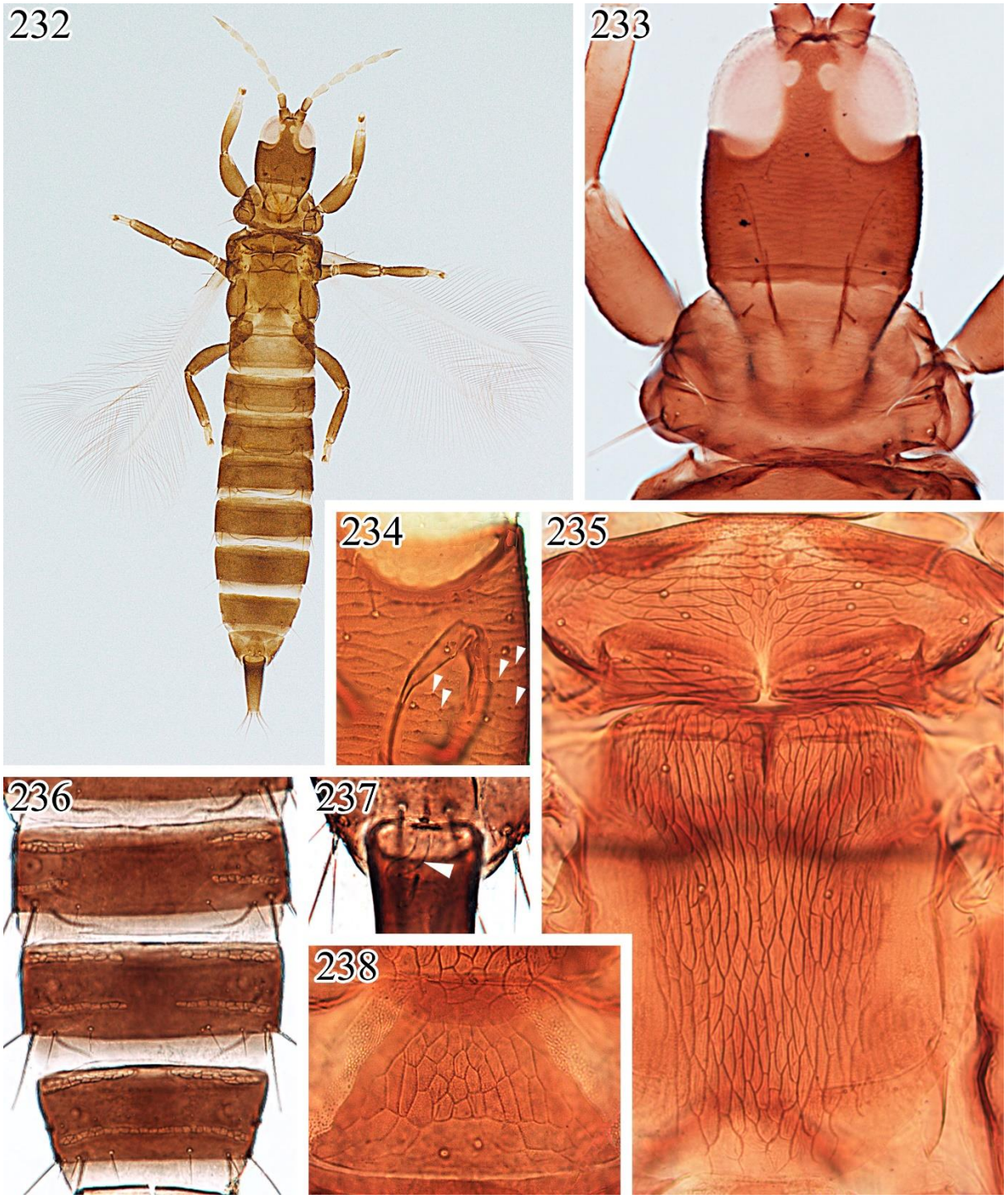


FIGURES 210–218. *Holopothrips permagnus* and *H. pictus*. 210–215. *Holopothrips permagnus* paratype: (210) head; (211) pelta; (212) pronotum, showing almost complete to complete epimeral sutures (white arrows); (213) spermatheca; (214) detail of mesonotal and part of metanotal sculpture; (215) mesonotum and metanotum; 216–218. *Holopothrips pictus*: (216) head and pronotum; (217) mesonotum and metanotum; (218) pelta and abdominal tergites II–III.

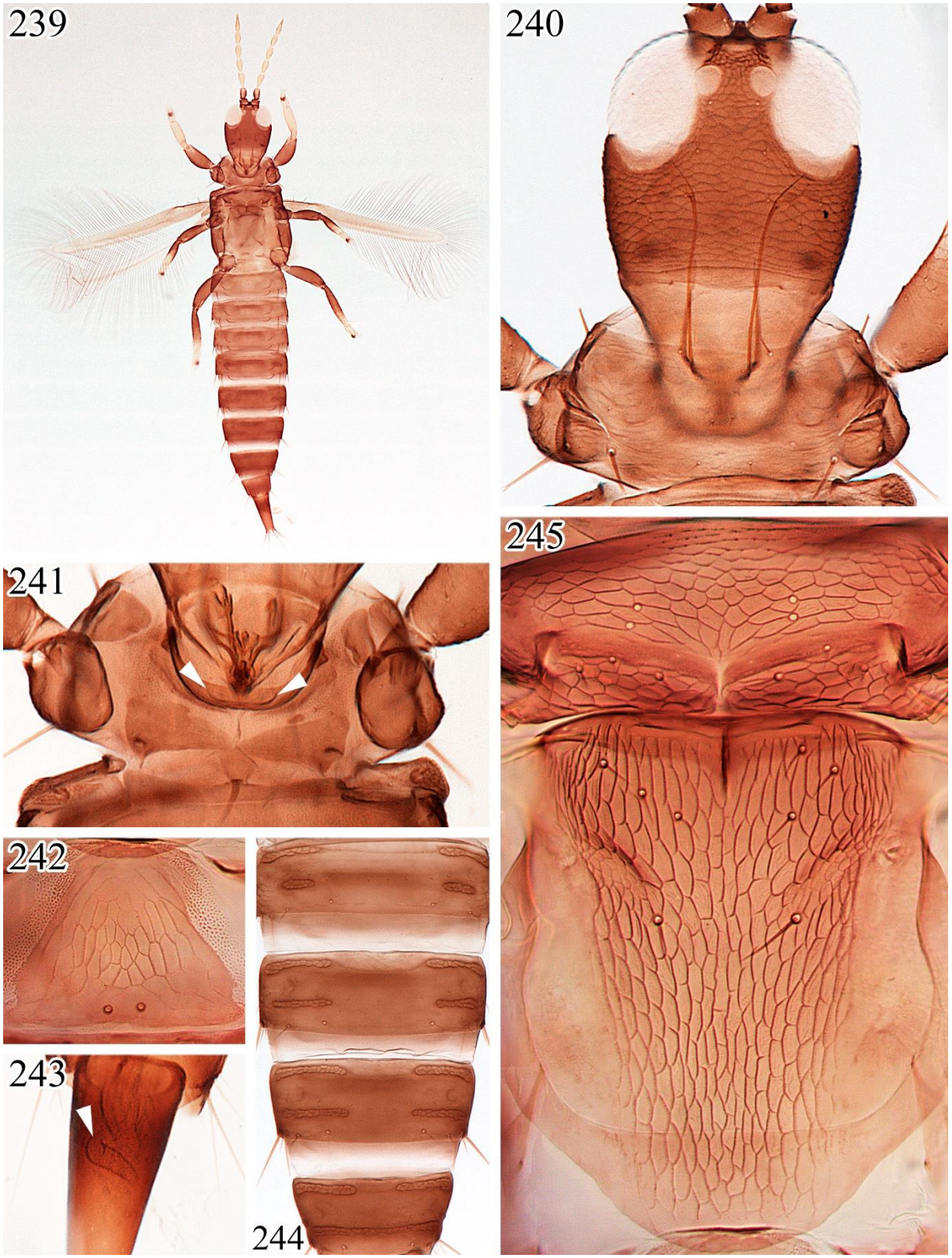
FIGURES 219–223. *Holopothrips porrosati* and *H. signatus*. (219) *Holopothrips porrosati* paratype, body; 220–223. *Holopothrips signatus* paratype and topotype: (220) body; (221) head and pronotum; (222) mesonotum and metanotum; (223) pore plates on abdominal sternites V–VIII.



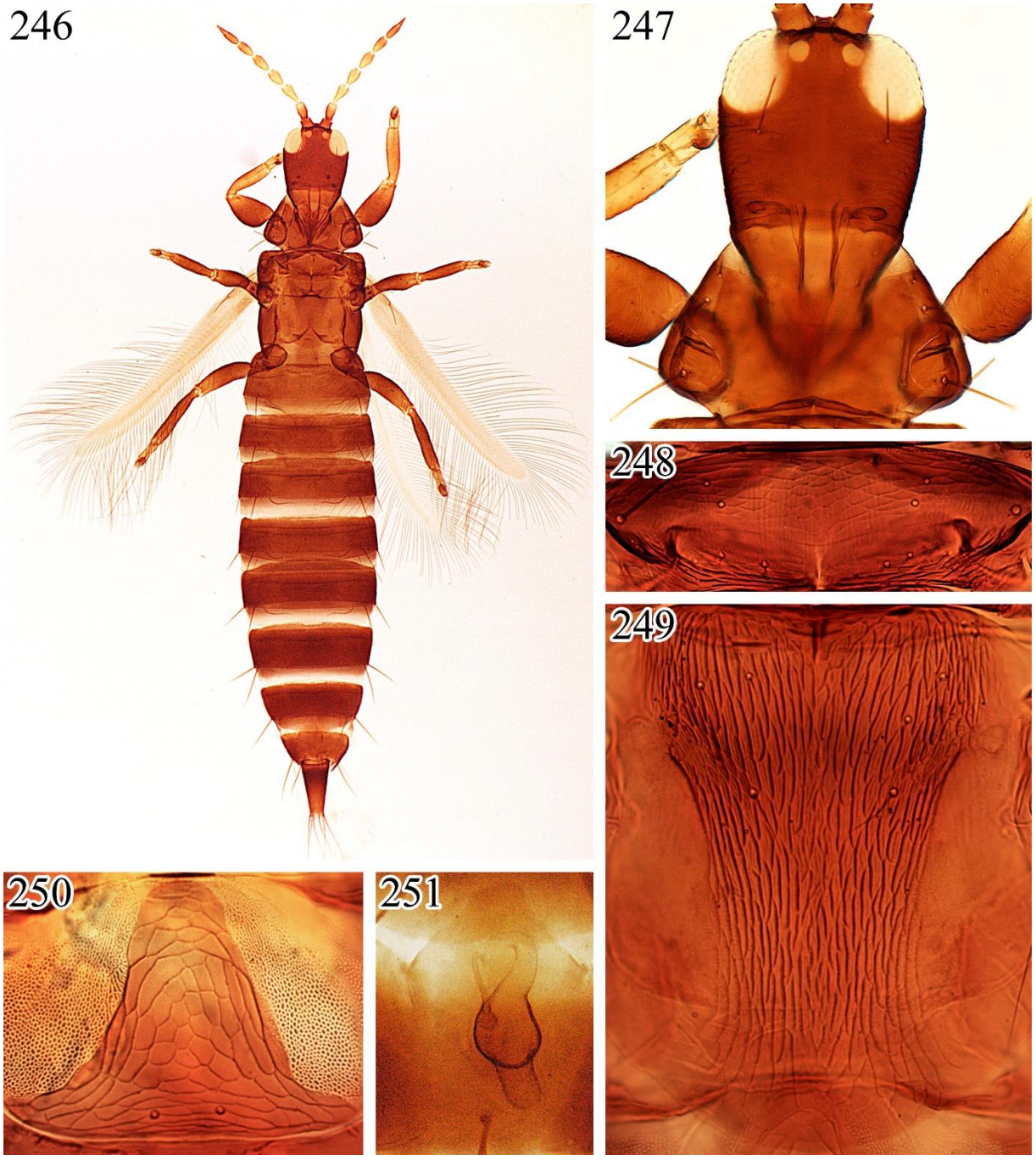
FIGURES 224–231. *Holopothrips punctatus* **sp. nov.** holotype and paratypes. (224) body; (225) head and pronotum; (226) detail of pronotum, showing the forking of the epimeral suture around the base of pa setae (white arrow); (227) mesonotum; (228) pelta; (229) spermatheca; (230) male abdominal sternites VII–VIII, pore plate visible on VII (white arrow) but hidden by internal content on VIII; (231) metanotum.



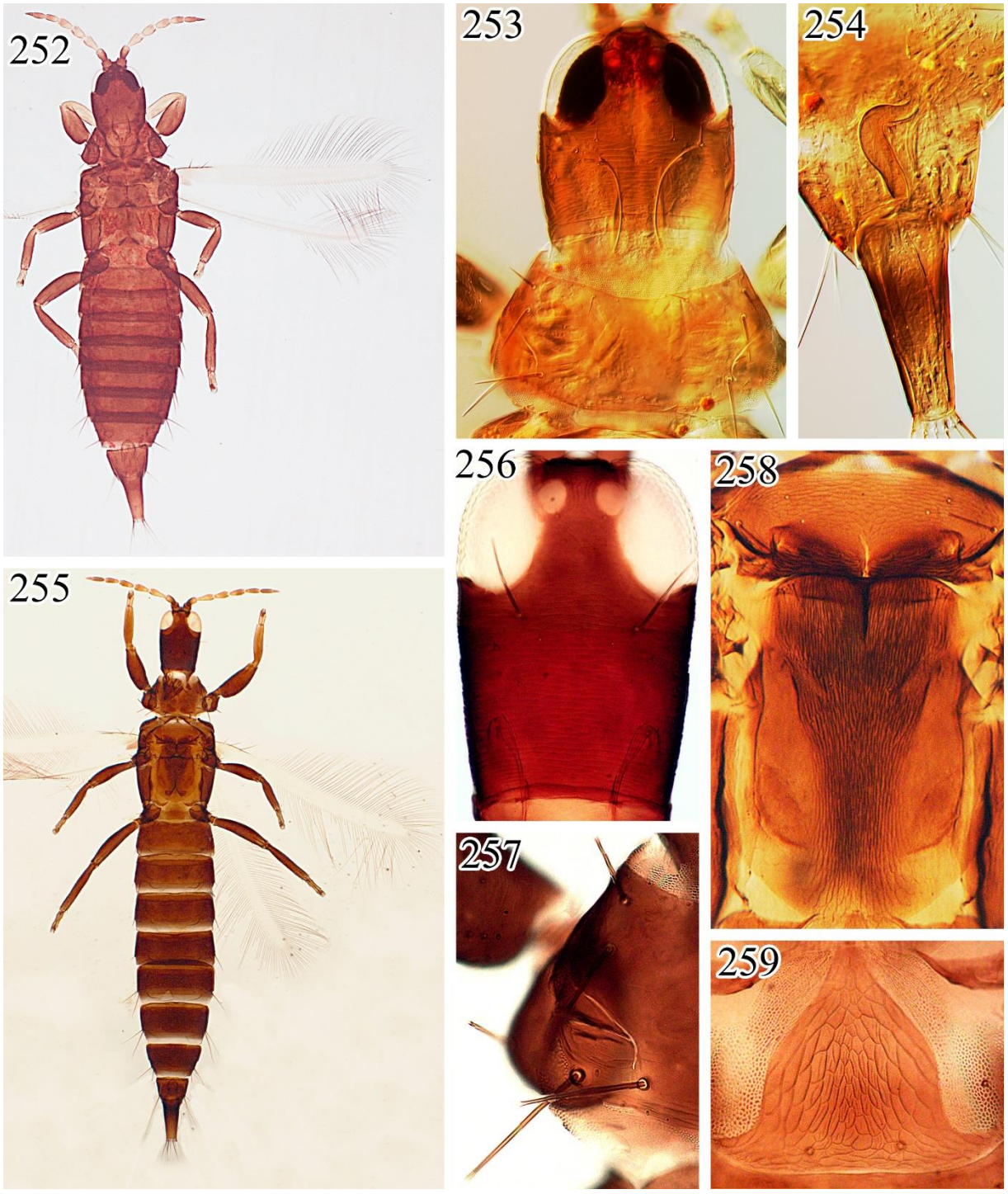
FIGURES 232–238. *Holopothrips reticulatus* **sp. nov.** holotype and paratypes. (232) body; (233) head and pronotum; (234) detail of head, showing microteeth on sculpture (white arrows); (235) mesonotum and metanotum; (236) pore plates on abdominal sternites VI–VIII; (237) spermatheca, dislocated (white arrow); (238) pelta.



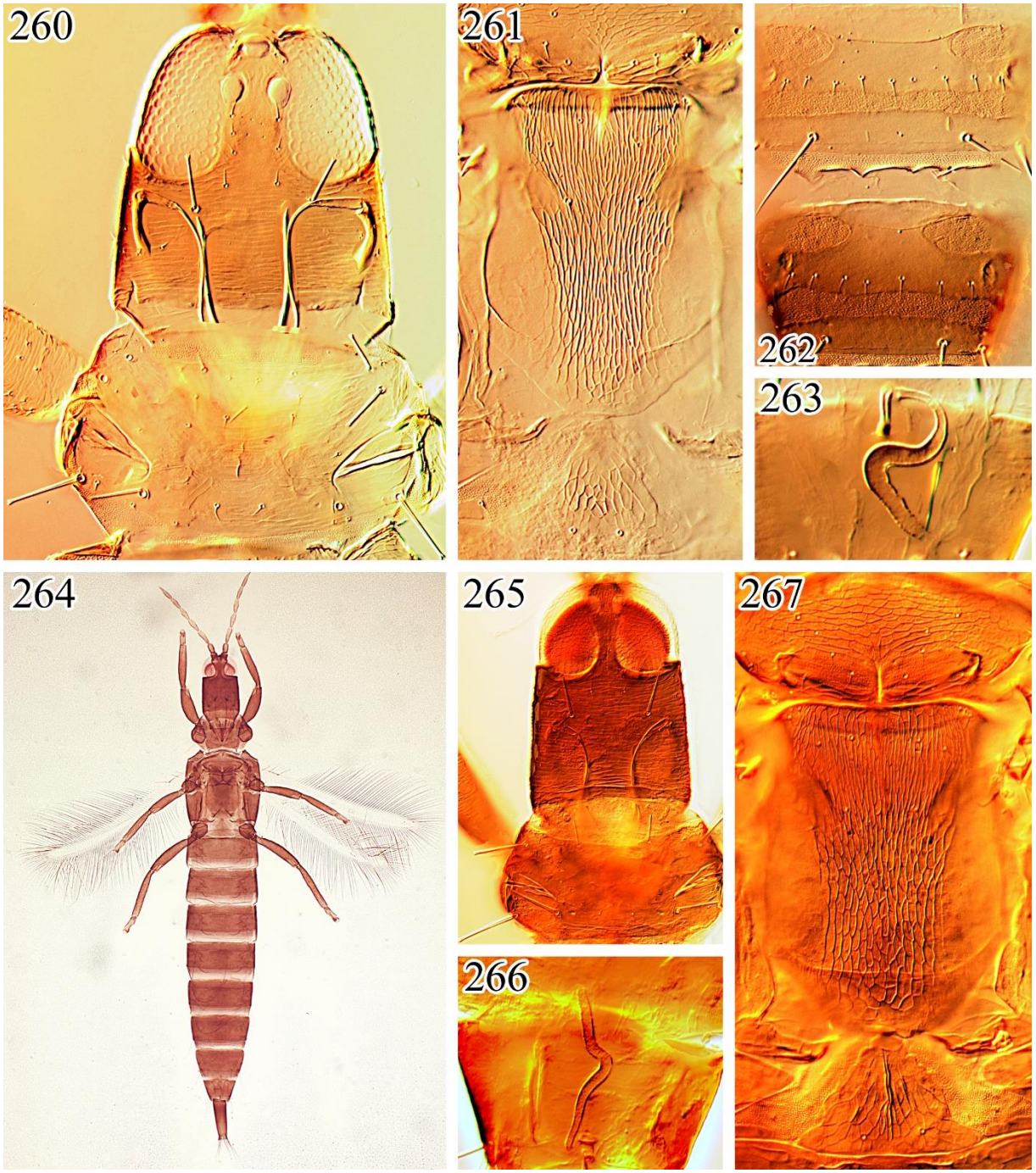
FIGURES 239–245. *Holopothrips singularis* **sp. nov.** holotype and paratypes. (239) body; (240) head and pronotum; (241) prosternum, showing vestigial labial palps (white arrows); (242) pelta; (243) spermatheca, dislocated (white arrow); (244) pore plates on abdominal sternites V–VIII; (245) mesonotum and metanotum.



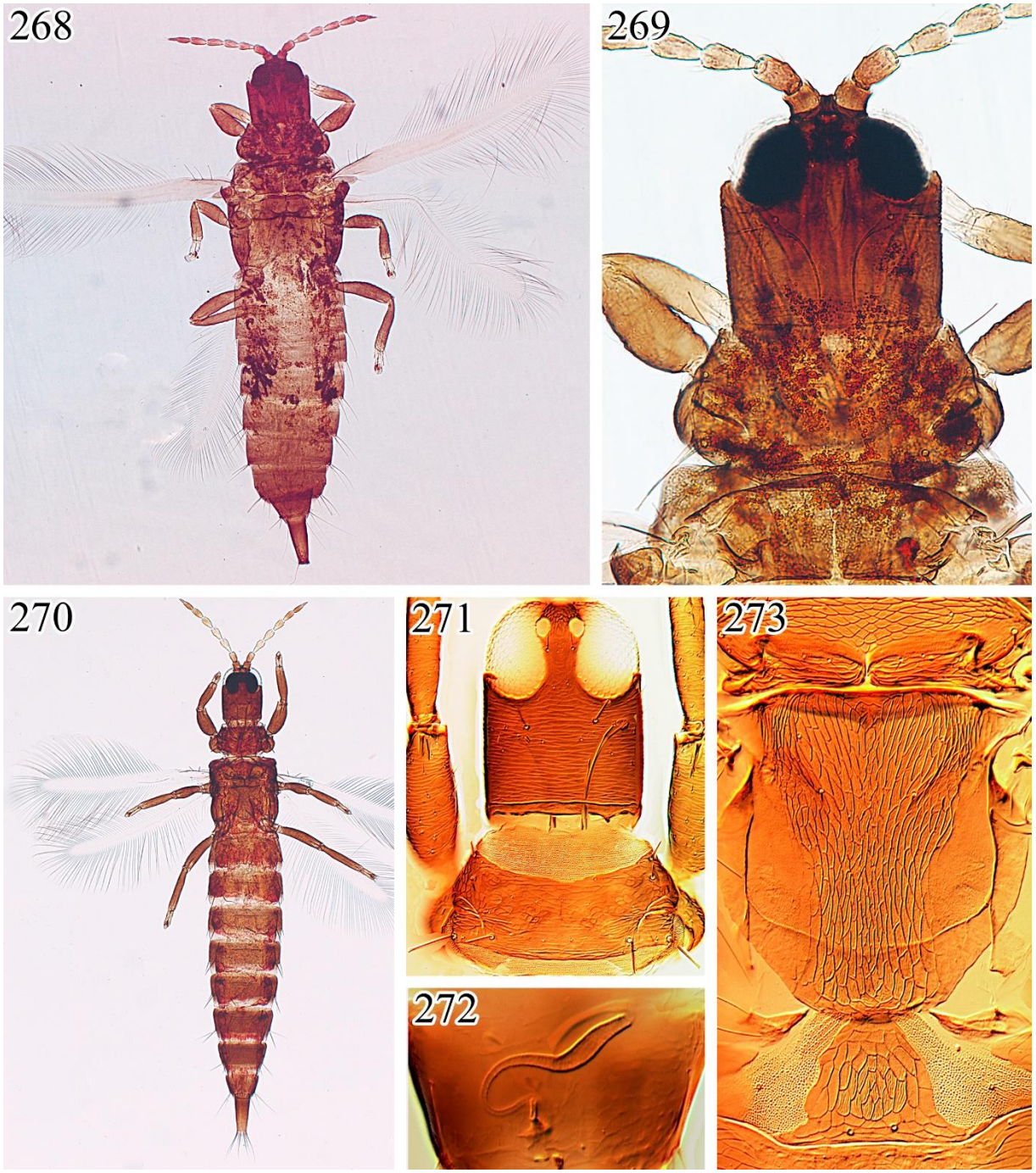
FIGURES 246–251. *Holopothrips spermathecus* **sp. nov.** holotype and paratype. (246) body; (247) head and pronotum; (248) mesonotum; (249) metanotum; (250) pelta; (251) spermatheca.



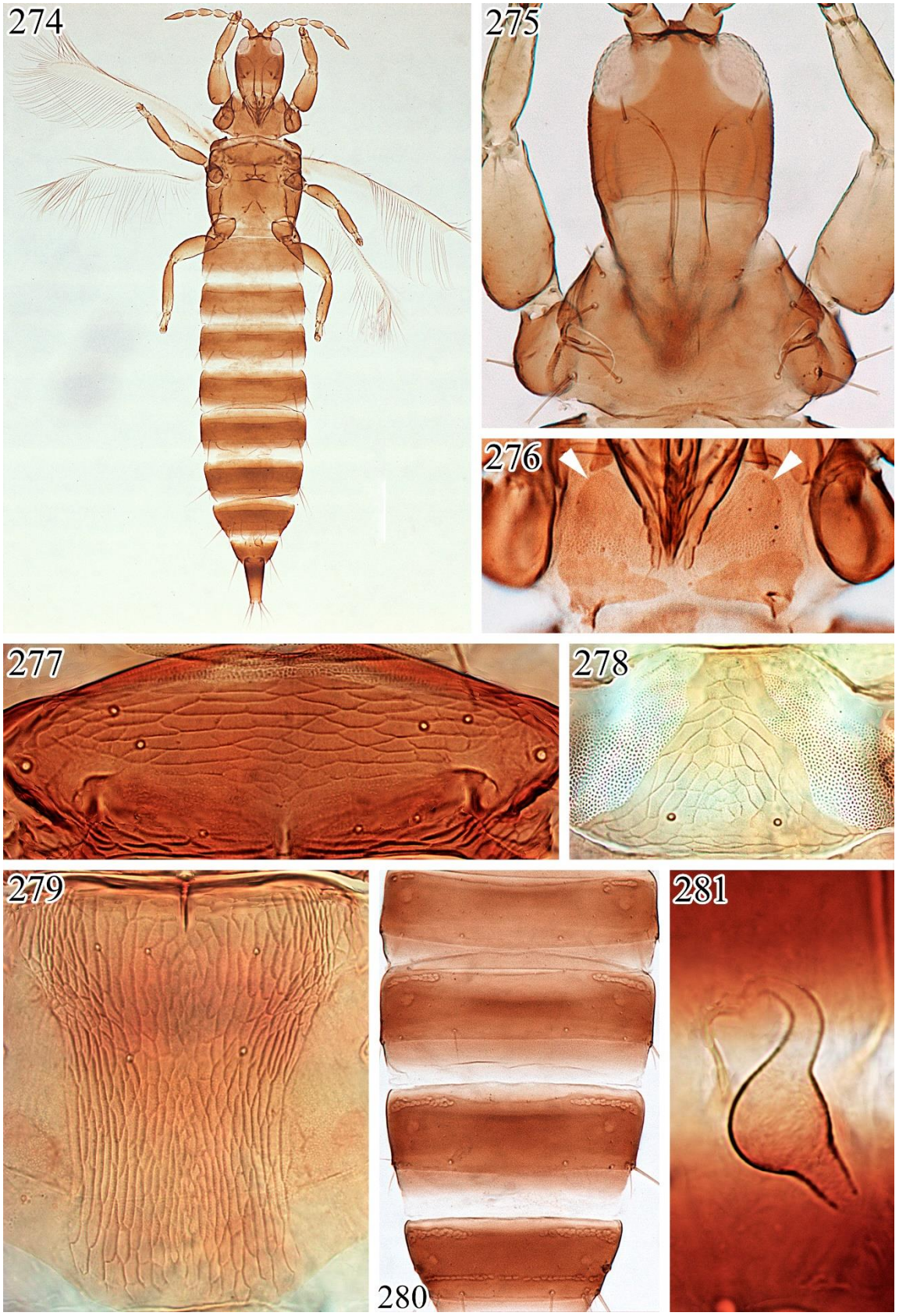
FIGURES 252–259. *Holopothrips stannardi* and *H. striatus*. 252–254. *Holopothrips stannardi* paratypes: (252) body; (253) head and pronotum; (254) spermatheca; 255–259. *Holopothrips striatus* holotype and paratypes: (255) body; (256) head; (257) pronotal setae; (258) mesonotum and metanotum; (259) pelta.



FIGURES 260–267. *Holopothrips tabebuia* and *H. tenuis*. 260–263. *Holopothrips tabebuia*: (260) head and pronotum; (261) mesonotum, metanotum and pelta; (262) pore plates on abdominal sternites VII–VIII; (263) spermatheca; 264–267. *Holopothrips tenuis* paratype: (264) body; (265) head and pronotum; (266) spermatheca; (267) mesonotum, metanotum and pelta.



FIGURES 268–273. *Holopothrips tillandsiae* and *H. tupi*. 268–269. *Holopothrips tillandsiae* paratype: (268) body; (269) head and pronotum; 270–273. *Holopothrips tupi* paratype: (270) body; (271) head and pronotum; (272) spermatheca; (273) mesonotum, metanotum and pelta.



FIGURES 274–281. *Holopothrips varicolor* **sp. nov.** holotype and paratypes. (274) body; (275) head and pronotum; (276) prosternum, showing weakly defined basantra (white arrows); (277) mesonotum; (278) pelta; (279) metanotum; (280) pore plates on abdominal sternites V–VIII; (281) spermatheca.

TABLE 1. Habit and host plants for *Holopothrips* species.

Species	Habit	Host Plant - Family	Distribution	Reference
H. acrioris **sp. nov.**	Gall inducer	*Myrcia selloi* - Myrtaceae	Southern Brazil	This work
H. affinis	Unknown	-	Brazil	Bagnall (1924)
H. ananasi	Phytophagous, damaging pineapple	*Ananas sativus* - Bromeliaceae	Southeastern Brazil	Costa Lima (1935b)
H. atlanticus **sp. nov.**	Gall inducer	*Myrcia brasiliensis* - Myrtaceae	Southeastern Brazil	This work
H. balteatus	Unknown	-	Southern Brazil	Hood (1955)
H. bicolor **sp. nov.**	Phytophagous	*Myrcia palustris*, *Myrcia guianensis* - Myrtaceae	Southern and Northeastern Brazil	This work
H. brevicapitatum **sp. nov.**	Gall inducer	*Miconia* sp. - Melastomataceae	Southeastern Brazil	This work
H. cardosoi **sp. nov.**	Gall inducer	*Myrcia* sp. - Myrtaceae	Southeastern Brazil	This work
H. carolinae	Unknown	*Pentaclethra* sp. - Fabaceae	Costa Rica	Mound & Marullo (1996)
H. chaconi	Gall invader	Abandoned cecidomyiid galls in *Piper* spp. - Piperaceae	Costa Rica	Zamora *et al.* (2015)
H. clarisetis **sp. nov.**	Gall inducer	Unidentified Myrtaceae	Southern Brazil	This work
H. claritibialis	Gall inducer	*Mollinedia* spp. - Monimiaceae	Southern Brazil	Cavalleri & Kaminski (2007)
H. conducans	Gall inducer	*Myrcia splendens*; *Eugenia* sp. - Myrtaceae	Brazil; Nicaragua; Paraguay	Costa Lima (1935a); Mound & Marullo (1996)
H. curiosus **sp. nov.**	Gall inducer	*Siphoneugena reitzii* - Myrtaceae	Southern Brazil	This work
H. elongatus	Unknown	-	Mexico	Mound & Marullo (1996)
H. erianthi	Unknown	Collected from *Saccharum asperum* - Poaceae (mentioned as *Erianthus asper*); it is likely not the host plant.	Southeastern Brazil	Hood (1954)
H. ferrisi	Unknown	Collected from *Coccoloba* sp. - Polygonaceae; it is uncertain if this is the host plant	Mexico	Mound & Marullo (1996)
H. fulvus	Referred as pest on some plants	*Anacardium occidentale* - Anacardiaceae; *Caryocar villosum* - Caryocaraceae;	Northeastern Brazil	Morgan (1929); Mound & Marullo (1996); Lima *et al.* (2017)

		Gossypium sp. - Malvaceae		
H. graminis	Unknown	Collected from *Saccharum asperum* - Poaceae (mentioned as *Erianthus asper*); it is likely not the host plant.	Southeastern Brazil	Hood (1955)
H. graziae **sp. nov.**	Unknown	-	Peru	This work
H. hambletoni	Unknown	-	Southeastern Brazil	Hood (1938)
H. hilaris	Unknown	-	Southeastern Brazil	Hood (1938)
H. inconspicuus **sp. nov.**	Gall inducer	*Myrcia multiflora* - Myrtaceae	Southeastern Brazil	Maia *et al.* (2008); this work
H. infestans **sp. nov.**	Gall inducer	*Acca sellowiana* - Myrtaceae	Southern Brazil	Hickel & Ducroquet (1993) (mentioned as *Phrasterothrips* sp.); this work
H. inquilinus	Gall invader	Abandoned cecidomyiid galls	Guadeloupe; Panama	Bournier (1993)
H. inversus	Unknown	-	Southeastern Brazil	Hood (1955)
H. irregularis **sp. nov.**	Gall inducer	*Eugenia* sp. - Myrtaceae	Southeastern Brazil	This work
H. jaboticabae	Unknown	Collected from "jaboticaba" (no species name given)	Southeastern Brazil	Hood (1954)
H. johanseni **sp. nov.**	Possibly gall inducer	*Drymonia* sp. - Gesneriaceae	Costa Rica	Mound & Marullo (1996) (mentioned as sp. n. CR2); this work
H. kaminskii **sp. nov.**	Gall inducer	*Vochysia* cf. *obovata* - Vochysiaceae	Northeastern Brazil	This work
H. longihamus **sp. nov.**	Gall inducer	Unidentified Melastomataceae	Southeastern Brazil	This work
H. longisetus **sp. nov.**	Gall inducer	*Myrcia splendens* - Myrtaceae	Central Brazil	This work
H. magnus **sp. nov.**	Possibly gall inducer	*Smilax rufescens* - Smilacaceae	Southeastern Brazil	This work
H. maiae **sp. nov.**	Possibly gall inducer	*Marlierea* sp. - Myrtaceae	Southeastern Brazil	This work
H. mariae	Unknown	-	Peru	Mound & Marullo (1996)
H. molzi	Gall inducer	*Myrcia guianensis* - Myrtaceae	Southern Brazil	Lindner *et al.* (2016)
H. nigrisetis **sp. nov.**	Gall inducer	*Myrcia* sp. - Myrtaceae	Southeastern Brazil	Maia *et al.* (2014); this work

H. nigrum **sp. nov.**	Possibly gall inducer	*Acca sellowiana* - Myrtaceae	Southeastern Brazil	This work
H. oaxacensis	Unknown, possibly phytophagous	Collected from *Serjania racemosa* - Sapindaceae	Mexico	Johansen (1986)
H. omercooperi	Unknown	-	Brazil	Bagnall (1924)
H. orites	Unknown	-	Peru	Mound & Marullo (1996)
H. paulus	Unknown	-	Costa Rica	Mound & Marullo (1996)
H. pennatus	Unknown	Collected from an unidentified Apocynaceae, without indication of a host plant association	Southeastern Brazil	Moulton (1938)
H. permagnus	Unknown	-	Peru	Hood (1938)
H. pictus	Unknown	-	Southeastern and Southern Brazil	ThripsWiki (2018); this work
H. porrosati	Phytophagous, induces the formation of translucent spots in the leaves of its host plant	*Philodendron* sp. - Araceae	Costa Rica	Mound & Marullo (1996)
H. punctatus **sp. nov.**	Possibly invader on *H. claritibialis* galls	*Mollinedia elegans* - Monimiaceae	Southern Brazil	This work
H. reticulatus **sp. nov.**	Unknown	*Myrciaria dubia* - Myrtaceae	Northern Brazil	This work
H. seini	Unknown	-	Dominican Republic	Watson (1927)
H. signatus	Possibly gall inducer	*Hura crepitans* - Euphorbiaceae	Panama; possibly Southeastern Brazil and Peru	Hood (1914); Mound & Marullo (1996)
H. singularis **sp. nov.**	Possibly gall inducer	Myrtaceae	Southeastern Brazil	This work
H. spermathecus **sp. nov.**	Gall inducer	*Myrciaria floribunda* - Myrtaceae	Southeastern Brazil	Santana (2014); this work
H. stannardi	Possibly gall inducer or invader	*Eugenia axillaris* - Myrtaceae	Florida (USA)	Stannard (1968); Mound & Marullo (1996)
H. striatus	Gall inducer	*Myrcia retorta* - Myrtaceae	Southern Brazil	Jorge *et al.* (2016)
H. tabebuia	Gall inducer	*Tabebuia* spp. - Bignoniaceae	Dominican Republic, Florida (USA), Puerto Rico	Cabrera & Segarra (2008)

H. tenuis	Possibly gall inducer	*Hura crepitans* - Euphorbiaceae	Guadeloupe; Panama	Hood (1914); Bournier (1993)
H. tillandsiae	Unknown	Collected from *Tillandsia compressa* - Bromeliaceae	Costa Rica	Mound & Marullo (1996)
H. tupi	Unknown	-	Southeastern Brazil	Hood (1955)
H. urinator	Unknown	-	Argentina	Mound & Marullo (1996)
H. varicolor **sp. nov.**	Gall inducer	*Neomitranthes obscura* - Myrtaceae	Southeastern Brazil	Carvalho-Fernandes *et al*. (2016)

Capítulo 2

PHYLOGENETIC ANALYSIS OF *HOLOPOTHRIPS* HOOD (THYSANOPTERA: PHLAEOTHRIPIDAE) BASED ON MORPHOLOGY

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Phylogenetic analysis of *Holopothrips* Hood (Thysanoptera: Phlaeothripidae) based on morphology

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Abstract. In the Neotropical region, *Holopothrips* is a diverse group of thrips associated to galls, with a variety of plant hosts and wide morphological diversity. Relationships to other Neotropical groups have been proposed, but are still untested, and the monophyly of the genus remains doubtful. Here, we perform a phylogenetic analysis of *Holopothrips*, based on morphological characters. Both discrete and continuous characters were coded and organized into two separated matrices, and a total matrix merging all data. These datasets were analyzed with a Parsimony criterion, both weighted and unweighted, using the New Technology search implemented in TNT. A total of six analyses were performed, and all of them failed to recover *Holopothrips* as a monophyletic grouping. However, Bremer and Bootstrap support values were very low, and the topologies varied among all analyses. We explore the topologies obtained, looking for tendencies presented by the data, and discuss some possible causes for these low support values. While our analyses lack the support to make any taxonomic decisions, the fact that none of them recovered *Holopothrips* as it is currently composed indicates that further studies are needed to provide a better generic delineation and character evolution in this group.

Key words. Neotropics, plant galls, *Fourbethrips*, *Jersonithrips*, *Johansenthrips*, *Mixothrips*, *Plagiothrips*.

Introduction

The thysanopteran genus *Holopothrips* (Phlaeothripidae) is a diverse group of thrips known only from the Americas. It has an interesting ecological standing, as the main group of thrips in the Neotropical region associated with plant galls. Half of the 60 described species have been collected or recorded inside galls of a variety of plant families, especially Myrtaceae (Lindner *et al.*, in prep.). Most *Holopothrips* species collected from galls are the inducers of such plant modifications, but at least two species have been recorded invading abandoned Cecidomyiidae galls (Bournier, 1993; Zamora *et al.*, 2015), or inside galls induced by other *Holopothrips* (Lindner *et al.*, in prep.). These thrips also have the ability to become pests of cultivated plants by altering growth and architecture, as well as tissue composition (Jorge *et al*., 2016). Serious injuries caused by *Holopothrips* species have been reported to cashew, pineapple, feijoa crops in Brazil and to ornamental *Tabebuia* trees in Central America (Costa Lima, 1935; Cabrera & Segarra, 2008; Lima *et al*., 2017).

The genus was established by Hood in 1914, based on two species collected from leaf galls in Panama. Between 1929 and 1986, 16 new species from several neotropical countries were described to the genus, most of them by Hood in his works of 1938, 1942 and 1955. Mound & Marullo (1996) made the most comprehensive revision of the group so far, describing six new species and synonymizing four genera (*Anoplothrips* Hood, *Caraibothrips* Bournier, *Homorothrips* Hood and *Phrasterothrips* Bagnall), which shared several morphological similarities with *Holopothrips*. In the following two decades, five additional new species were described, two from Central America and three from Southern Brazil. More recently, Lindner *et al.* (in prep.) revisited the genus, describing 24 new species in *Holopothrips*, the majority from Brazil.

Holopothrips is included in the family Phlaeothripidae, subfamily Phlaeothripinae, which is itself probably a paraphyletic assemblage of species (Buckman *et al.*, 2013). While several proposals for tribal classifications in the subfamily have been produced, none of them had a phylogenetic study to support such propositions. Currently, only one tribe comprising 35 genera is satisfactorily recognized, Haplothripini (Mound & Minaei, 2007). The remaining Phlaeothripinae species are traditionally divided between two loosely defined lineages, the leaf-feeding *Liothrips* lineage and the fungus-feeding *Phlaeothrips* lineage (Mound, 1994; Mound & Marullo, 1996). Members of the *Liothrips* lineage usually have one sense cone on antennal segment III and three on IV, basantra absent, and fore wings parallel-sided. However, there is not a defined suit of characters to diagnose a member of the *Phlaeothrips* lineage, and several

genera have been included in it lacking a proper justification (Mound & Marullo, 1996). *Holopothrips* itself has not been formally included in either of the lineages; while it has parallel wings and the galling habit, it does not possess the same sense cone formula as in *Liothrips* lineage members, and some species of the genus possess weakly defined basantra.

Holopothrips was first considered by Hood (1914), without further comments, to be related to *Gynaikothrips*, an Oriental genus of galling thrips. However, Mound & Marullo (1996) suggested that this group might be closely related to two other Neotropical genera, also associated with galls: *Plagiothrips* Priesner and *Mixothrips* Stannard, the latter included within the *Phlaeothrips* lineage (Mound, 1994; mentioned as "*Myxothrips*"). Another three genera were recently proposed from Costa Rica to be related to *Holopothrips*: the gall-inducers *Jersonithrips* and *Johansenthrips* (Retana-Salazar & Nishida, 2007; Retana-Salazar & Soto-Rodríguez, 2008) and *Fourbethrips*, found living inside galls of Cecidomyiidae (Soto-Rodríguez, Nishida & Retana-Salazar, 2012; Mound, 2013). Each of these genera has only one or two species, having been diagnosed on particular unusual traits not shared by *Holopothrips* species. However, *Holopothrips* itself is a group that currently has a wide morphological diversity, and the traits used to differentiate these other genera could very well fall within the range of variation of the group.

The diagnosis of *Holopothrips* is usually made by a combination of the following morphological characters: presence of a third pair of wing-retaining setae on abdominal tergites II–VII; presence of anterior discal setae on metanotum; males usually with multiple and complex pore plates on abdominal sternite VIII, frequently on VI–VII as well; and females with a visible spermatheca (Mound & Marullo, 1996; Zamora *et al.*, 2015; Lindner *et al.*, in prep.). However, most of these characters are variable, and one or more of them is absent in some of the species placed in the genus. At the same time, some of these characters are not exclusive to *Holopothrips*: several phlaeothripid species bear anterior discal setae on metanotum, and some genera, such as *Plagiothrips*, also bear a third pair of wing-retaining setae in most tergites.

Due to such morphological variation (Fig. 1), since Mound & Marullo's (1996) revision of the group, questions about the monophyly of *Holopothrips* with respect to the proposed related genera have arisen. The only attempt to test these relationships through a phylogenetic framework (Retana-Salazar, 2016) included mostly literature data of 36 *Holopothrips* taxa, of which 5 were undescribed species; and only *Jersonithrips* and *Johansenthrips* as outgroups. Based on the results of this analysis, the author informally proposed (but did not officialize) the redefinition of *Holopothrips* to exclude the species *H. ananasi*, *H. ferrisi*, *H. oaxacensis* and *H.*

tillandsiae, and revalidation of the genus *Phrasterothrips*, synonymized by Mound & Marullo (1996), to include the species *H. conducans*. However, the reliability of this work is uncertain, due to the few characters used (25 characters for 38 taxa, of which only 16 were indeed informative), and the presence of characters with confusing definitions or dependent on each other.

Here, we perform a phylogenetic analysis of *Holopothrips* using morphological data, comprised of discrete characters, as well as measurements used as continuous characters. Phylogenetic studies on Thysanoptera are often difficult. In almost all cases, taxonomic work involves macerating specimens with NaOH and further permanent mounting on microscopic slides using Canada Balsam. Such procedure dissolves most of the internal contents of thrips, thus making DNA extraction of mounted specimens virtually impossible. In addition, most thrips species are known only from the type series, such as in *Holopothrips*, where about 75% of the species have never been recollected, and this lack of fresh material currently limits molecular approaches. Thus, the main objective of this work is to test if the available morphological data supports the monophyly of *Holopothrips*. Due to the limited size of most phylogenetic studies using morphology in the order Thysanoptera, we also propose an extensive list of new and recoding of traditional characters, mostly from external morphology. Finally, we also test if the proposed suprageneric relationships for *Holopothrips* can be recovered (Mound & Marullo, 1996; Retana-Salazar & Nishida, 2007; Retana-Salazar & Soto-Rodríguez, 2008; Mound, 2013).

Material and Methods

Taxon sampling

A total of 87 species were included in the analysis, as detailed on Table 1. The ingroup was comprised of 55 *Holopothrips* species, more than 90% of the valid species of the genus. Due to the lack of information in the original descriptions and impossibility to examine any specimen, the following species were not included in the analysis: *H. affinis* (Bagnall), *H. balteatus* Hood, *H. elongatus* Moulton, *H. seini* (Watson), *H. urinator* De Santis. The outgroup comprised 30 different genera belonging to subfamily Phlaeothripinae, divided into two groups. Outgroup 1 included the five genera proposed to be closely related to *Holopothrips*, with all six species described for them. Outgroup 2 included 25 genera, involving species with a wide variety of habits and from several regions of the world. Most of Outgroup 2 were not considered to be related to *Holopothrips* in previous taxonomic studies. These taxa belong to the three

lineages proposed within Phlaeothripinae, and have been included to explore what could be the standing of *Holopothrips* and related genera within the subfamily (Mound, 1994; Mound & Marullo, 1996). Some of the outgroups are species with gall-inducing behaviour, which could share some morphological adaptations with *Holopothrips*. The analysis was rooted on an unidentified species of *Elaphrothrips*, a genus belonging to the other subfamily within Phlaeothripidae, Idolothripinae.

Specimens from the following collections were studied for this work: Australian National Insect Collection (ANIC - Canberra, Australia), The Natural History Museum (BMNH - London, England), Smithsonian National Museum of Natural History, which is held at United States Department of Agriculture (USDA - Beltsville, USA), Senckenberg Museum (SMF - Frankfurt, Germany) and Universidade Federal do Rio Grande do Sul (UFRGS - Porto Alegre, Brazil).

Morphological studies

Slide-mounted specimens of most included taxa were observed using an optical microscope for morphological studies. Most specimens were macerated with Sodium Hydroxide prior to mounting, which modifies the colours in relation to fresh specimens and dissolves most of the internal contents. Thus, mostly characters for all external body parts of adults were used.

The characters used for this work were defined after observations of several *Holopothrips* species, and from surveys of their original descriptions and some morphological studies (Mound & Marullo, 1996; Bhatti, 1998; Zamora *et al.*, 2015; Eow, 2016; Lindner *et al.*, in prep.). We included in the analysis several morphological traits commonly used to differentiate *Holopothrips* species, or traditionally mentioned as diagnostic of the group, being coded in a phylogenetic framework for the first time here. We also propose characters based on structures that are not commonly used in *Holopothrips* taxonomy, such as mesonotal chaetotaxy, and traits from the ventral surface of thoracic segments, among others. Finally, some characters that are not variable within the ingroup but are diverse in the outgroup were also included, to help structure the topology of outgroup taxa.

We used the same morphological terminology from Lindner *et al.* (in prep.), in which can also be found a discussion of several of the traits used for the characters proposed here. All characters used in this analysis are given in detail, with a brief discussion, on Supporting File 1. Photos of studied specimens were taken using the microscope Nikon AZ 100M and the software NIS-Elements AR, and posteriorly edited using the software Photoshop CS5.

Character coding

A total of 140 characters from all body parts of adult thrips were included in the analysis. Of these, 109 were coded as discrete characters, 75 binary and 34 multistate, and all of them treated as unordered. Thirty-one continuous characters were included in the analysis, scaled to 1, and treated as ordered (Goloboff *et al.*, 2006). We used observed range instead of the mean for continuous characters, whenever more than one specimen were available for a terminal taxon, to include the studied variation. We did not use the mean plus standard deviation of each character, as suggested by Goloboff *et al*. (2006), due to having access to a limited number of specimens for most of the terminals. All character statements are written following Sereno (2007), however, we did not distinguish the "neomorphic" characters from the "transformational" ones as in the original proposal.

Non-applicable characters were coded as "-", missing data was coded as "?". We coded a character as polymorphic when two or more states were observed in different specimens of a terminal taxon. If in a terminal taxon it was difficult to define which of two states was present, out of three or more proposed states, it was coded as polymorphic for the two doubtful states instead of just leaving it as "?". This way, the analysis would consider only the two states as possible, instead of all states of the character. A discrete character matrix was built on Mesquite (v 3.04, Maddison & Maddison, 2015), and the continuous characters were manually added to the file exported for TNT. The full data matrix, with discrete and continuous characters, is provided on Supporting File 2, the discrete-only matrix is provided on Supporting File 3, and the continuous-only matrix is provided on Supporting File 4; all as TNT files (.tnt).

Phylogenetic analysis

Parsimony analysis was implemented in TNT (v. 1.5, Goloboff *et al*., 2008; Goloboff & Catalano, 2016), and heuristic search strategies were conducted using the new technology option. Data was organized into three alternate subsets: only discrete data (Discrete matrix, D), only continuous data (Continuous matrix, C), and both data combined (All Data, total matrix, T). Each subset was then analyzed with both equal weights (EW) and implied weighting (IW), as described on Figure 2. The continuous data was analyzed alone mostly as a means of comparison with the discrete dataset, to see if both types of characters would yield congruent results; it is still uncertain if continuous characters by themselves have useful phylogenetic information despite the wide phenotypic variation inherent in this type of data (Goloboff *et al.*,

2006). The discrete dataset was also analyzed by itself to observe if the addition of continuous data in the total matrix modifies the support values observed for recurrent groupings. Due to some uncertainties about the complete independency of body setae characters, we performed a search using only Matrix T, where all chaetotaxy characters were excluded (except the two diagnostic for *Holopothrips*).

The value of k to be used on IW searches was defined using Mirande's script (Mirande, 2009). We used the script on the All Data matrix to find the k value that better fits this dataset, which was then used for the other two datasets (matrix D and C) as well. Despite the possibility of this value of k not being the best for the separated data, using the same k in all IW analysis allows better comparisons between results. The Mirande's value defined was 8.964, based on the arithmetic mean of the k values of the trees with the smallest sum of SPR distances.

The following parameters were used for all searches: random seed 1, slack for sectorial searches 500, search level 4, ten cycles of ratchet and ten cycles of tree drift with default parameters, hitting three times the shortest tree (except for EW-C search, which entered a looping and was stopped after two hours of search). One round of TBR was performed after the main search to find if there were any more optimal trees. If there were multiple most parsimonious trees, the strict consensus of all trees was calculated. A list of all commands used for each of the searches is given in Supporting File 5.

Support

We calculated here Bremer (absolute and relative) and Bootstrap/Bootstrap GC supports. For Bremer supports we used 50000 suboptimal trees with up to ten extra steps for EW searches, and 90000 suboptimal trees with up to 1.0 fit above the optimal value for IW searches (Supporting Files 6 and 7). For bootstrapping, 500 replications were performed for each search listed in Figure 2, using the following parameters: random seed 1, slack for sectorial searches 500, search level 7, ten cycles of ratchet and ten cycles of tree drift with default parameters, with one round of TBR after the search. No minimum amount of hits was set as this would turn resampling prohibitively long, except for minimum of two hits in the EW-D search. A list of commands used for resampling each of the searches is given in Supporting File 5.

In all searches using the Continuous matrix, the taxon *Holopothrips ferrisi* was inactivated due to lacking any continuous data. It was left active in searches using the All Data matrix. All trees generated by the analysis were saved with their support values as SVG files, and subsequently edited in the software Inkscape.

Results

Each of the six analyses performed obtained a different topology, all of them with low support values (relative Bremer <50, Bootstrap/Bootstrap GC <50). The EW-D analysis resulted in 51 most parsimonious trees, and the strict consensus of these trees is presented on Figure 3. All other searches found a single most parsimonious or with best fit tree, with EW-T, IW-D and IW-T presented on Figures 4–6, respectively. The number of steps or fit values for each tree obtained is listed on Table 2.

The strict consensus of all results obtained does not have any resolution except for the pairing (*Mirothrips* + *Adraneothrips*), indicating that this is the only grouping in common between all trees. The agreement subtree between EW-D and IW-D has 23 taxa, while the agreement subtree between EW-T and IW-T has 50 taxa, indicating that the addition of continuous characters, which appear to be less sensitive to the effect of weighting, doubled the congruence between both trees. SPR distances between trees shows that the two most similar trees are EW-D and IW-D, with a difference of 25 steps between both. The most different trees are EW-C with IW-D and IW-D with IW-C, both pairings with 84 steps of distance. All SPR distances between the different searches are given on Table 3.

In none of the searches was *Holopothrips* recovered as a monophyletic grouping, and all topologies obtained include *Jersonithrips galligenus* among *Holopothrips*, in varying positions. In all EW and in IW-T searches the species *H. brevicapitatum*, *H. longihamus* and *H. longisetus* were not recovered together with the rest of *Holopothrips*, being in varying positions among the outgroups. A clade that groups a large amount of *Holopothrips* species was recovered in each of the four searches with only discrete data and with all data. Despite these clades not having the same composition and topology, thus not being comparable, we have named them as "Clade A" in each tree for easier reference (Figs 3–6). The analysis including only continuous data recovered a very different topology when compared to the other analysis. The IW-D data search recovered all *Holopothrips* species together in the same clade, but also included *Fourbethrips fiorella*, *Jersonithrips galligenus*, both *Mixothrips* species and *Plagiothrips eugeniae* within it.

The support values obtained for all analyses were very low, with only the two searches using continuous data alone recovering few clades with Relative Bremer Support of 50% or more. The clade A, indicated in in each of the EW-D, EW-T, IW-D and IW-T searches, had particularly low support values in all four topologies.

Discussion

Our analyses could not find any groupings resistant to the different treatments and datasets used on this work (Fig. 2). The absence of common clades between the analyses can be related to the effects of homoplasy, or incongruences between discrete and continuous data. Besides the instability of these results across different treatments, the results of all analyses performed are weakly supported by the data. The low Bremer and Bootstrap support values found in all searches are somewhat surprising, and while we will discuss some tendencies observed in the topologies, none of the trees obtained is considered to be representative of the actual relationships of *Holopothrips* species here. Thus, we will propose here some of the possible causes for such low support values and explore the behaviour of data and the diagnostic characters of the genus in the obtained topologies, without making any propositions regarding the systematics of *Holopothrips*.

Topology comparisons

Holopothrips was not recovered as a monophyletic grouping in any of the analysis performed. Even if the low support values do not allow us to select any of the topologies obtained here as preferred, the failure to recover *Holopothrips* as a natural group with the different datasets and treatments used is an indication that this should be further investigated.

The largest SPR distances being between EW-C and IW-D topologies is expected, as these analyses deal with different datasets and treatments. The results obtained from the two different datasets are highly incongruent with each other, even when under the same treatment, as observed by IW-D and IW-C topologies having the same highest value of SPR distance. At the same time, while weighting the characters does influence the results, the effect is smaller than the usage of different datasets, as observed by EW-D and IW-D topologies having the lowest value of SPR distance. This is also an indication that our discrete matrix does not contain too much homoplasy, or else it would have been penalized strongly in the weighted analysis.

The addition of continuous characters to the matrix (EW-T and IW-T analysis) did not change significantly the support values obtained when compared to only discrete data (EW-D and IW-D analysis). However, it is clear that these characters have increased the overall number of taxa in the agreement subtrees (23 taxa between EW-D and IW-D, against 50 taxa between EW-T and IW-T). The effect of including continuous characters in phylogenetic analysis is still not fully understood, and apparently is variable between analyses: it can in some works increase

the overall support and resolution of topologies (Goloboff *et al*. 2006), while in others their addition seems to reduce the support of some groupings (Pereyra & Mound, 2010). The way such characters are coded (discretized, as means, ranges, ratios between measures, standard deviation from the mean, etc.) surely can influence how informative they will be. Despite the topologies being highly incongruent to each other, some tendencies were observed for some taxa, and might deserve further investigation. For these observations, we will consider only the EW-D, EW-T, IW-D and IW-T topologies, which managed to recover a clade that included most *Holopothrips* species (although of varying composition between the different analyses), which are denoted as "Clade A" in each tree.

Three species in the genus (*H. brevicapitatum, H. longihamus* and *H. longisetus*) were recovered outside of "Clade A" in most of these topologies. In the EW-D consensus the three species are in the polytomy that includes some *Holopothrips* species, a clade reuniting several outgroups and "Clade A"; and in both analyses with all data these species are basal to "Clade A". IW-D recovered these three species inside its "Clade A", but in a somewhat basal grouping that also includes *Fourbethrips fiorella* and the two *Mixothrips* species.

The four analyses considered here (Figs 3–6) recovered a grouping with the eight *Holopothrips* species whose body is mostly lightly coloured (*H. bicolor, H. carolinae, H. fulvus, H. graziae, H. inquilinus, H. paulus, H. porrosati* and *H. tabebuia*). The topology of such grouping remained the same with or without the presence of continuous data in the weighted analyses. However, it is not possible to confirm at the moment if this clade indicates a possible natural grouping or if it is a bias artifact of the colour characters, which are 21 out of 140 characters used in the analysis. The use of body colour as source for characters in phylogenetic analysis is inconstant, due to uncertainty over the effect of plasticity of colour in the data, and the limitations on accessing the natural colour of a species through mounted specimens. Aposematic or mimetic colour patterns show a certain level of constraint and structure in their evolution, which may result in strong phylogenetic signal that goes against the signal found in morphological data (Areekul & Quicke, 2006). While the biological role of this difference in colour within *Holopothrips* (dark-bodied species x light-bodied species) was never studied empirically, we believe that this is not a case of aposematic or mimetic colouration, due to the reduced size of thrips and their usual habit of living inside enclosed spaces such as plant galls. Both analyses with only continuous data did not recover such grouping.

Jersonithrips , one of the genera proposed to be related to the ingroup, has been recovered amidst *Holopothrips* species in all topologies obtained. The original description of

this genus (Retana-Salazar & Nishida, 2007) comments that it would be identified as a *Holopothrips* species if following the key provided by Mound & Marullo (1996), but then proceeded to justify its establishment as its own genus by the unique habit of inducing a gall in a species of fern. These authors also argued that describing a new species within *Holopothrips* would not contribute to a natural classification, due to the genus being considered a "problematic" group and possibly paraphyletic. The phylogenetic analysis performed by Retana-Salazar (2016) in *Holopothrips* included *J. galligenus* as one of the outgroups, and while it was recovered in a polytomy with *Johansenthrips galligena* and two *Holopothrips* species, the author supported its maintenance as its own genus. However, the inclusion of *Jersonithrips* within *Holopothrips* in all of the analyses performed here, is an indication that the relationships of this genus deserves more study.

The two *Mixothrips* species had varying positions in the different topologies, but as sister taxa only in IW-D and IW-T. It was included within "Clade A" only in the IW-D analysis, in a small grouping including *Fourbethrips fiorella* and three other *Holopothrips* species, as described above. The two species had a basal position relative to the node of "Clade A" in EW-D, EW-T and IW-T, but in the first two, one *Mixothrips* was basal to the other. Curiously, in both analysis including only continuous characters, the two *Mixothrips* species were very distant from each other, with *M. nakaharai* being recovered closer to the base of the three. This genus might not be related to *Holopothrips*, and might even require a revision if these results are to be repeated in an analysis with higher support values.

Plagiothrips eugeniae was recovered in a basal position to "Clade A" nodes in all analyses, except IW-D, in which it was recovered among "*Holopothrips*" species. This genus is differentiated by the presence of a tarsal tooth on fore legs, which is not found in any *Holopothrips* species, but in all topologies *Plagiothrips* was not recovered among species with this character. *Plagiothrips eugeniae* was originally described within the genus *Gynaikothrips*, but in none of the analyses were both groups recovered together.

Johansenthrips galligenus was located near the base of the tree in five out of the six topologies, and within an outgroup clade in the sixth, which may be an indication of this genus being actually not related to *Holopothrips*. Similarly, *Fourbethrips fiorella* was located near the base of the tree in four out of six topologies; however, in the EW-D analysis it was paired with *Holopothrips longisetus*, and both were located in a polytomy close to the base of the tree. In the IW-D analysis *F. fiorella* was actually included within "Clade A", in a small grouping including the two *Mixothrips* species, *H. longisetus* and other two *Holopothrips* species. While

it seems that *F. fiorella* is possibly also not related, further investigation is required to confirm or refute any of the relationships proposals discussed in this section.

Behaviour of diagnostic characters

We have considered here four characters to be "diagnostic" of *Holopothrips*, based on previous taxonomic reviews of the group (Mound & Marullo, 1996; Zamora *et al.*, 2015; Lindner *et al.*, in prep.): presence of anterior discal setae on metanotum (C94); presence of a third pair of wing-retaining setae on abdominal tergites II–VII (C114); "complex" male pore plates - included as presence, texture, appearance and occurrence (C119–C122); and visible female spermatheca (C124) (Supplementary file 1). On Table 4 we present the number of steps for each of these characters in each analysis they were present.

None of these characters was recovered as exclusive of *Holopothrips* in any of the analysis. The anterior pair(s) of metanotal discal setae, present in all *Holopothrips* species analyzed, is also found in a variety of unrelated outgroups, including species from South America, Asia and Oceania (see Bhatti, 1998 for a discussion on the chaetotaxy of metanotum and further examples). The third pair of wing-retaining setae was not exclusive of *Holopothrips* (being found all genera of Outgroup 1 except for *Mixothrips*, and in *Pistillothrips* from Outgroup 2), and was also not consistent within the genus: *H. clarisetis* and *H. infestans* lack these setae, and at least three or four further species in the genus have the presence of this pair of setae inconsistent among individuals.

The male sternal pore plates were evaluated with four different characters, in an attempt to explore the diversity found, especially within *Holopothrips* species. While the presence of these plates is far from being exclusive to the genus (being observed in 14 out of 30 outgroup genera analyzed), some traits of pore plates seemed to be exclusive to *Holopothrips*. For instance, reticulate texture was recorded with certainty only in *Holopothrips* species, but only in 14 out of 55 species. Thus, the usefulness of this trait as a diagnostic character is limited. The appearance of pore plate(s) in sternite VIII seems to be useful as well, with two of the states (S3 - single median pore plate posterior to discal setae; S4 - two anteroangular plates and a transverse band posterior to discal setae) being found only in *Holopothrips* species (with S4 also being found in *Jersonithrips galligenus*, which has been recovered together with other *Holopothrips* species in all analysis). The occurrence of pore plates seems to be informative to some degree as well: none of the outgroups included in this analysis had pore plates in any sternite besides VIII, thus any occurrence on sternites IV–VII seems to be exclusive to

Holopothrips. However, *H. brevicapitatum,* a species with three pore plates on sternite VIII and occurrence on sternites IV–VIII, was recovered outside of "Clade A" in three out of four analyses considered here; an indication that these characters might not be exclusive to the genus. Moreover, six *Holopothrips* species lack any pore plates, and other two are known only from females, thus pore plates cannot be used as a diagnostic character of the genus without creating exceptions for these species.

Finally, the female spermatheca seemed to be the closest to a "diagnostic" feature of *Holopothrips*: it was visible in all species of the genus where females were studied, and present in five out of the six Outgroup 1 species (a female of *Jersonithrips* was not available for study to confirm this character). The only Outgroup 2 terminal that also has a visible spermatheca is *Pistillothrips*, a genus originally described from Mexico, whose relationship to *Holopothrips* deserves further investigation. The presence of a visible spermatheca might be a useful trait for identifying the clade of Neotropical galling thrips, if the relationships of *Holopothrips* with Outgroup 1 species are confirmed in the future.

Possible causes for low support values

Low support values scattered across branches at several points of a topology have been previously observed in some phylogenetic studies with Thysanoptera. In a morphological phylogeny of *Desmothrips* (Aeolothripidae), while the genus itself had high GC support, the clades within it had low support; adding continuous characters to the dataset further reduced these support values, with most values of relative Bremer support below 50 (Pereyra & Mound, 2010). A phylogenetic analysis of Idolothripinae species, based on discrete morphological characters, recovered several clades with Bremer support of only one or zero steps (Eow, 2016). The molecular phylogeny of Thysanoptera recovered high Bootstrap support values for most families tested and for several species groups, but also had various clades with low support values at different points of the tree (Buckman *et al.*, 2013). Despite that, all of these studies have recovered at least some clades with high support, which indicates that there are other factors other than the group itself that may be influencing the low support values of our analyses. Here we do not affirm that low support values are a pattern within Thysanoptera studies; however, the frequent presence of such low values in different metrics still deserves a mention. To access if this is indeed a pattern within the group or an artifact of the few analyses performed, more phylogenetic studies, with different Thysanoptera taxa, and using the same support metrics for comparison, should be performed.

Most of the characters used in this analysis were coded for a phylogenetic framework for the first time here, with some notable difficulties in defining and coding them. Observations of available material show that several characters have a continuum of variation, thus defining boundaries between states end up being difficult and arbitrary at times. Choosing between states when the observed specimen had an intermediate state was a frequent problem as well, especially noticed in characters such as shape of setae apex, which could not be treated as a continuous character despite the continuum of variation observed. At the same time, much of the variation observed is associated with few types of morphological traits: 36 characters in the analysis are associated with chaetotaxy, 21 with colouration of specimens, 19 with body sculpture, representing more than 50% of our data matrix. Performing a test by removing all of these characters is not feasible, as the removal would reduce greatly the amount of available information, which would not be enough to define relationships with a good level of support for the 87 taxa included.

Part of the reason, for using so many characters of the same type, are the limitations imposed on the study of thrips by the way specimens are mounted on microscopic slides. Most characters available are from external morphology, with very few internal characters remaining after specimen maceration. Thrips are mounted in a way that most characters from dorsal and ventral surface are visible, but cover slip pressure may influence the apparent size and shape of body parts. At the same time, due to being isolated in balsam or other mounting media, thrips cannot be accessed for extraction of DNA nor Scanning Electron Microscope imaging.

Especially in the case of chaetotaxy characters, it is unclear how much inter-dependency there is among them. Due to the variation observed between different setae in the same species, we worked with one character for setal tip shape for every pair of pronotal seta (five in total). However, in most species, this shape is similar among all setae, which could indicate some sort of dependency among them. In some cases when the tip of setae did not agree among all pronotal setae, it was due to one or more of the setae having a reduced length in comparison; this was already coded also as a continuous character. However, a quick exploratory analysis removing all "tip of setae" characters, as well as one removing all chaetotaxy characters except for the two used as diagnostic features of *Holopothrips*, did not increase the overall support values obtained. Thus, even if chaetotaxy characters may have negative influence, they are not the only source of noise to the analyses.

While morphology seems to be a useful source of information for studies on *Holopothrips*, due to the wide range of morphological variation observed in the group (Lindner

et al., in prep.), this same variation might also be a source of noise for the phylogenetic analysis. One example is the observed difference in size between the smallest species of the genus (*H. inconspicuus*, around 1500 micrometers long) and the largest species (*H. permagnus*, almost 4000 micrometers long). Such differences in body size could influence all of the continuous characters measured, and this could explain why both of the analyses with only the continuous dataset failed to recover any structure to a possible "*Holopothrips*" group. However, it would be expected for this effect to be greatly reduced by the usage of stand = 1 and weighting in the analysis (Goloboff *et al*., 2006).

Another limitation of working with Thysanoptera morphology is the lack of studies involving sexual organs and their usage for species definitions. In several arthropod groups, characters from genitalia of either male or female are used to differentiate species, and offer a variety of characters informative at multiple levels in phylogenetic studies (Song & Bucheli, 2010). However, in Phlaeothripidae, the genitalia are inflatable, eversible sacs with limited structural information (Heming, 1970a; 1970b). In our study, the only characters associated with the sexual organs are the presence and shape of a visible spermatheca in females; and the presence, appearance and occurrence of sternal male pore plates, which are presumably associated with pheromone production (Mound, 2009). Thus, the phylogenetic signal found in genitalia, which is as informative as non-sexual characters, if not more (Song & Bucheli, 2010), could not be tested and accessed in these thrips.

Conclusions

While the results of our analyses were not consistent between datasets and treatments, and support values were very low in the majority of branches, our study still provides some interesting insights into the phylogeny of *Holopothrips*. The genus was not recovered as a monophyletic clade in any of the analysis performed; and of the proposed related genera, *Jersonithrips* was consistently recovered amidst *Holopothrips* species, while the remaining genera were mostly recovered as unrelated. None of the traits usually mentioned as diagnostic characters for *Holopothrips* is exclusive to the group or present in all of its members in all performed analyses. Here we do not make any proposals for a classification revision, but we underline all of these findings as indicative of *Holopothrips* being indeed a paraphyletic grouping, which needs further investigation and possible redefinition. Due to limitations associated with the way thrips are prepared for study, only morphological characters were available for this work, and it seems that this type of data was insufficient to define a stable

phylogeny with robust support. The characters proposed in this work should be tested further with different Phlaeothripidae species, and possibly modified and recoded, to improve their usefulness for phylogenetic analysis. At the same time, more effort in sampling areas for living thrips populations should be made, to allow collection of fresh specimens, from which molecular data could be extracted and sequenced for future analysis.

Supporting Information

File S1. Commented list of morphological characters.

File S2. Complete data matrix, including discrete and continuous characters.

File S3. Discrete data matrix.

File S4. Continuous data matrix.

File S5. List of commands used on TNT for each search.

File S6. TNT script used for Bremer support calculation, in equal weights analysis.

File S7. TNT script used for Bremer support calculation, in implied weighting analysis.

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References

Areekul, B. & Quicke, D.L.J (2006) The use of colour characters in phylogenetic reconstruction. *Biological Journal of the Linnean Society*, **88,** 193–202.

Bhatti, J.S. (1998) *New perspectives in the structure and taxonomy of Tubulifera*. Scientia Publishing, New Delhi.

Bournier, A. (1993) Thysanoptères de Martinique et de Guadeloupe. *Journal of Pure and Applied Zoology*, **3(3)**, 227–240.

Buckman, R.S., Mound, L.A. & Whiting, M.F. (2013) Phylogeny of thrips (Insecta: Thysanoptera) based on five molecular loci. *Systematic Entomology*, **38**, 123–133.

Cabrera, I. & Segarra, A. (2008) A new gall-inducing species of *Holopothrips* (Thysanoptera: Phlaeothripinae) from *Tabebuia* trumpet trees in the Caribbean region. *Florida Entomologist*, **91(2)**, 232–236.

Costa Lima, A.M. (1935) Um novo tisanoptero praga do abacaxi. *O Campo*, **6**, 43–45.

Eow, L.-X. (2016) The Phylogeny and Morphological Evolution of the Fungal Spore-feeding Thrips, Idolothripinae (Thysanoptera: Phlaeothripidae). PhD Thesis, 351 pp.

Goloboff, P.A. & Catalano, S. (2016) TNT, version 1.5, with a full implementation of phylogenetic morphometrics. *Cladistics*, **32**, 221–238.

Goloboff, P.A., Farris, J. & Nixon, K. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.

Goloboff, P.A., Mattoni, C.I. & Quinteros, A.S. (2006) Continuous characters analyzed as such. *Cladistics*, **22**, 589–601.

Heming, B.S. (1970a) Postembryonic development of the female reproductive system in *Frankliniella fusca* (Thripidae) and *Haplothrips verbasci* (Phlaeothripidae) (Thysanoptera). *Miscellaneous Publications of the Entomological Society of America*, **7**, 197–234.

Heming, B.S. (1970b) Postembryonic development of the male reproductive system in *Frankliniella fusca* (Thripidae) and *Haplothrips verbasci* (Phlaeothripidae) (Thysanoptera). *Miscellaneous Publications of the Entomological Society of America*, **7**, 235–272.

Hood, J.D. (1914) Two new Thysanoptera from Panama. *Insecutor inscitiae menstruus*, **2**, 49–53.

Hood, J.D. (1938) Studies in Neotropical Thysanoptera VII. *Revista de Entomologia*, **9**, 218–247.

Hood, J.D. (1942) A century of new American Thysanoptera III. *Revista de Entomologia*, **13**, 547–678.

Hood, J.D. (1955) Brasilian Thysanoptera VI. *Revista Brasileira de Entomologia*, **4**, 51–160.

Jorge, N.C., Cavalleri, A., Bedetti, C.S. & Isaias, R.M. (2016) A new leaf-galling *Holopothrips* (Thysanoptera: Phlaeothripidae) and the structural alterations on *Myrcia retorta* (Myrtaceae). *Zootaxa*, **4200(1)**, 174–180.

Lima, M.G.A., Dias-Pini, N.S., Lima, E.F.B, Maciel, G.P.S. & Vidal-Neto, F.C. (2017) Identification and pest status of *Holopothrips fulvus* (Thysanoptera: Phlaeothripidae) on dwarf-cashew crops in Northeastern Brazil. *Revista Brasileira de Entomologia*, **61(4)**,

271–274.
http://dx.doi.org/10.1016/j.rbe.2017.07.007

Lindner, M.F., Ferrari, A., Mound, L.A. & Cavalleri, A. (in prep.) *Holopothrips* diversity - a Neotropical genus of gall-inducing insects (Thysanoptera, Phlaeothripidae). Article to be submitted to Zootaxa.

Maddison, W.P. & Maddison, D.R. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.04. Available at http://mesquiteproject.org [Accessed 28.iv.2016]

Mirande, J.M. (2009) Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, **25**, 574–613.

Mound, L.A. (1994) Thrips and gall induction: a search for patterns. *Plant Galls* (ed. by M.A.J. Williams), pp. 131–149. Clarendon Press, Oxford, 1994.

Mound, L.A. (2009) Sternal pore plates (glandular areas) of male Thripidae (Thysanoptera). *Zootaxa*, **2129**, 29–46.

Mound, L.A. (2013) Homologies and Host-Plant Specificity: Recurrent Problems in the Study of Thrips. *Florida Entomologist*, **96(2)**, 318–322.

Mound, L.A. & Marullo, R. (1996) The thrips of Central and South America: an introduction (Insecta: Thysanoptera). *Memoirs on Entomology, International*, **6**, 1–488.

Mound, L.A. & Minaei, K. (2007) Australian insects of the *Haplothrips* lineage (Thysanoptera – Phlaeothripinae). *Journal of Natural History*, **41**, 2919–2978.

Pereyra, V. & Mound, L.A. (2010) Phylogenetic relationships within the genus *Desmothrips* (Thysanoptera, Aeolothripidae), an Australian genus of facultative flower-living predators. *Systematic Entomology*, **35**, 306–317.

Retana-Salazar, A.P. (2016) Filogenia de los grupos de especies de *Holopothrips* y grupos cercanos (Phlaeothripidae: Tubulifera: Thysanoptera). *Revista gaditana de Entomologia*, **VII(1)**, 549–586.

Retana-Salazar, A.P. & Nishida, K. (2007) First gall-inducing thrips on *Elaphoglossum* ferns: A new genus and species of thrips, *Jersonithrips galligenus* from Costa Rica (Insecta, Thysanoptera, Phlaeothripidae). *Senckenbergiana biologica*, **87(2)**, 143–148.

Retana-Salazar, A.P. & Soto-Rodríguez, G.A. (2008) A new genus and species of gall-inducing thrips (Thysanoptera: Tubulifera) from the neotropical region. *Brenesia*, **69**, 59–64.

Sereno, P.C. (2007) Logical basis for morphological characters in phylogenetics. *Cladistics*, **23(6)**, 565–587.

Song, H. & Bucheli, S.R. (2010) Comparison of phylogenetic signal between male genitalia

and non-genital characters in insect systematics. *Cladistics*, **26**, 23–35.

Soto-Rodríguez, G.A., Nishida, K. & Retana-Salazar, A.P. (2012) A new genus of gall-dwelling thrips from Costa Rica (Thysanoptera: Phlaeothripidae: Phlaeothripinae). *Revista Mexicana de Biodiversidad*, **83**, 605–610.

ThripsWiki (2018) *Thrips Wiki: providing information on the World's thrips.* URL. http://thrips.info/wiki/Main_Page [accessed on 21st February 2018].

Zamora, S., Hanson, P. & Mound, L.A. (2015) On the biology of *Holopothrips chaconi* **sp.n.** (Thysanoptera, Phlaeothripinae) from leaf-vein galls on *Piper* species in Costa Rica. *Revista Biologia Tropical*, **63(4)**, 1035–1042.

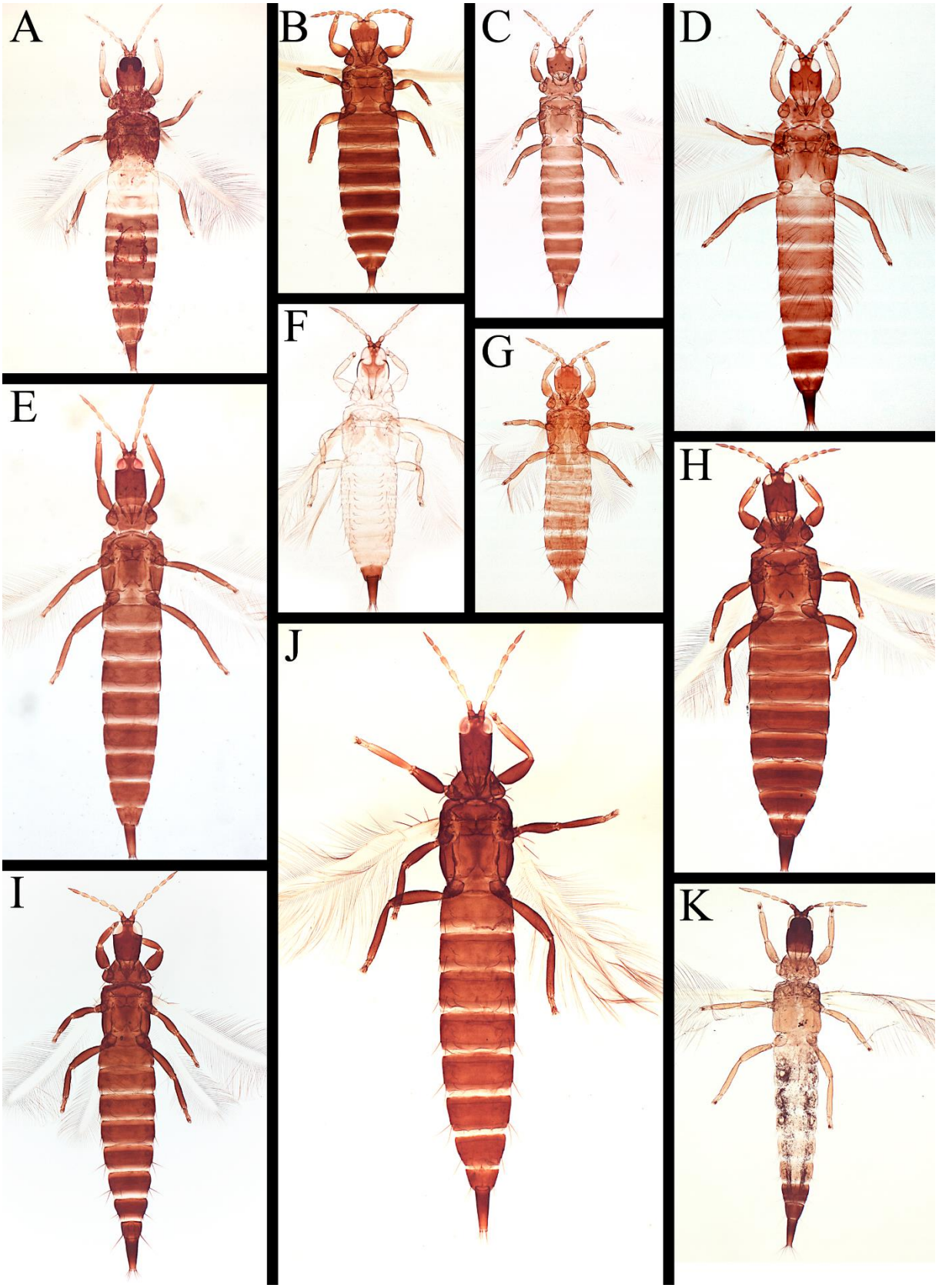

Figure 1. Morphological diversity within *Holopothrips*. All species scaled to represent correctly size differences. A, *H. signatus*; B, *H. clarisetis*; C, *H. mariae*; D, *H. chaconi*; E, *H. tenuis*; F, *H. fulvus*; G, *H. inconspicuus*; H, *H. cardosoi*; I, *H. atlanticus*; J, *H. orites*; K, *H. paulus*.

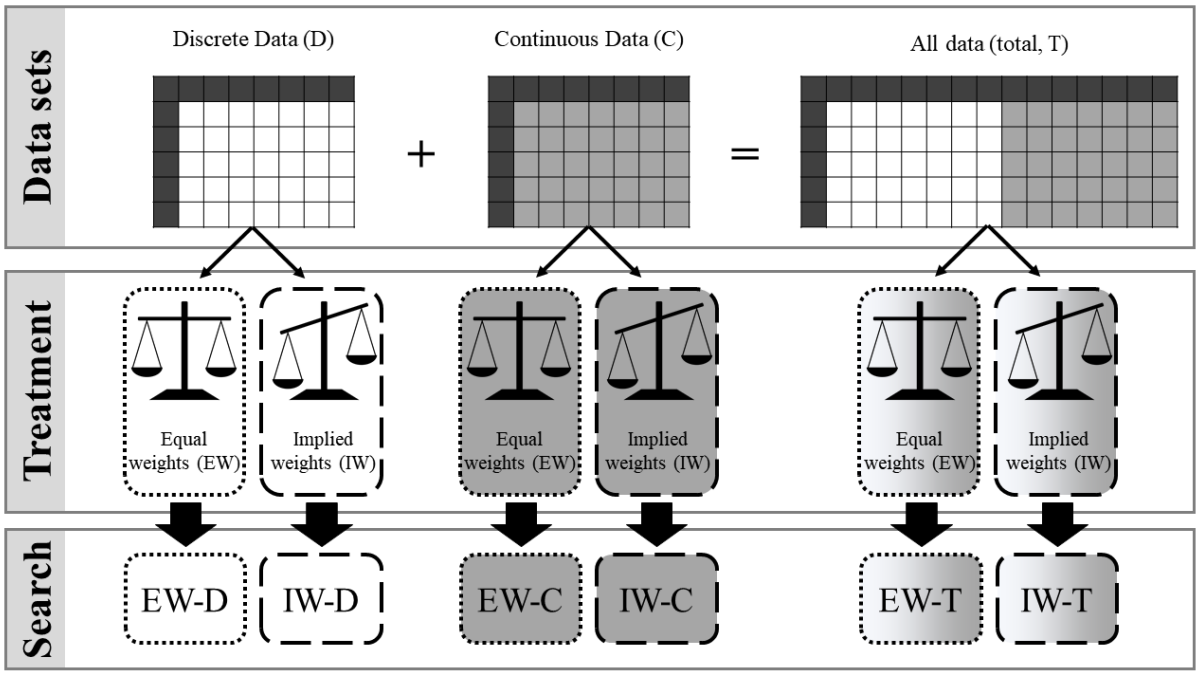

Figure 2. Combination of datasets (first row) and treatments (second row) used in each analysis performed in this work (third row).

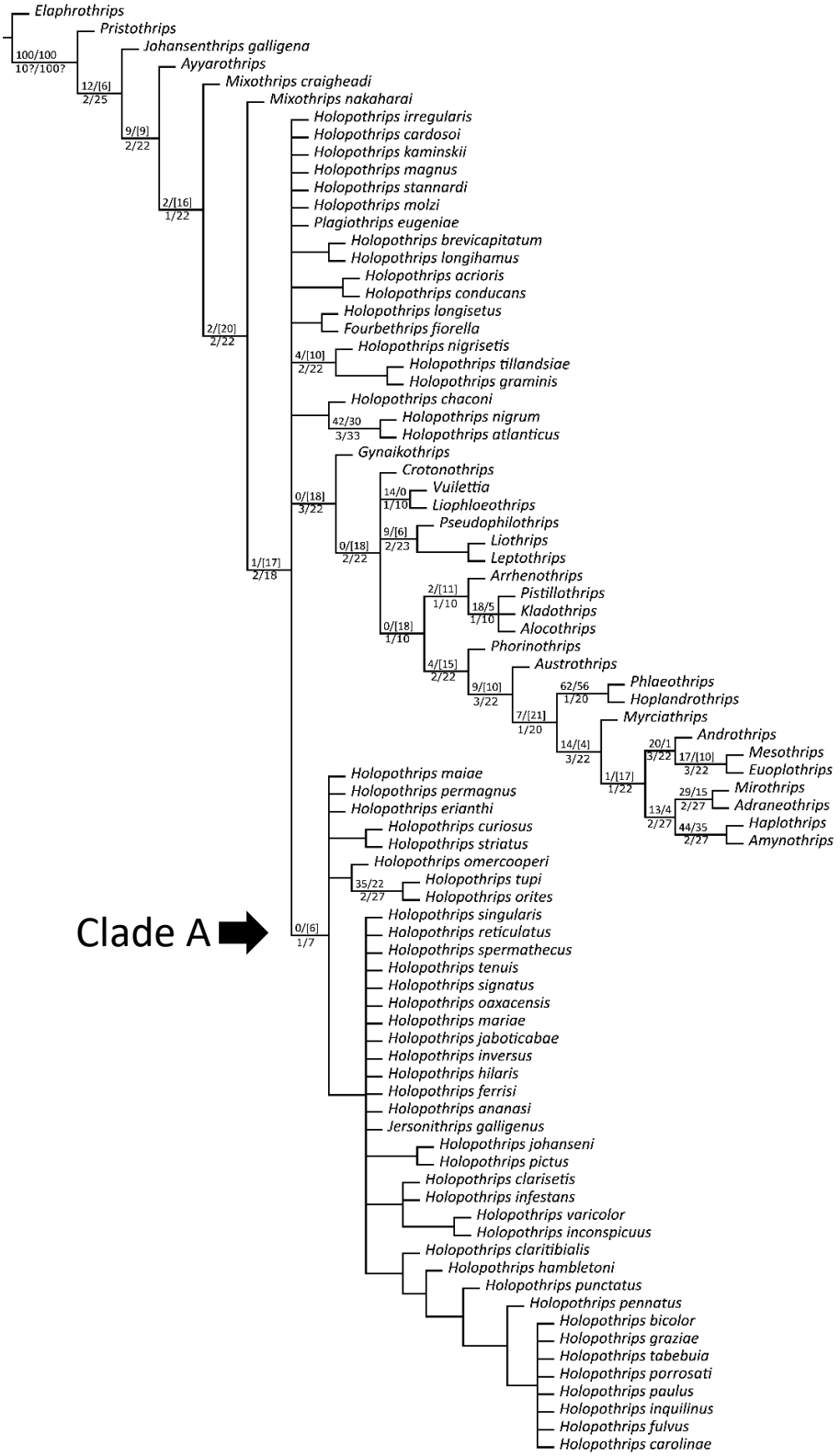

Figure 3. Equal weights, discrete-only dataset (EW-D) analysis: strict consensus of 51 most parsimonious trees obtained. Support values provided are Bootstrap/Bootstrap GC (above branch) and Bremer absolute/Bremer relative (below branch). Clade A represents the grouping that includes most *Holopothrips* species in this topology; this clade is not the same as the Clade A of other analyses. Some support values were not included in the tree.

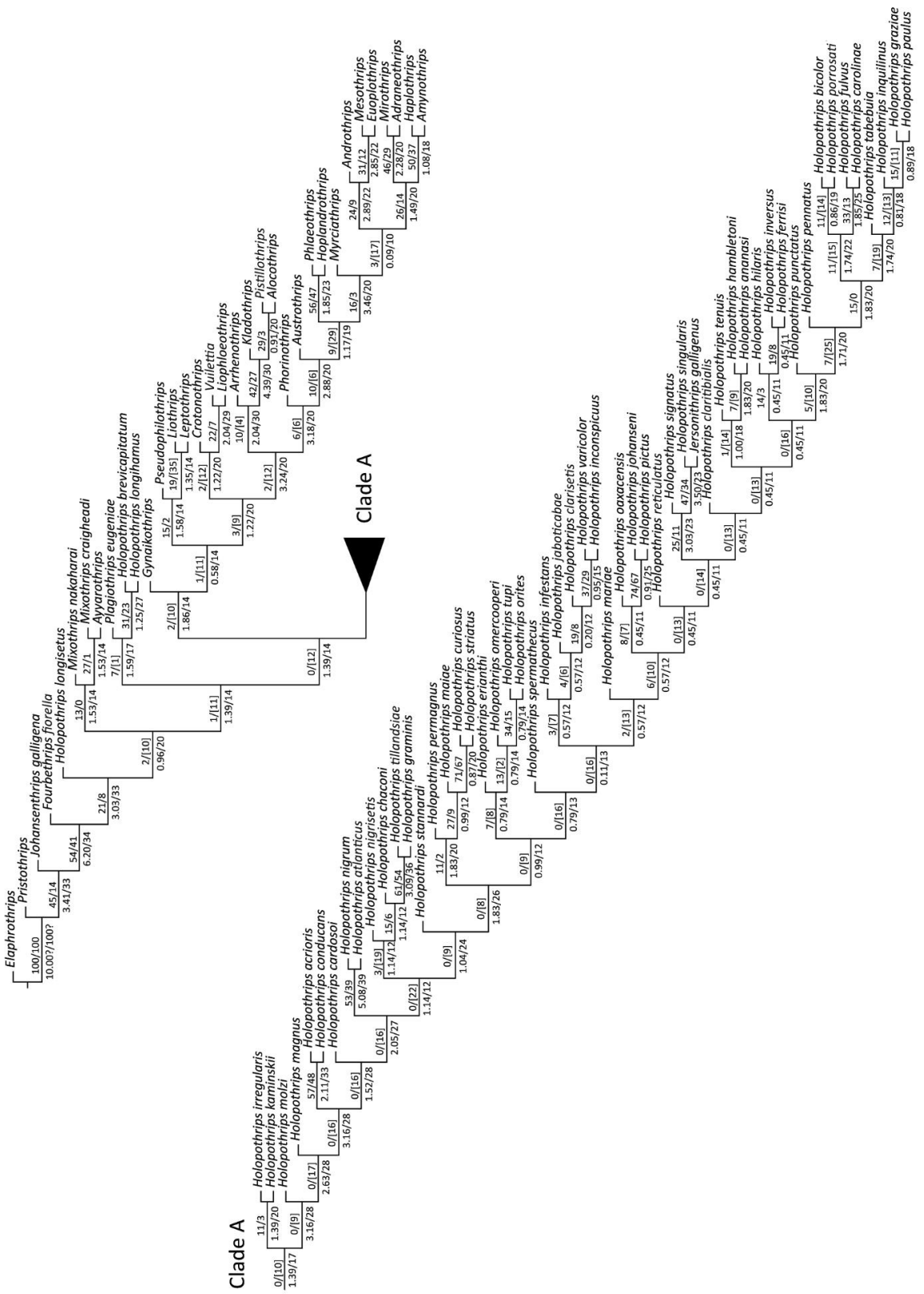

Figure 4. Equal weights, total dataset (EW-T) analysis: most parsimonious tree obtained. Support values provided are Bootstrap/Bootstrap GC (above branch) and Bremer absolute/Bremer relative (below branch). Clade A represents the grouping that includes most *Holopothrips* species in this topology; this clade is not the same as the Clade A of other analyses.

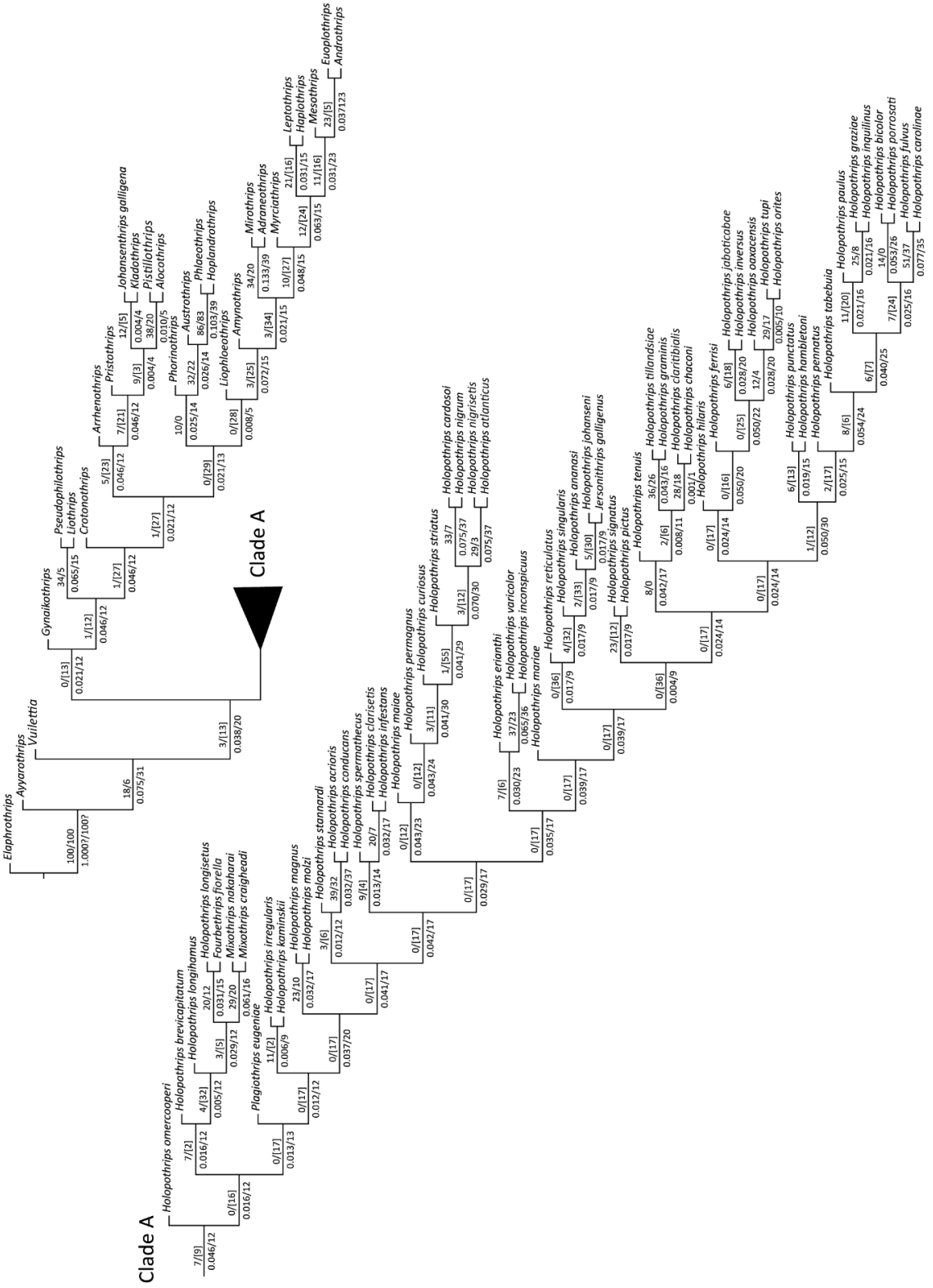

Figure 5. Implied weighting, discrete-only dataset (IW-D) analysis: most parsimonious tree obtained. Support values provided are Bootstrap/Bootstrap GC (above branch) and Bremer absolute/Bremer relative (below branch). Clade A represents the grouping that includes most *Holopothrips* species in this topology; this clade is not the same as the Clade A of other analyses.

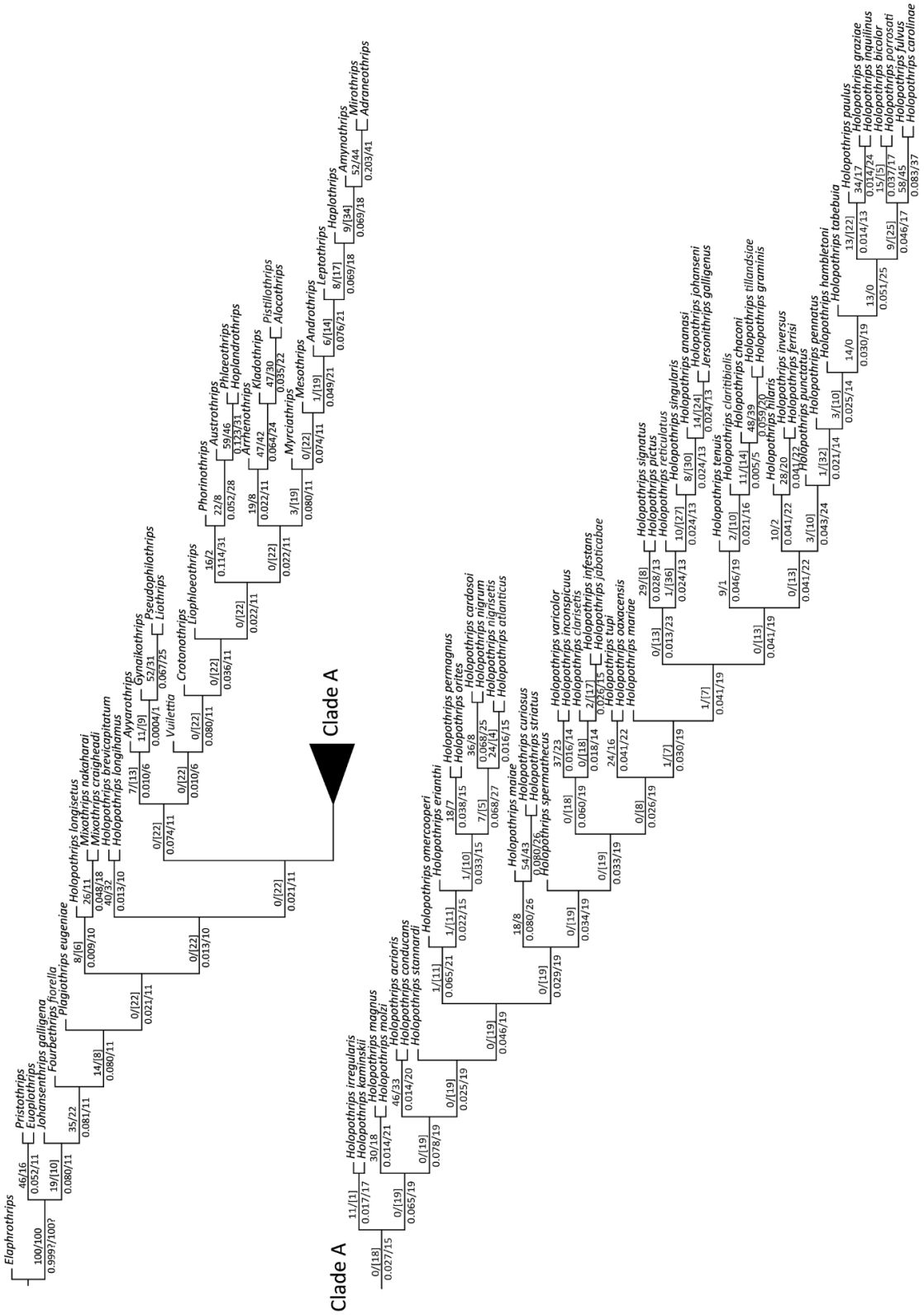

Figure 6. Implied weighting, total dataset (IW-T) analysis: most parsimonious tree obtained. Support values provided are Bootstrap/Bootstrap GC (above branch) and Bremer absolute/Bremer relative (below branch). Clade A represents the grouping that includes most *Holopothrips* species in this topology; this clade is not the same as the Clade A of other analyses.

Table 1. List of taxa included in the phylogenetic analyses.

Groupings and Species	Author	Material studied	Depositary
Ingroup			
Holopothrips acrioris	Lindner *et al.* (in prep.)	2♂ 3♀	UFRGS
Holopothrips ananasi	Costa Lima, 1935	2♂ 1♀	BMNH and NMNH
Holopothrips atlanticus	Lindner *et al.* (in prep.)	3♂ 1♀	UFRGS
Holopothrips bicolor	Lindner *et al.* (in prep.)	3♂ 3♀	UFRGS
Holopothrips brevicapitatum	Lindner *et al.* (in prep.)	3♂ 2♀	UFRGS
Holopothrips cardosoi	Lindner *et al.* (in prep.)	2♂ 3♀	UFRGS
Holopothrips carolinae	Mound & Marullo 1996	1♀	BMNH
Holopothrips chaconi	Zamora, Hanson & Mound, 2015	1♂ 1♀	BMNH
Holopothrips clarisetis	Lindner *et al.* (in prep.)	1♂ 2♀	UFRGS
Holopothrips claritibialis	Cavalleri & Kaminski, 2007	2♂ 2♀	UFRGS
Holopothrips conducans	(Priesner, 1921)	4♂ 5♀	BMNH and SMF
Holopothrips curiosus	Lindner *et al.* (in prep.)	2♂ 2♀	UFRGS
Holopothrips erianthi	(Hood, 1954)		
Holopothrips ferrisi	Moulton, 1929		
Holopothrips fulvus	Morgan, 1929	1♂ 2♀	BMNH and NMNH
Holopothrips graminis	Hood, 1955	1♀	NMNH
Holopothrips graziae	Lindner *et al.* (in prep.)	2♂ 2♀	UFRGS
Holopothrips hambletoni	Hood, 1938	1♂	NMNH
Holopothrips hilaris	Hood, 1938	1♀	NMNH
Holopothrips inconspicuus	Lindner *et al.* (in prep.)	3♂ 3♀	UFRGS
Holopothrips infestans	Lindner *et al.* (in prep.)	4♂ 2♀	UFRGS
Holopothrips inquilinus	(Bournier, 1993)	1♀	BMNH
Holopothrips inversus	Hood, 1955	1♂	NMNH
Holopothrips irregularis	Lindner *et al.* (in prep.)	3♂ 3♀	UFRGS
Holopothrips jaboticabae	(Hood, 1954)	1♀	NMNH
Holopothrips johanseni	Lindner *et al.* (in prep.)	2♂ 2♀	UFRGS
Holopothrips kaminskii	Lindner *et al.* (in prep.)	1♂ 3♀	UFRGS
Holopothrips longihamus	Lindner *et al.* (in prep.)	3♂ 3♀	UFRGS
Holopothrips longisetus	Lindner *et al.* (in prep.)	3♂ 4♀	UFRGS
Holopothrips magnus	Lindner *et al.* (in prep.)	1♂ 1♀	UFRGS
Holopothrips maiai	Lindner *et al.* (in prep.)	3♂ 3♀	UFRGS
Holopothrips mariae	Mound & Marullo, 1996	1♂ 1♀	BMNH
Holopothrips molzi	Lindner, Mendonça Jr. & Cavalleri, 2016	2♂ 2♀	UFRGS
Holopothrips nigrisetis	Lindner *et al.* (in prep.)	2♂ 3♀	UFRGS
Holopothrips nigrum	Lindner *et al.* (in prep.)	3♂ 2♀	UFRGS

Holopothrips oaxacensis	Johansen, 1986	Literature only	-
Holopothrips omercooperi	(Bagnall, 1924)	1♂ 1♀	BMNH
Holopothrips orites	Hood, 1942	2♀	BMNH and NMNH
Holopothrips paulus	Mound & Marullo, 1996	1♂ 1♀	BMNH
Holopothrips pennatus	Moulton, 1938	1♀	BMNH
Holopothrips permagnus	Hood, 1938	1♀	NMNH
Holopothrips pictus	Hood, 1942	1♀	NMNH
Holopothrips porrosati	Mound & Marullo, 1996	1♂ 2♀	BMNH
Holopothrips punctatus	Lindner *et al.* (in prep.)	2♂ 3♀	UFRGS
Holopothrips reticulatus	Lindner *et al.* (in prep.)	5♂ 5♀	UFRGS
Holopothrips signatus	Hood, 1914	2♂ 1♀	BMNH and NMNH
Holopothrips singularis	Lindner *et al.* (in prep.)	2♂ 1♀	UFRGS
Holopothrips spermathecus	Lindner *et al.* (in prep.)	2♀	UFRGS
Holopothrips stannardi	Mound & Marullo, 1996	1♂ 2♀	BMNH and NMNH
Holopothrips striatus	Jorge, Cavalleri, Bedetti & Isaías, 2016	2♂ 4♀	UFRGS
Holopothrips tabebuia	Cabrera & Segarra, 2008	1♂ 1♀	NMNH
Holopothrips tenuis	Hood, 1914	1♂ 2♀	BMNH
Holopothrips tillandsiae	Mound & Marullo, 1996	1♂ 1♀	BMNH
Holopothrips tupi	Hood, 1955	2♀	BMNH
Holopothrips varicolor	Lindner *et al.* (in prep.)	3♂ 3♀	UFRGS
Outgroup 1			
Fourbethrips fiorella	Soto-Rodríguez, Nishida & Retana-Salazar, 2012	1♀	ANIC
Jersonithrips galligenus	Retana-Salazar & Nishida, 2007	1♂	ANIC
Johansenthrips galligena	Retana-Salazar & Soto-Rodríguez, 2008	1♂ 2♀	ANIC and UFRGS
Mixothrips craigheadi	Stannard, 1968	1♂ 1♀	BMNH
Mixothrips nakaharai	Mound & Marullo, 1996	1♂ 1♀	BMNH and NMNH
Plagiothrips eugeniae	(Costa Lima, 1935)	1♀	BMNH
Outgroup 2			
Adraneothrips alternatus	Hood, 1925	2♂ 3♀	UFRGS
Alocothrips hadrocerus	(Karny, 1926)	1♂ 1♀	BMNH
Amynothrips andersoni	O'Neill, 1968	1♂ 1♀	ANIC
Androthrips ramachandrai	Karny, 1926	3♂ 3♀	UFRGS
Arrhenothrips acuminatus	Ananthakrishnan, 1969	1♂ 1♀	BMNH
Austrothrips flavitibia	Moulton, 1940	2♀	BMNH
Ayyarothrips abstrusus	Ananthakrishnan, 1972	1♂ 1♀	BMNH
Crotonothrips gallarum	Ananthakrishnan, 1968	1♂ 1♀	BMNH
Euoplothrips carcinoides	Hood, 1937	1♂ 1♀	BMNH
Gynaikothrips uzeli	(Zimmermann, 1900)	3♂ 3♀	UFRGS

Haplothrips fiebrigi	Priesner, 1931	3♂ 3♀	UFRGS
Hoplandrothrips erythrinae	(Priesner, 1925)	3♂ 3♀	UFRGS
Kladothrips rugosus	Froggatt, 1906	1♂ 1♀	ANIC and UFRGS
Leptothrips astutus	Johansen, 1978	1♂ 1♀	BMNH
Liophloeothrips segnis	Ananthakrishnan & Jagadish, 1969	1♂ 1♀	BMNH
Liothrips sp.	-	3♂ 3♀	UFRGS
Mesothrips jordani	Zimmermann, 1900	1♂ 1♀	BMNH
Mirothrips arbiter	Cavalleri, Souza, Prezotto & Mound, 2013	3♂ 3♀	UFRGS
Myrciathrips variabilis	Cavalleri, Lindner & Mendonça Jr., 2016	3♂ 3♀	UFRGS
Phlaeothrips coriaceus	Haliday, 1836	1♂ 1♀	BMNH
Phorinothrips loranthi	Ananthakrishnan, 1968	1♀	BMNH
Pistillothrips sp.	-	1♀	UFRGS
Pristothrips aaptus	Hood, 1925	1♂ 1♀	BMNH
Pseudophilothrips obscuricornis	(Priesner, 1921)	3♂ 3♀	UFRGS
Vuilletia houardi	(Vuillet, 1914)	1♂ 1♀	BMNH
Root			
Elaphrothrips sp.	-	2♂ 3♀	UFRGS

Specimens from the following collections: Australian National Insect Collection (ANIC - Canberra, Australia); British Museum of Natural History (BMNH - London, England); Senckenberg Museum (SMF - Frankfurt, Germany); Universidade Federal do Rio Grande do Sul (UFRGS - Porto Alegre, Brazil); Smithsonian National Museum of Natural History (NMNH - held at USDA, Beltsville, United States of America).

Table 2. Number of steps and fit values of each search performed.

Analysis	Number of steps	Fit	Number of trees found
EW-D	1117	-	51
EW-C	79.681	-	1
EW-T	1239.381	-	1
IW-D	-	46.85452	1
IW-C	-	5.02469	1
IW-T	-	54.65451	1

Legends: EW-C: equal weights, continuous data analysis; EW-D: equal weights, discrete data analysis; EW-T: equal weights, all data analysis; IW-C: implied weighting, continuous data analysis; IW-D: implied weighting, discrete data analysis; IW-T: implied weighting, all data analysis.

Table 3. SPR distances between the trees obtained in each search.

	EW-D	EW-C	EW-T	IW-D	IW-C	IW-T
EW-D	-					
EW-C	74	-				
EW-T	52	68	-			
IW-D	25	84	65	-		
IW-C	77	32	66	84	-	
IW-T	56	63	31	67	58	-

Legends: EW-C: equal weights, continuous data analysis; EW-D: equal weights, discrete data analysis; EW-T: equal weights, all data analysis; IW-C: implied weighting, continuous data analysis; IW-D: implied weighting, discrete data analysis; IW-T: implied weighting, all data analysis.

Table 4. Number of steps of each "diagnostic" character of *Holopothrips* in each analysis. Definitions of each character and comments can be found on Supporting File 1.

Character (number of states)	**EW-D**	**EW-T**	**IW-D**	**IW-T**
Presence of metanotal discal setae (2)	7	7	5	7
Tergal wing-retaining setae (3)	7	6	9	6
Presence of male pore plates on sternite VIII (2)	13	12	9	11
Texture of male pore plates (2)	11	6	5	5
Appearance of male pore plate(s) on sternite VIII (5)	13	11	8	10
Occurrence of pore plates (5)	21	16	16	19
Presence of visible female spermatheca (2)	3	3	3	3

Legends: EW-D: equal weights, discrete data analysis; EW-T: equal weights, all data analysis; IW-D: implied weighting, discrete data analysis; IW-T: implied weighting, all data analysis.

Considerações Finais

Com este trabalho, *Holopothrips* passa a possuir 60 espécies descritas, metade delas sendo registradas em galhas. A chave de identificação ilustrada, incluindo mais de 90% da diversidade do grupo, constitui uma importante ferramenta na identificação das espécies, o primeiro e fundamental passo em qualquer estudo envolvendo o gênero. Ao descrever estas espécies detalhadamente, provendo fotos e informações das galhas em que foram coletadas, também estabelecemos as bases para futuros estudos na ecologia do grupo.

A variação morfológica presente dentro de *Holopothrips* foi extensivamente estudada e comentada, e posteriormente codificada na forma de caracteres morfológicos para estudos filogenéticos. Esta codificação, associada aos comentários feitos para cada caráter, poderá servir de ponto de partida para muitos estudos futuros feitos não só com *Holopothrips*, mas com outros gêneros da família Phlaeothripidae. Não afirmamos que os caracteres aqui propostos poderão ser utilizados sem a necessidade de modificações para diferentes grupos; ao contrário, esperamos que estes caracteres sejam analisados de forma crítica, testados em diferentes grupos, modificados e recodificados sempre que necessário por pesquisadores que os utilizarem em trabalhos filogenéticos.

Apesar dos resultados das análises filogenéticas não possuírem suporte alto e, portanto, não serem confiáveis como base para uma proposta de revisão de *Holopothrips*, ainda permitiram a observação de alguns padrões interessantes. *Holopothrips* não foi recuperado como um grupo monofilético em nenhuma das análises realizadas, e nenhum dos caracteres utilizados como diagnósticos do gênero é totalmente exclusivo do grupo ou presente em todos os atuais membros. Estes dois fatos já são indicativos de que a atual definição do gênero não é adequada, e possa precisar ser revisada. Apesar disso, escolhemos descrever espécies em *Holopothrips* antes de que o gênero pudesse ser revisado, mesmo com o risco de que uma futura nova definição do grupo signifique transferir algumas das novas espécies para outros gêneros. Todas estas novas espécies possuem algumas características em comum com *Holopothrips* em sua atual definição, e acreditamos que ao conhecer melhor a diversidade de tripes galhadores Neotropicais, mais próxima da realidade será qualquer tentativa de revisão futura.

Dos gêneros propostos como proximamente relacionados, a maioria não é recuperada agrupada com *Holopothrips*, com exceção de *Jersonithrips*; a possibilidade de sinonimizar os dois gêneros deve ser explorada no futuro.

Por fim, levantamos algumas questões acerca da utilidade de caracteres morfológicos

como base para estudos filogenéticos em Thysanoptera. Em nosso estudo, os caracteres que utilizamos não foram suficientes para encontrar uma topologia estável entre os diferentes tratamentos, e mesmo com o mesmo tratamento caracteres discretos e contínuos parecem ser altamente incongruentes. Homoplasias parecem ser comuns em Thysanoptera como um todo, com caracteres sendo facilmente perdidos em linhagens ou surgindo em outras, com reversões sendo comumente usadas na definição de alguns grupos. Isso se reflete na maneira como a classificação em Thysanoptera é feita, aonde muitos gêneros possuem uma única espécie, que é diferenciada com relação a outro grupo morfologicamente próximo pela presença ou ausência de uma característica única. Entretanto, não sabemos o quão facilmente estas características surgem ou são suprimidas neste grupo. Apesar de todas as dificuldades, contudo, morfologia ainda é a principal (e em muitos casos a única) fonte de informações para estudos filogenéticos em Thysanoptera. Nesse sentido, é necessário encontrar maneiras de melhor compreender e aplicar estes dados se quisermos explorar a história evolutiva da ordem.

ANEXOS

NORMAS DE FORMATAÇÃO DOS PERIÓDICOS ZOOTAXA E SYSTEMATIC ENTOMOLOGY

LISTA DE MATERIAL EXAMINADO - COLEÇÃO THYSANOPTERA UFRGS

LISTA COMENTADA DE CARACTERES

COMANDOS UTILIZADOS NAS ANÁLISES FILOGENÉTICAS

Anexo 1. Normas para submissão de artigos dos periódicos Zootaxa e Systematic Entomology.

Zootaxa (Magnolia Press) - Disponível em: http://www.mapress.com/j/zt/ [Acesso em 27 de Fevereiro de 2018].

Normas de submissão disponíveis em: http://www.mapress.com/j/zt/pages/view/forauthors [Acesso em 24 de Fevereiro de 2018].

Systematic Entomology (Wiley Online Library) - Disponível em: http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1365-3113 [Acesso em 27 de Fevereiro de 2018].

Normas de submissão disponíveis em: http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1365-3113/homepage/ForAuthors.html [Acesso em 24 de Fevereiro de 2018].

Anexo 2. Lista de códigos de coleção do material examinado proveniente da coleção de Thysanoptera da UFRGS (Material suplementar do Capítulo 1).

Holopothrips acrioris **sp. nov.**:

Holotype: UFRGS 3216 (1♀).

Paratypes: UFRGS 3217 (1♀); UFRGS 3218 (1♀); UFRGS 3219 (1♀); UFRGS 3220 (1♀); UFRGS 3221 (1♀); UFRGS 3222 (2♀); UFRGS 3223 (1♂); UFRGS 3224 (1♂); UFRGS 3226 (1♂); UFRGS 3227 (1♂); UFRGS 3228 (1♂); UFRGS 3229 (2♂); UFRGS 3544 (1♂ 1 immature); UFRGS 4512 (1♀); UFRGS 4514 (1♀); UFRGS 4515 (1♀); UFRGS 4516 (1♀); UFRGS 4517 (1♀); UFRGS 4518 (2♀); UFRGS 4519 (2♀); UFRGS 4520 (2♀); UFRGS 4521 (1♂1♀); UFRGS 4522 (1♂1♀); UFRGS 4523 (1♂1♀); UFRGS 4524 (1♂1♀);UFRGS 4528 (2♀).

Non-type specimens: UFRGS 2589 (2♀); UFRGS 2592 (2♀); UFRGS 2595 (2♂); UFRGS 2599 (1♂); UFRGS 2601 (1♀); UFRGS 2602 (1♀); UFRGS 2604 (2♂); UFRGS 2611 (1♂); UFRGS 2613 (1♀); UFRGS 2614 (1♂); UFRGS 2615 (1♂); UFRGS 2616 (1♂); UFRGS 2618 (2♀); UFRGS 2619 (1♂1♀).UFRGS 2624 (1♀); UFRGS 3067 (1♀); UFRGS 3068 (1♀); UFRGS 3069 (1♀); UFRGS 3070 (1♀); UFRGS 3071 (1♀); UFRGS 3072 (1♀); UFRGS 3073 (1♀); UFRGS 3074 (1♀); UFRGS 3075 (1♀); UFRGS 3076 (1♀); UFRGS 3077 (1♀); UFRGS 3078 (1♀); UFRGS 3079 (1♀); UFRGS 3080 (1♀); UFRGS 3081 (1♀); UFRGS 3082 (1♀); UFRGS 3083 (1♀); UFRGS 3084 (1♀); UFRGS 3085 (1♀); UFRGS 3086 (1♂); UFRGS 3087 (1♂); UFRGS 3088 (1♂); UFRGS 3089 (1♂); UFRGS 3090 (1♂); UFRGS 3091 (1♂); UFRGS 3092 (1♂); UFRGS 3093 (1♂); UFRGS 3094 (1♂); UFRGS 3096 (1♂); UFRGS 3097 (1♂).

Holopothrips atlanticus **sp. nov.**:

Holotype: UFRGS 0975 (1♂).

Paratypes: UFRGS 0974 (1♀); UFRGS 0976 (1♂); UFRGS 1208 (1♂).

Holopothrips bicolor **sp. nov.**:

Holotype: UFRGS 3771 (1♀).

Paratypes: UFRGS 3769 (1♀); UFRGS 3770 (1♀); UFRGS 3772 (1♀); UFRGS 3773 (1♀); UFRGS 3774 (1♀); UFRGS 3775 (1♀); UFRGS 3776 (1♀); UFRGS 3777 (1♀); UFRGS 3778 (1♀); UFRGS 3779 (1♀); UFRGS 3780 (1♀); UFRGS 3781 (1♂); UFRGS 3782 (1♂); UFRGS 3783 (1♂); UFRGS 3784 (1♂); UFRGS 3785 (1♂); UFRGS 3786 (1♂); UFRGS 3787 (1♂); UFRGS 3788 (1♂); UFRGS 3789 (1♂).

Non-type specimens: UFRGS 4776 (1♀); UFRGS 4777 (1♂).

Holopothrips brevicapitatum **sp. nov.**:

Holotype: UFRGS 1058 (1♀).

Paratypes: UFRGS 1036 (1♂); UFRGS 1038 (1♂); UFRGS 1039 (1♂); UFRGS 1040 (1♀); UFRGS 1041 (1♀); UFRGS 1042 (1♀); UFRGS 1043 (1♀); UFRGS 1044 (1♀); UFRGS 1045 (1♀); UFRGS 1046 (1♀); UFRGS 1047 (1♀); UFRGS 1048 (1♀); UFRGS 1049 (3♀); UFRGS 1050 (1♀); UFRGS 1051 (2♀); UFRGS 1052 (1♂1♀); UFRGS 1053 (2♀); UFRGS 1054 (2♀); UFRGS 1056 (1♀); UFRGS 1059 (1♀); UFRGS 1060 (1♂); UFRGS 1061 (1♀); UFRGS 1062 (1♀); UFRGS 1063 (1♀).

Holopothrips cardosoi **sp. nov.**:

Holotype: UFRGS 5065 (1♀).

Paratypes: UFRGS 5064 (1♀); UFRGS 5066 (1♀); UFRGS 5067 (1♂); UFRGS 5068

(1♂); UFRGS 5069 (1♀); UFRGS 5070 (1♀); UFRGS 5071 (1♀); UFRGS 5072 (1♀); UFRGS 5073 (2♀); UFRGS 5074 (1♀); UFRGS 5075 (2♀); UFRGS 5076 (2♀); UFRGS 5077 (1♀); UFRGS 5079 (2♀); UFRGS 5080 (2♀).

Non-type specimens: UFRGS 5078 (2♀); UFRGS 5081 (2♀).

Holopothrips clarisetis **sp. nov.**:

Holotype: UFRGS 4115 (1♀).

Paratypes: UFRGS 4116 (1♂); UFRGS 4117 (1♀).

Holopothrips curiosus **sp. nov.**:

Holotype: UFRGS 3436 (1♀).

Paratypes: UFRGS 3437 (1♀); UFRGS 3438 (1♂); UFRGS 3439 (1♂); UFRGS3443 (4 immature).

Holopothrips inconspicuus **sp. nov.**:

Holotype: UFRGS 1147 (1♀).

Paratypes: UFRGS 1136 (1♂); UFRGS 1137 (1♀); UFRGS 1138 (1♂); UFRGS 1139 (1♂1♀); UFRGS 1140 (1♀); UFRGS 1141 (1♂); UFRGS 1142 (1♂); UFRGS 1143 (1♂1♀);UFRGS 1144 (1♀); UFRGS 1145 (1♀); UFRGS 1146 (1♀); UFRGS 1148 (2♀); UFRGS 1149 (1♂); UFRGS 1180 (1♂); UFRGS 1181 (1♀); UFRGS 1182 (1♂); UFRGS 1183 (1♀); UFRGS 1184 (1♀); UFRGS 1185 (1♀); UFRGS 1186 (1♂); UFRGS 1187 (1♂);UFRGS 1188 (1♀); UFRGS 1189 (1♀).

Holopothrips infestans **sp. nov.**:

Holotype: UFRGS 3209 (1♀).

Paratypes: UFRGS 3204 (1♀); UFRGS 3205 (2♂); UFRGS 3206 (1♀); UFRGS 3207 (1♀); UFRGS 3208 (2♂); UFRGS 3444 (1♀); UFRGS 3445 (1♀); UFRGS 3447 (1♂ 2 immatures); UFRGS 3448 (3 immatures).

Non-type specimens: UFRGS 1014 (1♀); UFRGS 1015 (1♀); UFRGS 1016 (1♀); UFRGS 1017 (1♂); UFRGS 1018 (1♂); UFRGS 1019 (1♂); UFRGS 1020 (1♂); UFRGS 1068 (1♂); UFRGS 1070 (1♂); UFRGS 1071 (1♀); UFRGS 1072 (1♂); UFRGS 1214 (1♀); UFRGS 1215 (1♂); UFRGS 1216 (1♂); UFRGS 1217 (1♀); UFRGS 1218 (1♂); UFRGS 1219 (1♀); UFRGS 3354 (1♂); UFRGS 3355 (1♀).

Holopothrips irregularis **sp. nov.**:

Holotype: UFRGS 4618 (1♀).

Paratypes: UFRGS 4612 (1♀); UFRGS 4613 (1♀); UFRGS 4614 (1♀); UFRGS 4615 (1♀); UFRGS 4617 (1♀); UFRGS 4619 (1♀); UFRGS 4620 (1♀); UFRGS 4621 (1♀); UFRGS 4622 (1♀); UFRGS 4623 (1♀); UFRGS 4624 (1♀); UFRGS 4625 (1♀); UFRGS 4626 (1♀); UFRGS 4627 (1♀); UFRGS 4629 (1♀); UFRGS 4630 (1♀); UFRGS 4631 (1♀); UFRGS 4632 (1♀); UFRGS 4633 (1♀); UFRGS 4634 (1♀); UFRGS 4635 (1♀); UFRGS 4636 (1♂); UFRGS 4637 (1♀); UFRGS 4638 (1♀); UFRGS 4639 (1♀); UFRGS 4640 (1♀); UFRGS 4641 (1♂); UFRGS 4643 (1♂); UFRGS 4644 (1♂).

Holopothrips kaminskii **sp. nov.**:

Holotype: UFRGS 0990 (1♀).

Paratypes: UFRGS 0980 (1♂); UFRGS 0986 (1♀); UFRGS 0987 (1♀); UFRGS 0989 (1♀); UFRGS 0998 (1♀).

Non-type specimens: UFRGS 0994 (1♀); UFRGS 0997 (1♀).

Holopothrips longihamus **sp. nov.**:

Holotype: UFRGS 0962 (1♀).

Paratypes: UFRGS 0958 (1♀); UFRGS 0964 (1♀); UFRGS 0965 (1♀); UFRGS 0966 (1♂); UFRGS 0967 (1♂1♀); UFRGS 0968 (2♀); UFRGS 0969 (2♀); UFRGS 0970 (1♂1♀); UFRGS 1012 (1♀); UFRGS 1106 (1♂); UFRGS 1110 (1♀); UFRGS 1111 (1♀); UFRGS 1112 (1♀); UFRGS 1113 (1♂); UFRGS 1114 (1♀); UFRGS 1115 (2♀); UFRGS 1116 (1♀); UFRGS 1117 (1♂1♀); UFRGS 1118 (1♀ 1 immature); UFRGS 1119 (1♂); UFRGS 1120 (1♀); UFRGS 1121 (1♀); UFRGS 1122 (1♂); UFRGS 1123 (1♀); UFRGS 1124 (1♂); UFRGS 1125 (1♀); UFRGS 1126 (1♂); UFRGS 1127 (1♀); UFRGS 1128 (1♂1♀ 1 immature); UFRGS 1129 (1♀); UFRGS 1130 (1♀); UFRGS 1132 (1♀); UFRGS 1133 (1♂); UFRGS 1134 (2♀); UFRGS 1135 (1♀ 1 immature); UFRGS 1210 (1♀); UFRGS 1212 (1♂); UFRGS 1221 (1♀); UFRGS 1222 (1♀); UFRGS 1224 (1♂); UFRGS 1225 (1♂).

Non-type specimens: UFRGS 0959 (1 immature); UFRGS 1107 (1♀); UFRGS 1108 (1♀); UFRGS 1109 (1♂); UFRGS 1211 (1♀); UFRGS 1213 (1♀); UFRGS 1220 (1♀); UFRGS 1223 (1♀).

Holopothrips longisetus **sp. nov.**:

Holotype: UFRGS 4391 (1♀).

Paratype: UFRGS 4375 (1♀); UFRGS 4376 (1♀); UFRGS 4377 (1♀); UFRGS 4378 (1♀); UFRGS 4379 (1♀); UFRGS 4380 (1♀); UFRGS 4381 (1♀); UFRGS 4382 (1♀); UFRGS 4383 (1♀); UFRGS 4384 (1♀); UFRGS 4385 (1♀); UFRGS 4386 (1♀); UFRGS 4387 (1♀); UFRGS 4388 (1♀); UFRGS 4389 (1♀); UFRGS 4390 (1♀); UFRGS 4392 (1♀); UFRGS 4393 (1♀); UFRGS 4394 (1♀); UFRGS 4395 (1♀); UFRGS 4396 (1♀); UFRGS 4397 (1♀); UFRGS 4399 (1♀); UFRGS 4400 (1♀); UFRGS 4401 (1♀); UFRGS 4402 (1♀ 1 immature); UFRGS 4403 (1♀); UFRGS 4404 (1♀); UFRGS 4405 (1♀); UFRGS 4406 (1♀); UFRGS 4407 (1♀); UFRGS 4408 (1♀ 1 immature); UFRGS 4409 (1♀); UFRGS 4410 (1♀ 1 immature); UFRGS 4411 (1♀); UFRGS 4412 (1♀ 1 immature); UFRGS 4413 (1♀); UFRGS 4415 (1♀); UFRGS 4416 (1♀); UFRGS 4417 (1♀); UFRGS 4419 (1♀); UFRGS 4420 (1♀); UFRGS 4421 (1♀); UFRGS 4422 (1♀); UFRGS 4423 (1♀); UFRGS 4424 (1♀); UFRGS 4425 (1♀); UFRGS 4426 (1♀); UFRGS 4427 (1♀); UFRGS 4428 (1♀); UFRGS 4429 (1♀); UFRGS 4431 (1♀); UFRGS 4432 (1♀); UFRGS 4434 (1♀ 1 immature); UFRGS 4435 (1♀ 1 immature); UFRGS 4436 (1♀ 1 immature); UFRGS 4437 (1♀ 1 immature); UFRGS 4438 (1♀ 1 immature); UFRGS 4439 (1♀ 1 immature); UFRGS 4440 (1♀ 1 immature); UFRGS 4441 (1♀ 1 immature); UFRGS 4442 (1♀ 2 immatures); UFRGS 4443 (1♀ 2 immatures); UFRGS 4444 (1♂); UFRGS 4445 (1♂ 1 immature); UFRGS 4446 (1♂); UFRGS 4447 (1♂); UFRGS 4448 (1♂); UFRGS 4449 (1♂); UFRGS 4450 (1♂); UFRGS 4452 (1♂); UFRGS 4453 (1♂); UFRGS 4454 (1♂); UFRGS 4455 (1♂); UFRGS 4456 (1♂); UFRGS 4457 (1♂); UFRGS 4458 (1♂); UFRGS 4459 (1♂ 1 immature); UFRGS 4460 (1♂ 1 immature); UFRGS 4461 (1♂ 1 immature); UFRGS 4496 (1♀); UFRGS 4497 (1♀); UFRGS 4498 (1♀); UFRGS 4499 (1♀); UFRGS 4500 (1♀); UFRGS 4501 (1♀); UFRGS 4502 (1♀); UFRGS 4503 (1♀ 1 immature); UFRGS 4505 (1♂1♀) - UFRGS 4508 (1♂); UFRGS 4509 (1♂); UFRGS 4510 (1♂); UFRGS 4511 (1♂ 1 immature).

Non-type specimens: UFRGS 4398 (1♀); UFRGS 4414 (1♀); UFRGS 4430 (1♀); UFRGS 4504 (2♀); UFRGS 4506 (1♂1♀) - UFRGS 4507 (1♂1♀?); UFRGS 5082 (1♀); UFRGS 5083 (1♀); UFRGS 5084 (1♀); UFRGS 5085 (1♀); UFRGS 5086 (1♀); UFRGS 5087 (1♀); UFRGS 5088 (1♀); UFRGS 5089 (1♀); UFRGS 5090 (1♀); UFRGS 5091 (1♀).

Holopothrips magnus **sp. nov.**:

Holotype: UFRGS 4824 (1♀).

Paratypes: UFRGS 4825 (1♂).

Holopothrips maiae **sp. nov.**:

Holotype: UFRGS 4693 (1♀).

Paratypes: UFRGS 4685 (1♀); UFRGS 4686 (1♀); UFRGS 4687 (1♀); UFRGS 4689 (1♀); UFRGS 4691(1♀ 5 immatures);UFRGS 4692 (1♀ 1 immature); UFRGS 4694 (1♀ 1 immature); UFRGS 4695 (1♀ 1 immature); UFRGS 4696 (1♀ 1 immature); UFRGS 4698 (1♀ 1 immature); UFRGS 4699 (1♂); UFRGS 4700 (1♂); UFRGS 4701 (1♂); UFRGS 4702 (1♂); UFRGS 4703 (1♂); UFRGS 4704 (1♂); UFRGS 4705 (1♂); UFRGS 4706 (1♂); UFRGS 4707 (1♂); UFRGS 4708 (1♂); UFRGS 4709 (1♂); UFRGS 4710 (1♂ 1 immature).

Non-type specimens: UFRGS 4690 (1♀).

Holopothrips nigrisetis **sp. nov.**:

Holotype: UFRGS 1174 (1♀).

Paratypes: UFRGS 1168 (1♀); UFRGS 1171 (1♀); UFRGS 1173 (1♀); UFRGS 1175 (1♂); UFRGS 1176 (1♀); UFRGS 1177 (1♀); UFRGS 1178 (1♂); UFRGS 1179 (1♂).

Holopothrips nigrum **sp. nov.**:

Holotype: UFRGS 1191 (1♀).

Paratypes: UFRGS 1190 (1♂); UFRGS 1193 (1♂); UFRGS 1194 (1♀); UFRGS 1195 (1♂); UFRGS 1196 (1♂); UFRGS 1197 (1♂); UFRGS 1201 (1♀); UFRGS 1203 (1♂).

Non-type specimens: UFRGS 3520 (1♀); UFRGS 3521 (1♀); UFRGS 3522 (1♀); UFRGS 3523 (1♀); UFRGS 3526 (1♀); UFRGS 3527 (1♂1♀); UFRGS 3529 (1♂); UFRGS 3530 (1♂); UFRGS 3531 (1♂); UFRGS 3534 (1♀); UFRGS 3535 (1♀); UFRGS 3538 (1♂); UFRGS 3539 (1♂); UFRGS 3540 (1♂); UFRGS 3542(1♂).

Holopothrips punctatus **sp. nov.**:

Holotype: UFRGS 1083 (1♀).

Paratypes: UFRGS 1074 (1♀); UFRGS 1075 (1♀); UFRGS 1076 (1♀); UFRGS 1077 (1♀); UFRGS 1080 (1♀); UFRGS 1081 (1♀); UFRGS 1082 (1♀); UFRGS 1084 (1♀); UFRGS 1085 (1♂); UFRGS 1087 (1♀) UFRGS 1088 (1♀); UFRGS 1089(1♂); UFRGS 1090 (1♀); UFRGS 1091 (1♀); UFRGS 1093 (1♀); UFRGS 1096 (1♀); UFRGS 1099 (1♀); UFRGS 1101 (1♀); UFRGS 1102 (1♀).

Holopothrips reticulatus **sp. nov.**:

Holotype: UFRGS 3622 (1♀).

Paratypes: UFRGS 3590 (1♀); UFRGS 3591 (1♀); UFRGS 3592 (1♀); UFRGS 3593 (1♀); UFRGS 3594 (1♀); UFRGS 3595 (1♀); UFRGS 3597 (1♀); UFRGS 3598 (2♀); UFRGS 3599 (2♀); UFRGS 3600 (1♂1♀); UFRGS 3602 (1♂); UFRGS 3603 (2♂); UFRGS 3614 (1♀); UFRGS 3615 (1♀); UFRGS 3616 (1♀); UFRGS 3617 (1♀); UFRGS 3618 (1♀); UFRGS 3620 (1♀); UFRGS 3621 (1♀); UFRGS 3624 (1♂); UFRGS 3625 (1♂); UFRGS 3626 (1♂); UFRGS 3627 (1♂); UFRGS 3629 (1♂); UFRGS 3630 (1♂).

Non-type specimens: UFRGS 3596 (1♀); UFRGS 3628 (1♂).

Holopothrips singularis **sp. nov.**:

Holotype: UFRGS 1200 (1♂).

Paratypes: UFRGS 1202 (1♂); UFRGS 1207 (1♀).

Holopothrips spermathecus **sp. nov.**:

Holotype: UFRGS 3130 (1♀).

Paratypes: UFRGS 3130 (2 immatures); UFRGS 3131 (1♀).

Holopothrips variabilis **sp. nov.**:

Holotype: UFRGS 4793 (1♀).

Paratypes: UFRGS 4786 (1♀); UFRGS 4787 (1♀); UFRGS 4789 (1♀); UFRGS 4790 (1♀); UFRGS 4792 (1♀); UFRGS 4794 (1♀); UFRGS 4795 (1♀); UFRGS 4797 (1♀); UFRGS 4798 (1♀); UFRGS 4799 (1♀); UFRGS 4800 (1♂); UFRGS 4801 (1♂); UFRGS 4802 (1♂); UFRGS 4803 (1♂); UFRGS 4804 (1♂); UFRGS 4805 (1♂); UFRGS 4807 (1♂); UFRGS 4808 (1♂); UFRGS 4809 (1♂); UFRGS 4810 (1♂); UFRGS 4811 (1♂); UFRGS 4812 (1♂); UFRGS 4816 (1♀); UFRGS 4817 (1♀); UFRGS 4819 (1♀); UFRGS 4820 (1♀).

Non-type specimens: UFRGS 4788 (1♀); UFRGS 4791 (1♀); UFRGS 4806 (1♂); UFRGS 4818 (1♀); UFRGS 4821 (1♀).

Anexo 3: Lista comentada de caracteres (Supporting File 1 do capítulo 2)

Continuous Characters:

C1. Body, distended length.

Measured from the top of interantenal projection to the tip of abdominal segment X, without including antennal segments or anal setae. Some specimens were not completely distended when measured, but we preferred to use the brute measure and did not attempt to estimate the fully distended length.

C2. Antennal segment III, length.

C3. Antennal segment III, basal width.

C4. Antennal segment III, apical width.

C5. Antennal segment III, largest width.

C6. Antennal segment IV, length.

C7. Antennal segment IV, basal width.

C8. Antennal segment IV, apical width.

C9. Antennal segment IV, largest width.

Lengths were measured from the base to the apex of segment, not including membranous areas; basal width was measured at the extreme base of each segment; apical width was measured at the extreme apex of segment, not including the membranous area; largest width was measured at the widest part of the segment, independently if it was located medially or closer to either of the tips.

All antennal characters were measured from the same antenna. When both antenna were present, the one that was less inclined or curled was chosen for the measures.

These characters were proposed to try quantifying the variations observed especially in antennal segment III, which is more robust in some *Holopothrips* species, but very thin and elongate in others, such as *H. ananasi*.

C10. Head, length.

Measured dorsally, from the tip of interantenal projection to the posterior margin of sclerotized area, including any craspedum that might have been present. However, in *Johansenthrips galligena*, which has a clear median projection on posterior margin of head, the length of this projection was not included in the measure.

C11. Head, width.

Measured dorsally, right behind compound eyes, not including any tubercle or projected setal pore that might have been present.

C12. Head, postocular setae, length.

Measured from the base of setae, not including basal pore, to the tip, including capitate area if present. When both postocular setae were present, the least inclined or curled setae out of the two was measured. In cases there was a clear difference in length between both setae, the longest of the pair was measured. In some cases, both setae were strongly inclined or curled, so the measure taken was shorter than the real length; however, we preferred to not estimate the real length of the setae and use the brute measure.

C13. Head, compound eyes, dorsal length.

Measured from the anterior limit of eye, near antennal segment I, to the most posterior point of posterior margin.

C14. Head, compound eyes, dorsal width.

Measured from the external margin of the eye, near its contact with the lateral margin of head, to the most internal point of internal margin, including the projected margin of bean-shaped eyes. If the head was slightly tilted or turned to the side, the dorsal width of both eyes was measured, and the average between both values was used.

C15. Pronotum, median length.

Measured medially, from anterior margin to posterior margin of sclerotized area. Membranous areas were not included in the measure.

C16. Pronotum, anterior width.

Measured from one anterior angle to the other. In few specimens, where the anterior angles were not as well defined, the measure was performed at anteroangular setae level.

C17. Pronotum, posterior width.

Measured at epimeral setae level, from one lateral margin to the other of sclerotized area, not

including fore coxae, membranous areas or the basal pore of epimeral setae.

C18. Pronotum, anteromarginal setae, length.

C19. Pronotum, anteroangular setae, length.

C20. Pronotum, distance between anteroangular and midlateral setae.

C21. Pronotum, outer epimeral setae, length.

C22. Pronotum, posteroangular setae, length.

C23. Prothorax, fore coxae, coxal setae length.

C24. Metanotum, median major setae, length.

Lengths for all setae were measured from base of setae, not including basal pore, to the tip, including capitate area if present. The least inclined or curved setae of the pair was measured. In some cases, both setae were strongly inclined or curled, so the measure taken was shorter than the real length; however, we preferred to not estimate the real length of the setae and use the brute measure. Few times, when the setae were reduced to less than 5 micrometres, they could not be properly measured.

In specimens where two pairs of epimeral setae were present, always the outermost pair was measured.

Distance between setae was measured at the shortest distance, in a straight line, from the margin of one basal pore to the other, without including the basal pores in the measure.

C25. Abdominal segment X (tube), ventral length.

Measured from the base to the tip of tube, not including the membranous area at the apex where anal setae are placed. In males, who have an excavation at the base of tube ventrally, the excavated area was not discounted from the measure.

C26. Abdominal segment X (tube), basal width.

Measured at the widest part of tube near basal area, which might be slightly posterior to the extreme base.

C27. Pronotum, minor posteromarginal setae, number of pairs.

All minute setae near or at the posterior margin were counted, including ones occurring on epimeral region; the minor setae that is placed medially in the epimeral region was not included.

C28. Metanotum, anterior discal setae, number.

All discal setae anterior to the median major pair of metanotum, except for the three pairs at anteroangular margins, were counted. At first number of pairs was being considered, but due to several specimens having unpaired setae in either of the sides, the total number of anterior discal setae is now considered here.

C29. Abdominal tergite II, lateral setae, number.

All minor lateral setae of tergite II were considered. Lateral setae on sternite, the two major setae at posterior margin, and any curved setae that might have a function as wing-retaining setae, were not counted here. Due to specimens frequently having different numbers of setae from one side to the other, each side was counted and treated separately.

C30. Abdominal sternite III, discal and lateral setae, number.

All discal and lateral setae present in the sternite were considered. Setae placed on posterior margin were not included in the counting.

The counting in some specimens might be inexact, as some lateral setae may be harder to see, and internal contents of abdomen may hide some of the discal setae.

C31. Fore wings, duplicated cilia, number.

All duplicated cilia present at the posterior margin near the apex of fore wings were counted. Due to specimens frequently having different numbers of cilia from one wing to the other, each fore wing was counted and treated separately.

Discrete Characters:

Colouration group

C32. Head, colour: (0) yellow or light-coloured; (1) brown; (2) bicoloured.

Heads were considered state 0 if they were yellow or only slightly shaded with light brown. Any shade of brown, light or dark, was considered state 1. Only heads with a very clear distinction between a lighter/yellow and a darker/brown part were considered state 2.

C33. Thorax, colour: (0) yellow or light-coloured; (1) brown; (2) bicoloured.

Coding for states 0 and 1 was similar to what was done for head. In most observed cases, all three thoracic segments have the same colouration; thus, slight differences in the colour between

two segments or presence of a more shaded area in one of the segments was considered enough to code it as state 2.

C34. Abdomen, colour pattern: (0) uniform; (1) bicoloured.
An abdomen was considered bicoloured only if there was a striking difference in colour between two adjacent segments, such as one being clear yellow and the following one brown. Abdomens with basal segments slightly lighter and gradually becoming darker towards apical segments were considered uniformly coloured.

C35. Antenna, antennal segment III, colouration: (0) yellow or light-coloured; (1) brown; (2) bicoloured.
C36. Antenna, antennal segment IV, colouration: (0) yellow or light-coloured; (1) brown; (2) bicoloured.
C37. Antenna, antennal segment V, colouration: (0) yellow or light-coloured; (1) brown; (2) bicoloured.
C38. Antenna, antennal segment VI, colouration: (0) yellow or light-coloured; (1) brown; (2) bicoloured.
C39. Antenna, antennal segment VII, colouration: (0) yellow or light-coloured; (1) brown; (2) bicoloured.
C40. Antenna, antennal segment VIII, colouration: (0) yellow or light-coloured; (1) brown.
Colouration was sometimes harder to access for antennal segments. Only clear yellow or very faintly shaded segments were considered state 0. Any hint of a brown pigmentation, even if very light, was considered state 1: we coded this way so slight differences in colouration, especially on segments VII–VIII which tend to be slightly darker than segments III–VI, would be detected. Only segments with a clear differentiation between a lighter/yellow area and a darker/brown area were considered bicoloured.

C41. Fore legs, femur, colour pattern: (0) uniform; (1) bicoloured.
C42. Fore legs, femur, colouration (for uniformly-coloured ones): (0) yellow or light-coloured; (1) brown; (-) not applicable.
C43. Fore legs, tibia, colour pattern: (0) uniform; (1) bicoloured.
C44. Fore legs, tibia, colouration (for uniformly-coloured ones): (0) yellow or light-coloured; (1) brown; (-) not applicable.

C45. Hind legs, tibia, colour pattern: (0) uniform; (1) bicoloured.

C46. Hind legs, tibia, colouration (for uniformly-coloured ones): (0) yellow or light-coloured; (1) brown; (-) not applicable.

Only femora or tibiae with at least a third or fourth of it in clearly paler or darker than the base colour were considered bicoloured; when only the extreme base or extreme apex was lighter or shaded, it was considered uniformly coloured. The few cases where the femora or tibiae were dark basally and gradually turned yellow apically were considered bicoloured.

In some cases, even if fore tibia was light brown, it was coded as state 0 instead of 1 when it was clearly paler than the adjacent brown or dark brown femora.

C47. Mid and hind legs, tarsus, colouration in relation to tibia: (0) concolorous; (1) differently coloured.

The colour of tarsi was compared to the main colour of its adjacent tibiae in cases where the latter was bicoloured. If about half of the tibiae was dark and half was lighter, the colour on apical half was considered for the comparison. Same colouration or slight differences were considered state 0, only tarsi strongly lighter or darker than tibiae were considered state 1.

C48. Fore wings, apical half, colouration: (0) hyaline; (1) brown or shaded.

Fore wings were coded as state 0 only when there was no trace of pigmentation on it, or when it was a very faintly indicated yellow shading. Yellow, weakly shaded or brown wings were all considered state 1.

C49. Fore wings, median dark line: (0) absent; (1) present; (-) not applicable.

Any brown or darker pigmentation forming a median longitudinal line near base or medially on fore wings were considered as a median dark line. Median pigmentation that did not form a line, or that was not strikingly darker than the rest of the fore wing, was not considered as a median dark line.

C50. Fore wings, basal area, colouration in relation to apical half of forewing: (0) concolorous; (1) lighter; (2) darker.

Fore wings with a clearly defined basal area with differentiated pigmentation in relation to the rest of the fore wing were considered as state 1 (if lighter) or 2 (if darker). If the basal area was only slightly darker, or if it was darker but gradually turned paler towards the apical half of fore

wing, it would be considered as state 0.

C51. Wings, clavus, colouration: (0) hyaline or yellow; (1) brown or shaded.
Clavus colouration was coded slightly differently from fore wing colouration: only the presence of a clear brown pigmentation would constitute state 1, so yellow clavus were coded as state 0. In some specimens clavus was placed over the body, making it difficult to access its colouration - in these cases, it was either left as missing (?) data or it was tentatively coded as the same colouration as the basal area of fore wings.
C52. Major pronotal setae, colouration: (0) hyaline, yellow or light brown; (1) dark brown.
Only dark-coloured pronotal setae were considered as state 1, as the presence of dark brown setae has been previously used as a possible trait to differentiate *Holopothrips* species. An attempt was made to differentiate between hyaline or yellow setae and light brown setae, but the presence of intermediate states such as yellowish brown or lightly shaded setae made the distinction confusing; thus, all setae that are not clearly dark brown were considered as state 0.

Antenna group

C53. Antenna, segment III, number of sense cones: (0) 1 cone; (1) 2 cones; (2) 3 cones.
C54. Antenna, segment IV, number of sense cones: (0) 1 cone; (1) 2 cones; (2) 3 cones; (3) 4 cones.
In some specimens, an extra sense cone, about half of the size of the other cones of the same antennal segment, was present; this reduced sense cone was not included in the counting.

C55. Antenna, segment VI, pedicel: (0) absent; (1) present.
C56. Antenna, segment VII, pedicel: (0) absent; (1) present.
An antennal segment was considered to have a pedicel when its base was constricted into a small, neck-like structure, with parallel sides and its length about subequal to its width. Constrictions that did not form this structure with parallel sides, or that were much shorter that wide, were not considered as a pedicel.

C57. Antenna, segment VIII, shape of base: (0) with pedicel; (1) constrict but without pedicel; (2) not constricted; lateral margins discontinuous with lateral margins of segment VII; (3) segment VIII apparently fused or continuous with VII, with only a suture separating both.
The same definition of a pedicel from the previous characters was used here. The base was

considered constrict when the largest width of the segment was not located in the extreme base, but slightly above it. State 2 was used for segments VIII clearly separate from VII, forming an independent unit, while state 3 was used for segments VIII that seem to be almost fused to VII, having only a suture separating them.

Head group

C58. Head, dorsal surface, median area posterior to eyes, sculpture: (0) absent; (1) present.

Only the dorsal median area of head, posterior to compound eyes but anterior to posterior margin of sclerotized area, was considered for this character and the following one. Species that had lines of sculpture between eyes, near lateral margins of head, and close to posterior margin, but had the median area smooth, were considered state 0.

C59. Head, dorsal surface, median area posterior to eyes, type of sculpture: (0) reticulate; (1) transverse lines; (-) not applicable.

If the lines of sculpture in the median area of head enclosed several reticles, equiangular or elongate, it was considered state 0. When only few small or elongate reticles were present in the middle and the rest of the sculpture lines were mostly transversal, forming an almost striate pattern, it was considered state 1.

C60. Head, major postocular setae: (0) absent; (1) present.

C61. Head, major postocular setae, number: (0) 1 pair; (1) 2 pairs; (-) not applicable.

The longest dorsal pair of setae, positioned posterior to compound eyes, each seta somewhat aligned with the middle of each eye, was considered the postocular setae. The postocular setae was considered absent when there was no pair of setae posterior to the eyes clearly longer than the other discal setae of the head, even if there were one or more pairs of small setae posterior to the eyes.

In some cases, a third elongate seta or a second pair of elongate setae was present internally to the usual postocular pair, usually shorter. This second internal pair may represent in some species a dislocated and enlarged postocellar setae.

C62. Head, major postocular setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.

In cases there were two pairs of postocular setae, the shape of the tip of the outermost pair was

considered here. In species where it was difficult to determine if the apex was expanded or capitate, it was coded as "2&3" instead of simply "?", since it was clear that these setae were not acute nor blunt. To differentiate from actual polymorphisms, in the Mesquite matrix such cases of "tentative polymorphisms" had the cells coloured red.
Further comments on how the states for setae apex were defined and difficulties involved are written in the comments of characters C70–C76, under the Pronotum group.

C63. Head, dorsolateral region, minute teeth on sculpture: (0) absent; (1) present.
Few species have minute teeth in the angles of head sculpture, dorsally, near lateral margins, giving a somewhat punctuate appearance to the area. In cases where such teeth were present, but only in the sculpture immediate to the compound eye or in the sculpture between eyes, these species were coded as state 0.

C64. Head, cheeks, tubercles: (0) absent; (1) present.
A series of well-developed projections from the margin of head are here considered to be tubercles. However, the enlarged bases of robust lateral setae on head are not tubercles.

C65. Head, maxillary stylets, position: (0) parallel; (1) v-shaped.
Maxillary stylets that extend within the head capsule parallel to each other, usually distanced about a third of head width apart or less, are coded as state 0. Maxillary stylets that extend within the head capsule diagonally, forming a V shape, usually distanced about half of head width apart or more, are coded as state 1. In few cases, maxillary stylets might be more distanced from each other than a third of head width, but are still extending longitudinally, thus still being considered parallel to each other.

C66. Head, maxillary bridge: (0) absent; (1) present.
Maxillary bridge is not always clearly apparent within the head capsule, being very hard to see in specimens that were not macerated or whose maxillary stylets are dislocated from their natural position. Only clearly visible maxillary stylets were considered state 1. All other cases were considered state 0, which might include species that actually possess a maxillary bridge, but it was not detected in the observed specimens.

C67. Head, labial palps, size: (0) apparent, projecting from margin of mouth cone; (1) reduced,

not projecting from the margin of mouth cone, similar to a papilla.
Labial palps vary in length, with some species having them well defined and with the segmentation visible (state 0), which is usually associated with a long and pointed mouth cone. In other species, the labial palps are very reduced, being seen as vestigial papillae barely projecting from the margin of mouth cone (state 1); these seem to be associated with shorter and rounder mouth cones.

C68. Head, mouth cone, length: (0) reaches or surpasses posterior line of fore coxae; (1) does not reach posterior line of fore coxae.
Mouth cone in Phlaeothripinae seems to vary between two extremes: a short and round mouth cone, that barely reaches the anterior margin of ferna; and a long and pointed mouth cone, that extends between fore coxae and sometimes reaches close to mesosternum. Here we defined the line tangent to the posterior margin of fore coxae as the threshold, considering as state 0 any mouth cone that reaches or surpasses this line, and as state 1 the mouth cones that do not reach this line.

Prothorax group

C69. Pronotum, median region, sculpture: (0) absent; (1) present.
Only the median area of pronotum was considered for this character. If the species had lines or sculpture near margins or on epimeral region, but the middle of pronotum was smooth, then it was considered state 0. In few species there are very faint lines medially on pronotum, but unless these formed a defined pattern of sculpture, they were considered state 0 as well.

C70. Pronotum, anteromarginal setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.
C71. Pronotum, anteroangular setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.
C72. Pronotum, midlateral setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.
C73. Pronotum, epimeral setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.
C74. Pronotum, major epimeral setae, number: (0) 1 pair; (1) 2 pairs.
C75. Pronotum, posteroangular setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded;

(3) capitate.

C76. Pronotum, coxal setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.

Defining the shape of apex of pronotal and other major body setae may appear easy, but there is a wide variation of shapes and several species with intermediate states, so defining the limits between the different states was a complex task. In this work, we have considered as state 0 any setae with a fine, acute tip, without any sort of expansion; state 1 any setae with tip not acute but also not expanded, usually ending in a somewhat round shape; state 2 any setae slightly expanded at tip, either weakly swollen or forming an expanded and round, drop-shaped tip; and state 3 any setae with a wide, fan-shaped tip, usually showing minute and pointy rays in this capitate area.

However, the limits between each state were not always clear. Setae considered to be acute were thinner in some species but more robust in others, sometimes looking closer to a blunt seta than a finely acute seta. Sometimes the tip of a blunt setae could look slightly swollen due to slide pressure, or a slightly expanded seta could look almost blunt depending on its position. Capitate setae could be not as wide, and sometimes the rays could not be visible, making them appear closer to an expanded seta.

Particularly, the limits between states 2 and 3 are harder to define, due to the wide variety of expanded and capitate setae observed, and the size of the tip would be also influenced by the size of the seta. It is possible that considering all types of expanded and capitate setae to be a single state would bring less noise to an analysis.

In species where it was difficult to determine if the apex was expanded or capitate, it was coded as "2&3" instead of simply "?", since it was clear that these setae were not acute nor blunt. To differentiate from actual polymorphisms, in the Mesquite matrix such cases of "tentative polymorphisms" had the cells coloured red.

Regarding the number of epimeral setae: while a minor, second setae, is usually present in the middle of epimera, internally to the major epimeral setae, it is usually not larger than discal setae. In few species this seta might be clearly longer than other discal setae on pronotum, but they are still much smaller than the major epimeral setae, having a fourth or less of its length. Only in species where the internal epimeral setae is comparable to the outer epimeral setae, or at least half of its length, that it was coded as state 1.

C77. Pronotum, discal setae: (0) absent; (1) present.

Any small setae present in the pronotum that does not arises from its margins or in epimera is here considered to be discal setae. Small setae present on anterior margin are not considered, due to the risk of counting reduced anteromarginal or anteroangular setae as discal setae in some species. The minute setae on posterior margin is not considered here as they have two separate characters. The small setae in the middle of epimera is not considered as well, as it is hypothesized to be homologous to the second internal pair of epimeral setae in species that bear two pairs of epimeral setae.

C78. Pronotum, median discal setae, size: (0) small (comparable to other discal setae or only slightly longer, but not more robust); (1) large (clearly longer and more robust than other pronotal discal setae).

This character refers to the pair of setae that is present on pronotum medially to the posteromarginal setae, but distanced enough from the posterior margin to not be confused with marginal setae. It is usually comparable in size to other pronotal discal setae, being identified by its positioning, or only slightly longer.

The definition of the states of this character was not easy to do. At first, we thought of considering any median discal setae longer than other discal setae to be state 1, even if they were otherwise the same in appearance. However, our objective here is to separate the species whose median discal setae is clearly enlarged, thus we have added the robustness of the setae to the definition of the state: if the median discal setae is longer than other discals, but has the same robustness, it is then considered to be state 0.

C79. Pronotum, minor posteromarginal setae: (0) absent; (1) present.

Similar to character C27, we have considered here to be minor posteromarginal setae all minute setae near or at the posterior margin of pronotum, including ones occurring on epimeral region. If no minute seta was present in either side of pronotum, it was considered absent. If a single minute seta was present in one side but not in the other, it was considered present.

C80. Pronotum, epimeral suture: (0) incomplete and short (not reaching the basal pore of posteroangular setae); (1) almost complete (distance between the end of the suture and posterior margin not greater than the diameter of basal pore of posteroangular setae); (2) complete.

Epimeral suture is usually very short in *Holopothrips* species, sometimes formed only by the

anterior part and lacking the longitudinal suture towards the posterior margin of pronotum. In some species the length of the suture varies between individuals or even between sides of the same specimen. All of these cases were coded as polymorphic if more than one state was observed in different specimens.

C81. Prosternum, basantra: (0) absent; (1) present.
C82. Prosternum, basantra, development: (0) faintly indicated; (1) strongly sclerotized; (-) not applicable.
C83. Prosternum, basantra, shape: (0) wider than long; (1) length and width subequal; (-) not applicable.
Basantra was considered present if there was any indication of a pair of sclerotized plates anterior to the fernal plates. In some *Holopothrips* the coding for presence or absence was uncertain, as some specimens may give the impression of having a weak basantra, but this might be actually the effect of the prosternal membrane being folded by the mouth cone positioning. When it seemed that there was some hint of a sclerotized area in the middle of the folding, we considered basantra to be present.
When present, basantra was considered faintly indicated when it was weakly defined, with margins barely differentiating from the membrane, or when the plate was irregular or reduced. Basantras with regular and well-defined margins, clearly differentiated from the membrane, were considered strongly sclerotized.
Shape separates between transversely rectangular basantras, where the width was clearly longer than height (state 0), and quadrate basantras where width and length were similar (state 1).

C84. Prosternum, chitinous islets above ferna: (0) absent; (1) present.
Chitinous islets refer to sclerotized spots smaller than a basantra and placed closer to the anterior margin of ferna. It was observed in few *Holopothrips* species. In some species, the anterior margin of ferna seems to have a projection, which might be an indication that the chitinous islets are projections of ferna that were isolated from it.

C85. Prosternum, ferna, median contact between both plates: (0) absent; (1) present.
The distance between fernal plates is variable, from being very far apart to touching each other medially. Here instead of trying to measure or quantify this distance, which could be influenced by prothorax size and slide quality, we accessed if the fernal plates touch each other or not. In

few species, where the fernal plates were very close to each other but did not touch by two or three micrometres only, we considered to be state 1.

Mesothorax group

C86. Mesonotum, anteromedian region, sculpture: (0) absent; (1) present.

Only the anteromedian area of mesonotum was considered to score the presence/absence character. If the mesonotum had sculpture laterally and/or posteriorly, but was mostly smooth or had only faint and undefined lines medially, sculpture would be considered absent.

C87. Mesonotum, median region, type of sculpture: (0) almost equiangular reticles; (1) transverse lines, sometimes enclosing few elongate reticles; (-) not applicable.

Type of mesonotal sculpture was hard to access in some cases: frequently the sculpture seen medially is different from the sculpture near margins, so only the median region was considered. If this region was mostly covered by equiangular or elongate reticles, it was coded as state 0; if it had mostly transverse lines rarely enclosing reticles, it was then considered as state 1. In cases where few median reticles were surrounded by very elongate reticulation or transverse lines, or when it was difficult to define which of the states the sculpture should be judged as, we coded as 0&1.

C88. Mesonotum, sculpture, internal markings: (0) absent; (1) present; (-) not applicable.

We considered here as internal markings any lines or granulations occurring in between the main lines of sculpture, being frequently shorter and fainter. If internal markings were present in any part of the sculpture in the main area of mesonotum, even if restricted to few reticles or a small area, it would be considered as state 1.

C89. Mesonotum, posterior discal setae, positioning: (0) all pairs arising within the area of differentiated sculpture; (1) at least one pair arising at the margin or anterior to the posterior area of differentiated sculpture.

Besides the major setal pair at the extreme lateral tip of mesonotum, at least two or three pairs of smaller setae are observed near the posterior margin, usually within two oval areas marked with thick but short lines, rarely reticulate. If all setae arise within this area, it's coded as state 0; but if at least one of the pairs was anteriorly placed, at the margin or outside this area, then it was considered state 1.

C90. Mesosternum, spina: (0) absent; (1) present.

C91. Mesosternum, mesopresternum, shape: (0) entire; (1) divided.

The mesopresternum is the transverse plate anterior to the major mesosternal plate. It's usually a single and entire rectangular plate (state 0), but in several groups this plate is eroded into two lateral triangles, or even into two triangles and an oval or irregular plate medially (state 1).

C92. Mesosternum, mesopresternum, anterior margin (when entire): (0) straight; (1) one median "excavation"; (2) two "excavations" and with projection medially; (-) not applicable.

Only an entire mesopresternum was considered for this character. The most frequent state was for the anterior margin to have two curves/"excavations", forming two lateral and one median tips (state 2). In some cases the median tip is absent, and the anterior margin has one single curve/"excavation" (state 1). Finally, when no curve is seen, and the anterior margin is a straight transverse line, it was coded as state 0.

C93. Mesosternum, major sternal plate, shape of anterior margin: (0) straight; (1) curved or sinuous.

The coding of this character was difficult at times, as the difference between a straight and a weakly curved margin is small, and sometimes found within the same species. Several times this trait was coded as 0&1, due to differences between the observed specimens making it impossible to assign with certainty to one or the other state.

<u>Metathorax group</u>

C94. Metanotum, anterior discal setae: (0) absent; (1) present.

In this work we considered to be metanotal anterior discal setae any setae that: (1) is placed medially in the metanotum, never in its margins (which excludes the three anteroangular pairs); and (2) arises anteriorly to the metanotal median major setae (which is usually the longer pair of setae on metanotum and is present in all Phlaeothripinae species).

C95. Metanotum, anteromedian region, sculpture: (0) absent; (1) present.

C96. Metanotum, anteromedian region, type of sculpture: (0) equiangular reticles; (1) longitudinally elongate reticles; (2) longitudinally striate; (-) not applicable.

We considered in these two characters only the area of metanotum anterior to the median major

setae, excluding the extreme lateral area since this part is almost always striate. If metanotum had sculpture elsewhere but it was very weak or absent in this region, it was considered absent. Within *Holopothrips* the metanotal sculpture is highly variable, and different types of sculpture can occur together in some species, thus why only the anteromedian region was considered. Reticles were considered equiangular when all sides were similar in length, giving each reticle a shape closer to a hexagon, square or circle. Reticles were considered elongate when they had a shape closer to a rectangle or an oval, being longer in one of the planes than in the other, usually longitudinally longer. Finally, when the sculpture was formed by longitudinal lines which would not enclose well defined reticles, it was considered striate.

C97. Metanotum, sculpture, internal markings: (0) absent; (1) present.
We used here the same definition of internal markings from character C88. In some species few faint lines were seen in between the thicker lines of sculpture only adjacent to anterior margin of metanotum; these were considered as state 0 unless there were further internal markings in other parts of metanotum. We have not considered here the internal markings that are always present inside the lateral oval/circular sculpture.

C98. Metanotum, craspedum, shape of posterior margin: (0) straight; (1) angular; (2) curved/rounded.
The external plate over the dorsum of metathorax extends laterally and posteriorly past the limits of metanotum, forming the craspedum. Posteriorly, the craspedum margins can be either straight, without any curving (state 0); the lateral margins may smoothly curve into a round margin (state 2); or the lateral margins sharply curve in an almost 90° curve, then curve once more to form an elongate and sometimes almost acute posterior craspedum (state 1).

C99. Metanotum, sculpture, lateral limits of sculpture area: (0) closely parallel; (1) tapering towards posterior margin.
The sculptured area may have its lateral limits almost parallel to each other, having a somewhat rectangular area of covering over the metanotum (state 0). Alternatively, the sculptured area may look like a triangle, with the lateral limits tapering as they approach the posterior area (state 1). Here we considered to be state 1 when the width of the sculptured area near posterior margin of metanotum was half or less of its width at the anterior margin.

C100. Metanotum, sculpture, posterior limits of sculpture area: (0) reaching posterior margin of craspedum; (1) reaching close to posterior margin of craspedum but not touching it; (2) not reaching close to posterior margin of craspedum.

We coded as state 0 species whose metanotal sculpture clearly extended all the way to the posterior limit of craspedum, with the lines being interrupted only at the margin. Species where the metanotal sculpture extended close to the posterior margin, but with lines being interrupted before reaching the margin, were coded as state 1. Finally, in few specimens the metanotal sculpture is mostly absent on the craspedum area, with its lines barely extending past the limit of the metanotal plate underneath; these were coded as state 2.

C101. Metasternum, metafurca, anterior spina: (0) absent; (1) present.

Ventrally, the metafurca is seen as two dark lines that approach each other anteriorly. In some species, these two lines are actually fused into a single longitudinal line, here called an anterior spina. Whenever this fusion occurred and the spina was visible, it was considered to be state 1.

C102. Metasternum, metapleural sutures: (0) absent; (1) present.

Metapleural sutures originate from the socket where the midcoxa is included, extending longitudinally towards the posterior area of metasternum. Whenever these sutures were identified, even when reduced, we coded as state 1.

<u>Pelta group</u>

C103. Abdomen, pelta, shape: (0) triangular (all sides subequal in length); (1) bell-shaped (constrict medially and with lateral wings basally); (2) oval (longer than wide, no median constriction nor lateral wings basally); (3) transversal (much wider than long).

Pelta shows a noticeable variation in shape, which we have tried to code here into four states. Triangular (state 0), where the three sides are somewhat straight or only slightly curved, without any constriction medially, and with similar lengths. Bell-shaped (state 1), which presents a transverse constriction medially, and pelta has broad lateral wings basally adjacent to this constriction. Oval (state 2), where pelta is longer than wide, has lateral margins almost parallel, without basal wings. Transversal (state 3), where the pelta is much broader than long, with posterior margin much larger than either of the lateral margins.

Species where pelta had a more arcuate shape (anterior margin looking like a semi-circle, posterior margin straight) were considered to be state 0. All species with a small, but visible

median constriction, were considered to be state 1.

C104. Abdomen, pelta, lateral wings on triangular-shaped pelta: (0) absent; (1) present; (-) not applicable.

We have considered the presence of lateral wings only on triangular-shaped peltas since mention to this structure was already included in the definition of the other types or does not occur in them, at least in the specimens observed in this study.

Lateral wings are lateral projections at the base of pelta, which extend parallel to the anterior margin of tergite II. Minute projections, which could be just an irregularity of the margins of pelta, were not considered as lateral wings here.

C105. Abdomen, pelta, anterior margin shape: (0) straight; (1) round; (2) acute.

Anterior margin of pelta was considered to be state 0 when it formed a straight line parallel to the posterior margin; in cases where the lateral margins formed what would be an acute angle, but ended in a straight tip, were considered to be state 0 as well. Curved anterior margins, no matter if wide or more strongly curved, were all considered as state 1. When the lateral margins joined each other in an anterior angle with an acute tip (not a straight or curved tip), it was considered to be state 2.

In some species the pelta had irregular margins and could have projections on anterior margin. In these cases, the anterior margin of said projection was considered for coding.

C106. Abdomen, pelta, campaniform sensilla: (0) absent; (1) present.

Here we considered only the presence of campaniform sensilla, no matter their position or number. Species where one both sensilla were changed into small setae in all observed specimens we considered as state 0; if only one of the sensilla was changed or some but not all specimens had them changed into setae, we considered as state 1.

C107. Abdomen, pelta, area of occupation of sculpture: (0) covers the whole pelta; (1) present medially and/or anteriorly, but weak or absent posteriorly; (2) present on the margins, but weak or absent medially.

Sculpture on pelta is usually well defined and covers the structure thoroughly, and this was coded as state 0. However, in some species, the sculpture seems to be very weakened or fully absent posterior to campaniform sensilla, sometimes near the other margins as well; these were

coded as state 1. Finally, cases where the sculpture was well defined near margins, but weakened to absent medially, were coded as state 2.

C108. Abdomen, pelta, sculpture, shape of median reticles: (0) very thin, longitudinally elongated and smaller in relation to marginal reticles; (1) not longitudinally elongated and thin.
In most observed species the sculpture on pelta is formed by reticles, usually equiangular or only slightly elongate, with median reticles having the same appearance as marginal reticles, if not smaller (state 1). However, in some species, the median reticles on pelta are clearly differentiated from marginal reticles: they are longitudinally elongate and very thin (usually more than two or three times longer than wide), close to each other, and frequently bear internal markings.

C109. Abdomen, pelta, internal markings on sculpture: (0) absent; (1) present.
Here we used the same definition of internal marking as characters C88 and C97. We considered these markings to be present in a species if most of the specimens observed had at least some of them in few reticles, no matter how weak or restricted. Cases where only one specimen had few internal markings, or they were restricted to a single reticle, would be coded as 0&1.

<u>Abdomen group</u>
C110. Tergite II, posteroangular major setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.
We used here the same definitions for setae tip from characters C62 and C70–C76.

C111. Tergite II, median area, sculpture: (0) absent; (1) present.
C112. Tergite II, median area, type of sculpture: (0) reticulate or irregularly reticulate; (1) transverse lines; (-) not applicable.
C113. Tergite II, sculpture, internal markings: (0) absent; (1) present; (-) not applicable.
We considered for our observations in these three characters the area in between the wing-retaining setae, excluding the area immediately adjacent to anterior and posterior margins. If a species had sculpture on the lateral thirds of tergite, or near the margins, but the median area was mostly smooth, it would be coded as absent (state 0).
Our definitions of type of sculpture here are similar to the ones used for mesonotum, in C. If the lines of sculpture formed reticulation, equiangular or elongate, they would be considered as

state 0 in C112. If these lines were mostly transverse, without forming clear reticulation or only few irregular reticles in between the lines, then it would be coded as state 1.
Internal markings follow the same definitions as character C88, C97 and C109.

C114. Tergites II-VII, wing-retaining setae, number: (0) up to two pairs; (1) three pairs; (2) four or more pairs.
We have considered to be wing-retaining setae any tergal setae that was: (1) distanced at least a fourth or fifth of tergite's width from the lateral margins; (2) were sinuous or curved towards the middle of tergite; and (3) located close to each other, in the same line or diagonally. Small and straight lateral setae and the long straight setae at posterior margins were not considered as wing-retaining setae.
Most Phlaeothripinae species seem to have two pairs of such setae per tergite, sometimes reduced to a single pair (state 0). In *Holopothrips*, one of the traditionally used characters to diagnose the group is the presence of a third wing-retaining seta, usually smaller, not as curved, and very close to the anterior pair, either laterally or anterolaterally to it (state 1). Few Phlaeothripinae species, usually ones with a large body, have multiple setae externally to the two usual wing-retaining pairs, some of them curved like wing-retaining ones, others straight like lateral ones, and the differentiation between both groups become muddled. All species fitting this latter case were coded as state 2, even if it was not possible to confirm with certainty that there was four or more actual wing-retainers in all observed tergites.
At first, we tried to code the presence of a third wing-retaining seta per tergite, for tergites II to VII. This was an attempt to capture variations in the presence of this setae seen in some *Holopothrips* species, which may have them in some median tergites and lack in others. However, the cases where the third pair was not present in all of tergites II–VII were few, and we were also pooling together species with only an extra pair and species with multiple extra pairs. Thus, to avoid coding possibly dependent characters and differentiate having a third or having multiple setae, we decided to make this single character as presented here.

C115. Tergite IX, setae S2, length in males: (0) similar or longer than setae S1; (1) shorter than setae S1.
C116. Tergite IX, setae S3, length in males: (0) similar or longer than setae S1; (1) shorter than setae S1.
Here we refer to the row of multiple setae present near the posterior margin of tergite IX, of

which the innermost major pair is called S1, the next major pair is called S2, and the outermost major pair is called S3. Males having setae S2 smaller than the other two pairs, sometimes comparable in size to the shorter setae present in between the major pairs, is considered to be a trait exclusive of some Phlaeothripinae groups, and not found within Idolothripinae. However, this trait is possibly a homoplasy within Phlaeothripinae.

The reduction on S2 in males does not occur within *Holopothrips*, but was present in several of the included outgroups. We have included a character for reduction on S3 size as well to evaluate if this seta could also vary.

C117. Tergite IX, setae S1, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.

C118. Tergite IX, setae S2, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.

We used here the same definitions for setae tip from characters C62, C70–C76 and C110.

Pore plates group

C119. Abdominal sternite VIII, male pore plate: (0) absent; (1) present.

Here we considered to be a pore plate any area present on sternite VIII with defined limits, and whose appearance (usually a punctuate texture) was clearly differentiate from the rest of sternite surface. While in most observed cases the pore plates had well-defined margins, in some species they seemed to smoothly change into the usual sternite surface appearance, making it hard to define where were the limits of the plate. Nonetheless, if they still had the clear appearance of a pore plate, with the characteristic punctuate texture, the were considered to be present.

In few species it was hard to confirm the presence of pore plates, since the observed specimens were not previously clarified, thus the internal contents of abdomen were still present and making difficult to observe properly the sternite surface. These were either left as a question mark or coded as state 0, if we could see no hint of a possible pore plate at all, nor find any mentions to its presence in literature.

C120. Sternites, male pore plates, gland texture: (0) punctuate; (1) reticulate; (-) not applicable.

Pore plates usually have a distinct punctuate texture, with each of the "dots" apparently "shining" as the focus of the image changes in a microscope (state 0). This punctuate appearance differs from the usual smooth texture of sternites, making them easy to differentiate. However,

within *Holopothrips*, several species have also a reticulate pattern, as if the overall area of the pore plate is subdivided into reticles (state 1). The punctuate texture is still seen underneath this reticulate texture in most species as well, thus this character could be also interpreted as "presence of reticulate texture over the base punctuate appearance". Few *Holopothrips* species have indications of lines that could be forming reticles near the limits of the pore plates, but no clear reticulate texture is seen over the punctuate area; these were all coded as state 0.

C121. Abdominal sternite VIII, male pore plate, appearance: (0) small median circular, oval or irregular pore plate; (1) transverse band reaching the laterals of sternite or close to it, covering from a fourth to a half of sternite length; (2) large pore plate, covering almost or all of sternite area; (3) thin transverse band restricted to median area of sternite, always posterior to the row of discal setae, less than a fourth of sternite length; (4) three plates: two anteroangular plates and one transverse band posterior to discal setae, which might be interrupted medially or not; (-) not applicable.

Pore plates vary wildly in appearance between different genera, and even within *Holopothrips*. Here we coded only the types we observed in this work, thus other states could be present in other groups not considered here. We also considered only the appearance on sternite VIII, as most Phlaeothripinae species that have pore plates bear them only in this sternite.

Few species had small spots, irregular, circular or oval, placed medially in the sternite, usually over the area with the discal setae or slightly posterior to it (state 0). In others, a single transverse band, posterior to discal setae, is present in the sternite; this plate usually extends until the lateral limits of sternite, and occupy at least a fourth of sternite length (state 1). Some species have the pore plate covering most of the sternite surface, reaching its lateral limits and close to the anterior and posterior margins (state 2). In few *Holopothrips* species there is a single transverse pore plate posterior to discal setae, thin but wide (state 3); it is larger and better defined than state 0 plates, but smaller than state 1 plates, never extending laterally beyond the median third or fourth of sternite. Finally, the most common pore plates conformation within *Holopothrips* is the presence of three plates: two at the anterior angles, and one transverse band posterior to discal setae (state 4); the anteroangular plates may be thinner or thicker, and the posterior band may be interrupted medially or not, sometimes being fully separated into two lateral bands.

C122. Abdominal sternites, occurrence of male pore plates: (0) VIII; (1) VIII-VII; (2) VIII-VI; (3) VIII-V; (4) VIII-IV; (-) not applicable.

Pore plates usually occur only on sternite VIII in Phlaeothripinae, whenever present. In several *Holopothrips* species, however, pore plates occur in further sternites, more frequently VII and VI, few times V, and in one species even on sternite IV.
This character may be ordered, as no species has been observed with pore plates just on sternite VII or VI, but not on VIII. Whenever there are pore plates in one sternite, all subsequent sternites will have plates as well, until sternite VIII.

C123. Abdominal tergite VIII, male pore plate: (0) absent; (1) present.
In few *Holopothrips* species, the posterior plate of sternite VIII extends beyond the lateral limits of sternite, reaching over the tergite as well (state 1). Apparently how much the plate extends over the tergite is variable, in some species only a small tip that does not surpasses the spiracle; in others it covers the lateral thirds, and in at least one observed specimen the two sides almost contact each other medially on tergite VIII.
There is a report of some populations of *Gynaikothrips uzeli* having males with pore plates extending towards tergite VIII similarly; however, we did not code this character as state 1 for *Gynaikothrips* as we did not observe any specimen with such plates.

Spermatheca group

C124. Abdominal segment IX, visible female spermatheca: (0) absent; (1) present.
In all observed *Holopothrips* species, the female spermatheca remains visible in the abdominal segment IX even after maceration of the specimen for slide mounting. Such characteristic has been observed only in few groups outside *Holopothrips*, namely *Plagiothrips*, *Mixothrips*, *Johansenthrips*, *Fourbethrips*, and an unidentified specimen believed to be close to *Pistillothrips*. A visible spermatheca seems to be restricted to some neotropical groups of thrips. This character, combined with the other diagnostic characters of the genus, seems to be useful for identifying specimens as belonging to *Holopothrips*.

C125. Abdominal segment IX, female spermatheca, shape: (0) slender (up to 12.5 micrometres of diameter); (1) thickened (more than 15 micrometres of diameter, but not clearly enlarged medially); (2) enlarged medially; (-) not applicable.
In the observed specimens, the spermatheca could be divided into two basic types: swollen, having a somewhat round enlarged area medially (state 2); or not enlarged, having about the same diameter in the whole length of the structure, and being frequently curled (states 0 and 1).

Not swollen spermathecas were further divided between thin (state 0) and thickened (state 1); we based the limiting diameter value for each state off measures of spermathecas of different species and our impressions of what would be thin or thickened.

Swollen spermathecas have shown some variation as well. Some *Holopothrips* have the spermatheca only slightly enlarged medially, with the tips of the structure looking similar to the tips of not swollen spermathecas; others had greatly enlarged spermathecas, which appeared to be almost fully round. However, due to the difficulty to clearly separate between these two variations, we decided on keeping a single state for swollen spermathecas.

Curiously, *Holopothrips tillandsiae* has a very long spermatheca, extending all the way to abdominal segment VI and curling back to segment IX. This one was considered to be state 1, due to the thickened appearance of the spermatheca.

Fore legs group

C126. Fore legs, femur, maximum width in relation to mid femora's maximum width, in females: (0) up to 1.5x larger; (1) more than 1.5x larger.

C127. Fore legs, femur, maximum width in relation to mid femora's maximum width, in males: (0) up to 1.5x larger; (1) more than 1.5x larger.

In some groups thrips have the fore femora enlarged, a trait sometimes associated to sexual dimorphism, thus why we have separated the coding for both genders. We proposed a proportion here to define enlarged fore femora in comparison to the width of mid femora. Traditionally, only fore femora much larger than this proportion and associated to other modifications (such as presence of tubercles) would be considered enlarged. However, we wanted to separate here between *Holopothrips* species where all legs are similar in size and species where the fore femora are slightly but clearly stouter than mid and hind femora, to verify if this difference could have any phylogenetic signal.

C128. Fore legs, femur, tubercle: (0) absent; (1) present.

C129. Fore legs, tibia, tubercle: (0) absent; (1) present.

The definition of tubercle used here is similar to the one on character C64, but isolated projections on femora or tibia were also counted. Position of tubercle(s) was not considered here, thus non-homologous structures were pooled in the same state. We considered on adding a character for position of these tubercles for each segment of fore leg, but decided against it due to a reduced amount of species studied in this work bearing a tubercle in either fore femora

or tibiae.

While none of the *Holopothrips* species observe in this work has any sort of tubercle on fore legs, we included these characters as they occur in some of the outgroups, and could be useful for structuring the topology for these species.

C130. Fore legs, hamus, size: (0) not enlarged (thin, small curving, not projecting beyond lateral margin of tarsus); (1) enlarged (thick hamus; projecting beyond the lateral margin of tarsus).

The hamus within *Holopothrips* is usually a small and thin curved hook (state 0), which is frequently placed to the side due to the fore legs position, making it hard to see in some specimens. We have considered here the hamus to be enlarged only if it was thicker and longer in comparison to the usual small hamus, and proposing that it should extend enough sideward for the tip to surpass the lateral limit of fore tarsus (state 1).

Only one *Holopothrips* species, *H. longihamus*, filled the full definition of an enlarged hamus; however, two other species in the genus were coded to be state 1: *H. longisetus* (whose hamus is greatly thickened and long, but does not surpass the lateral of fore tarsus) and *H. brevicapitatum*. In the latter, most specimens had the fore legs placed over the body instead of being spread out, which might difficult seeing the tarsal area correctly. Despite that, in several specimens the hamus seemed to be long enough to surpass the lateral margin of tarsus, despite not being particularly thickened.

In the outgroups, some species had a greatly enlarged hamus associated to a fore tarsal tooth and enlarged fore legs. *Mixothrips*, a genus considered close to *Holopothrips*, was differentiated from the latter for possessing an enlarged hamus and lacking the third pair of wing-retaining setae.

C131. Fore legs, tarsal tooth in females: (0) absent; (1) present.

C132. Fore legs, tarsal tooth in females, size: (0) small (length equal or less than half of basal width of tarsus); (1) enlarged (length more than half of basal width of tarsus).

C133. Fore legs, tarsal tooth in males: (0) absent; (1) present.

C134. Fore legs, tarsal tooth in males, size: (0) small (length equal or less than half of basal width of tarsus); (1) enlarged (length more than half of basal width of tarsus).

Here we considered a tarsal tooth to be a lateral pointed projection from the fore tarsus, differentiating it from the hook-like ventral projection that is the hamus. Similarly to enlarged fore femora, the tarsal tooth seems to be associated to sexual dimorphism in some species, being

frequently present only in males.

We also accessed the size of such tarsal teeth, by comparing its length (measured from the lateral margin of tarsus where it is inserted to the tip of the tooth) to the basal width of the same fore tarsus, not including the tooth length. Any teeth with length equal or shorter than half of tarsal width was considered small (state 0), and any teeth longer than half of tarsal width was considered enlarged (state 1).

Within *Holopothrips* no species has a fore tarsal tooth, but this character was included due to it being the main character used to differentiate it from the genus *Plagiothrips*. Moreover, several species in the outgroup bear tarsal tooth, thus these characters could help structuring the topology of these taxa.

Fore wings group

C135. Wings: (0) absent; (1) present.

All observed species in this work had developed wings in at least one of the sexes. In *Alocothrips* and *Fourbethrips* only females were macropterous, while males were apterous; these genera were coded as 0&1. In *Vuilettia* only one of the four observed specimens was macropterous, while all of the other were micropterous; the genus was coded as having wings, but some of the following characters could be observed only in the macropterous specimen, being not applicable to the rest.

C136. Fore wings, duplicated cilia: (0) absent; (1) present; (-) not applicable.

Some species, in the subapical posterior margin of fore wings, present a secondary row of cilia (state 1), while in other species only the main row that extends from apex to base of wing is present (state 0). The number of these cilia, which is highly variable and frequently differs between both wings of the same individual, was considered on character C31. Within *Holopothrips* only *H. carolinae* lacks such setae, which is one of the defining traits of the species.

C137. Fore wings, margins, shape: (0) parallel-sided; (1) with median constriction; (-) not applicable.

The anterior and posterior margins of fore wings can be mostly parallel to each other until reaching the apex of the wing, giving it a somewhat homogeneous width from base to apex (state 0). In some species in the outgroup, the margins approach each other medially, forming

a constriction in the middle of fore wing; this makes the fore wing be thinner medially than subapically (state 1).

While constrict fore wings do not occur within *Holopothrips*, we included this character for its presence in some of the outgroups and for being one of the defining traits of the only tribe formally recognized in Phlaeothripidae, Haplothripini.

C138. Fore wings, first pair of sub-basal setae, size in relation to second pair: (0) shorter; (1) sub equal or longer; (-) not applicable.

C139. Fore wings, first pair of basal setae, shape of apex: (0) acute; (1) blunt; (2) weakly expanded; (3) capitate.

Fore wings bear three or four pairs of setae on anterior margin, near the base. In the observed specimens the outermost pair (third or fourth) is usually longer than the other pairs and frequently has an acute tip, independently from the shape of tip of the other pairs. Due to that, this pair was not included in the comparisons for the two characters above.

For size, we considered state 0 only when the first pair was clearly shorter than second pair, usually two thirds or less of its length. All other cases were considered to be state 1.

We used here the same definitions for setae tip from characters C62, C70–C76, C110 and C117–C118.

C140. Fore wing clavus, sculpture on dorsal surface: (0) absent; (1) present; (-) not applicable.

We considered sculpture to be a group of well-defined lines, usually forming a reticulate pattern (state 1). It was not considered to be sculpture having only one or two lines, or weakly defined irregular lines; these cases and when clavus was fully smooth were all considered to be state 0.

Anexo 4: Lista de comandos utilizados no programa TNT para as análises filogenéticas (Supporting File 5 do capítulo 2).

Discrete data, equal weights (EW-D)

Search + Bremer support

Command	Comments
`log Holopothrips_EW-D_LOG.txt`	Creates log file for the analysis
`proc discrete.tnt`	Opens matrix with only discrete data (Supporting file 3)
`keep 0`	Discards any trees from memory
`ttags -`	Discards any tree tags from memory
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`xmu= hit 3 level 4 rat 10 drift 10; bb`	New Technology search, lists parameters to be used, completes with a round of TBR branch-swapping
`tsave *Trees_EW-D.tre`	Opens tree file
`save; tsave /`	Saves trees to file, and closes it
`nelsen *`	Calculates strict consensus, saving as the last tree in memory
`tchoose /`	Keeps only last tree on memory
`tsave *ConsensusTree_EW-D.tre`	Opens tree file
`save; tsave /`	Saves consensus to file, and closes it
`run bew.run`	Runs Bremer support script created by Augusto Ferrari
`Log /`	Closes Log file

Bootstrap

Command	Comments
`log Holopothrips_EW-D_BOOT_LOG.txt`	Creates log file for the analysis
`proc discrete.tnt`	Opens matrix with only discrete data (Supporting file 3)
`proc ConsensusTree_EW-D.tre`	Opens consensus tree file
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`ttags =`	Activates tree tags

`resample boot replications 500 [xmult= hit 2 level 7 rat 10 drift 10; bb] frequency from 0;`	Bootstrap calculation, with 500 replications and similar parameters as the search, except for the number of hits
`Keep 0`	Discards any trees from memory
`proc ConsensusTree_EW-D.tre`	Opens consensus tree file
`ttag &Bootstrap500rep_EW-D.svg`	Creates svg file, adding the bootstrap values to the branches
`Log /`	Closes Log file

Continuous data, equal weights (EW-C)

Search + Bremer support

Command	Comments
`log Holopothrips_EW-C_LOG.txt`	Creates log file for the analysis
`proc continuous.tnt`	Opens matrix with only continuous data, with values already scaled to 1 (Supporting File 4)
`keep 0`	Discards any trees from memory
`ttags -`	Discards any tree tags from memory
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`taxcode -37`	Turns terminal 37 (*Holopothrips ferrisi*) inactive, due to this species not having any data in this matrix
`xmu= hit 3 level 4 rat 10 drift 10; bb`	New Technology search, lists parameters to be used, completes with a round of TBR branch-swapping
`tsave *Trees_EW-C.tre`	Opens tree file
`save; tsave /`	Saves trees to file, and closes it
`run bew.run`	Runs Bremer support script created by Augusto Ferrari
`Log /`	Closes Log file

Bootstrap

Command	Comments
`log Holopothrips_EW-C_BOOT_LOG.txt`	Creates log file for the analysis
`proc continuous.tnt`	Opens matrix with only continuous data, with values already scaled to 1 (Supporting File 4)
`proc Trees_EW-C.tre`	Opens tree file

`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`ttags =`	Activates tree tags
`taxcode -37`	Turns terminal 37 (*Holopothrips ferrisi*) inactive, due to this species not having any data in this matrix
`resample boot replications 500 [xmult= level 7 rat 10 drift 10; bb] frequency from 0;`	Bootstrap calculation, with 500 replications and similar parameters as the search, except for the number of hits
`Keep 0`	Discards any trees from memory
`proc Trees_EW-C.tre`	Opens tree file
`ttag &Bootstrap500rep_EW-C.svg`	Creates svg file, adding the bootstrap values to the branches
`Log /`	Closes Log file

All (total) data, equal weights (EW-T)

Search + Bremer support

Command	Comments
`log Holopothrips_EW-T_LOG.txt`	Creates log file for the analysis
`proc AllData.tnt`	Opens all data matrix, with values of continuous characters already scaled to 1 (Supporting File 2)
`keep 0`	Discards any trees from memory
`ttags -`	Discards any tree tags from memory
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`xmu= hit 3 level 4 rat 10 drift 10; bb`	New Technology search, lists parameters to be used, completes with a round of TBR branch-swapping
`tsave *Trees_EW-T.tre`	Opens tree file
`save; tsave /`	Saves trees to file, and closes it
`run bew.run`	Runs Bremer support script created by Augusto Ferrari
`Log /`	Closes Log file

Bootstrap

Command	Comments
`log Holopothrips_EW-T_BOOT_LOG.txt`	Creates log file for the analysis

`proc AllData.tnt`	Opens all data matrix, with values of continuous characters already scaled to 1 (Supporting File 2)
`proc Trees_EW-T.tre`	Opens tree file
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`ttags =`	Activates tree tags
`resample boot replications 500 [xmult= level 7 rat 10 drift 10; bb] frequency from 0;`	Bootstrap calculation, with 500 replications and similar parameters as the search, except for the number of hits
`Keep 0`	Discards any trees from memory
`proc Trees_EW-T.tre`	Opens tree file
`ttag &Bootstrap500rep_EW-T.svg`	Creates svg file, adding the bootstrap values to the branches
`Log /`	Closes Log file

Discrete data, implied weighting (IW-D)

Search + Bremer support

Command	Comments
`log Holopothrips_IW-D_LOG.txt`	Creates log file for the analysis
`proc discrete.tnt`	Opens matrix with only discrete data (Supporting file 3)
`keep 0`	Discards any trees from memory
`ttags -`	Discards any tree tags from memory
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`piwe= 8.964`	Activates implied weighting, sets the value to 8.964
`piwe`	Confirms value of implied weighting, to be added to log
`xmu= hit 3 level 4 rat 10 drift 10; bb`	New Technology search, lists parameters to be used, completes with a round of TBR branch-swapping
`tsave *Trees_IW-D.tre`	Opens tree file
`save; tsave /`	Saves trees to file, and closes it
`run biw.run`	Runs Bremer support script created by Augusto Ferrari
`Log /`	Closes Log file

Bootstrap

Command	Comments
`log Holopothrips_IW-D_BOOT_LOG.txt`	Creates log file for the analysis
`proc discrete.tnt`	Opens matrix with only discrete data (Supporting file 3)
`proc Trees_IW-D.tre`	Opens consensus tree file
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`ttags =`	Activates tree tags
`piwe= 8.964`	Activates implied weighting, sets the value to 8.964
`piwe`	Confirms value of implied weighting, to be added to log
`resample boot replications 500 [xmult= level 7 rat 10 drift 10; bb] frequency from 0;`	Bootstrap calculation, with 500 replications and similar parameters as the search, except for the number of hits
`Keep 0`	Discards any trees from memory
`proc Trees_IW-D.tre`	Opens consensus tree file
`ttag &Bootstrap500rep_IW-D.svg`	Creates svg file, adding the bootstrap values to the branches
`Log /`	Closes Log file

Continuous data, implied weighting (IW-C)

Search + Bremer support

Command	Comments
`log Holopothrips_IW-C_LOG.txt`	Creates log file for the analysis
`proc continuous.tnt`	Opens matrix with only continuous data, with values already scaled to 1 (Supporting File 4)
`keep 0`	Discards any trees from memory
`ttags -`	Discards any tree tags from memory
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`taxcode -37`	Turns terminal 37 (*Holopothrips ferrisi*) inactive, due to this species not having any data in this matrix
`piwe= 8.964`	Activates implied weighting, sets the value to 8.964

`piwe`	Confirms value of implied weighting, to be added to log
`xmu= hit 3 level 4 rat 10 drift 10; bb`	New Technology search, lists parameters to be used, completes with a round of TBR branch-swapping
`tsave *Trees_IW-C.tre`	Opens tree file
`save; tsave /`	Saves trees to file, and closes it
`run biw.run`	Runs Bremer support script created by Augusto Ferrari
`Log /`	Closes Log file

Bootstrap

Command	Comments
`log Holopothrips_IW-C_BOOT_LOG.txt`	Creates log file for the analysis
`proc continuous.tnt`	Opens matrix with only continuous data, with values already scaled to 1 (Supporting File 4)
`proc Trees_IW-C.tre`	Opens tree file
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`ttags =`	Activates tree tags
`taxcode -37`	Turns terminal 37 (*Holopothrips ferrisi*) inactive, due to this species not having any data in this matrix
`piwe= 8.964`	Activates implied weighting, sets the value to 8.964
`piwe`	Confirms value of implied weighting, to be added to log
`resample boot replications 500 [xmult= level 7 rat 10 drift 10; bb] frequency from 0;`	Bootstrap calculation, with 500 replications and similar parameters as the search, except for the number of hits
`Keep 0`	Discards any trees from memory
`proc Trees_IW-C.tre`	Opens tree file
`ttag &Bootstrap500rep_IW-C.svg`	Creates svg file, adding the bootstrap values to the branches
`Log /`	Closes Log file

All (total) data, implied weighting (IW-T)

Search + Bremer support

Command	Comments
`log Holopothrips_IW-T_LOG.txt`	Creates log file for the analysis
`proc AllData.tnt`	Opens all data matrix, with values of continuous characters already scaled to 1 (Supporting File 2)
`keep 0`	Discards any trees from memory
`ttags -`	Discards any tree tags from memory
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`piwe= 8.964`	Activates implied weighting, sets the value to 8.964
`piwe`	Confirms value of implied weighting, to be added to log
`xmu= hit 3 level 4 rat 10 drift 10; bb`	New Technology search, lists parameters to be used, completes with a round of TBR branch-swapping
`tsave *Trees_IW-T.tre`	Opens tree file
`save; tsave /`	Saves trees to file, and closes it
`run biw.run`	Runs Bremer support script created by Augusto Ferrari
`Log /`	Closes Log file

Bootstrap

Command	Comments
`log Holopothrips_IW-T_BOOT_LOG.txt`	Creates log file for the analysis
`proc AllData.tnt`	Opens all data matrix, with values of continuous characters already scaled to 1 (Supporting File 2)
`proc Trees_IW-T.tre`	Opens tree file
`hold 99999`	Sets tree buffer to hold 99999 trees
`rseed 1`	Sets random seed to 1
`sect:slack 500`	Sets slack for sectorial searches
`ttags =`	Activates tree tags
`piwe= 8.964`	Activates implied weighting, sets the value to 8.964
`piwe`	Confirms value of implied weighting, to be added to log
`resample boot replications 500 [xmult= level 7 rat 10`	Bootstrap calculation, with 500 replications and similar parameters as the search, except for the number of hits

drift 10; bb] frequency from 0;	
Keep 0	Discards any trees from memory
proc Trees_IW-T.tre	Opens tree file
ttag &Bootstrap500rep_IW-T.svg	Creates svg file, adding the bootstrap values to the branches
Log /	Closes Log file