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Os estágios imaturos de Asopinae e taxonomia de *Tynacantha* Dallas, *Tylospilus* Stål *e Podisus* Herrich-Schäffer (Hemiptera: Pentatomidae)

PORTO ALEGRE
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Tese 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 Doutor em Biologia Animal.

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SUMÁRIO

RESUMO

Os percevejos (Heteroptera) compõem o grupo mais diverso de insetos hemimetábolos, reunindo linhagens com diferentes hábitos alimentares, dentro eles, fitófagos, micófagos, hematófagos e predadores. A maioria dos populares percevejos fede-fede (Pentatomoidea) é fitófaga, mas a subfamília Asopinae (Pentatomidae) se destaca por conta do hábito predador zoofitófago, se alimentando principalmente de outros insetos, mas incluindo também recursos vegetais na dieta. O grupo apresenta cerca de 300 espécies descritas, no entanto, a maioria carece de informações taxonômicas e biológicas básicas. Esta tese tem como objetivos investigar os hábitos de vida e a morfologia dos estágios imaturos de Asopinae, e solucionar problemas taxonômicos nos gêneros *Tynacantha* Dallas, *Tylospilus* Stål e *Podisus* Herrich-Schäffer. A descrição do ciclo de vida e da morfologia dos ovos e ninfas de sete espécies (*Oplomus catena* (Drury), *Alcaeorrhynchus grandis* (Dallas), *Brontocoris tabidus* (Signoret), *Marmessulus brasilianus* Schouteden, *Podisus fuscescens* (Dallas), *Podisus nigrispinus* (Dallas), e *Supputius cincticeps* (Stål)) é apresentada. A partir de técnicas de microscopia eletrônica de varredura, características relevantes em ambos os estágios de vida foram estudadas, dentre elas, os processos aeromicropilares e a superfície do cório dos ovos, o lábio, e o sistema odorífero das ninfas. Dentre os resultados obtidos, destaca-se a variabilidade morfológica e interespecífica observada em ambos os estágios. Esta diversidade permite a identificação em nível de espécie ou de gênero na maioria dos casos e, portanto, pode ser aplicada na taxonomia e sistemática dos asopíneos. Revisitando o histórico taxônomico, consultando espécimes-tipo, e examinando exemplares de diferentes coleções, se procedeu a revisão taxonômica com descrição de duas novas espécies de *Tynacantha*, a redescrição de *Tylospilus nigrobinotatus* (Berg) e descrição de *Tylospilus armatussimilis* Brugnera, Paim & Grazia, e atualizações taxônomicas em *Podisus*, incluindo a descrição de cinco novas espécies. Nestes trabalhos, são fornecidas imagens dos exemplares e de estruturas importantes para a identificação, novas descrições, chaves de identificação, e mapas de distribuição. A importância de examinar exemplares-tipo para a tomada de decisões taxonômicas em Asopinae é destacada, e problemáticas taxonômicas que envolvem os gêneros estudados são discutidas.

Palavras-chave: percevejos predadores, sistemática, estágios imaturos, fede-fede, espécies novas.

ABSTRACT

The true bugs (Heteroptera) compose the most diverse group of hemimetabolous insects, containing lineages with different alimentary habits, such as phytophagous, mycetophagous, hematophagous, and predators. The majority of stink bugs (Pentatomoidea) are phytophagous, however, the members of Asopinae (Pentatomidae) are zoophytophagous, feeding mainly on other insects, but also including plants in the diet. The group has about 300 species described, in which most lack basic taxonomic and biological information. This thesis aims to investigate the natural history and morphology of the immature stages of Asopinae, and to solve taxonomic problems in the genera *Tynacantha* Dallas, *Tylospilus* Stål and *Podisus* Herrich-Schäffer. The description of the life cycle and morphology of eggs and nymphs of six species (*Oplomus catena* (Drury), *Alcaeorrhynchus grandis* (Dallas), *Brontocoris tabidus* (Signoret), *Marmessulus brasilianus* Schouteden, *Podisus fuscescens* (Dallas), *Podisus nigrispinus* (Dallas), and *Supputius cincticeps* (Stål)) is presented. Using scanning electron microscopy technics, relevant features in the eggs and nymphs were studied, such as the aeromicropilary processes and chorion of the eggs, and the labium, and odoriferous system of nymphs. The obtained results highlights the morphological variability observed in both stages. This diversity allows the identification of the specie or genus in most cases, thus, should be explored in the taxonomy and systematics of the asopines. By revisiting the taxonomic history, and consulting type and pinned specimens of different collections, are presented: the taxonomic revision and description of two new species of *Tynacantha*; the redescription of *Tylospilus nigrobinotatus* (Berg) and description of *Tylospilus armatussimilis* Brugnera, Paim & Grazia; the correction of taxonomic problems in *Podisus,* including the description of five new species. Photographies, new descriptions, identification keys, and maps of distribution are provided. The importance of examining type specimens of Asopinae is highlighted, and the major taxonomic problems involving the studied genera are discussed.

Keywords: predatory stink bugs, systematics, immature stages, stink bugs, new species.

Introdução Geral

Os percevejos (Heteroptera) compõem um dos grupos mais diversos de insetos, com mais de 40 mil espécies descritas. Ocupam nichos em ambientes aquáticos e terrestres e participam de diversos processos ecológicos como predadores, sugadores de seiva, e outros (Schuh and Weirauch, 2020). Certos táxons são conhecidas por serem danosas para plantas, enquanto outras são eficientes controladoras biológicas (*e.g.* Asopinae, Thaumastocoridae) (De Clercq, 2008; Souza et al. 2012). Com o avanço de estudos genômicos, as relações entre grandes grupos de Heteroptera (famílias, superfamílias) foram melhor compreendidas e já existem hipóteses sobre a origem e diversificação das principais linhagens (Li et al. 2012; Weirauch et al. 2018). Porém, em diversas famílias, como Pentatomidae com mais de 5 mil espécies descritas, as relações entre tribos, gêneros e espécies são pouco resolvidas, havendo diversos agrupamentos taxonômicos possivelmente não monofiléticos (Rider et al. 2018; Roca-Cusachs, et al. 2022).

Pentatomidae inclui percevejos popularmente conhecidos como maria-fedida ou fede-fede. Dentre as diversas linhagens com hábito alimentar predominantemente fitófago, a subfamília Asopinae se destaca pela presença do hábito zoofitófago predador (Grazia et al. 2015; Rider et al. 2018). Os asopíneos se alimentam principalmente de outros insetos, injetando toxinas e compostos salivares que matam e promovem digestão extra-oral da presa (Plata-Rueda et al. 2022). O tipo de presa varia entre as espécies, havendo grupos generalistas (como *Eocanthecona* Bergroth, *Podisus* Herrich-Schäffer, *Tynacantha* Dallas*, Tylospilus* Stål) que predam basicamente qualquer inseto que conseguirem capturar, desde larvas e adultos de besouros, lagartas, mariposas, abelhas, moscas, outros percevejos, e até aracnídeos como aranhas e opiliões; e grupos que tendem a capturar essencialmente coleópteros, como algumas espécies dos gêneros *Stiretrus* Laporte, *Oplomus* Spinola e *Cazira* Amyot & Serville (Schaefer, 1996). Também podem ingerir fluidos vegetais com frequência, principalmente em períodos de escassez de presas (Pires et al. 2015). Porém, ao que se sabe, necessitam obrigatoriamente incluir fontes de origem animal na dieta para completar o desenvolvimento ninfal e atingir a fase adulta, onde o hábito também influenciará em fatores biológicos como na sobrevivência e longevidade, e nas taxas de fecundidade e fertilidade das fêmeas (Torres et al. 2006; Lemos et al. 2010).

A diversidade de Asopinae é representada por cerca de 300 espécies e 65 gêneros atualmente descritos, com ampla distribuição mundial (Thomas 1992, 1994; Roca-Cusachs et al. 2019; Roell et al. 2019). Estes percevejos predadores apresentam características singulares, como o lábio geralmente robusto e inserido próximo ao labro, búculas unidas distalmente, e genitália masculina com a presença de *pseudoclaspers* e *phallotheca* dividida em *basal theca* e *thecal shield* (Gapud 1991; Gapon & Konstantinov, 2006; Roell et al. 2020). Outras características distintivas de alguns gêneros são a presença de espinhos nos fêmures, expansões nas tíbias anteriores, grande número de cerdas no aparato tibial, e polimorfismo cromático (Thomas, 1992; 1994; Barão et al. 2013; Brugnera et al. 2019; Roell et al. 2019). A subfamília tem sido considerada um grupo monofilético, porém as relações internas são pouco resolvidas, havendo algumas proposições de tribos feitas no passado, mas que não foram adotadas nas classificações atuais (Thomas 1992; 1994; Rider et al. 2018; Roell, 2019; Roca-Cusachs et al. 2021).

São registrados 26 gêneros no Novo Mundo, e pelo menos 21 gêneros ocorrem na região Neotropical, sendo pelo menos 15 no Brasil. O trabalho de Thomas (1992) representa o último compilado taxonômico publicado com foco nestes gêneros, o qual contém chaves de identificação, diagnoses, listas sinonímicas, dados de distribuição e importantes comentários adicionais sobre as espécies. *Podisus* Herrich-Schäffer é o gênero mais diverso, composto por 33 espécies, com ocorrência registrada em todos os países localizados nas regiões Neotropical e Neártica, exceto Chile (Thomas, 1992; Roell et al. 2021).

Historicamente, *Podisus* passou por diversas alterações em sua classificação, incluindo a descrição de novas espécies, gêneros, e sinonimías (Thomas, 1992; Gapon, 2009). Certas espécies hoje classificadas em *Podisus* já pertenceram ao gênero *Telepta* Stål, atualmente considerado um sinônimo júnior. Outras, foram classificadas como subgêneros de *Apateticus* Dallas, por Schouteden 1907 (*A*. (*Eupodisus*)) e Kirkaldy 1909 (*A. (Podisus*)). Mais recentemente, os gêneros *Brontocoris* Thomas (duas espécies) e *Tyrannocoris* Thomas (quatro espécies) em 1992, e *Conquistator* Gapon (monotípico) em 2009, foram descritos a partir de espécies previamente classificadas em *Podisus*.

Ainda como parte da história taxonômica de *Podisus*, se destaca o gênero *Tylospilus*, descrito por Stål em 1870 como um subgênero de *Podisus*, ao qual incluiu três espécies: *P.* (*T.*) *chilensis* Spinola (espécie-tipo), *P.* (*T.*) *acutissimus* Stål e *P.* (*T.*) *cloelia* Stål. Foi apenas com a proposição de Thomas (1992) que *Tylospilus* passou ao ranking de gênero, sendo incluídas mais cinco espécies: *T. distans* (Bergroth), *T. megaspilus* (Walker), *T. nigrobinotatus* (Berg), *T. peruvianus* (Horvath) e *T. armatus* Thomas, descrita na mesma publicação. Exceto por *T. acutissimus*, que também ocorre nos Estados Unidos, as demais espécies ocorrem apenas na região Neotropical. O gênero é caracterizado pela presença de faixas e máculas pálidas e calosas na cabeça, pronoto e escutelo, frequentemente presentes também na região ventral, e pelo peritrema distintamente curto, quando comparado a outros gêneros morfologicamente parecidos, como *Brontocoris* e *Podisus*.

Em duas hipóteses (não publicadas) de relacionamento filogenético entre gêneros de Asopinae (Gapon, 2009; Roell, 2019, teses de doutorado), *Podisus* é apontado como sendo próximo aos gêneros do Novo Mundo: *Brontocoris*, *Conquistator*, *Supputius* Distant, *Tylospilus*, *Tynacantha* e *Tyrannocoris* Thomas*.* Assim como aos gêneros do Velho Mundo: *Arma* Hahn, *Troilus* Stål, *Oechalia* Stål e *Amyotea* Ellenrieder (Fig. 1). Estes gêneros compartilham algumas características, tais como: o corpo de formato pentagonal e coloração marrom ou amarelada, o fêmur anterior sem espinho, tíbia anterior sem expansão, e projeções globosas nos *pseudoclaspers* da genitália masculina (Roell, 2019); além da morfologia dos ovos, caracterizada por processos aeromicropilares bastante longos que ultrapassam o raio do opérculo, sendo este um padrão morfológico único em Pentatomoidea (Javahery, 1994; Brugnera et al. 2022).

Podisus, *Tylospilus*, e *Tynacantha* apresentam algumas espécies abundantes e amplamente distribuídas, encontradas com facilidade em ambientes naturais e antropizados, e utilizadas como importantes modelos em estudos relacionados ao controle biológico de insetos danosos a plantas cultivadas, contribuindo para o desenvolvimento de métodos de manejo que visam reduzir o uso de defensivos agrícolas (De Clercq, 2008; Zanuncio et al. 2014; Roca-Cusachs et al. 2020; Plata-Rueda et al. 2022). Para essa finalidade, destacam-se *Podisus maculiventris* (Say) e *Tylospilus acutissimus* na região Neártica; e *Podisus nigrispinus* (Dallas), *Podisus fuscescens*, e *Tynacantha marginata* Dallas na região Neotropical, sendo estas, estudadas em diversos centros de pesquisa brasileiros, como na Universidade Federal de Viçosa e Embrapa. Porém, a falta de estudos filogenéticos e taxonômicos modernos tornam a identificação das espécies um desafio, sobretudo no gênero *Podisus* (Brugnera et al. 2020). O gênero apresenta sete agrupamentos de espécies (aenescens, sculptus, falcatus, cornutus, congrex, sagitta, e maculiventris), propostos por Thomas (1992) com base apenas em características morfológicas do pronoto. Exceto pelas ilustrações dos parâmeros de algumas espécies, características da genitália masculina e feminina importantes para a identificação não são apresentadas nas descrições.

O baixo número de estudos e a falta de acesso a informações taxonômicas robustas, atrelados à crescente importância econômica associada a algumas espécies de *Podisus,* representam atualmente um problema científico. Por exemplo, entre 1992 e 2020, *Podisus fuscescens* (Dallas), foi erroneamente identificada como *Podisus distinctus* (Stål), como consequência de ambiguidades presentes nas descrições e na chave de identificação disponível (Thomas, 1992), incluindo a ausência de imagens e ilustrações que possibilitassem fazer relação entre as descrições e a espécie a ser identificada. Em quase duas décadas, pelo menos 30 artigos científicos foram publicados citando *Podisus distinctus* Stål, mas que provavelmente se referiam a *Podisus fuscescens* (Brugnera et al.

2020). A questão se estende ainda à publicação de novos registros de ocorrência, como *P. maculiventris* na Amazônia brasileira (a espécie ocorre apenas na América do Norte) (Silva, 2018) e *P. sagitta* (Fabricius) no estado de Minas Gerais (a ocorrência da espécie é restrita à América Central, México e norte da América do Sul) (Oliveira-Junior et al. 2021; Brugnera et al. 2022a).

Figura 1. Espécies de *Podisus* e possíveis gêneros relacionados. a) *Podisus tinctus* (Dallas); b) *Podisus mactans* Thomas; c) *Podisus curvispina* Bergroth; d) *Podisus maculiventris* (Say); e) *Brontocoris tabidus* (Bergroth); f) *Supputius cincticeps* (Stål); g) *Tynacantha marginata* (Dallas); h) *Tylospilus cloelia* (Stål); i) *Oechalia schellenbergi* (Burmeinster); j) *Arma custos* (F.); k) *Troilus luridus* (F.); l) *Amyotea hamata* (Walker).

Assim como a sistemática, estudos relacionados aos estágios imaturos de percevejos predadores são escassos (Brugnera & Grazia, 2018). É sabido que os ovos e as ninfas de Pentatomidae podem ter importância na taxonomia, além de representar caracteres com significância no estabelecimento de hipóteses filogenéticas, embora tenham sido pouco explorados até então (Javahery, 1994; Matesco et al. 2009; 2014). Os ovos de Asopinae se destacam por conta dos longos processos aeromicropilares, geralmente mais longos que o raio do opérculo, sendo considerados os mais longos conhecidos dentro de Pentatomoidea (Matesco et al. 2014). Esta característica está presente nos gêneros mais estudados (e.g. *Podisus*, *Supputius*), e por esse motivo, acreditava-se que ela seria dominante dentro da subfamília. Porém, hoje sabe-se que o tamanho e o número dos processos, e outras características dos ovos (e.g. esculturação do cório), apresentam grande variação entre os gêneros, podendo ser bastante curtos e até inconspícuos, como no gênero *Alcaeorrhynchus* Bergroth (Brugnera et al. 2022b). Da mesma forma, as ninfas apresentam diferenças interespecíficas em diversas partes do corpo, como nas placas abdominais, no formato da cabeça e pronoto, e no padrão de coloração, as quais possibilitam uma identificação confiável na maioria dos casos, principalmente a partir do terceiro ínstar de desenvolvimento (Brugnera et al. 2022b).

Diante das problemáticas apresentadas, nomeadamente a falta de informações básicas sobre os estágios imaturos e a taxonomia de Asopinae, os estudos desenvolvidos nesta tese atendem a dois principais objetivos: (i) investigar a morfologia e história natural dos ovos e ninfas de Asopinae, através de uma extensiva busca por literatura e a partir da criação e observação de diferentes espécies em condições controladas de laboratório; (ii) analisar e corrigir problemáticas taxonômicas e descrever espécies novas em três gêneros de Asopinae.

Estrutura da tese

Esta tese apresenta um compilado de informações sobre os estágios imaturos de Asopinae, assim como revisões, atualizações taxonômicas e descrições de novas espécies em três gêneros: *Tylospilus*, *Tynacantha* e *Podisus*. Este trabalho encontra-se dividido em: Introdução geral, capítulos e conclusão geral. Esta tese está estruturada em formato de artigos, que compõem sete capítulos, diagramados de acordo com as normas das respectivas revistas.

O capítulo I trata da descrição dos ovos e ninfas de *Oplomus catena* (Drury), assim como informações sobre a história natural e documentação das variações de coloração encontradas nos adultos da espécie (publicado na *Neotropical Entomology* – DOI: 10.1007/s13744-019-00713-5).

O capítulo II traz um compilado de informações da literatura sobre os estágios imaturos de Asopinae, guiado por categorias previamente selecionadas, além de imagens de fêmeas em oviposição e ninfas de 34 espécies e 30 gêneros. O trabalho também apresenta descrições morfológicas comparativas de seis espécies criadas em laboratório (publicado na *Zoology* – DOI: 10.1016/j.zool.2021.125991).

O capítulo III trata da revisão taxonômica do gênero *Tynacantha* com descrição de duas novas espécies. Apresentamos uma nova chave de identificação, imagens detalhadas de estruturas da genitália masculina e feminina, e mapas de distribuição (publicado na *Zootaxa* – DOI: 10.11646/zootaxa.4656.3.3).

O capítulo IV aborda aspectos taxonômicos do gênero *Tylospilus*. A espécie *Tylospilus nigrobinotatus* Berg é redescrita, uma nova sinonímia é feita, uma espécie nova é descrita, e uma chave de identificação atualizada para o gênero é disponibilizada. (publicado na *Zootaxa* – DOI: 10.11646/zootaxa.4766.1.6).

O capítulo V traz a redescrição de duas espécies de *Podisus*, uma delas com grande importância econômica. Apresentamos correções taxonômicas, novas sinonímias, imagens de espécimes-tipo e estruturas do corpo e genitália, e mapas de distribuição (publicado na *Zootaxa* – DOI: 10.11646/zootaxa.4751.3.7).

O capítulo VI trata da correção de uma nota científica contendo a ocorrência de *Podisus sagitta* (Fabricius) no estado de Minas Gerais (Brasil) (publicado na *Brazilian Journal of Biology* – DOI: 10.1590/1519-6984.255757).

O capítulo VII apresenta atualizações taxonômicas dentro do gênero *Podisus*, e a descrição de cinco espécies novas. Imagens de espécimes-tipo são disponibilizadas, espécies previamente consideradas válidas são sinonimizadas, e outras são revalidadas. *Ornithosoma rivierei* Kormilev é proposta como sinônimo júnior de *Podisus semialbus* Walker.

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CAPÍTULO I

Morphology of immature stages, chromatic polymorphism of adults and natural history of *Oplomus catena* (Heteroptera: Pentatomidae: Asopinae)

[Brugnera et al. (2019). Neotropical Entomology, 48:1046–1057, doi.org/10.1007/s13744-019-00713-5]

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Abstract

The predatory stink bugs are well known by their behavior, but the knowledge of the immature morphology and their natural history are scarce. Studies on predatory stink bugs are important to better understand their evolution and their use as biological controllers. Here, we describe the morphology of egg and the five nymphal instars of *Oplomus catena* (Drury, 1782), using optical and scanning electron microscopy. In general, *O. catena* immatures are very distinctive from other Asopinae species already studied. The egg is black, with short aero-micropylar processes and similar to those described for Stiretrus species. The nymphs can be diagnosed by the abdominal plates very large and bright blue. The color polymorphism of adults is fully illustrated, and four color patterns are proposed. The natural history of the species is described based on field and laboratory observations. The known prey of the species is reviewed and new preys are reported. The morphological and biological traits here described are discussed in order to better understand the biological role of predatory stink bugs.

Keywords: Hemiptera, color morphs, sexual dimorphism, predatory stink bugs, biological control

Introduction

Predatory stink bugs (Asopinae) are well known as important agents in biological control programs, with several species used in all continents of the world (De Clercq 2000, Richman & Mead 2001, Zanuncio *et al* 2014, Grazia *et al* 2015). The use of alternative methods to control pests in crops is increasingly important to reduce the use of pesticides and keep a balance between agricultural and ecological systems. However, the biology and morphology of immature stages of these predators are poorly studied which makes their application in biological control and pest management programs difficult (Cohen 2000, Schaefer & Panizzi 2000, Brugnera & Grazia 2018). *Oplomus* Spinola, 1837 is a genus of predatory stink bugs, composed of 12 species distributed through the American Continent from the USA to Argentina and remarkable by the bright and aposematic colorations and intraspecific color variation (Thomas 1992). Species of *Oplomus* can be recognized by the frenal margin of scutellum shorter than the postfrenal and presence of foretibial expansions and abdominal glandular patches in males (Thomas 1992, Brugnera *et al* 2019).

Oplomus catena (Drury, 1782) was one of the first asopines studied in Brazil by Silva (1933) who provided information about the life cycle and the morphology of immature and adults (see Pires *et al* 2015). The species is widely distributed in Austral South America, easily recognized by the angulated apex of mandibular plates (Thomas 1992), and it is known to prey on Lepidoptera (Silva 1933, Paluch *et al* 1999) and Coleoptera (Silveira et al 2002 Gomes 2012). Among *Oplomus* species, the morphology of immatures of *O. cruentus* Burmeister, 1835was studied by Saini (1990), and the biology of *O. dichrous* Herrich-Schäffer, 1838 by Drummond *et al* (1987).

Here we describe the external morphology of the egg and the five nymphal instars of *O. catena*, emphasizing the postembryonic changes. Additionally, we describe the chromatic polymorphism of adults proposing color patterns, provide details on the natural history, and review the known preys of the species.

Materials and Methods

Adults were collected in São Domingos do Sul, RS, Brazil (28°33′51.1″S 51°49′56.8″W). Specimens were reared in laboratory in mesh boxes (12 × 12 cm) composed of a structure made of wood (floor and four lateral pilaster), surrounded by a fine and translucide tulle; the door is also made with tulle and coupled to the box with velcro (Fig 4d). The boxes were maintained in a control chamber at 25 ± 1°C, 70 ± 10 RH, and 12 L:12Dh photoperiod. The boxes were sprayed daily with water and the specimens fed with larvae of Lepidoptera and larvae and pupae of *Tenebrio molitor* Linnaeus (Coleoptera: Tenebrionidae) ad libitum (see “Discussion”). Additionally, leaves of *Eugenia uniflora* (L.) (Myrtaceae) were offered once a week.

Pinned adult specimens used in this study were obtained from the following institutions (Supplementary 1):

EMG Entomologisches Museum Geyer, Insekten Dauerausstellung, Geyer, Germany.

NMPC National Museum, Prague, Czech Republic.

MNRJ Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil.

MPEG Museu Paraense Emílio Goeldi, Belém, Brazil.

MZUSP Museu de Zoologia, Universidade Estadual de São Paulo, São Paulo, Brazil.

UFRG Universidade Federal do Rio Grande do Sul. Departamento de Zoologia, Porto Alegre, Brazil

Immature and adults were photographed in multiple focal planes with a Nikon AZ100M scope coupled with a DS-Fi2 digital camera. Pictures were stacked in a single focused image using the NIS Elements software. Alive specimens were photographed with a Nikon D3100 digital camera. Photographs were processed in Photoshop® CS5 software.

Measurements and morphological data were obtained from 10 eggs and 10 nymphs of each instar, fixed in 70% ethanol, and maintained in freezer. The description of color patterns was carried out *in vivo*. Measurements are presented in millimeters (mean ± standard deviation [maximum - minimum]) and were obtained according to Brugnera & Grazia (2018) (Table 1). Voucher specimens were deposited at the Entomological Collection of the Department of Zoology, Federal University of Rio Grande do Sul (UFRG).

For scanning electron microscopy (SEM) analysis, two eggs and two specimens of each instar (preserved in 70% ethanol) were dehydrated in an increasing concentration of ethanol series (70%, 80%, 90%, and 99.9%) for 10 min each, and transferred to 100% acetone. Samples were critical point dried (10 cycles), mounted in stubs, sputter-coated with gold, and observed and photographed in a scanning electron microscope (JEOL JSM 6060).

Terminologies for immature follow Matesco *et al* (2007, 2009, 2014) for general morphology, and Vilimová & Kutalová (2012), Bottega *et al* (2015), and Bianchi *et al* (2016) for dorsal abdominal glands. Terminologies for adult morphology follow Thomas (1992).

Results

Morphology of immature

Egg

Barrel-shaped (Figs 1a and 2b); chorion thick, pale after oviposition, becoming dark brown few minutes later; egg color becoming reddish with the development of the embryo; lateral wall of chorion reticulated, with rounded projections (Figs 1a and 2b); operculum with a projected circle medially, sometimes with tiny projections in the center; lateral of operculum smooth; 15 to 23 translucent aero-micropylar processes surrounding the operculum (Figs 1b and 2a, b); openings of aero-micropylar processes subapical and directed inward (Fig 2d); aero-micropylar processes dilated at base (Fig 2c); distance between processes almost equal to one process length. Measurements: egg length (1.56 ± 0.04 [1.64–1.48]); egg width (1.17 ± 0.02 [1.2–1.12]).

First instar

Head and thorax dark brown to black (except intersegmental areas of antennae and discal region of thorax that are red). Abdomen red; abdominal plates dark brown to black; spiracles and trichobothria dark brown (Fig 1c, d). Body oval; surface smooth, without punctures; lateral margin of the body, antennae, and legs with setae. Head rounded, declivent; clypeus longer than mandibular plates; apex of labium slightly surpassing themetacoxae; proportion of labial segments I < II > III < IV, fourth segment longest; proportion of antennal segments I < II > III < IV, fourth segment longest. Seven dorsal median plates in abdomen; first two plates slender, shorter than the III plate; II–IV plates with the openings of dorsal abdominal glands (DAGs). Eight pairs of semicircular lateral plates in abdomen, first plate smaller than the following, XI segment entirely covered by a plate; ventral median plates not visible (Fig 1c, d); 1 + 1 spiracles on II–VII abdominal segments and 1 + 1 pre-trichobothria and 1 + 1 trichobothria on III–VI abdominal segments (Fig 2g). Ventral plates covered by comb-like projections (Fig 2h). Ornamentation of evaporatorium of anterior dorsal abdominal glands (DAG1) with wrinkles located anteriorly and posteriorly to the ostiole; ostioles slit-like (Fig 2e); ostioles of median (DAG2) and posterior (DAG3) attended by cuticular fold; surface of evaporatorium with spiked projections (Fig 2f).

Second to fifth instar

From second to fifth instar, the morphology of the nymphs is very similar, differing only in the size (Table 1) and some aspects of the antennae, mandibular plates, and legs that are detailed below. Head, thorax and dorsal abdominal plates somewhat bright blue. Intersegmental areas of antennae, discal region of thorax and abdomen red (Fig 1e–n).

Body oval (Fig 1e–j) slightly elongated in the fifth instar (Fig 1i, j); dorsal surface slightly punctured on the second instar, becoming more dense and deep in the following instars (Figs 1e–j and 2n, o), each puncture with a basiconic sensilla (Fig 2n, o); clypeus slightly longer than mandibular plates on second instar (Fig 1k), subequal on third instar (Fig 2l); and shorter than mandibular plates on fourth and fifth instars (Fig 1m,n); apex of labium surpassing the metacoxae on second instar (Fig 1f), becoming increasingly shorter along the development, slightly surpassing the mesocoxae on fifth instar (Fig 1j). II and IV antennal segments equally in length in the second instar (Fig 1e); III antennal segment longest from that of the third instar (Fig. 1g, h, j). Lateral margins of pronotum serrated. Development of wing pads, femoral spine and foretibial expansion visible from the third instar (Fig 1e, f), and abdominal spine in the fifth instar (Fig 1j). Dorsal and lateral plates of abdomen almost touching each other; abdomen with six dorsal plates, plate I not distinctly separated from thorax; plate II long and slender, slightly shorter than III; six dorsal median plates and five ventral median plates present; IX segment entirely covered by a plate. A pair of slender ventral plates on the posterior margins of II and III abdominal segments; a pair of mesolateral plates on the III abdominal segment; openings of dorsal abdominal scent glands on II–IV dorsal median plates (Fig 1e, g–i); 1 + 1 spiracles on II–VIII segments and 2 + 2 trichobothria on III–VII ventral abdominal segments (Fig 2m). Ostiole of DAG1 slit-like surrounded by cuticular wrinkles and reticulated evaporatorium with shallow alveoli composed of low bridges and trabeculae (Fig 2i). DAG2 (Fig 2j) and DAG3 bearing spout peritreme, surrounded by a reticulate evaporatorium; peritreme lip and postostiolar fold present (Fig 2j–l).

Chromatic polymorphism of adults

Seventy-four adults of *Oplomus catena* were analyzed from different localities of Brazil. Four color patterns were observed among males and females, with drab and bright variations (Fig 3). Each specimen analyzed was classified in one of the patterns described below (Supplementary 1). Color patterns: (1) entirely bright blue, sometimes with the abdominal spine and the apex of abdomen yellow (Figs 3a, b and 4h). (2) Head drab black with the apex of mandibular plates reddish or yellow; thorax drab reddish or yellow dorsally, with two black and semicircular maculae in the center of pronotum, and one macula in the center of each corium (sometimes not present or very reduced). Scutellum red or yellow, with a black macula at base and a black macula in the middle of postfrenal portion. Ventral drab red or yellow, with several black maculae. Legs brown, with red or yellow areas on femur and tibia (Figs 3e–h and 4e, f, h, j). (3) Head generally totally black; dorsal and ventral bright blue or drab black; apex of corium and posterolateral portion of pronotum red or yellow, apical margin of scutellum pale or concolor with scutellum. Ventral bright blue or drab black, sometimes with pale spots; abdominal spine pale. Legs bright blue or drab black (Figs 3i–l and 4g). (4) Dorsal and ventral drab black; base and lateral of pronotum and apex of corium red or yellow; basal angles and apex of scutellum red or yellow. Ventral red or yellow at the apex of abdomen, abdominal spine, and medial part of the IV segment (frequently with a black spot in the middle). Legs drab black with red or yellow spots in the femur (Figs 3m–p and 4i, k). Among the patterns proposed, 1 and 2 were observed in both sexes, pattern 3 was present only in females and 4 observed only in males (Supplementary 1). Pattern 2 is the most common variation, observed in 38 (51, 3%) individuals. Pattern 3 was observed in four individuals from Paraná and São Paulo states. Among the adults obtained from our rearing (bold individuals in Supplementary 1) were observed all the patterns except 3, and pattern 2 was observed only in females. No yellow forms of pattern 2 were obtained from our rearing; we observed that the red pigmentations tend to fade with the age of adult, becoming pale/yellow (Supplementary 1).

Natural history

Several immature and adults were found among December and February in a relative small portion of native Atlantic Rain Forest (see “Material and Methods”) in different plants (Fig 4a). Frequently these bugs were collected in small shrubs of *Eugenia uniflora* (L.) (Fig 4b), but also in climbing plants tangles (Fig 4c). Usually larvae of Lepidoptera and Coleoptera were found in the same plant. Eggs are laid in two rows, with about to 24 eggs per cluster, but sometimes with less than 10 eggs (Fig 4l). After hatching, the first instar nymphs stay around the egg cluster, feeding on water until the molt. Few hours after molting to second instar, nymphs start to walk around the box, usually alone, apparently to find food. When a larva is found, the nymph made fast movements with the antennae and immediately tries to insert the stylets on the prey. Usually the prey try to escape but the bugs are successful in almost all the cases. Right after the nymphs start to feed, more nymphs come and share the prey (Fig 4m–p). Generally, in second and third instars, the nymphs do not avoid to share their prey, even if it is small. In fourth and fifth instars, the nymphs try to escape with the prey when other nymphs come closer. This behavior was also observed in adults (Fig 4 k). After feeding, the nymphs stay a long time motionless, frequently until the next molt.

Oplomus catena seems to be very generalist, having preference for soft body larvae. The adults are voracious and attack the prey holding it with the claws of forelegs (Fig 4f). Initially in laboratory, we have tried to feed adults and nymphs with larvae and pupae of *Tenebrio molitor* but apparently, they cannot pierce the external cuticle to access the internal tissues and feed. So we offered any Lepidoptera or Coleoptera larvae, daily collected in a remnant of Atlantic Rain Forest in Campus do Vale—UFRGS, Porto Alegre, Brazil. All the larvae offered to nymphs and adults were eaten. Because of the difficulty to frequently find and collect soft body larvae, we made small cuts on the sides of the body of

Tenebrio molitor larvae and offered to the bugs. Apparently, with the help of antennae and apex of labium, they could find the cuts and feed on the larvae without difficulties (Fig 4p, q). Almost all the specimens reared for this study were fed with this method, and the mortality index was almost zero. Additionally, nymphs from second instar and adults were frequently observed feeding on leaves of *Eugenia uniflora* (Fig 4r).

Adults exhibit thanatosis behavior when they are perturbed, usually extending the legs and antennae and staying in that position for about 10 s. This behavior was not observed in the nymphs (Fig 4j).

Discussion

Morphology of immature

Only about 1% of the immature stages of predatory stink bugs that occur in the neotropics have been studied so far. This lack of knowledge makes it difficult the identification of most of immature stages collected and prevents to include immature characters in taxonomic diagnosis and phylogenetic analysis (Matesco *et al* 2014, Brugnera & Grazia 2018). Taking into consideration the species of Asopinae whose morphology is known, the egg of *Oplomus catena* has the similar characteristics with *O. cruentus*, *Stiretrus decastigmus* Herrich-Schäffer, 1838, and of *S. anchorago* Fabricius, 1775 [as *S. fimbriatus* (Germar)] (Oetting & Yonke 1971, Saini 1990, Richman & Mead 2001). According to unpublished phylogenetic hypotheses (Gapon 2008, Roell 2019), *Oplomus* is the sister group of the *Stiretrus* + *Discocera* clade. The similarities between the egg of *Oplomus* and *Stiretrus* and their hypothetical phylogenetic relationship reinforce the phylogenetic importance of the egg structure in Pentatomidae, as tested by Matesco *et al* (2014) for *Chinavia* Orian, 1965 and *Nezara* Amyot & Serville, 1843.

Besides the underexplored morphology of Asopinae eggs, some studies show their remarkable diversity in size, shape, chorion sculpture, and size of aeromicropylar processes. Eggs of predatory stink bugs are known by the aero-micropylar processes, generally much longer than in other subfamilies of Pentatomidae (De Clercq 2000, Matesco *et al* 2009, 2014), as observed in *Podisus* Herrich-Schäffer, 1851 (Oetting & Yonke 1971, Grazia *et al* 1985, De Sá *et al* 2013), *Brontocoris* Thomas 1992, *Supputius* Distant, 1889 (Dimaté *et al* 2014), *Tynacantha* Dallas, 1851 (Brugnera & Grazia 2018), *Conquistator* Gapon, 1992 (Costello *et al* 2002), *Troilus* Stål, 1867 (Hinton 1981) among others. However, as *Oplomus* and *Stiretrus*, many genera exhibit short aero-micropylar processes, as *Euthyrhynchus* Dallas, 1851 (Richman & Mead 2000), *Alcaeorrhynchus* Bergroth, 1891 (Mead & Richman 2000), *Picromerus* Amyot & Serville, 1841, and *Pinthaeus* Stål, 1867

(Rieger 2000) These egg patterns observed among Asopinae genera seems to be correlated with their phylogenetic relationship, which can be useful for the systematics of the group and should be more investigated.

First instar nymphs of Asopinae generally show similar characteristics: red abdomen and black to dark brown head and thorax (Grazia *et al* 1985, Brugnera & Grazia 2018, this study) which makes their identification difficult. From the second instar on, the nymphs show more evident differences between the species that allow distinguishing them. In *Oplomus catena* the most diagnostic characteristic is the dorsal and lateral abdominal plates that almost touch each other, occupying nearly the entire dorsal surface of abdomen (Fig 2e–i). These features are not observed in any other species of Asopinae whose morphology is known, presenting always much shorter plates (see Brugnera & Grazia 2018 for an example), except for *Stiretrus anchorago*. Although not described by Richman & Mead (2001), the nymphs of *S. anchorago* seem to have fused dorsal and lateral plates from the second instar on, forming a single plate that covers the entire dorsal surface of abdomen. The femoral spine and the angulated apex of mandibular plates, features present in adults (Thomas 1992), can be recognized in the nymphs from the third instar, which progressively increases in size on fourth and fifth instar (Fig 2e–i). Additionally, *O. catena* nymphs present a pair of pre-trichobothria and a pair of trichobothria in III–VI abdominal segments on first instar (Fig 2g). Generally pentatomids exhibit only a pair of trichobothria on first instar, but some contrary examples can be found in species of *Chinavia* (Schaefer 1975, del Vecchio *et al* 1988, Schwertner *et al* 2002). This is the first time that a pair of pre-trichobothria is reported for the subfamily Asopinae.

The intraspecific color variation is a feature present in some bugs of the superfamily Pentatomoidea and can be expressed in nymphs and adults (Schwertner *et al* 2002, Sánchez-Soto *et al* 2004, Campos *et al* 2007). Among adults, the condition is observed in drab bugs such in the well-known green stink bug, *Nezara viridula* (Linnaeus, 1758) (Pentatomidae) (Harris *et al* 1984, Esquiavel *et al* 2018) and frequently observed among species that exhibit bright and/or aposematic coloration, as in *Pachycoris torridus* (Scopoli, 1772) (Scutelleridae) (Sánchez- Soto *et al* 2004), in Catachantini (Pentatomidae) species such as in the genus *Arocera* Spinola, 1837 (Rider 1992), and in many Asopinae (Pentatomidae) species (Thomas 1992, 1994, Paleari 2013, Roell *et al* 2019, this work), among others. From the second instar on, nymphs of *O. catena* exhibit a bright blue coloration on head, thorax, and abdominal plates, without intraspecific variation (Figs 1e-j). Similar condition was already reported for other asopines: *Tynacantha marginata* Dallas, 1851 (Brugnera & Grazia 2018), *Euthyrhynchus floridanus* Linnaeus, 1767 (Richmann & Mead 2000), and *Alcaeorrhynchus grandis* (Dallas, 1851) (Mead & Richman 2000). Among the possible biological roles of this condition, the defensive behavior, sexual selection, type of food and diapause have been studied so far, which directly influences the systematic studies on these taxa (Please, replace this citation by Schwertner *et al* 2002 , Souza *et al* 2012, Musolin & Saulich 2018); however, the intraspecific color variation is not yet well understood in stink bugs.

The evolutionary implications and the biological role of this variation in Asopinae are yet unclear but were discussed by Schaefer (1996). The author suggests bright asopines prefer to feed on bright beetles compared with drab asopines, and may derive defensive allomones by feeding, mainly from chrysomelid and coccinellid beetles. Schaefer (1996) also suggested the bright condition of these bugs may trace an evolutionary progression from drab bugs that commonly feed on other insects besides beetles. However, in laboratory and natural conditions *O. catena* was frequently reported feeding on Lepidoptera larvae, especially of the genus *Actinote* (Fig 4, Table 2) which suggests that the species may not have a preference for beetles, as reported for *Stiretrus decemguttatus* (Paleari 2013) for example. It is suggested the species seems to be generalist and able to feed on any insect they can pierce, but more studies on the predatory behavior are needed to confirm this hypothesis.

As in other pentatomids, first instar nymphs of *Oplomus catena* do not feed and only need moisture to survive (Schuh & Slater 1995). From the second instar, the nymphs need to feed on other insects to continue the development and some species need to feed also on plants, probably to obtain water for saliva and to complete the development (De Clercq 2000, 2008, Grazia *et al* 2015). Early instar nymphs of *O. catena* seem to prefer group feeding; this behavior could improve the efficiency of the predation especially on large size preys, as reported for *Andrallus spinidens* (Fabricius) (Hyodo *et al* 2014).

Although yet underexplored, the knowledge about the predatory behavior and feeding strategies of asopines has been improved in the last decades. These stink bugs use essentially visual, chemical, and tactile senses to detect potential preys, which are then selected based on their nutritional quality and their defense capacity (Marston *et al* 1978, De Clercq 2000, Lemos *et al* 2003). However, the influences of remarkable features like body coloration and some body structures (e.g. foretibial apparatus and foretibial expansion) in the predation are yet poorly understood (Barão *et al* 2013, Brugnera *et al* 2019). In general, the knowledge about the biology of asopines is very scarce and focused only in species with economic importance. Studies in less known species are important to better understand the evolutionary traits and feeding strategies of these bugs.

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Authors' Contribution

RB planned, designed, collected data, and executed experimental work of the study. RB, LAC, and JG wrote and approved the final manuscript.

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Table 1 Measurements (in millimeters) (mean ± standard deviation [maximum-minimum] of the morphometric characters of nymphs of *Oplomus catena*.

Character	**First instar**	**Second instar**	**Third instar**	**Fourth instar**	**Fifth instar**
Total length	1.75 ± 0.04 (1.80–1.70)	3.59 ± 0.11 (3.76–3.40)	4.74 ± 0.24 (5.28–4.24)	7.84 ± 0.67 (8.83–6.83)	9.84 ± 0.58 (11.08–9.25)
Head length	0.55 ± 0.01 (0.58–0.54)	0.85 ± 0.04 (0.88–0.80)	0.98 ± 0.04 (1.08–0.92)	1.32 ± 0.15 (1.58–1.08)	1.69 ± 0.07 (1.75–1.42)
Head width	0.82 ± 0.03 (0.88–0.76)	1.06 ± 0.02 (1.08–1.04)	1.32 ± 0.02 (1.36–1.28)	1.80 ± 0.03 (2.20–1.79)	2.10 ± 0.05 (2.28–2.00)
Interocular distance	0.61 ± 0.02 (0.64–0.58)	0.75 ± 0.02 (0.80–0.72)	0.80 ± 0.01 (0.84–0.76)	1.04 ± 0.08 (1.25–0.92)	1.26 ± 0.06 (1.32–1.16)
Rostral length	0.89 ± 0.02 (0.92–0.86)	1.49 ± 0.03 (1.52–1.46)	2.01 ± 0.05 (2.12–1.92)	2.97 ± 0.18 (3.42–2.58)	1.69 ± 0.08 (1.75–1.42)
Rostral width of I segment	0.16 ± 0.01 (0.16–0.14)	0.26 ± 0.03 (0.28–0.20)	0.32 ± 0.01 (0.36–0.32)	0.46 ± 0.03 (0.48–0.40)	0.59 ± 0.01 (0.60–0.52)
Length of I antennal segment	0.14 ± 0.00 (0.14–0.14)	0.23 ± 0.01 (0.24–0.22)	0.36 ± 0.04 (0.40–0.30)	0.52 ± 0.04 (0.60–0.44)	0.62 ± 0.03 (0.72–0.60)
Length of II antennal segment	0.31 ± 0.02 (0.34–0.28)	0.72 ± 0.01 (0.74–0.70)	0.92 ± 0.03 (1.00–0.90)	1.50 ± 0.12 (1.84–1.28)	2.00 ± 0.01 (2.04–2.00)
Length of III antennal segment	0.25 ± 0.01 (0.26–0.24)	0.52 ± 0.00 (0.54–0.52)	0.70 ± 0.01 (0.72–0.68)	1.05 ± 0.04 (1.20–0.96)	1.40 ± 0.00 (1.40–1.40)
Length of IV antennal segment	0.52 ± 0.01 (0.54–0.52)	0.80 ± 0.00 (0.80–0.80)	0.92 ± 0.02 (0.98–0.90)	1.28 ± 0.06 (1.40–1.12)	1.47 ± 0.04 (1.56–1.40)
Pronotal length	0.18 ± 0.01 (0.20–0.16)	0.45 ± 0.04 (0.52–0.40)	0.63 ± 0.03 (0.68–0.60)	1.22 ± 0.13 (1.67–1.00)	1.74 ± 0.03 (1.83–1.67)
Pronotal width	1.10 ± 0.02 (1.14–1.06)	1.61 ± 0.02 (1.64–1.60)	2.20 ± 0.00 (2.20–2.20)	3.57 ± 0.33 (4.42–2.83)	4.58 ± 0.13 (4.96–4.42)
Abdominal width	1.40 ± 0.02 (1.44–1.34)	2.49 ± 0.11 (2.68–2.36)	3.66 ± 0.16 (4.00–3.33)	5.13 ± 0.33 (5.67–4.50)	6.22 ± 0.20 (6.75–5.83)

Table 2 Review of the known prey of *Oplomus catena*. The scientific name of the species is written as in the references.

Family (Order)	Genus/Species	Reference
Nymphalidae (Lepidoptera)	*Actinote pellenea* Huebn.	Silva 1933; Grazia & Hildebrand 1987
Nymphalidae (Lepidoptera)	*Actinote pyrrha pyrrha* (Fabricius)	Rezende *et al*. 2008
Nymphalidae (Lepidoptera)	*Actinote surima* (Schaus)	Paluch *et al.* 1999
Nymphalidae (Lepidoptera)	*Actinote* sp.	This study (Fig 4e)
Papilionidae (Lepidoptera)	*Heraclides* sp.	This study (Fig 4m)
Papilionidae (Lepidoptera)	*Heraclides anchisiades capys* (Hübner)	Costa Lima 1968
Crambidae (Lepidoptera)	*Duponchelia fovealis* Zeler	Bischoff *et al*. 2013
Saturniidae (Lepidoptera)	cf. *Dyrphia* sp.	This study (Fig 4e)
cf. Noctuidae (Lepidoptera)	–	This study (Fig 4o)
Chrysomelidae (Coleoptera)	*Coelomera lanio* (Dalman)	Silveira *et al.* 2002
Chrysomelidae (Coleoptera)	*Stolas chalybea* Germar	Nogueira-de-Sá & Vasconcellos-Neto 2003
Chrysomelidae (Coleoptera)	–	This study (Fig 4g)

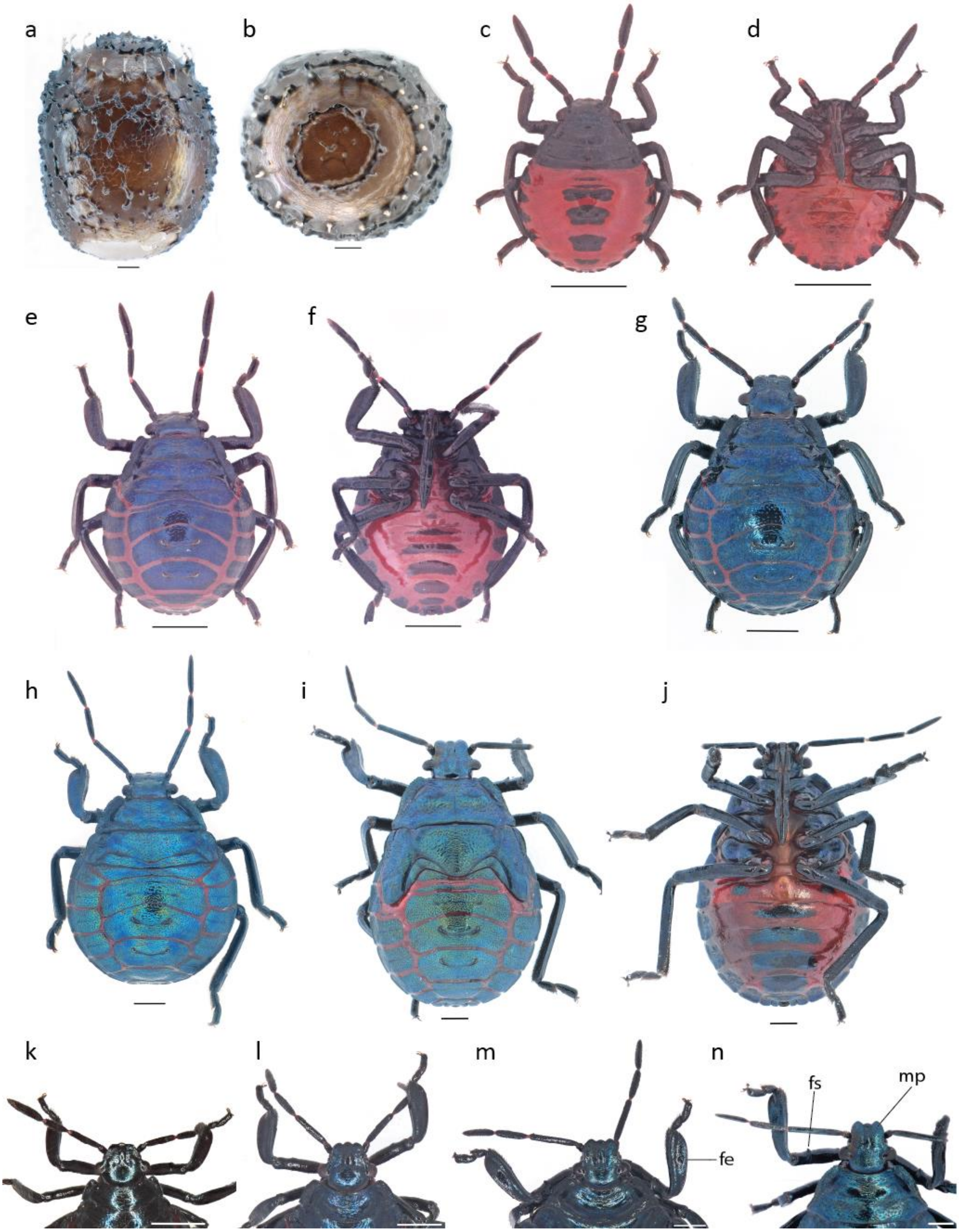

Fig 1 Immature stages of *Oplomus catena*. a, b egg; c, d first instar; e, f, k second instar; g, l third instar; h, m fourth instar; i, j, m fifth instar. fe, foretibial expansion; fs, foretibial spine; mp, mandibular plate. Scale bars = a, b 0,1 mm; c–n 1 mm

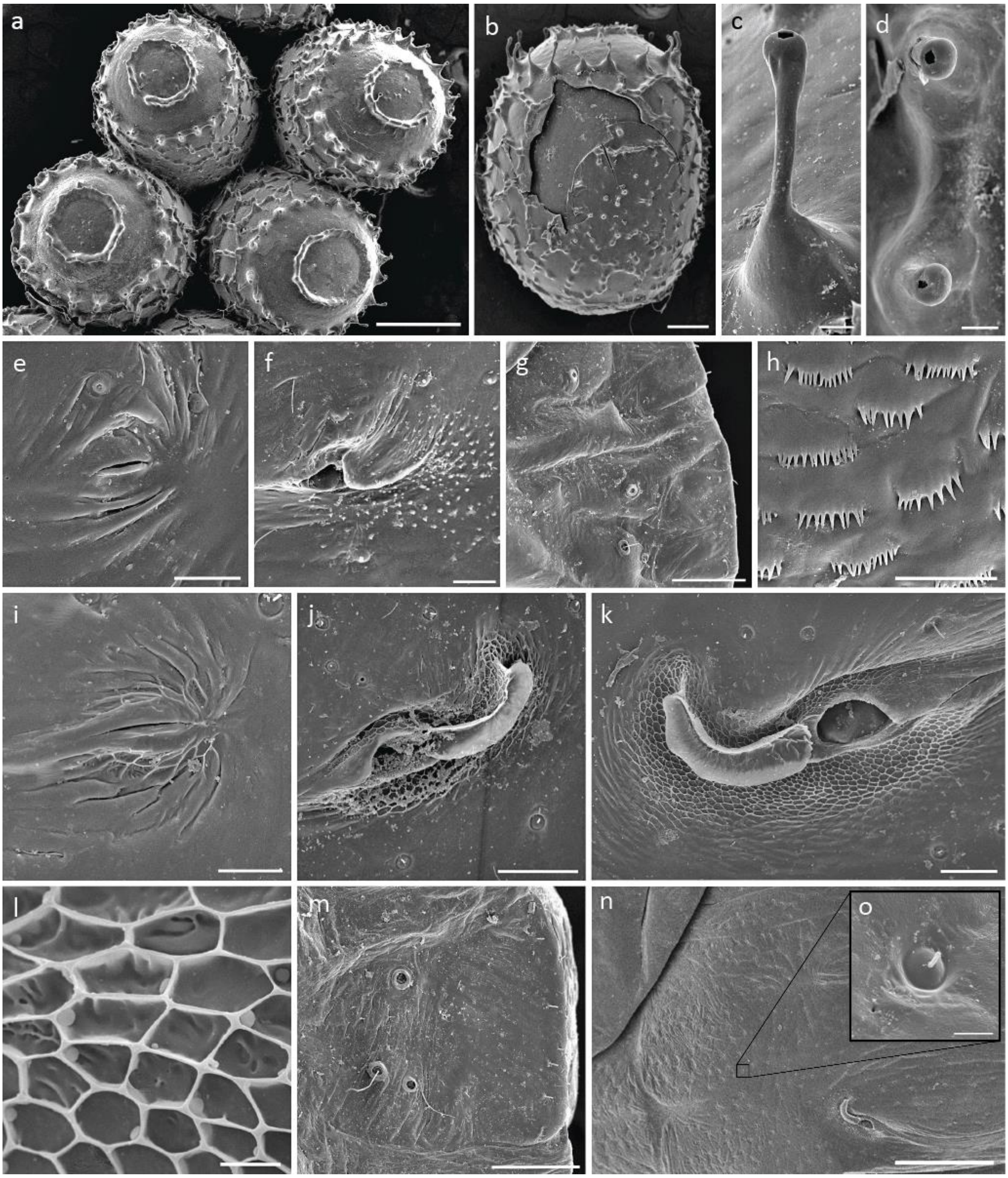

Fig 2 Immature stages of *Oplomus catena* under scanning electronmicroscopy. a–d egg; a dorsal view; b lateral view; c, d aero-micropylar process; e–h first instar; e DAG1; f DAG2; g spiracle and trichobothria of II and III ventral abdominal segments; comb-like projection on VI abdominal segment; i, j, m; second instar; i DAG1; j DAG2; k, l, n, o fifth instar; k DAG2; l evaporatorium; m spiracle and trichobothria of II ventral abdominal segment; n, o punctures with a basiconic sensilla. e, evaporatorium; o, ostiole; p, peritreme; ptr, pre-trichobothria; s, spiracle; tr, trichobothria. Scale bars = 500, 200, 20, 20, 10, 20, 100, 10, 20, 50, 50, 5, 100, 500, 10 μm, respectively.

Fig 3 Patterns of chromatic polymorphism in adults of *Oplomus catena*. a–d pattern 1; e–h pattern 2; i–l pattern 3;m–p pattern 4. Scale bars = 1 mm.

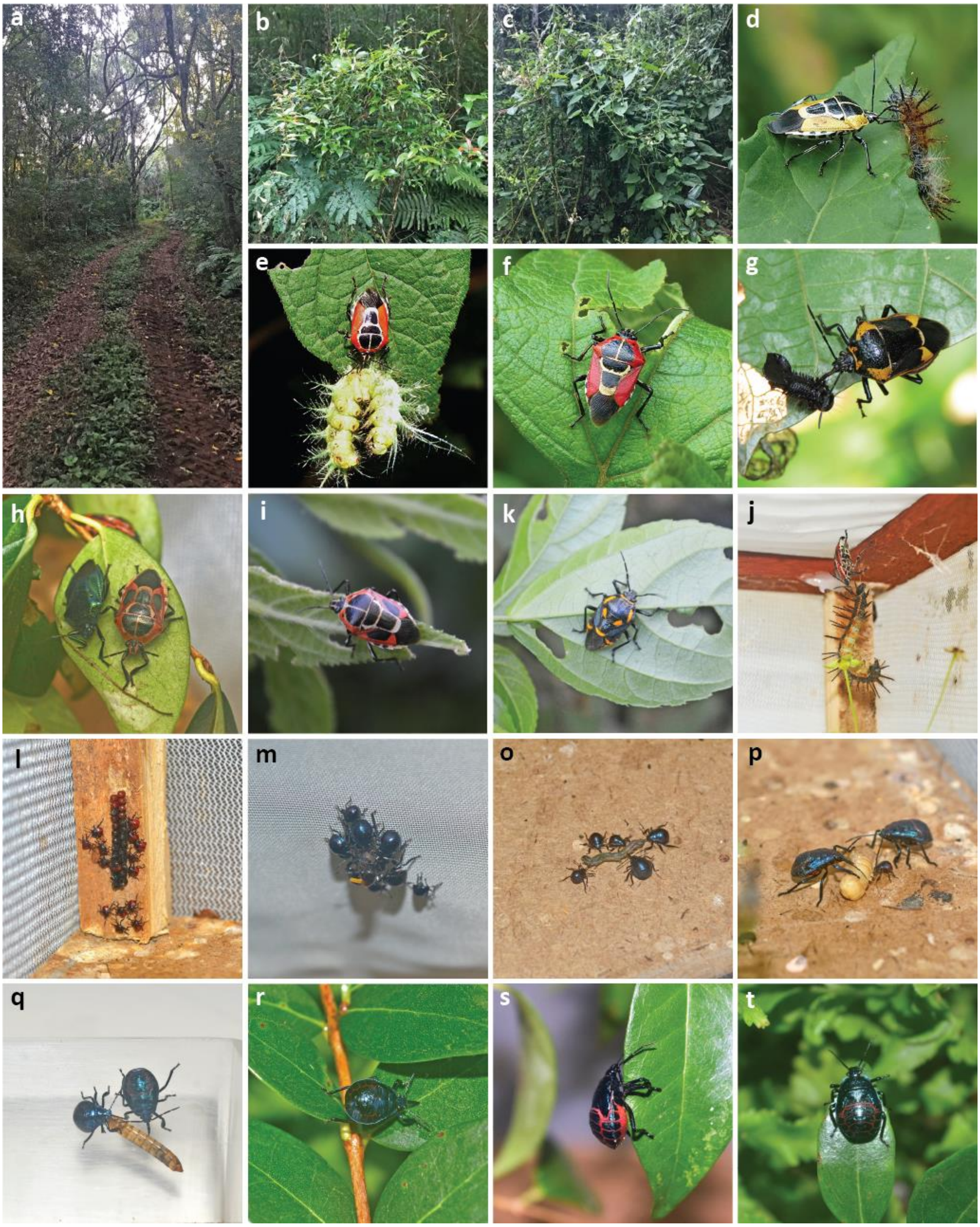

Fig 4 Habitat and photos of *Oplomus catena*. a general aspects of site of collection (São Domingos do Sul, Brazil); b shrub of *Eugenia uniflora*; c climbing plants tangles; d mesh box; e–j habit of live adults; l–t habit of live immature; j male displaying thanatosis behavior; l egg cluster and first instar; m second and third instar preying *Heraclides* sp. larva; n second and third instar preying cf. Noctuidae larva; p fifth and second instar preying Tenebrio molitor pupa; q fourth and fifth instar preying *Tenebrio molitor* larva; r fourth instar feeding on *Eugenia uniflora* leave; s lateral view of fifth instar; t dorsal view of fifth instar. Photos e–f by Antonio C. F. Junior. Photo g by Diogo J. Luiz.

Morphology of immature stages, chromatic polymorphism of adults and natural history of *Oplomus catena* (Heteroptera: Pentatomidae: Asopinae)

Ricardo Brugnera, Luiz A. Campos, Jocelia Grazia

Neotropical Entomology

Online Supplementary Material 1

Supplementary 1: Label information, sex and collection of deposition of adult specimens of *Oplomus catena* with the color variation classified for each specimen. Bold records represent the individuals obtained from our rearing.

Label information	Sex	Collection	Color pattern
Brazil, MG, Viçosa. 20.I.1995. R.D. Silveira leg.	M	UFRG	2
Brazil, MG, Viçosa. 20.I.1995. R.D. Silveira leg.	M	UFRG	2
Brazil, MG, Viçosa. 20.I.1995. R.D. Silveira leg.	M	UFRG	2
Brazil, RJ, Rio de Janeiro. X.1951. Nestor Fagundez leg.	F	MNRJ	2
Brazil, RJ, Rio de Janeiro. IX.1966. E. Mendes leg.	F	MNRJ	2
Brazil, RJ, Rio de Janeiro. 1956. Zaj Civ. leg.	F	MNRJ	2
Brazil, RJ, Petrópolis. II-III.1941	F	MNRJ	2
Brazil, RJ, Rio de Janeiro. 4.IV.1960. M. Alvarenga leg.	F	MZUSP	2
Brazil, RJ, Muriqui. 10.IV.1960. M. Alvarenga leg.	F	MZUSP	2
Brazil, RJ, Tijuca. G. Barb. Frey leg.	F	EMG	2
Brazil, SP, Barueri. 18.XII.1954. K. Lenko leg.	M	MNRJ	2
Brazil, SP, Barueri. 18.XII.1954. K. Lenko leg.	M	MNRJ	2
Brazil, SP, Sorocaba. I.1990. G. Accacio leg.	F	UFRG	1
Brazil, SP. F. Jahn leg.	M	EMG	2

Brazil, SP, São Paulo	M	NMPC	2
Brazil, SP, São Paulo	M	NMPC	2
Brazil, SP, São Paulo	F	NMPC	2
Brazil, SP, São Paulo	M	NMPC	4
Brazil, SP, São Paulo	F	NMPC	3
Brazil, SP, São Paulo	F	NMPC	3
Brazil, SP, São Paulo	F	NMPC	2
Brazil, SP, São Paulo	M	NMPC	2
Brazil, SP, São Paulo	M	NMPC	2
Brazil, SP, São Paulo	F	NMPC	3
Brazil, SP, São Paulo	M	NMPC	2
Brazil, PR. J.M. Carvalho leg.	M	MNRJ	4
Brazil, PR, Arapongas. XII.1952. J. Maller leg.	M	MNRJ	4
Brazil, PR, Palmeira. I.1929	M	UFRG	4
Brazil, PR, Iguassú. XII.1941. E.N.V. leg.	M	UFRG	4
Brazil, PR, Tibagi. XII.1957	F	MZUSP	2
Brazil, PR. Ponta Grossa. 1940	F	MZUSP	2
Brazil, PR, Ponta Grossa. X.1942	F	MZUSP	1
Brazil, PR, Ponta Grossa. X.1942	F	MZUSP	3
Brazil, PR, Ponta Grossa. X.1942	M	MZUSP	4

Brazil, PR, Ponta Grossa. X.1944	M	MZUSP	4
Brazil, PR, Ribeirão do Pinhal. XII.1955. A. Maller leg.	M	MZUSP	4
Brazil, PR, Curitiba. 08.IV.2013. Bischoffia leg.	F	UFRG	2
Brazil, PR, Curitiba. 08.IV.2013. Bischoffia leg.	M	UFRG	4
Brazil, SC, Nova Teutônia. III.1981. F. Plaumann leg.	M	MZUSP	4
Brazil, SC, Nova Teutônia. 20.X.1950	F	EMG	2
Brazil, SC, Nova Teutônia. 20.X.1950	F	EMG	2
Brazil, SC, Nova Teutônia. 27.III.1951	F	EMG	2
Brazil, SC, Nova Teutônia. 17.IX.1950	F	EMG	2
Brazil, SC, Nova Teutônia. 27.III.1951	F	EMG	2
Brazil, SC, Nova Teutônia. 17.I.1950	M	EMG	4
Brazil, SC, Nova Teutônia. 27.XII.1944	M	EMG	4
Brazil, SC, Urussanga. 15.I.2008. F. M. Bianchi & R. A. Teixeira leg.	F	UFRG	2
Brazil, SC, Urussanga. 15.I.2008. F. M. Bianchi & R. A. Teixeira leg.	M	UFRG	4
Brazil, RS, Maquiné. 17.IX.2006. J. L. C. Bernardes leg.	M	UFRG	4
Brazil, RS, Maquiné. 17.IX.2006. J. L. C. Bernardes leg.	F	UFRG	2
Brazil, RS, São Francisco de Paula. 20.XII.1959. Ditadi, Petersen, Meyrer & Volkmer leg.	M	UFRG	2
Brazil, RS, Santa Maria. 20.iv.1984. L.F. Gnoatto leg.	M	UFRG	4
Brazil, RS, Caxias do Sul, Vila Oliva. II.1963.	M	UFRG	2

Brazil, RS, Nonoai. IV.1994. J.A.M. Fernandes leg.	F	UFRG	1
Brazil, RS, Bozano. 22.XI.2001. F. L. Santos leg.	M	UFRG	1
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**1**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**1**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**M**	**UFRG**	**4**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**F**	**UFRG**	**2**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**F**	**UFRG**	**2**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**F**	**UFRG**	**2**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**F**	**UFRG**	**2**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**F**	**UFRG**	**2**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**F**	**UFRG**	**2**
Brazil, RS, São Domingos do Sul. 07-13.1.2018. R. Brugnera leg.	**F**	**UFRG**	**1**

CAPÍTULO II

The eggs and nymphs of predatory stink bugs (Hemiptera: Pentatomidae: Asopinae): what do we know?

[Brugnera et al. (2022). Zoology, 151, 125991, doi.org/10.1016/j.zool.2021.125991]

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Abstract

The Asopinae are known for their predatory behavior, differing from the phytophagous habits of most pentatomoids, feeding mostly on soft body insects such as larvae of Lepidoptera and Coleoptera. For this reason, asopines have been studied as biological controllers in integrated pest management programs. Notwithstanding their clear relevance, the general knowledge about Asopinae has important gaps, especially regarding immature. Thus, the importance of studying eggs and nymphs of true bugs (Heteroptera) is evident, contributing to understand their classification, biology, and evolution. In this perspective, we conducted a research about immature of predatory stink bugs, highlighting critical features for identification. We present: (1) a literature overview about eggs and nymphs of predatory stink bugs guided by selected categories; (2) images of females laying eggs of ten species and nymphs of thirty-four species, obtained on websites with a citizen science approach; (3) a comparative morphology of immature of six species reared under laboratory conditions, which we examined using light and scanning electron microscopy. We found a remarkable morphological diversity of both eggs and nymphs of Asopinae, revealing key features to establish diagnoses for identification and potential characters to phylogenetics, such as the aero-micropylar processes and chorion scultpturing of the eggs; and the coloration, labium and abdominal plates morphology of nymphs. The results show that little is known about Asopinae immature considering the diversity of the group; however, information obtained by citizen science initiatives, for instance, can improve this knowledge.

Key words: Pentatomoidea, comparative morphology, citizen science, immature stages, ontogeny

1. Introduction

True bugs (Heteroptera) are among the most diverse groups of hemimetabolous insects, with more than 40,000 species widespread in terrestrial and aquatic ecosystems (Schuh and Weirauch, 2020). Among this diversity, the predatory stink bugs (subfamily Asopinae: Pentatomidae) composes a cosmopolitan group, with about 300 species and 65 genera, most of them recorded in the Neotropical and Indo-Malayan zoogeographical regions (Thomas 1992, 1994; Rider et al., 2018; Roca-Cusachs et al., 2019). These species differs from the phytophagous habits of most pentatomids (Schuh and Slater, 1995), being obligatory predators (Grazia et al., 2015), feeding primarily on larvae of beetles, butterflies, and moths (Schaefer, 1996; De Clercq, 2000). Asopines have been studied as effective organisms to control populations of harmful insects in crops through integrated pest management (IPM) programs (De Clercq, 2000; De Bortoli et al., 2011). Citing a few examples, in South America, *Podisus nigrispinus* (Dallas, 1851) was demonstrated to have more than 90% of predation effectiveness on the southern armyworm *Spodoptera eridania* (Cramer, 1782) (De Carvalho et al., 2020). In North America, *Podisus maculiventris* (Say, 1831) and *Perillus bioculatus* (Fabricius, 1775) are known as important natural enemies of the Colorado potato beetle *Leptinotarsa decemlineata* (Say, 1824) (Hough-Goldstein and McPherson, 1996).

Around the world, many other Asopinae species such as *Arma custos* Hahn, 1832 (Zou et al., 2012, 2013), *Eocanthecona furcellata* Bergroth, 1915 (Shylesha and Sravika, 2018), and *Brontocoris tabidus* (Signoret, 1863) (Zanuncio et al., 2014; Pires et al., 2020) have been studied for IPM purpose. These and other investigations point out the relevance of studying the biology and ontogeny of these insects, thus better understanding their ecological role as predators and allowing a precise identification and management in IPM programs (De Clercq, 2000, 2008).

Less than 1% of the Neotropical Asopinae species have the immature described (Brugnera and Grazia, 2018), and this proportion in unknown for other regions. Similar values are found in other Pentatomidae subfamilies, and most species described are of economic importance (Matesco et al. 2014). Among the importance of knowing the immature stages of stink bugs, stands out their potential to contribute to taxonomic and phylogenetic purposes (Cobben, 1968; Javahery, 1994).

Eggs of pentatomids are generally ovoid, ellipsoidal, or barrel-shaped with a crown of aero-micropylar processes (AMPs) surrounding the top of the chorion (Esselbaugh, 1946; Javahery, 1994; Matesco et al., 2014). These aero-micropylar processes can vary in number, size, and shape, being important for egg fertilization, possibly displaying a role in the gas exchange of the embryos (Southwood, 1956; Cobben, 1968; Javahery, 1994). In Asopinae, the AMPs are very long in some genera, considered the longest found in Pentatomidae (Javahery, 1994; Matesco et al., 2009, 2014). Regarding the nymphs, they have five instars and lacks one antennomere and one tarsomere compared to adults (Yonke, 1991; Schuh and Slater, 1995). The dorsal abdominal scent glands (DAGs) are important features at this phase, composed of three exocrine glands that produce semiochemicals used, among other functions, for intraspecific communication and protection (Yonke, 1991; Aldrich, 1997). Each DAG opens to the exterior by a pair of orifices called ostioles, located on anterior margins of tergites 4, 5, and 6, where a complex set of morphological structures, the external scent efferent system (ESES) allows quick evaporation of the product (Aldrich, 1988; Yonke, 1991; Schuh and Slater, 1995; Kment and Vilímová, 2010). Nymphs of Asopinae frequently present metallic and contrasting colorations such as red and orange, and displays gregarious behavior (Oetting and Yonke, 1975; Brugnera et al., 2019).

The description of immature of stink bugs has been growing over the years, from little detailed descriptions in the early 20th century (e.g., Kirkaldy, 1907; Withmarsh, 1916; Miller, 1943), later improved with the use of drawings (e.g., Southwood, 1956; De Coursey and Essebaugh, 1962; Grazia et al., 1985; Bundy and McPherson, 2018) and digital photographs (e.g., Jones and Coppel, 1963; Schwertner et al., 2002; Zou et al., 2012; Matesco et al., 2014). From the 1970s, the access to new techniques for entomologists such as the scanning electron microscopy (SEM) (Friedrich et al., 2014) has enabled the study of structures yet underexplored, such as egg sculpturing (Ren, 1992; Matesco et al., 2009; 2014), ESES of DAGs (Biasotto et al., 2013; Bottega et al., 2015; Bianchi et al., 2016), and the trichobothria (e.g., Vecchio et al., 1998; Schwertner et al., 2002; Brugnera et al., 2019), abdominal mechanoreceptive sensilla with importance in Heteroptera classification (Schaefer, 1975; Gao et al., 2017).

Recently, researchers have access to other tools to improve the knowledge about immature insects, reducing important gaps of information. Amongst them, modern citizen science (e.g. Silvertown, 2009; Vohland et al., 2021) has successfully contributed to the advance of scientific research in many fields (Bonney et al., 2009), which were promoted by the increasing accessibility to the internet and mobile devices by citizens across the world (Bonney et al., 2014). Among hundreds of citizen science projects currently available, several of them include insects as target organisms (e.g., iNaturalist, Bug Guide). These databases can provide useful information to species distribution, including monitoring of invasive species (Hiller and Haelewaters, 2019; Werenkraut et al., 2020; Brugnera et al., 2021), conservation (Prudicet al., 2017; Koffler et al., 2021), and biodiversity studies (Theobald et al., 2015; Chandler et al., 2017). Regarding true bugs, the predatory behaviors of millipede assassin bugs (Reduviidae: Echtricodiinae) (Forthman and Weirauch, 2012), the monitoring of the brown marmorated stink bug *Halyomorpha halys* (Stål, 1855) (Maistrello et al., 2016; Malek et al., 2019), and the redescription of two African genera of stink bugs (Pentatomidae) (Silva et al., 2021) are among the few studies using this source of data.

Although the predatory stink bugs are being recognized as important organisms for human society and ecosystems (De Clercq, 2000, 2008), the understanding of their systematics, behavior, and natural history is in an early stage. As an initiative to contribute to the information of Asopinae immature, we conducted a literature review guided by previously selected categories representing important information about immature stages. In addition, to explore possible new data sources, we searched for images of eggs and nymphs of Asopinae species, using a citizen science approach. We also provide a redescription of the immature of four species, *Alcaeorrhynchus grandis* (Dallas, 1851), *Brontocoris tabidus* (Signoret, 1863), *Podisus nigrispinus*, and *Supputius cincticeps* (Stål, 1860); redescription of the egg and first description of nymphs of *Podisus fuscescens* (Dallas, 1851); and the first description of immature of *Marmessulus brasilianus* Schouteden, 1907.

2. Material and Methods

2.1. Literature and citizen science data

We searched for literature in the bibliometric databases Web of Science (https://www.webofknowledge.com) and Google Scholar (https://www.scholar.google.com) (see Harzing and Alakangas, 2016). The keywords used were “Asopinae” and “Predatory stink bug” in combination with “immature”, “egg”, and “nymph” for all Asopinae genera currently described and published until December 2020. Another search was made in the physical bibliographic depository of the Laboratório de Entomologia Sistem´atica at UFRGS. Publications containing meaningful information regarding any of the following categories were selected: morphological description, natural history, drawings, digital photographs, SEM images, and laboratory rearing (Fig. 1). Publications with species presenting outdated taxonomic status are presented based on the current classification (Thomas, 1992; Thomas, 1994).

A search for images of females laying eggs and nymphs was made on the websites iNaturalist (http://www.inaturalist.org) and Flickr (https://www.flickr.com) (Supplementary file S2). We searched for images of all Asopinae genera, prioritizing high-definition photographs of fifth instar specimens. Identification was made consulting taxonomists and based on the literature. The presence of the adult in the same image (e.g., *Perillus circumcinctus* in Fig. 4I), the geographical distribution of the species (Thomas, 1992, 1994), and the information available in the citizen science projects (e.g. Apateticus sp. in 3B-C) were also considered for identification. We selected only images in which identification at genus or species level was possible, and to avoid any ambiguity, some species were identified as conferring (Cf.). Fifty-eight citizens were contacted, asking for authorization to use the photographs in this publication (Supplementary file S2). Only authorized images were selected and are presented in Figs. 2–5, Supplementary file S2. Original images were cropped, and the light levels and contrast were adjusted on Photoshop software (Adobe Inc.).

2.2. Rearing

Adult specimens were collected in three locations in the state of Rio Grande do Sul, Brazil. *Alcaeorrhynchus grandis*, *Brontocoris tabidus*, *Podisus nigrispinus* and *Supputius cincticeps* were collected in a natural area of Atlantic Rain Forest in São Domingos do Sul (long -51.8324, lat -28.5641). Podisus fuscescens was collected at Campus do Vale, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre (long -51.1230, lat -30.0726). A female of Marmessulus brasilianus was manually collected on the ground, under a decomposing trunk at Estaç˜ao Ecol´ogica do Taim, Rio Grande (long -52.5379, lat -32.5384).

Specimens were reared in a control chamber at 25 ± 1 ◦C, 70 ± 10% RH, and 12 L:12Dh photoperiod, following the procedures described in Brugnera et al. (2019). Specimens were fed ad libitum with larvae and pupae of *Tenebrio molitor* L. (Coleoptera: Tenebrionidae), and branches of *Eugenia uniflora* (L.) (Myrtaceae). Water was provided every two days. During rearing, specimens of each instar were selected, cold anesthetized for 10 minutes, put in plastic vials with cold ethanol 85%, and stored in a freezer for posterior analysis. Voucher specimens are deposited at the Entomological Collection of the Departamento de Zoologia at UFRGS (UFRG).

2.3. Morphological characterization

Eggs and nymphs of all reared species were examined in a stereomicroscope. Selected individuals were photographed in multiple focal planes with a Nikon AZ100 M scope coupled with a DS-Fi2 digital camera. Pictures were stacked in a single focused image using the NIS Elements software. Alive specimens were photographed with a Nikon D3100 digital camera (Figs. 16–21). Photographs were processed in Photoshop software (Adobe Inc.).

Five eggs and five nymphs of each instar were measured in a Leica MZ 12.5 light stereomicroscope (Leica Microsystems, Heerbrugg, Switzerland), using a coupled micrometer eyepiece. Measurements are in millimeters (mean ± standard deviation [maximum-minimum]), and the parameters were obtained according to Brugnera and Grazia (2018) (Supplementary file S3).

Eggs and first, second, and third instar nymphs of each species were examined under scanning electron microscopy (SEM) using JEOL JSM 6060 and JEOL JSM 6610 microscopes (JEOL, Akishima, Tokyo). Samples were critical point dried (10 cycles), mounted in stubs, sputtercoated with gold for 3 min, then observed and photographed at 10 kV. The procedures followed Brugnera et al. (2019). Light and contrast levels were edited using Photoshop software (Adobe Inc.).

Terminology follows Bundy and McPherson (2000) and Matesco et al. (2008) for the general morphology of eggs, and Vilímovà and Kutalovà (2012) and Bottega et al. (2015) for the ESES of nymphs.

3. Results

3.1. Literature and citizen science data

The literature search resulted in 51 selected publications (Fig. 1), and comprises 41 species and 30 genera of Asopinae. Regarding the category ‘morphological description’, a total of 28 species have both eggs and nymphs described, five species have only eggs described, and four have only its nymphs described. Drawings or photographs of the egg and nymph are available for 33 and 34 species, respectively. Examination under SEM comprises the egg of 14 species and nymphs of two species. Information regarding the natural history covers 26 species. A total of 28 species were reared under laboratory conditions.

Using citizen science projects, 52 records of immature Asopinae from 48 citizens (Supplementary file S2) were accounted. The photographs comprise at least 31 genera and 40 species of Asopinae. Twenty-seven records were from the Nearctic, Neotropical, and Andean zoogeographical regions (52.94%), eighteen records were from the Palearctic region (35.29%), five records were from Indo-Malaysian, Australian and Polynesian regions (9.80%), and a single record was from the Afrotropical region (1.96%).

Records of ten females during oviposition were selected, covering eight different genera (Fig. 2). In all records, fresh eggs were pale white subsequently changing to a grayish coloration in most species. Females selected both the ventral and dorsal surface of leaves (Fig. 2B, C, G, H, J), trunk (Fig. 2D), branches (Fig. 2A, E, F), and an inflorescence (Fig. 2I) as substrates for oviposition. The egg posterior pole always contacts the substrate, except in *Alcaeorrhynchus grandis* and *Jalla dumosa* in which some eggs were attached to their adjacent, and not on the substrate (Fig. 2A, F). Similar features were observed, that is, the *Eocanthecona* species shared a rounded egg shape in dorsal view, with a characteristic circle at the top of the operculum surrounded by a crown of middle-sized aero-micropylar processes (Fig. 2C–E); *A. grandis* and *J. dumosa* shared the cluster configuration, with eggs tightly laid with their adjacent, and very short aero-micropylar processes (Fig. 2A, F); *Oechalia schellenbergii, Podisus crassimargo* (Stål, 1860), and *Supputius typicus* Distant, 1889 shared distinctly longer aero-micropylar processes (Fig. 2G, H, J). *Stiretrus decemguttatus* was the only species in which the eggs were organized in two rows (Fig. 2I). The images did not allow a detailed characterization of the chorion sculpturing; however, they were useful to estimate the number of eggs laid and the number and size of aeromicropylar processes (depending on the magnification and resolution of the images).

Images of nymphs comprised 34 species and 30 genera (Figs. 3–5, Supplementary file S2). To the best of our knowledge, these are the first published images in the scientific literature of *Apateticus marginiventris* (Stål, 1870) (Fig. 3B), *Apateticus lineolatus* (Herrich-Schaffer, 1840) (Fig. 3C), *Amyotea cf. malabarica* (Fabricius, 1775) (Fig. 3E), *Brontocoris nigrolimbatus* (Spinola, 1852) (Fig. 3F), *Comperocoris roeheneri* (Phillipi, 1862) (Fig. 3I), *Dorycoris pavoninus* (Westwood, 1837) (Fig. 3L), *Ealda minax* Walker, 1867 (Fig. 3O), *Oplomus cf. dichrous* (Fig. 4B), *Parajalla sanguineosignata* (Fig. 4D), *Platynopus cf. melanoleuchus* (Westwood, 1837) (Fig. 4G), *Perillus cincumcinctus* Stål, 1862 (Fig. 4I), and *Tylospilus acutissimus* Stål, 1870 (Fig. 5C). The images show a high diversity of coloration and morphology among species. Shades of green, blue, and copper iridescence were observed on the dorsal surface of the head, thorax, and in the dorsal and lateral abdominal plates of at least 17 species. The presence of red, orange, and vivid yellow coloration, especially in the abdomen was observed in at least 15 species. Pronotum is always trapezoidal, with the lateral margins rectilinear (e.g., Figs. 3H, J, 4 E, L, 5 A, B), sinuous (e.g., Figs. 3C, K, 4 A, B), or distinctly concave (e.g., Figs. 3B, F, 4H, I), besides being smooth (e.g., Figs. 3G, 4 D, I) or serrated (e.g., Figs. 3C, 5 C). In species with adults presenting developed humeri, a distinct concavity on the posterior angles of pronotum was observed in the fifth instar (Figs. 3M, O, 4 C, K, 5 A). Both lateral and dorsal abdominal plates were diverse regarding their number (dorsal), size, and shape, besides having a contrasting, variegated or concolorous coloration compared to the surrounding abdominal surface. At least four dorsal plates were observed in all species: the first three surrounding the ESES and one placed posteriorly. Their shape and width are highly diverse among species, especially the width correlation between the dorsal plate I (surrounding DAG1) and dorsal plate II (surrounding DAG2), which can be equally wide (e.g., Figs. 3B, 4 A), or with the dorsal plate I shorter (e.g., Figs. 3G, 4 C, 5 B) or longer (e.g., Fig. 4B, D) than dorsal plate II. The plates were elongated, subrectangular, or globose, with rounded or reticulated lateral margins. The plates of some species are more developed, covering most of the dorsal abdominal surface, as in *Oplomus catena* (Fig. 4A) and *Stiretrus anchorago* (Fig. 4M). The colorations of the remaining dorsal abdominal surface were uniform, variegated, or with spots or maculae. Among genera with more than one species sampled, similar morphological patterns were observed, as in *Podisus* (Fig. 4J, K), *Oplomus* (Fig. 4A, B), and *Perillus* (Fig. 4H, I), but not in *Apateticus* (Fig. 4B, C). See additional images in Supplementy file S1.

3.2. Comparative morphology of reared species

3.2.1. Egg. Three morphological patterns were observed: (i) the egg of *A. grandis* was oblong, with a smooth and light-brown chorion; the aeromicropylar processes were very short and upward directed (~12); the surface of the operculum had shallow polygonal excavations (Figs. 6A–B, 7 A–C). (ii) In *M. brasilianus*, the egg was barrel-shaped, the chorion was bright brown, smooth in the lower portion with shallow polygonal excavations from the middle up; the aero-micropylar processes were middle-sized and innerly curved with openings presenting an "X" shape (~14); the surface of the operculum had circular projections (Figs. 5E–F, 6 D–F). (iii) Eggs of *B. tabidus, P. fuscescens, P. nigrispinus*, and *S. cincticeps* were similar; they were oval in shape, with gray or light-brown to brown coloration; the chorion and operculum were covered by dark-brown spines; the aero-micropylar processes were translucent, outward-directed and very long, distinctly surpassing the top of operculum (~14–15) (Figs. 5C–D, G–L, 6 G–L).

In all species, egg color was almost white right after oviposition, changing to the color described above a few minutes later. With embryonic development, the egg turned redder, and the eyes and the *ruptor ovis* became visible through operculum. Unfertilized eggs maintained the original color that was acquired right after oviposition.

During rearing, we observed a single egg mass of *A. grandis* with 114 eggs, longitudinally laid in a twig (Fig. 16A–B). Females of *B. tabidus, P. fuscescens, P. nigrispinus* (Fig. 20A), and *S. cincticeps* tended to oviposit few circular egg masses with about 20 to 50 eggs on any surface of the rearing box. The female of *M. brasilianus* oviposited a single mass with 72 eggs on the wall of the plastic pot (Fig. 18A). A layer of adhesive material covered the external egg surface in all species; such layer was distinctly thicker in *A. grandis* and *M. brasilianus*, keeping the eggs attached to their adjacent, while a thinner layer was found in the other species, in which the eggs easily detach from the egg mass.

3.2.2. Nymphs

3.2.2.1. First instar. First instar nymphs were very similar among species, with head, thorax, and abdominal plates dark brown, and abdominal surface reddish (Fig. 8). The body was oval and elongated; the abdomen was slightly wider than thorax in *A. grandis* (Fig. 8A–C) and *M. brasilianus* (Fig. 8F–G); and it was distinctly wider than thorax in *B. tabidus* (Fig. 8D–E), *P. fuscescens* (Fig. 8H–I), *P. nigrispinus* (Fig. 8J–K), and *S. cincticeps* (Fig. 8L–M). The body surface was smooth, without punctures. The head was rounded and declivous. The proportion of antennomeres was I < II > III < IV in all species. The antennae were distinctly longer in *A. grandis* and *M. brasilianus*, reaching 70% and 76% of the body length, respectively, while about 60% in the other species (Supplementary file S3). The last antennomere was the longest and fusiform, wider in *B. tabidus, P. fuscescens, P. nigrispinus,* and *S. cincticeps*, and narrower in *A. grandis* and *M. brasilianus* (Fig. 8). The proportion of labiomeres was I < II > III < IV and the fourth was the longest (Fig. 9A–C, E), except for *S. cincticeps* in which the first labiomere was the longest. *M. brasilianus* had the second and third labiomeres fused (Fig. 9C). Bucculae were poor developed in all species (Fig. 9). The first labiomere width ranged from 0.11 to 0.16 mm and exceeded the bucculae; the labial apex surpassed the metacoxae in all species, except in *M. brasilianus* (Fig. 8G). Under light microscopy, the abdomen had dorsal plates in the segments I to IX, lateral plates in segments I to VII, and no ventral plates; the first two dorsal plates were slender, followed by the three subrectangular plates (around ostioles), plus two smaller plates. Abdominal sternites II–VII contained 1 + 1 spiracles plus 1 + 1 trichobothria in III–VI (Fig. 13A–E).

Morphology of external scent efferent system (ESES): DAG1 with slitlike ostiole surrounded by winkles, without evaporatorium (Fig. 10A–D). ESES of DAG2 and DAG3 with rounded ostioles attended by a cuticular fold; evaporatorium was composed by spiked projections (Fig. 10E–K). Ostioles of DAG1 was positioned laterally to those of that DAG2, and DAG3.

Compared with the first instar, distinct body modifications were observed from the second instar, especially the shape of head, thorax, and abdominal plates. Dorsal surface of the head, thorax, and abdominal plates with inconspicuous punctures was observed in *B. tabidus*. In *Podisus* spp. and *S. cincticeps* it was deeply punctured. In *A. grandis* and *M. brasilianus* the surface was smooth. The proportion of antennae and body length were similar to that observed in the first instar, but it increased in *A. grandis* and *M. brasilianus*, reaching 82% and 83% of body length, respectively (Supplementary file S3). A pair of narrow mesolateral plates were observed in all species. The first two dorsal plates were slender in *A. grandis* (Fig. 11A) and *M. brasilianus* (Fig. 11E), but only one plate was observed in *Podisus* spp. (Figs 11G, I) and *S. cincticeps* (Fig. 11K), and none in *B. tabidus* (Fig. 11C). Five ventral plates were seen in sternites V–X, in which the second plate was the widest in *B. tabidus*, *Podisus* spp. and *S. cincticeps*, while in *A. grandis* and *M. brasilianus* the widest was the first plate. Abdominal sternites II–VII with 1 + 1 spiracles, plus 2 + 2 trichobothria in III–VI (13F–K). At least one of the trichobothria was located inside or near the edge of the respective lateral plate in *B. tabidus*, *Podisus* spp. and *S. cincticeps*, while in *A. grandis* and *M. brasilianus* the trichobothria was distinctly away from the lateral plates.

Regarding the morphology of the external scent efferent system (ESES), DAG1 had slit-like ostioles (Figs 12A–D) that were surrounded by wrinkles; some alveoli (characteristic of reticulated evaportorium) were observed in *B. tabidus* (Fig. 12B) and *S. cincticeps* (Fig. 12D). ESES of DAG2 and DAG3 with rounded ostiole, bearing spout peritreme, surrounded by a reticulate evaporatorium with shallow alveoli; trabeculae in most of the alveoli, more densely in the anterior ones; peritreme lip and post-ostiolar projection observed (Fig. 12E–K). Ostioles of DAG1 were positioned laterally to those of DAG2 and DAG3, except in *A. grandis* where all ostioles were aligned.

3.2.2.3 Third and fourth instars. In these stages, the most remarkable changes were the coloration and the development of structures found in the adult phase, as detailed below. Coloration changes: lateral margins of pronotum in *A. grandis* became reddish from the fourth instar (Fig. 14B); in *B. tabidus* abdomen and pronotum became yellowish/orange, but lateral margins of pronotum remained dark brown (Figs 14C–D, 17B–D); a pair of yellowish spots were observed in the second abdominal tergite in *M. brasilianus* (Figs 14E–F); at least seven yellowish spots were observed between the dorsal and lateral abdominal plates in *P. fuscescens* (Figs 14G–H, 19A–D), and a pair of yellowish spots in urostenite III;

yellowish elongated macula were observed between dorsal and lateral abdominal plates in *P. nigrispinus* (Figs 14I–J, 20C); in *S. cincticeps* the pronotum, coxae, trochanters, anterior half of femora and abdomen ranging from orange, red, to yellow (Figs 14K–L, 21A–G). Specimens of *B. tabidus* and *S. cincticeps* had intraspecific color variation, mainly from the fourth instar; some individuals had the head, thorax, and abdominal plates entirely or in part faded, completely reddish in some cases (Figs 17D–E, 21A–G). Different shades of iridescence were observed in the head, thorax, and abdominal plates of all species, notably in *A. grandis* (Figs 14A–B, 16D–H).

The development of wing pads was observed from the third instar, at least doubling its size in the fourth instar (Fig. 14). The development of a femoral spine was observed in the fourth and fifth instars in *A. grandis* and *M. brasilianus* (Figs 14B, F).

3.2.2.4 Fifth instar. We provide below a short description of the diagnostic features for species identification. It was constructed based on morphological features of the fifth instar but is useful for identification of the third and fourth instars in most cases.

In the fifth instar, the wing pads reached the posterior margin of abdominal tergite III (Figs 15A, C, E, G, I, K). In all species, labium and labrum were closely inserted; the first labiomere was longer and free of the bucculae (Figs 15B, D, F, H, J, L).

Alcaeorrhynchus grandis: Body large (average body length 11.00mm), mandibular plates longer than clypeus, labium wider than femur (averaging 1.32 mm width), lateral margins of pronotum distinctly expanded and red, iridescence frequently observed in the head, thorax, and abdominal plates (Figs 15A–B, 16F–I).

Brontocoris tabidus: Lateral margins of pronotum distinctly concave and dark brown in most specimens, ventral body surface including labium, coxae, trochanters, and anterior half of femora yellowish (average body length 9.40mm) (Figs 15C–D, 17D–E).

Marmessulus brasilianus: Body with dark coloration, frequently with a pair of yellowish spots in the second abdominal tergite, lateral margins of pronotum often red, labiomere IV twice the length of labiomere III (average body length 8.58mm) (Figs 15E–F, 18E–G).

Podisus fuscescens: Head, thorax, and abdominal plates dark brown frequently with greenish iridescence, abdomen red with at least five rounded yellowish spots between the dorsal and lateral plates; abdominal sternites red, with a pair of yellowish spots on sternite III (average body length 8.92mm) (Figs 15G–H, 19C–D).

Podisus nigrispinus: Head, thorax, and abdominal plates dark brown, often with pale spots on head and thorax; at least the last two labiomeres light brown; abdomen with yellowish elongated maculae between dorsal and lateral plates, frequently with white spots between the dorsal plates; abdominal sternites pale yellow with red stripes (average body length 6.08mm) (Figs 15I–J, 20 B–C).

Supputius cincticeps: Highly polychromatic species, can be identified by the length of labiomere II which is at least twice the length of III and IV combined (average body length 7.42mm) (Figs 15K–L, 21A–G).

4. Discussion

We recovered literature information from 51 publications, gathering more than half of predatory stink bugs genera currently described (40 of 66). Most publications have over two decades; however, they bear relevant information about morphology, natural history, and laboratory rearing methods. We observed an expressive diversity of eggs and nymphs in the selected images taken by citizens across the world. These images highlight the potential of citizen science projects to contribute with valuable information of immature and adults of asopines and other heteropterans. Only in the iNaturalist, there were more than 60,000 records of Heteroptera in the Neotropical region, and about 800,000 worldwide (iNaturalist.org, accessed on 3.30.2021).

This study provides an overview of the current knowledge about immature of predatory stink bugs. A comparative morphological examination was conducted based on six species of five genera reared in laboratory conditions. Our study shows that features of eggs and nymphs are useful data to improve taxa identification and possibly represent relevant characters to explore the phylogenetic relationships within Asopinae.

4.1. Eggs

The eggs of Asopinae have been characterized as having long aeromicropylar processes with chorion and operculum covered by spines (Javahery, 1994). Although that combination of features seems unique among pentatomoids, we found a high diversity of egg morphology among the species studied here. Furthermore, our results showed distinct size variations regarding the aero-micropylar processes, chorion and operculum sculpturing, and coloration.

The well-known combination of long aero-micropylar processes and spined chorion is present in species of eight genera (*Amyotea*, *Arma*, *Brontocoris*, *Conquistator*, *Oechalia*, *Podisus*, *Supputius*, and *Troilus*). In these taxa, the processes clearly exceed the top of the operculum, and each process length is usually similar to the opercular radius, reaching 0.32mm in *Podisus placidus* and 0.28mm in *Podisus maculiventris* (Coppel and Jones, 1962), equivalent at least to twice the length of medium-sized processes, like those of *S.*

anchorago (0.11mm) (Oetting and Yonke, 1971). *Tynacantha marginata* is the only species (with egg description) that combines long aero-micropylar processes and smooth chorion (Brugnera and Grazia, 2018). The species of *Cazira, Oplomus*, *Perillus*, and *Stiretrus* presented a similar morphological pattern: the eggs have a reticulated chorion with the top of operculum with a circular projection, and middle-sized and innerly curved aero-micropylar processes (Esselbaugh, 1946; Richman and Withcomb, 1978; Saini, 1990; Ren, 1992; Brugnera et al., 2020; Fig. 2I). Other similarities among taxa that stand out are: the very short aero-micropylar processes of *Alcaeorrhynchus grandis* and *Jalla dumosa* (the shortest reported for Asopinae), composed by a minute projection with a circular opening at the apex (Putshkova, 1961; Richman and Mead, 2000; Fig. 6C); a circular projection in the operculum of *Eocanthecona* species (Srikumar et al., 2018; Figs 2C-E); and the X-shaped opening of the aero-micropylar processes of *Marmessulus brasilianus* (Fig. 6F), *Andrallus spinidens*, and *Cantheconidea humeralis* (Ren, 1992), which differs from the circular opening of other species (Ren, 1992; Matesco et al., 2014; Brugnera et al., 2019).

The number of aero-micropylar processes is reduced in many Asopinae species compared with other pentatomids, ranging from 10 to 20 in most genera (Javahery, 1994; Bundy and Mcpherson, 2000; Matesco et al., 2014) such as *Podisus* (Sá et al., 2013) and *Oplomus* (Saini, 1990; Brugnera et al., 2019). However, this number can average from 28 in *Eocanthecona furcellata* (Kumar et al., 2002) and 34 in *Picromerus bidens* (Javahery, 1994) to only 5 in *Jalla dumosa* (Putshkova, 1961). Eggs of other pentatomids can reach up to 70 aero-micropylar processes, as in *Chinavia obstinata* (Pentatominae: Nezarini) (Matesco et al. 2009). This feature can be used as a diagnostic character at the generic level, but not to congeneric species, as the number can overlap between them (Bundy & McPherson 2000, Matesco et al. 2009). As a phylogenetic character, the number of aero-micropylar processes is little explored in low taxonomic levels because of the missing data for most species (Matesco et al. 2014).

The egg features may represent important characters for phylogenetic purposes in Asopinae. However, the tribal classification of the group is currently unresolved, as well as the relationship among genera (Rider et al., 2018; Roca-Cusachs et al. 2021). Additionally, few asopine species have been included in phylogenetic analysis, preventing us from discussing a possible correlation between morphological characters and phylogenetic relationships. However, similar morphological patterns among some genera (as *Oplomus*, *Stiretrus* and *Perillus*) may reflect their phylogenetic relationships, and should be explored in future investigations.

The arrangement of egg masses, the number of eggs laid, and the incubation period greatly varies among Asopinae species. Eggs more ornamented tended to be laid loose and in circular shapes, as in *A. custos*, *B. tabidus*, *Podisus* spp., *Eocanthecona* spp., and *Supputius* spp. (Zou et al., 2012; Dimaté et al., 2014). Less ornamented eggs as in *A. grandis*, *A. cynicus*, and *J. dumosa* were oviposited in rows and very close to their adjacent (Jones and Coppel, 1963; Richman and Mead, 2000). More ornamented eggs, especially those with spiked chorion as found in *Podisus* spp., may play a role to stabilize the humidity gradient of the egg surface, preventing water loss and possibly acting as protection in combination with the long aero-micropylar processes (Lumbin and Lu, 1984; Matesco et al., 2009). Egg masses generally have no more than 50 eggs; however, they can be composed of up to 200 eggs, as observed in *A. grandis*, and about 100 eggs in *E. floridanus* (Richman and Withcomb, 1978). This feature can be linked to the natural differences between female body size and condition, for instance. Abiotic conditions, such as temperature and humidity have direct influence on the incubation period of the eggs. Richman and Withcomb (1978) found significant differences regarding the time of embryo development between *A. grandis* (16 days), *E. floridanus* (19 days), *P. maculiventris* (5 days), and *S. anchorago* (6-7 days) at 26°C.

Several authors have reported that freshly laid eggs are completely pale white in Asopinae species, changing their color a few minutes later (Rieger, 2000; Costello et al., 2002; Zou et al., 2012). A layer of adhesive material covering the external egg surface is commonly reported for stink bugs in different families of Pentatomoidea and was also described for asopines (Cobben*,* 1968; Matesco et al., 2014; Brugnera et al., 2020). This material is produced and secreted by females, then used to stick one egg to another, and can enhance protection against predators (Cobben, 1968; Kumar, 2002). However, the adhesive layer may have other functions in Asopinae. Abram et al. (2015) evidenced that egg pigmentation of *Podisus maculiventris* is affected by the structure of the leaf surface and the luminosity levels of the environment. The variations in these conditions predict if the female will lay darker or lighter eggs, revealing high phenotypic plasticity and one of the few animals capable of select egg pigmentation in response to environmental conditions (Abram et al., 2015). We observed this color variation in all species reared and in the images received. However, this phenomenon is unreported for other pentatomoids (Javahery, 1994) and needs more investigation.

4.2 Nymphs

The paucity of information about the nymphs is notorious in Pentatomidae, limiting the understanding of the family in many aspects, including taxonomy, ecological role, behavior, and evolution (Bundy and McPherson, 2000). Diagnostic characters for identifying nymphs of Asopinae are little explored, and the overall knowledge is mostly limited to species of economic importance (Evans, 1985; Saini, 1989). Bellow we discuss the major features that are helpful for identification of nymphs of Asopinae: (i) the coloration, (ii) labium morphology, and (iii) abdominal plates morphology.

The coloration is a notorious feature of predatory stink bugs. Many species have drab colorations when adults (such as brown and light yellow), however, at least 37% of genera are bright-colored (usually iridescent); some of them have contrasting coloration, possibly reflecting an aposematic role against predators or even a mimetic adaptation with their prey (Thomas, 1992; Schaefer, 1996; Lupoli, 2019). Chromatic polymorphism is also observed in adults of some genera, such as *Stiretrus* and *Oplomus* (Brugnera et al. 2019). The coloration of Asopinae first instar nymphs is black and red most species. This pattern is usually maintained in the second instar and represents a useful feature for early recognition of Asopinae nymphs (Evans, 1985). First instar of the phytophagous groups of Pentatomidae are commonly brown, yellow, or green, being the red and black pattern less common as in *Mormidea quinqueluteum*, and *Oebalus poecilus* (Martins et al., 1986; Greve et al., 2003). From the third instar on, nymphs of Asopinae generally exhibit other colorations besides those black and red, including contrastingly spots, mainly on the pronotum and abdomen. The iridescence (if present) is also observed from the third instar, becoming more conspicuous in the fourth and fifth instars (Mead and Richman, 2000; Brugnera et al. 2019). The chromatic polymorphism of nymphs is unusual, including in species with polymorphisms when adults; *Supputius cincticeps* is the only species with distinct color variation, with at least four morphotypes described, especially in fourth and fifth instars (Zanuncio et al. 1993b). The applicability of coloration as a tool for identification of nymphs at the species level is relevant, including among congeneric species, as demonstrated in this work for *Podisus nigrispinus* and *Podisus fuscescens*; however, it need to be done with caution since only a small part Asopinae nymphs are described (~10%), and some features can overlap among taxa, as in the species of Nearctic *Podisus*, for instance (Evans, 1985).

The labial morphology of Asopinae nymphs is underexplored, being this study the pioneer to detail and describe the labium of the first instar under SEM. In adults, a thick and wide labium is considered a key adaptation to the predatory behavior, and an important diagnostic character to differentiate asopines from other pentatomids (Rider et al. 2018; Wang et al., 2020). The labiomere I is usually distinctly wider than the following labiomeres and free of bucculae, contrasting with a well-developed bucculae and a thinner and uniform labium of phytophagous species (Thomas, 1992; Grazia et al., 2015; Rider et al., 2018). Examining the labium of nymphs, we observed the presence of diagnostic characters since the first instar, especially regarding the undeveloped bucculae, and the close insertion of labrum and labium (Fig. 8), which is also a characteristic of the group (Gapud, 1991). At the species level, features of labium can be useful in identification, as observed in *M.*

brasilianus (i.e. third and fourth labiomeres fused) and *S. cincticeps* (i.e. length of labiomere II). These results highlight the importance of the labium to the identification of Asopinae nymphs in early stages, especially when associated with the brown to black coloration of the labium in the majority of Asopinae species in the first and second instar.

We documented a high variation of the abdominal plates is seen in the Asopinae. In Pentatomidae, Yonke (1991) diagnosed the nymphs by comparing the length of the dorsal plates surrounding the DAG1, which is no longer than half of the following two plates. This characteristic corresponds to most Asopinae species, with the plate of DAG1 slender and frequently shorter than the following two plates. However, in some species as *Oplomus* spp., *Stiretrus anchorago*, and *Parajalla sanguineosignata*, the dorsal plates are distinctly larger, which, combined with the remaining plates cover most of the dorsal abdominal surface (Oetting and Yonke, 1971, Brugnera et al., 2019, Figs 4A, B, M). Moreover, in some species the plate that surrounds the DAG1 is distinctly longer than the following plates, as in *A. marginiventris*, *C. roehneri*, *P. sanguineosignata*, and *Z. caerulea*. This feature is unusual in Pentatomidae, but it was reported in other families such as Scutelleridae and Thyreocoridae (Yonke, 1991). On the other hand, some species have greatly reduced dorsal and lateral plates as in *A. custos*, *E. floridanus*, and *J. dumosa*. Regarding the morphology of ESES, we observed little variation among the investigated species, including previous descriptions of these structures (Bianchi et al., 2016; Brugnera et al., 2018; Brugnera et al., 2019). However, the high variation of size, shape, and proportion of dorsal and lateral plates may represent informative characters for Asopinae classification, and future studies should account for it.

5. Conclusion

Considering the diversity of Asopinae, few species have the immature described, most from Nearctic and Neotropical regions. Our comparative approach revealed a significant diversity variation of characters of both eggs and nymphs, which can further contribute to taxonomic and phylogenetic investigations, such as the aero-micropylar processes, and chorion sculpturing of the eggs; and the coloration, and the morphology of labium, and abdominal plates of nymphs. Identifying eggs and nymphs of first and second instars at infrageneric levels can be inaccurate because of shared similarities. From the third to fifth instar, the identification is more accurate. Citizen science has proven to be a relevant tool to access immature information, enabling species recognition and habits of natural history. Therefore, we strongly recommend investigating stink bug immature through different approaches and data sources.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.zool.2021.125991.

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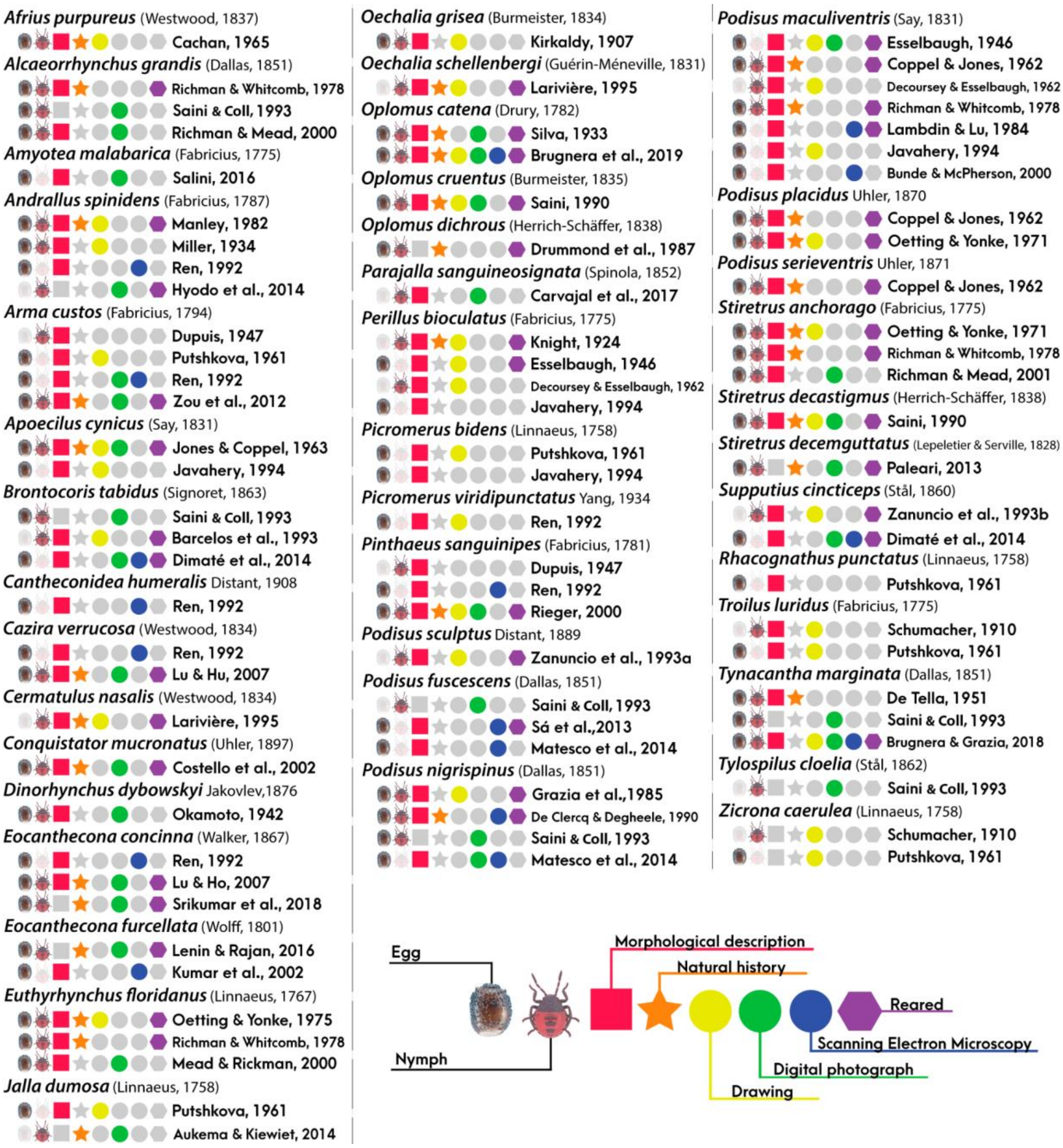


Fig. 1. Compilation of publications of Asopinae eggs and nymphs. The presence of the selected category is represented by colored symbols and the absence by gray symbols. References uncited in the main text: Aukema and Kiewiet, 2014; Barcelos et al., 1993; Cachan, 1965; Carvajal et al., 2017; De Clercq and Degheele, 1990; Tella, 1951; Drummond et al., 1987; Dupuis, 1947; Hyodo et al., 2014; Knight, 1924; Larivière, 1995; Lenin and Rajan, 2016; Lu and Ho, 2007; Manley, 1982; Okamoto, 1942; Paleari, 2013; Sá et al., 2013; Saini and De Coll, 1993; Salini, 2016; Schumacher, 1910; Silva, 1933; Richman and Mead, 2001; Zanuncio et al., 1993a. All cited references are presented in full in the References List.

Fig. 2. Females of Asopinae species during oviposition. Authors: A, ©Richard Stovall (2018). B, ©Joseph Montes de Oca (2017). C, ©Mac Lin (2019). D, ©Taewoo Kim (2001). E, ©Chung-Yi Liu (2016). F, ©Ingeborg M.M. van Leeuwen (2020). G, ©Reiner Richter (2019). H, ©Sergio Monteiro (2013). I, ©Yuuki Nakatani. J, ©Kel Silva (2016).

Fig. 3. Nymphs of Asopinae species, part 1. Authors: A, ©Ryszard Szczygieł (2011). B, ©Juan Carlos Garcia Morales (2019). C, ©Karen Yukich (2018). D, ©John Guerin (2016). E, ©Arijit Patra (2019). F, ©Diego Ghigliotto Urzúa (2020). G, ©Xiong Shengzhi (2019). H, ©Robin Booth (2018). I, ©Francisco Agustín Aliaga Villagrán 2020). J, ©Brian Magnier (2019). K, ©Alexander Ganse (2014). L, ©Jane Trembath (2019). M, ©Kit Chang (2019). N, ©Felix Fleck (2018). O, ©Julien Barrault (2019). P, ©Roland Lupoli (2020).

Fig. 4. Nymphs of Asopinae species, part 2. Authors: A, ©Carlos Eduardo Zuma (2020). B, ©Felix Fleck (2018). C, ©Andrew Allen (2016). D, ©Vicente Valdés Guzmán. E, ©Andrei E. Humala (2012). F, ©Jesús Tizón Taracido (2018). G, ©Cheng Wai Keung (2017). H, ©Dave Beaudette (2011). I, ©Mia Marcellus (2019). J, ©Doug Wechsler. K, ©Jeffrey Gruber (2015). L, ©Tristan Bantock (2012). M, ©Jeff O’Connell (2020). N, ©Ricardo A. Palonsky (2020).

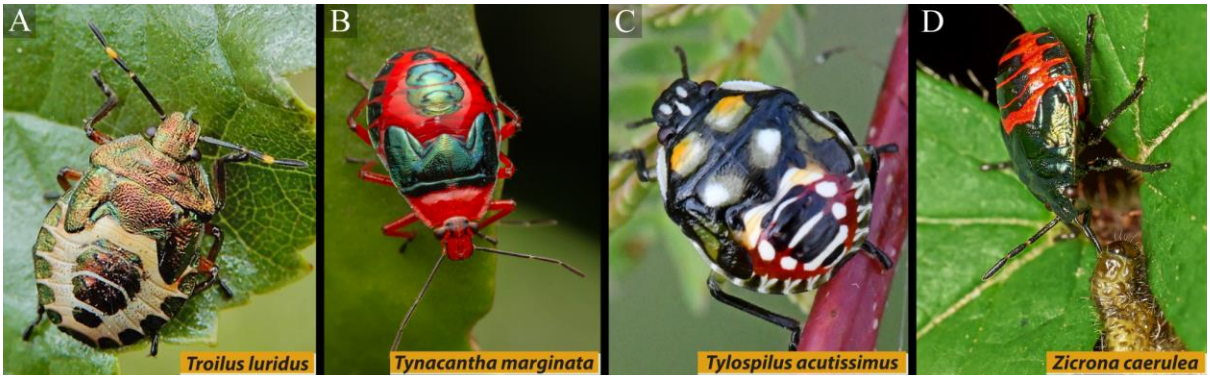


Fig. 5. Nymphs of Asopinae species, part 3. Authors: A, ©Maria Justamond (2018). B, ©Andrès Costa (2020). C, ©Ryan McDaniell (2019). D, ©David W. Williams (2017).

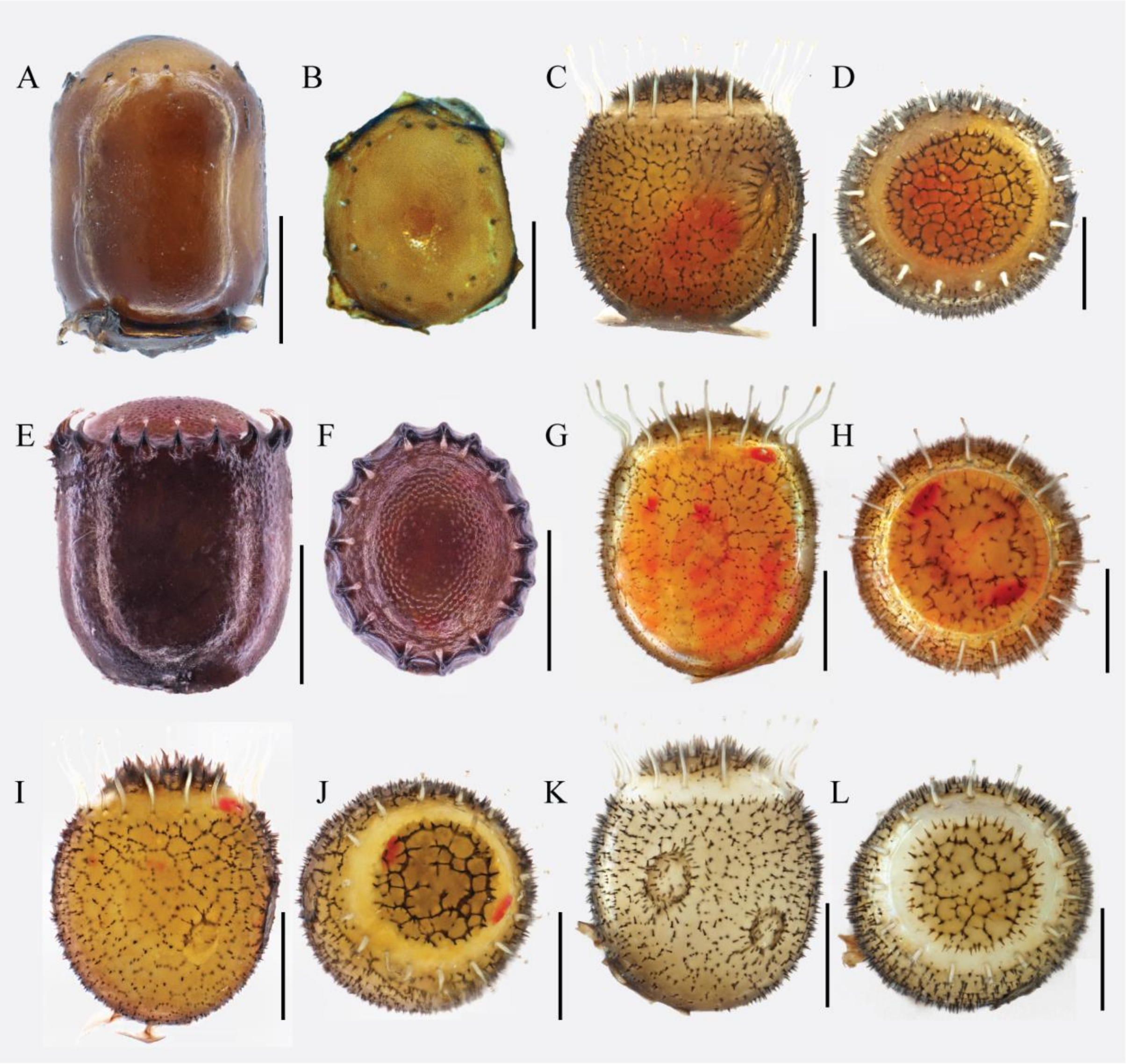


Fig. 6. Eggs of reared species. A-B, *Alcaeorrhynchus grandis* (Dallas). C-D, *Brontocoris tabidus* (Signoret). E-F, *Marmessulus brasilianus* Schouteden. G-H, *Podisus fuscescens* (Dallas). I-J, *Podisus nigrispinus* (Dallas). K-L, *Supputius cincticeps* (Stål). A, C, E, G, I, K, lateral view. B, D, F, H, J, L, dorsal view. Scales: 0.4mm.

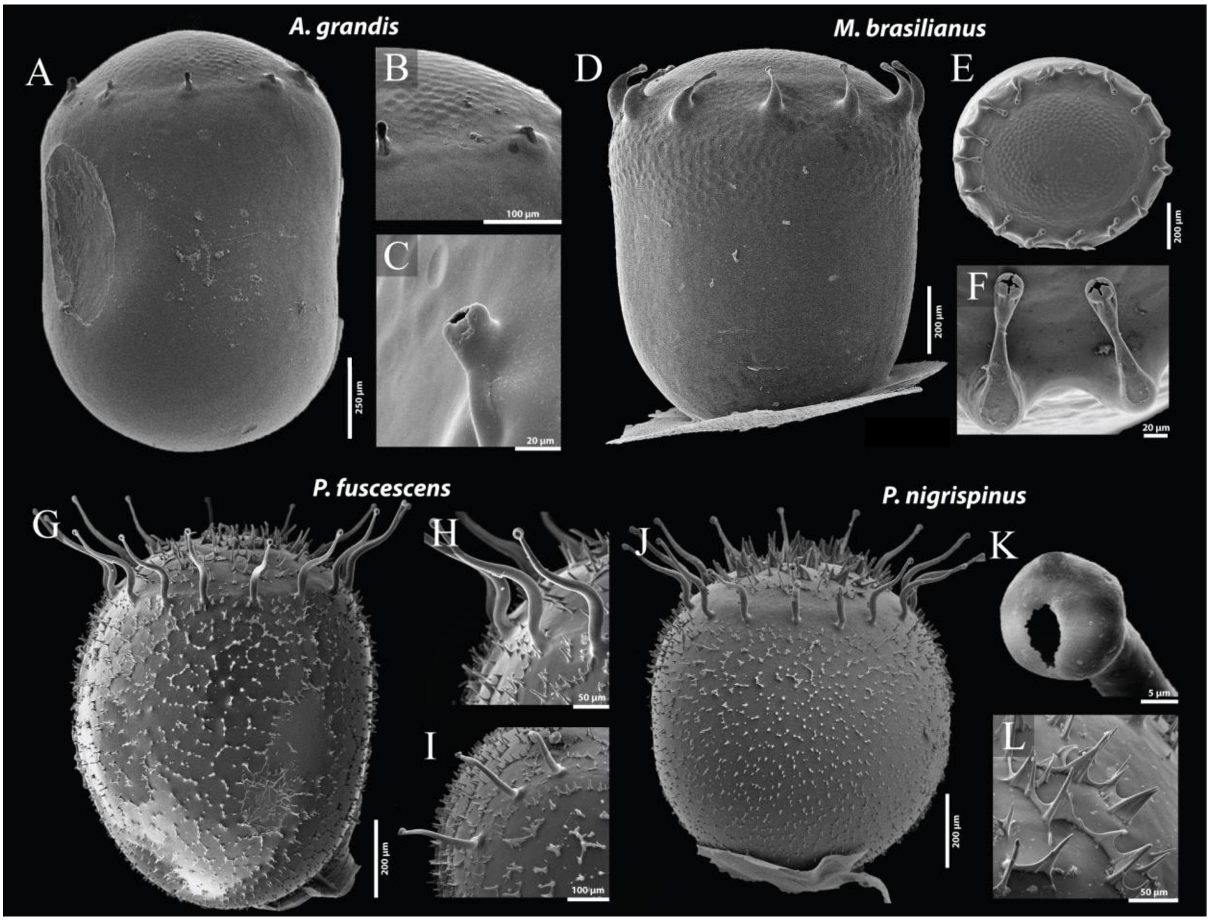


Fig. 7. Eggs of reared species under scanning electron microscopy. A-C, *Alcaeorrhynchus grandis* (Dallas). D-F, *Marmessulus brasilianus* Schouteden. G-I, *Podisus fuscescens* (Dallas). *Podisus nigrispinus* (Dallas). A, D, G, J, lateral view of egg. C, F, H, K, details of aero-micropylar processes. B, I, L, details of chorion sculpturing.

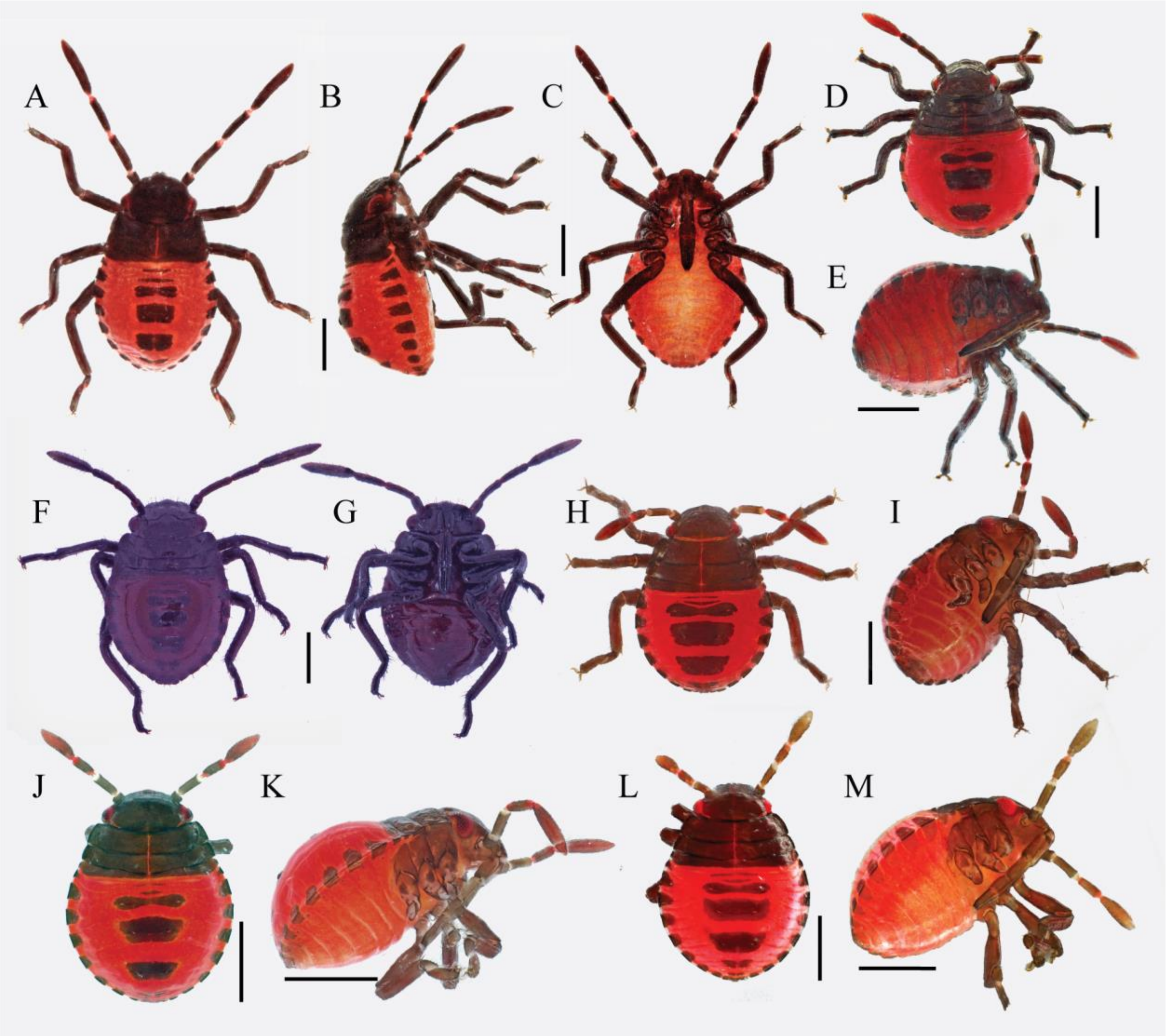


Fig. 8. First instar nymphs of reared species. A-C, *Alcaeorrhynchus grandis* (Dallas). D-E, *Brontocoris tabidus* (Signoret). F-G, *Marmessulus brasilianus* Schouteden. H-I, *Podisus fuscescens* (Dallas). J-K, *Podisus nigrispinus* (Dallas). L-M, *Supputius cincticeps* (Stål). A, D, F, H, J, L, dorsal view. B, lateral view. C, G, ventral view. E, I, K, M, ventrolateral view. Scales: 0,4mm.

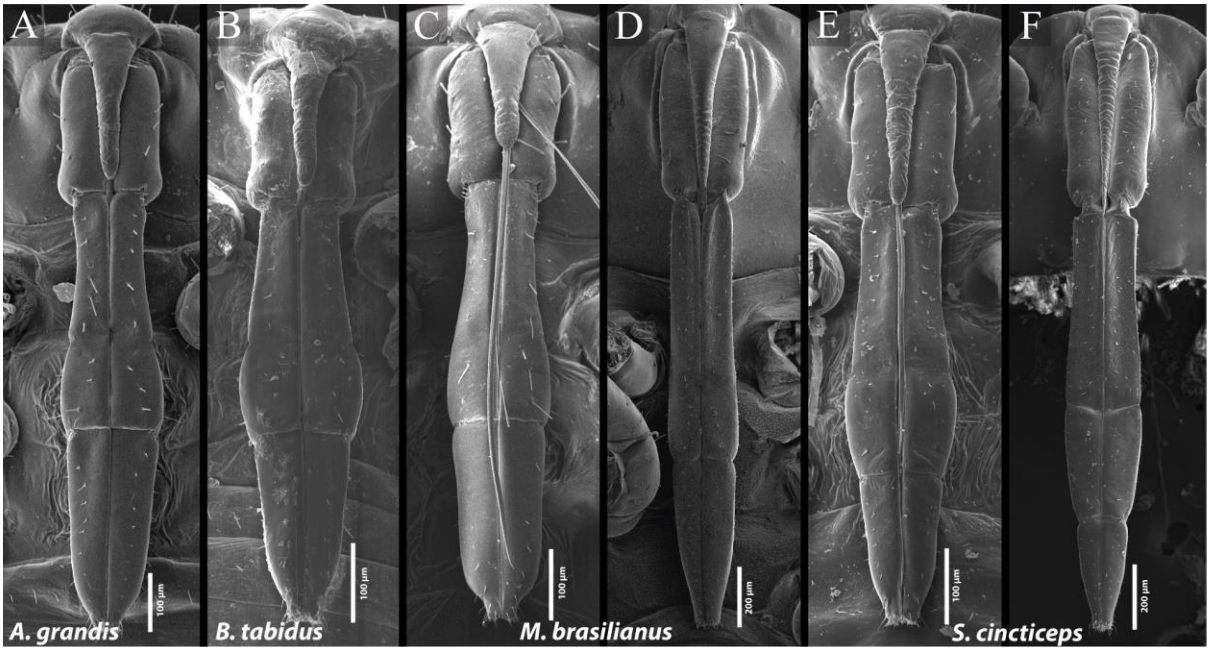


Fig. 9. Labium of reared species under scanning electron microscopy. A, *Alcaeorrhynchus grandis* (Dallas). B, *Brontocoris tabidus* (Signoret). C-D, *Marmessulus brasilianus* Schouteden. E-F, *Supputius cincticeps* (Stål). A-C, E, first instar. D, F, third instar.

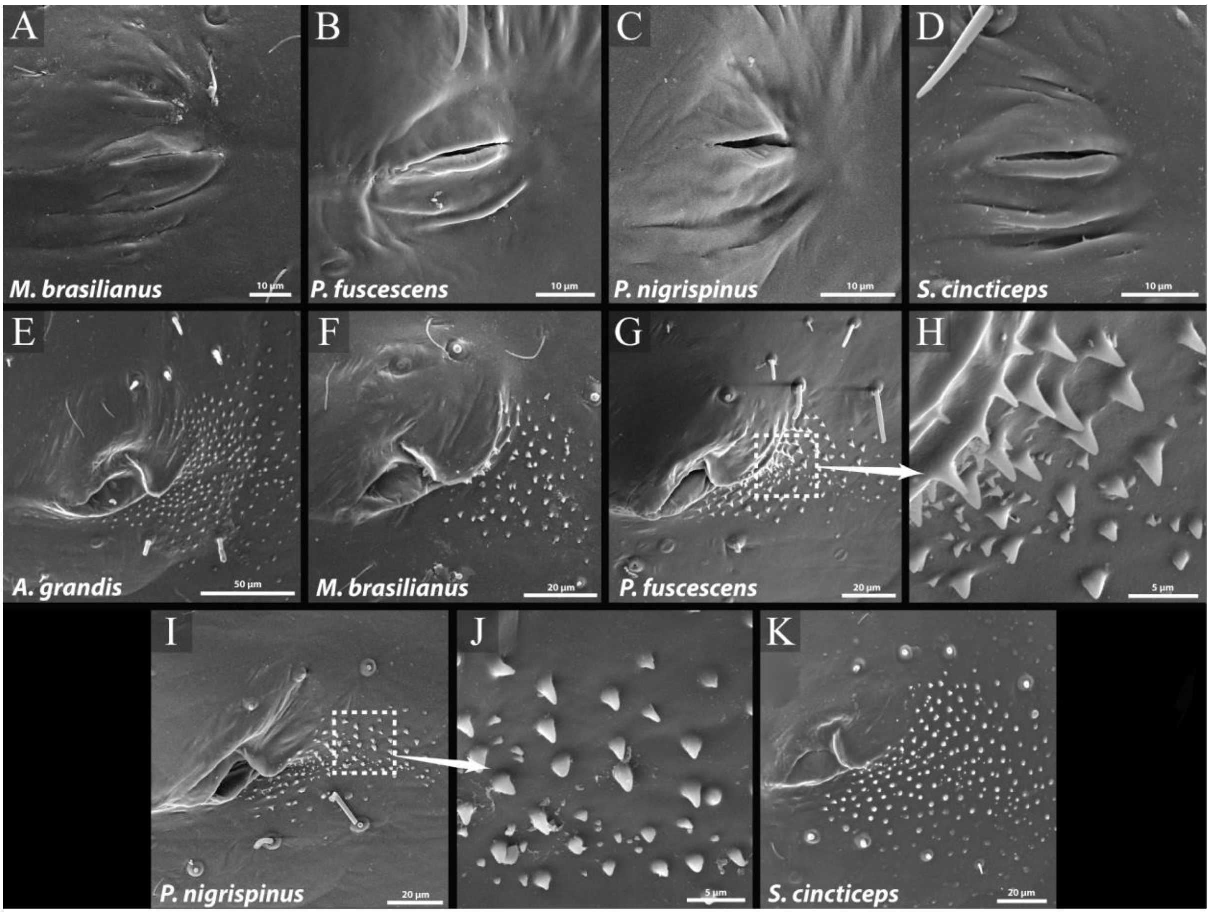


Fig. 10. External scent efferent system of dorsal abdominal glands (DAGs) of first instar nymphs under scanning electron microscopy. A, F, *Marmessulus brasilianus* Schouteden. B, G-H, *Podisus fuscescens* (Dallas). C, I-J, *Podisus nigrispinus* (Dallas). D, K, *Supputius cincticeps* (Stål). E, *Alcaeorrhynchus grandis* (Dallas). A-D, right DAG1. E-K, right DAG2. H, J, details of evaporatorium.

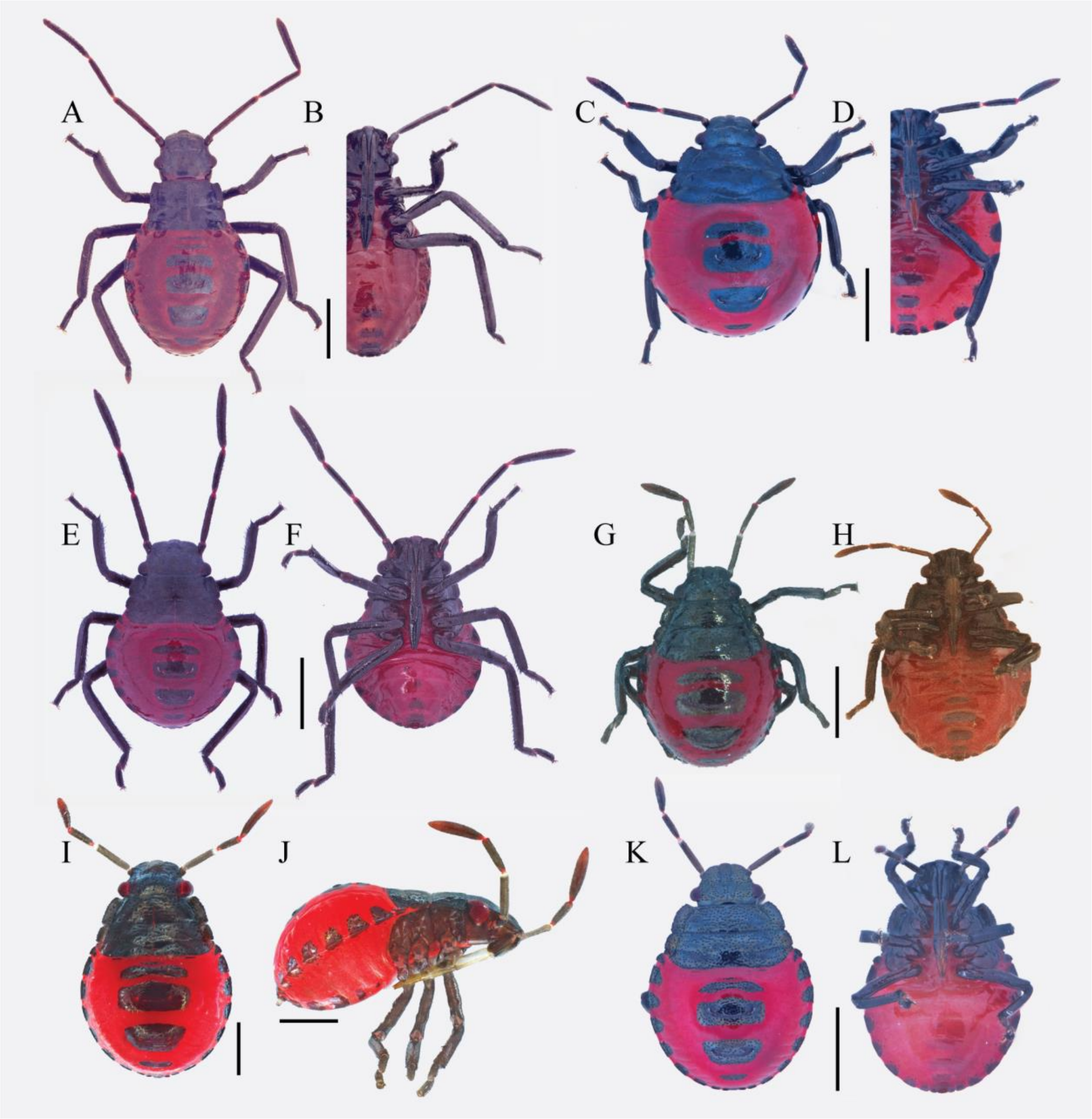


Fig. 11. Second instar nymphs of reared species. A-B, *Alcaeorrhynchus grandis* (Dallas). C-D, *Brontocoris tabidus* (Signoret). E-F, *Marmessulus brasilianus* Schouteden. G-H, *Podisus fuscescens* (Dallas). I-J, *Podisus nigrispinus* (Dallas). K-L, *Supputius cincticeps* (Stål). A, C, E, G, I, K, dorsal view. B, D, F, H, L, ventral view. J, lateral view. Scales: 1 mm.

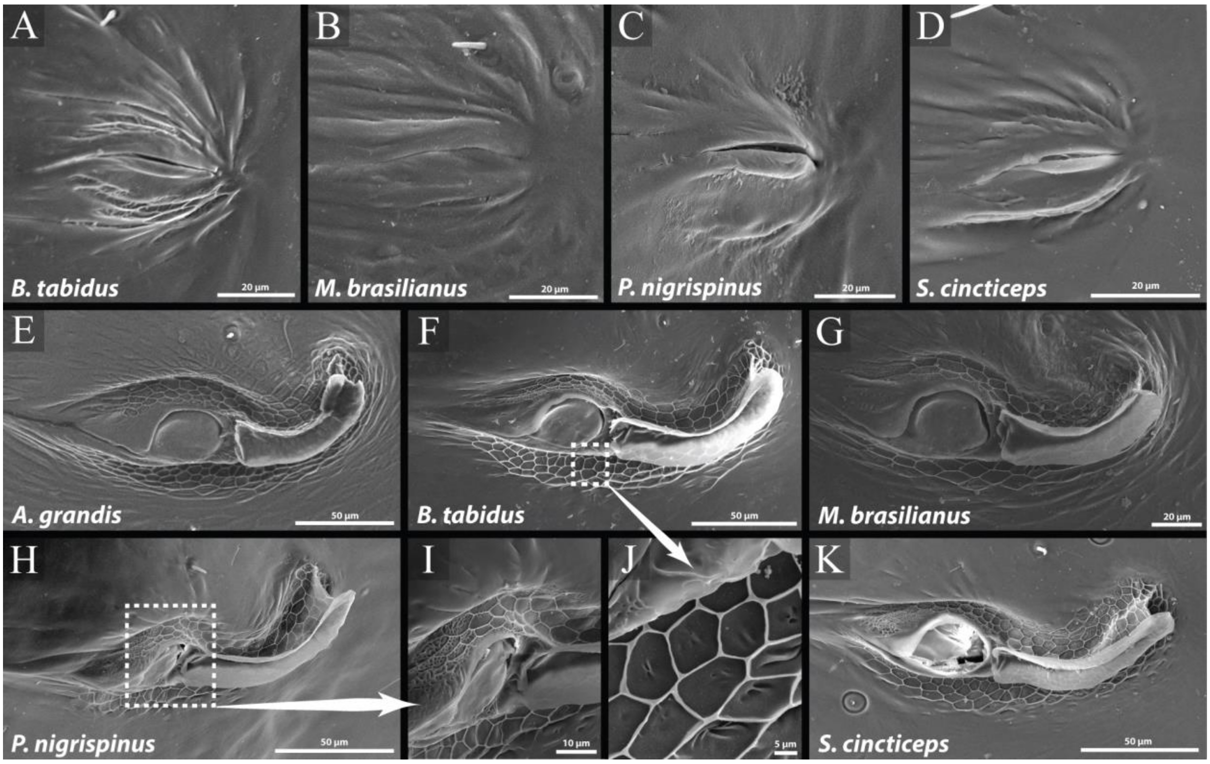


Fig. 12. External scent efferent system of dorsal abdominal glands (DAGs) of second instar nymphs under scanning electron microscopy. A, F, J, *Brontocoris tabidus* (Signoret). B, G, *Marmessulus brasilianus* Schouteden. C, H-I, *Podisus nigrispinus* (Dallas). D, K, *Supputius cincticeps* (Stål). E, *Alcaeorrhynchus grandis* (Dallas). A-D, right DAG1. E-K, right DAG2. I-J, details of evaporatorium.

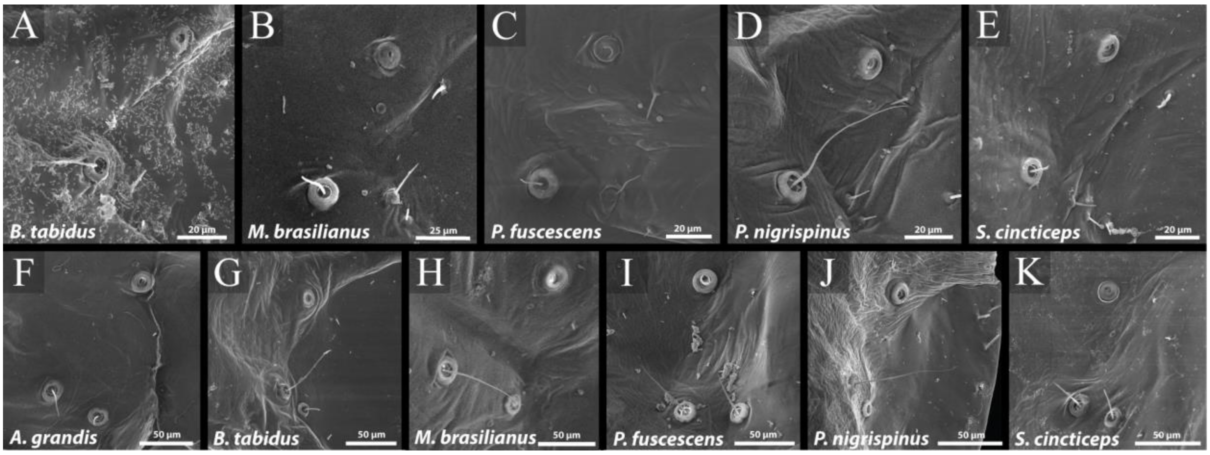


Fig. 13. Spiracle and trichobothria under scanning electron microscopy. A, G, *Brontocoris tabidus* (Signoret). B, H, *Marmessulus brasilianus* Schouteden. C, I, *Podisus fuscescens* (Dallas). D, J, *Podisus nigrispinus* (Dallas). E, K, *Supputius cincticeps* (Stål). F, *Alcaeorrhynchus grandis* (Dallas). A-E, first instar nymphs. F-K, second instar nymphs.

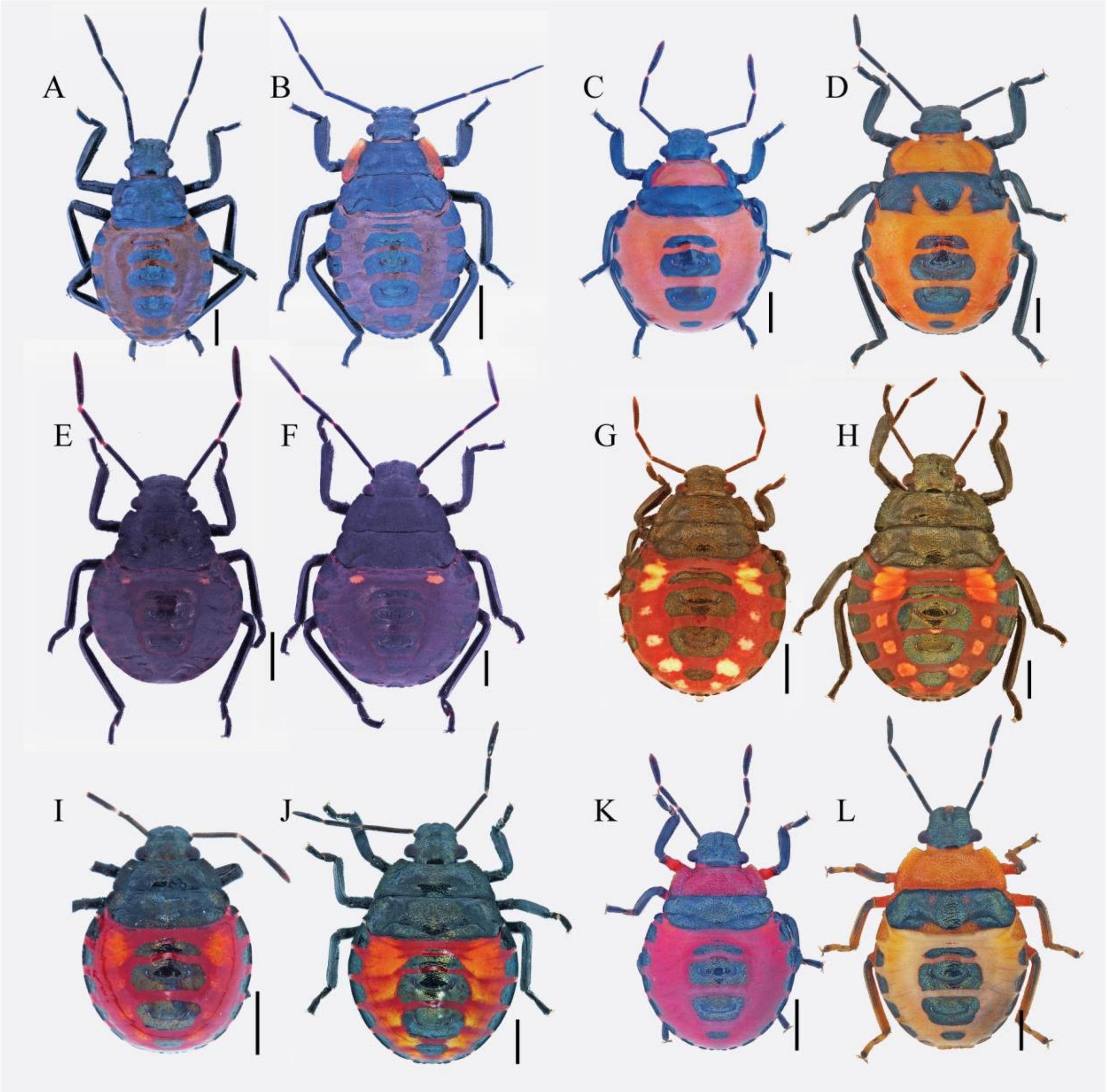


Fig. 14. Third and fourth instars nymphs of reared species in dorsal view. A-B, *Alcaeorrhynchus grandis* (Dallas). C-D, *Brontocoris tabidus* (Signoret). E-F, *Marmessulus brasilianus* Schouteden. G-H, *Podisus fuscescens* (Dallas). I-J, *Podisus nigrispinus* (Dallas). K-L, *Supputius cincticeps* (Stål). Scales: 1 mm.

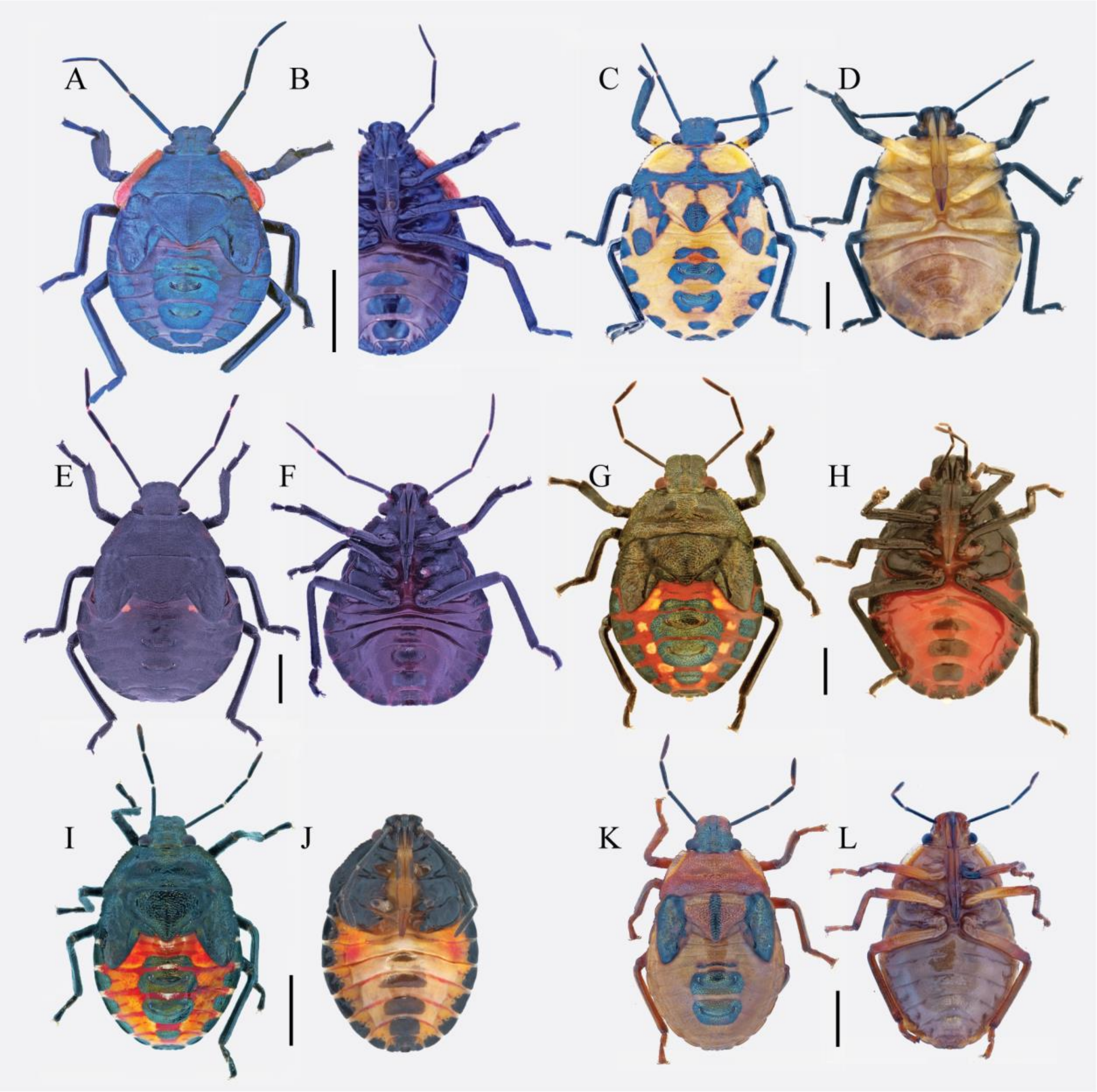


Fig. 15. Fifth instar nymphs of reared species. A-B, *Alcaeorrhynchus grandis* (Dallas). C-D, *Brontocoris tabidus* (Signoret). E-F, *Marmessulus brasilianus* Schouteden. G-H, *Podisus fuscescens* (Dallas). I-J, *Podisus nigrispinus* (Dallas). K-L, *Supputius cincticeps* (Stål). A, C, E, G, I, K, dorsal view. B, D, F, H, J, L, ventral view. Scales: 2 mm.

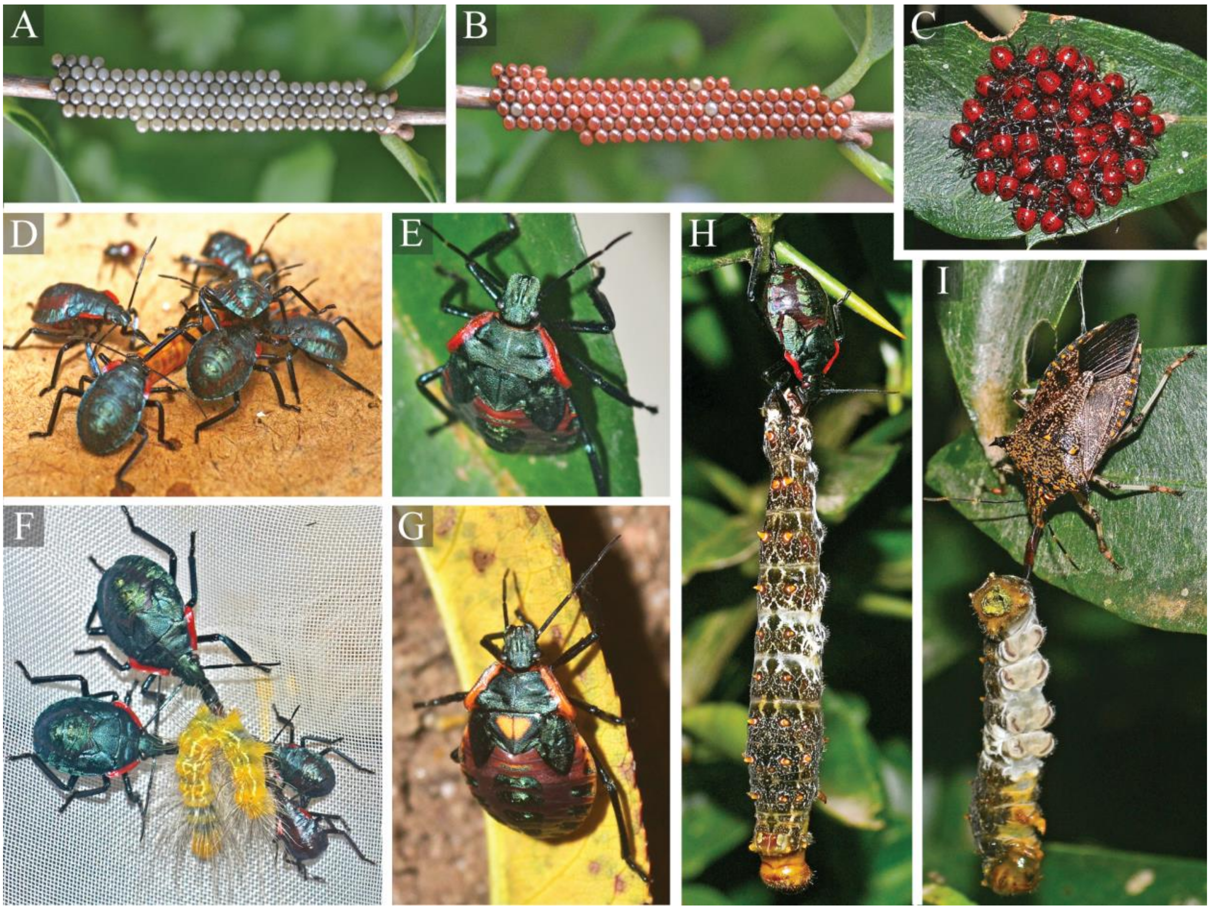


Fig. 16. *Alcaeorrhynchus grandis* (Dallas) during laboratory rearing. A-B, eggs after laying (A), and near hatching (B). C, aggregation of first instar nymphs. D, fourth instar nymphs feeding on *T. molitor* larvae. E, fifth instar nymph. F, fifth (left) and fourth instar (right) nymphs feeding on Lepidoptera larvae. G, fifth instar nymph with an unusual pale spot on thorax. H-I, fifth instar (H) and adult (I) feeding on Lepidoptera larvae.

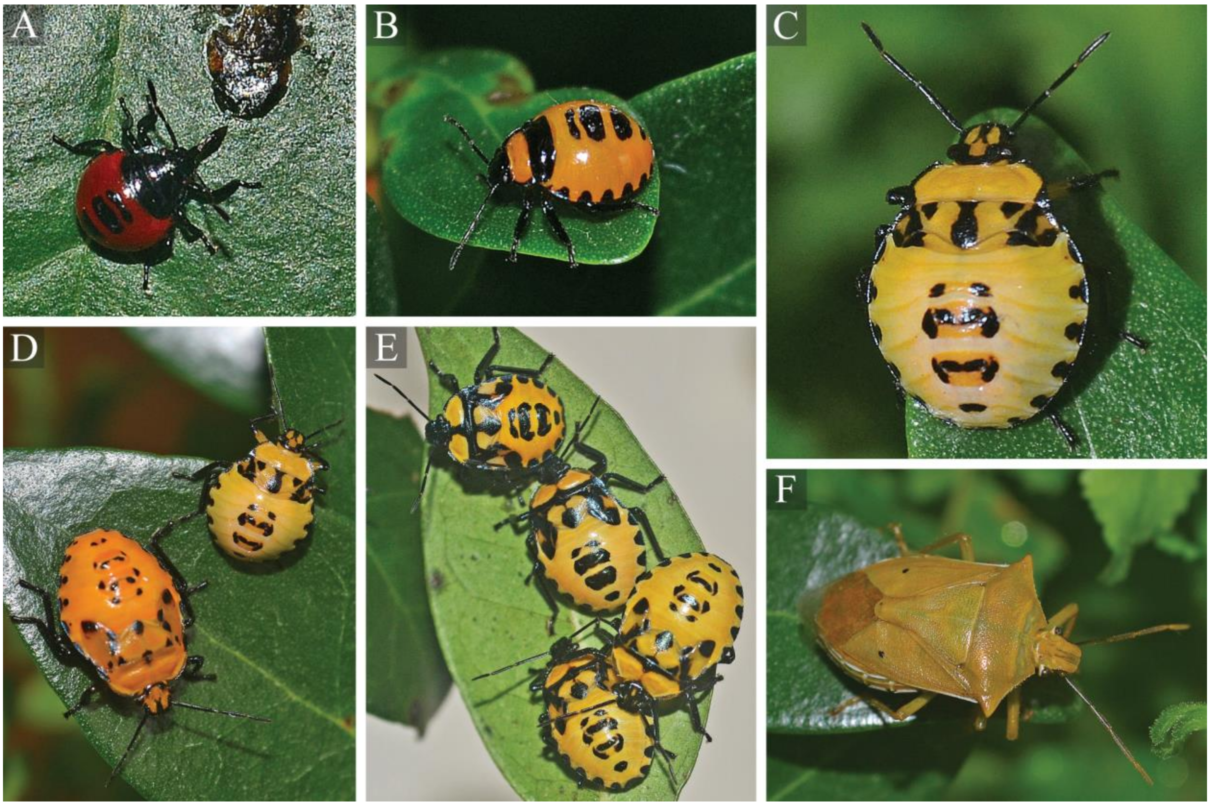


Fig. 17. *Brontocoris tadibus* (Signoret) during laboratory rearing. A, second instar nymph. B, third instar nymph. C, fourth instar nymph. D, Fourth (right) and fifth (left) instar nymphs. E, fifth instar nymphs showing variations of black pigmentation. F, adult.

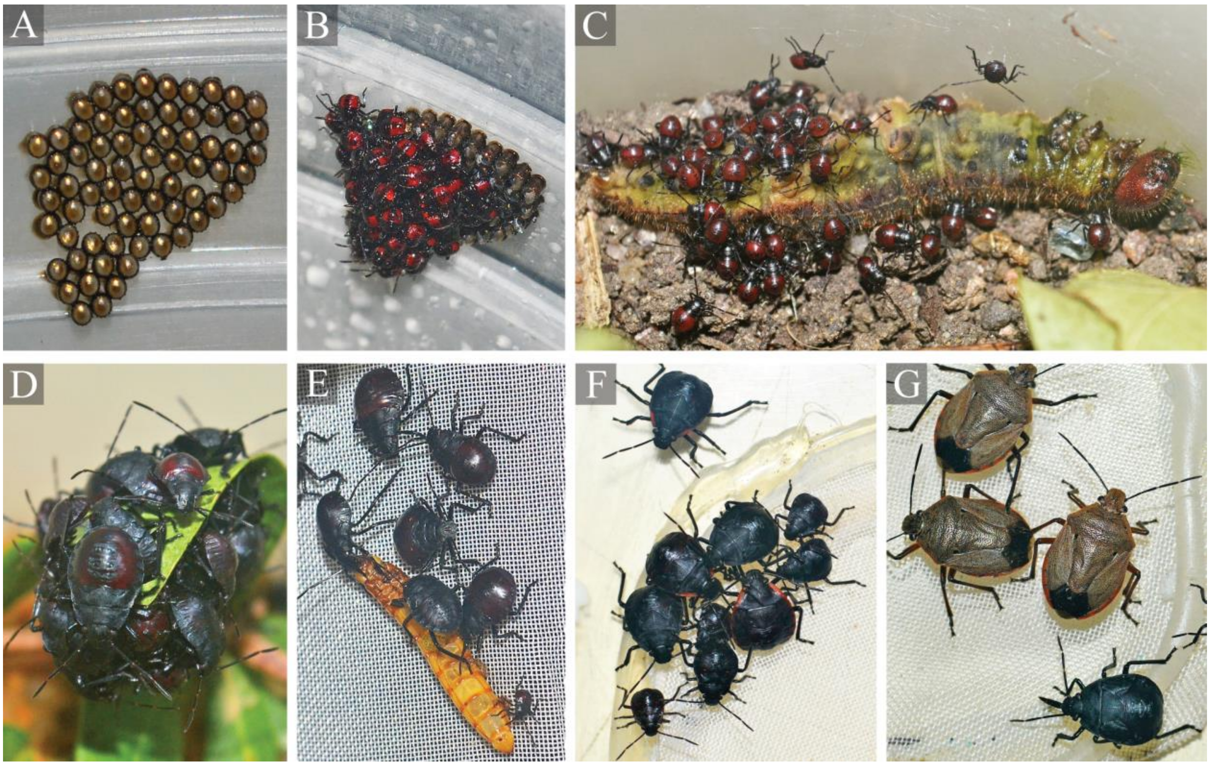


Fig. 18. *Marmessulus brasilianus* Schouteden during laboratory rearing. A, eggs. B, first instar nymphs after hatching. C, second instar nymphs feeding on Lepidoptera larvae. D, nymphs' aggregation. E, fourth and second (bottom right) feeding on *T. molitor* larvae. F, fourth and fifth instar nymphs aggregation. G, adults and fifth instar nymph (bottom right).

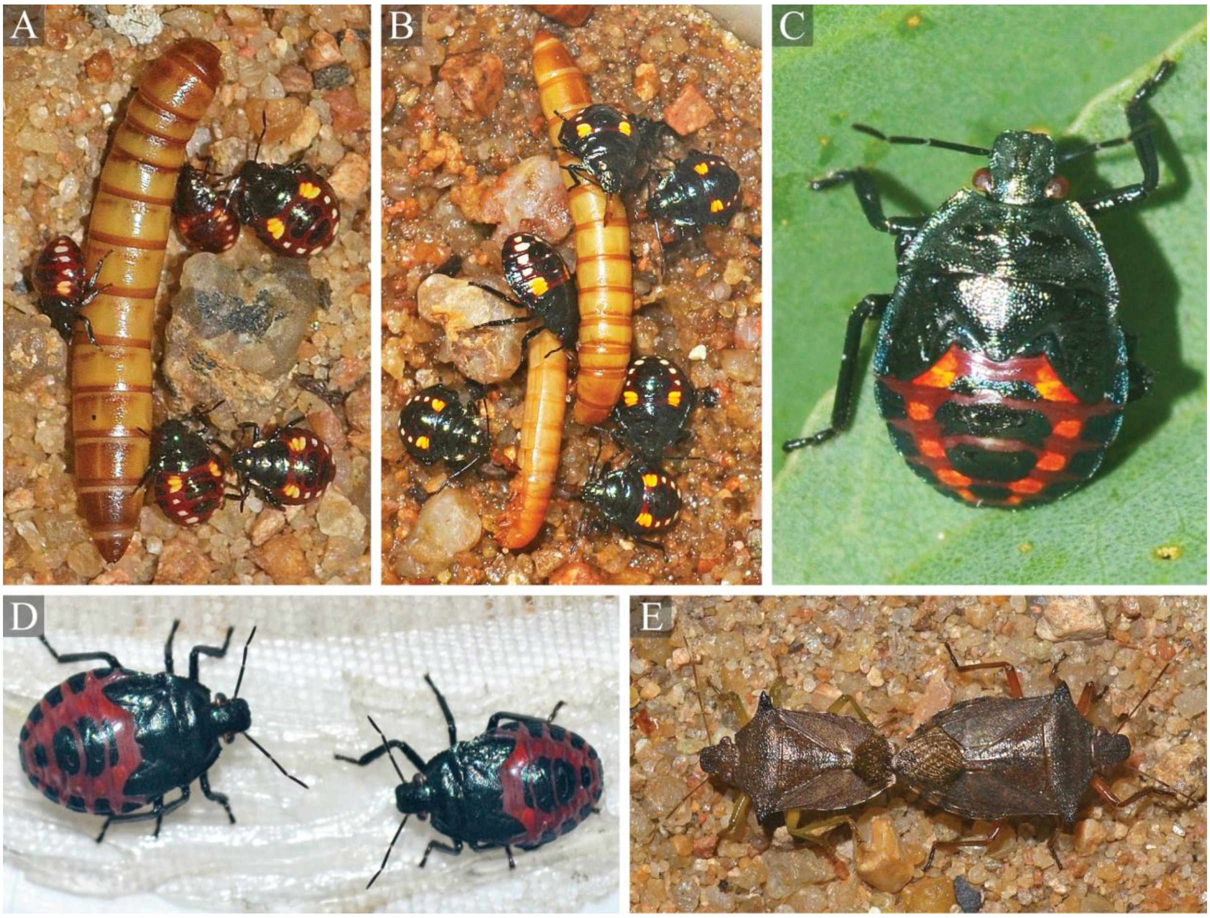


Fig. 19. *Podisus fuscescens* (Dallas) during laboratory rearing. A-B, third (A) and fourth (B) instar nymphs feeding on *T. molitor* larvae. C-D, newly emerged (C) and near of imaginal molt (D) fifth instar nymphs. E, adults mating.

Fig. 20. *Podisus nigrispinus* (Dallas) during laboratory rearing. A, first instar nymphs after hatching. B-D, third and fourth instar nymphs (B-C) and adult feeding on *T. molitor* larvae.

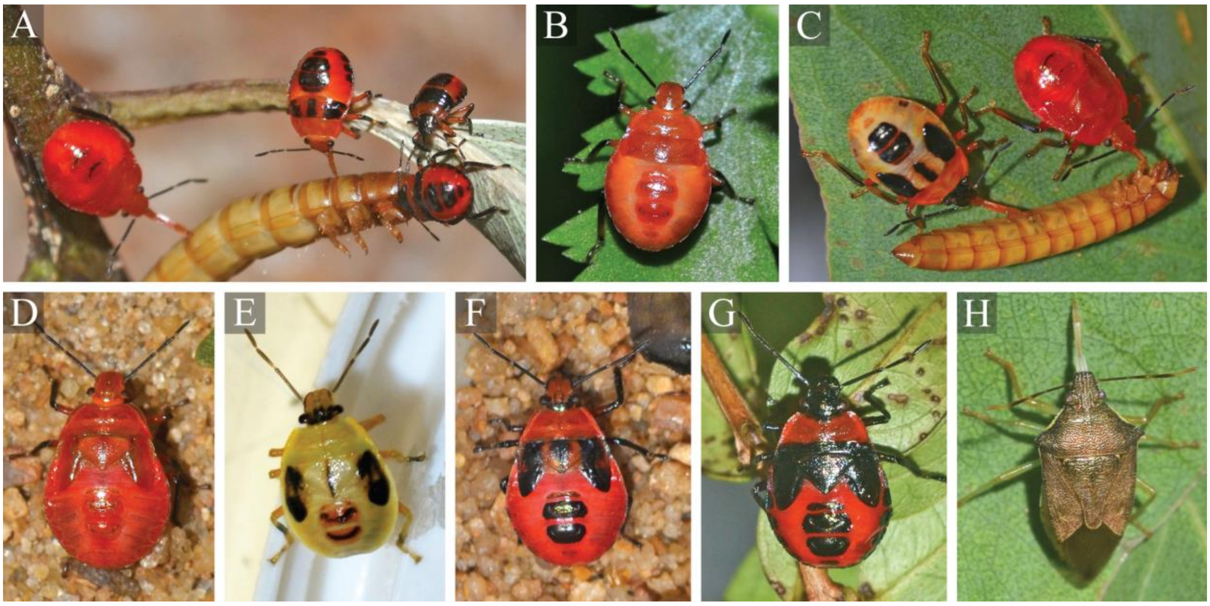
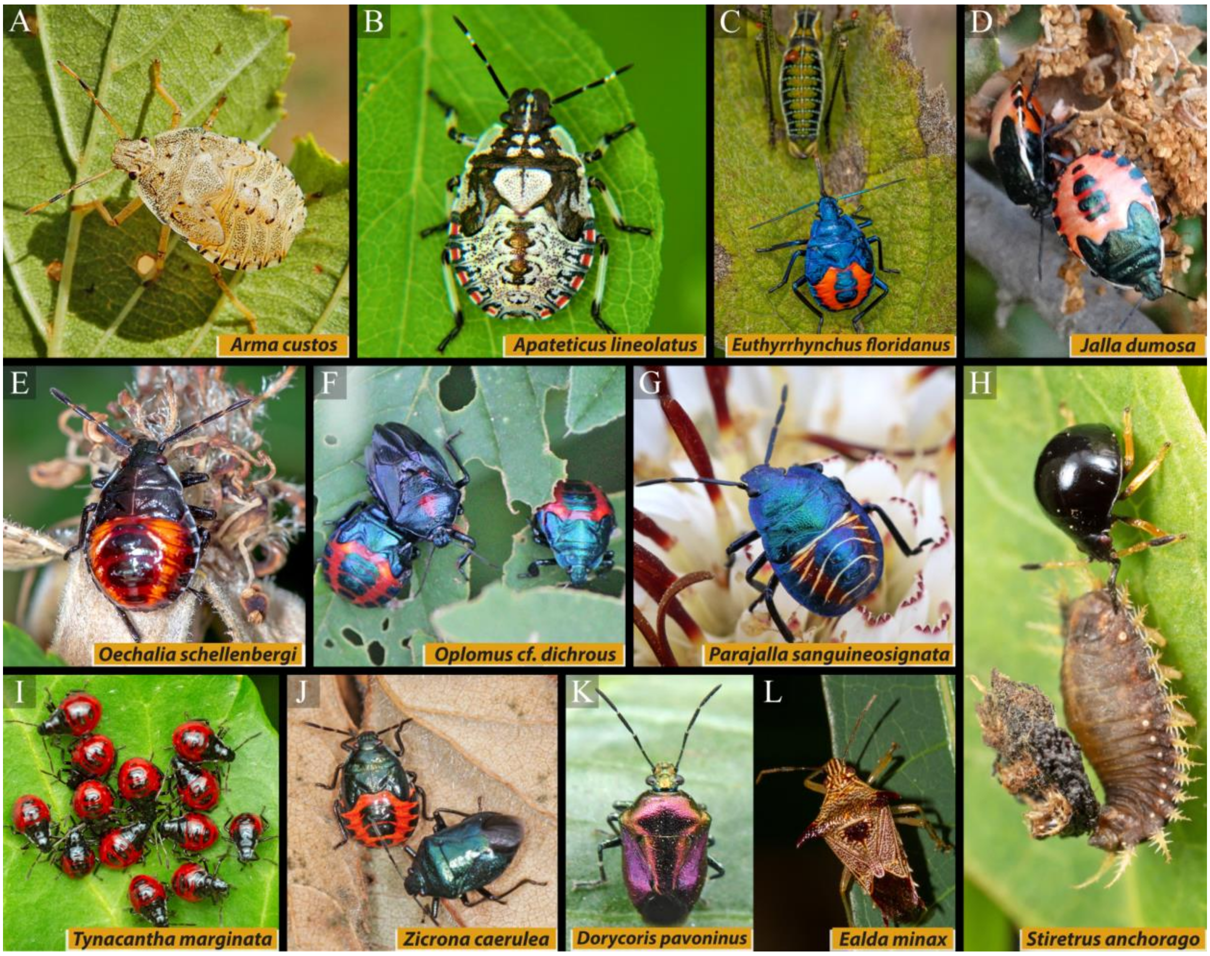


Fig. 21. *Supputius cincticeps* (Stål) during laboratory rearing. A, third and fourth instar nymphs feeding of *T. molitor* larvae. B, fourth instar nymph. C, fifth instar nymphs feeding on *T. molitor* larvae. D-G, chromatic variations of fifth instar nymphs. H, adult.

Brugnera R, Limberger GM, Campos LA, and Grazia J. The eggs and nymphs of predatory stink bugs (Hemiptera: Pentatomidae: Asopinae): what do we know?

Supplementary File S1



A-J, Nymphs of Asopinae species, part 4. K-L, Habit of adults used for identification of nymphs. Authors: A, Maria Justamond (2019). B, Bruno Govaerts (2019). C, Felix Fleck (2017). D, Kostas Zontanos (2015). E, Andrew Allen (2016). F, José B. H. Díaz (2017). G, Sebastián Lescano (2019). H, Doug Wechsler (2019). I, Andrès Costa (2020). J, Frank Porch (2017). K, Jane Trembath (2019). L, Julien Barrault (2019).

Brugnera R, Limberger GM, Campos LA, and Grazia J. The eggs and nymphs of predatory stink bugs (Hemiptera: Pentatomidae: Asopinae): what do we know?

Supplementary File S2

Species	**Stage**	**Figure**	**Author**	**Link**
Alcaeorrhynchus grandis (Dallas)	Egg	2A	Richard Stovall	https://www.inaturalist.org/observations/12792933
Amyotea cf. malabarica (Fabricius)	Nymph	3E	Arijit Patra	https://www.inaturalist.org/observations/21174834
Andrallus spinidens (Fabricius)	Egg	2B	Joseph Montes de Oca	https://www.inaturalist.org/observations/7243483
Apateticus lineolatus (Herrich-Schäffer)	Nymph	S1B	Bruno Govaerts	https://www.inaturalist.org/observations/33094586
Apateticus lineolatus (Herrich-Schäffer)	Nymph	3C	Karen Yukich	https://www.inaturalist.org/observations/18384893
Apateticus marginiventris (Stål)	Nymph	3B	Juan C. G. Morales	https://www.inaturalist.org/observations/30401827
Apoecilus cf. cynicus (Say)	Nymph	3D	John Guerin	https://www.inaturalist.org/observations/18366490
Arma custos (Fabricius)	Nymph	S1A	Maria Justamond	https://live.staticflickr.com/65535/48598497726_5b5336f89a_b.jpg
Arma custos (Fabricius)	Nymph	3A	Ryszard Szczygieł	https://www.flickr.com/photos/ricosz/16414410170/
Brontocoris nigrolimbatus (Spinola)	Nymph	3F	Diego Ghigliotto Urzúa	https://www.inaturalist.org/observations/38107548
Cazira verrucosa (Westwood)	Nymph	3G	Xiong Shengzhi	https://www.inaturalist.org/observations/29440462
Cermatulus nasalis (Westwood)	Nymph	3H	Robin Booth	https://www.inaturalist.org/observations/9942962

Comperocoris roehneri (Phillipi)	Nymph	3I	Francisco A. A. Villagrán	https://www.inaturalist.org/observations/41303452
Conquistator mucronatus (Uhler)	Nymph	3J	Brian Magnier	https://www.inaturalist.org/observations/33769968
Dinorhynchus dybowskyi Jakovlev	Nymph	3K	Alexander Ganse	https://www.inaturalist.org/observations/16178432
Dorycoris pavoninus (Westwood)	Nymph	3L/S1K	Jane Trembath	https://www.inaturalist.org/observations/34732280
Ealda minax Walker	Nymph	3O/S1L	Julien Barrault	https://www.inaturalist.org/observations/36368395
Eocanthecona cf. concinna (Walker)	Egg	2C	Mac Lin	https://www.inaturalist.org/observations/27144431
Eocanthecona cf. concinna (Walker)	Nymph	3M	Kit Chang	https://www.inaturalist.org/observations/24924439
Eocanthecona cf. formosa (Horváth)	Egg	2D	Taewoo Kim	https://www.inaturalist.org/observations/8729882
Eocanthecona cf. parva (Distant)	Egg	2E	Liu Chung-Yi	https://www.flickr.com/photos/hellomumu/27170926533/in/photostream/
Euthyrhynchus floridanus (Linnaeus)	Nymph	S1C	Felix Fleck	https://www.inaturalist.org/observations/8786500
Euthyrhynchus floridanus (Linnaeus)	Nymph	3N	Felix Fleck	https://www.inaturalist.org/observations/18661052
Jalla dumosa (Linnaeus)	Egg	3F	Ingeborg M.M. van Leeuwen	https://www.inaturalist.org/observations/48138328
Jalla dumosa (Linnaeus)	Nymph	S1D	Kostas Zontanos	https://www.inaturalist.org/observations/8411351

Jalla dumosa (Linnaeus)	Nymph	3P	Roland Lupoli	https://www.inaturalist.org/observations/56760385
Oechalia schellenbergi (Guérin-Méneville)	Nymph	4C/S1E	Andrew Allen	https://natureshare.org/item?i=andrew_allen%2Fitems%2Fns%2F2016%2F58633b8fed2a89748000b777.yaml
Oechalia schellenbergi (Guérin-Méneville)	Egg	2G	Reiner Richter	https://www.inaturalist.org/observations/32996978
Oplomus catena (Drury)	Nymph	4A	Carlos Eduardo Zuma	https://www.inaturalist.org/observations/37620771
Oplomus cf. dichrous (Herrich-Schäffer)	Nymph	4B	Felix Fleck	https://www.inaturalist.org/observations/15657259
Oplomus cf. dichrous (Herrich-Schäffer)	Nymph	S1F	José B. H. Díaz	https://www.inaturalist.org/observations/7759772
Parajalla sanguineosignata (Spinola)	Nymph	4D	Vicente Valdés Guzmán	-
Parajalla sanguineosignata (Spinola)	Nymph	S1G	Sebastián Lescano	https://www.inaturalist.org/observations/36731956
Perillus cf. bioculatus (Fabricius)	Nymph	4H	Dave Beaudette	https://www.flickr.com/photos/48912028@N05/6051626396/
Perillus cf. circumcinctus Stål	Nymph	4I	Mia Marcellus	https://www.inaturalist.org/observations/55457874
Picromerus bidens (Linnaeus)	Nymph	4E	Andrei E. Humala	https://www.inaturalist.org/observations/18986642
Pinthaeus sanguinipes (Fabricius)	Nymph	4F	Jesús Tizón Taracido	https://www.inaturalist.org/observations/37278104
Platynopus cf. melanoleucus (Westwood)	Nymph	4G	Cheng Wai Keung	https://www.inaturalist.org/observations/7035788

Podisus crassimargo (Stål)	Egg	2H	Sergio Monteiro	https://www.projectnoah.org/spottings/31543077
Podisus cf. maculiventris (Say)	Nymph	4J	Doug Wechsler	-
Podisus placidus Uhler	Nymph	4K	Jeffrey Gruber	https://www.flickr.com/photos/7432824@N07/23597829649/in/photostream/
Rhacognathus punctatus (Linnaeus)	Nymph	4L	Tristan Bantock	https://www.flickr.com/photos/tristanba/7997045359/in/photolist-dbEX4F-dbEXfP-dbEXar-dbEWYp
Stiretrus anchorago (Fabricius)	Nymph	4M	Jeff O'Connell	https://www.inaturalist.org/observations/58468958
Stiretrus anchorago (Fabricius)	Nymph	S1H	Doug Wechsler	https://bugguide.net/node/view/1713761/bgimage
Stiretrus decemguttatus (Lepeletier & Serville)	Egg	2I	Yuuki Nakatani	-
Supputius cincticeps (Stål)	Nymph	4N	Ricardo A. Palonsky	https://www.inaturalist.org/observations/39275892
Supputius typicus Distant	Egg	2J	Kel Silva	https://www.biofaces.com/post/52925/percevejo-predador-supputius-predatory-stink-bug/
Troilus luridus (Fabricius)	Nymph	5A	Maria Justamond	https://www.flickr.com/photos/rock_wolf/33369956918/
Tylospilus acutissimus Stål	Nymph	5C	Ryan McDaniell	https://www.inaturalist.org/observations/39075970
Tynacantha marginata Dallas	Nymph	5B/S1I	Andrès Costa	https://www.inaturalist.org/observations/41896662
Zicrona caerulea (Linnaeus)	Nymph	5D	David W. Williams	https://www.flickr.com/photos/dwilliams1971/35713672834

Brugnera R, Limberger GM, Campos LA, and Grazia J. The eggs and nymphs of predatory stink bugs (Hemiptera: Pentatomidae: Asopinae): what do we know?

Supplementary File S3 – Measurements

Table 1: Measurements (mm): mean ± standard deviation (maximum-minimum) of morphometric characters of nymphs of *Alcaeorrynchus grandis*.

Character	***Alcaeorrynchus grandis* (Dallas)**				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Total length	2.12 ± 0.10 (2.24–2.00)	3.56 ± 0.18 (3.84–3.40)	5.91 ± 0.49 (6.66–5.41)	8.05 ± 0.48 (8.71–4.42)	11.02 ± 0.93 (12.14–9.85)
Head length	0.72 ± 0.01 (0.74–0.70)	0.984 ± 0.06 (1.06–0.90)	1.344 ± 0.14 (1.56–1.22)	2.104 ± 0.07 (2.16–2.00)	2.784 ± 0.17 (3.00–2.56)
Head width	0.74 ± 0.03 (0.76–0.70)	1.02 ± 0.01 (1.04–1.00)	1.42 ± 0.09 (1.54–1.30)	2.14 ± 0.06 (2.24–2.08)	2.85 ± 0.15 (3.04–2.68)
Interocular distance	0.53 ± 0.02 (0.56–0.50)	0.72 ± 0.02 (0.74–0.70)	0.95 ± 0.06 (1.00–0.86)	1.28 ± 0.05 (1.36–1.24)	1.70 ± 0.09 (1.80–1.60)
Labiomere I width	0.16 ± 0.00 (0.16–0.16)	0.24 ± 0.03 (0.28–0.22)	0.40 ± 0.01 (0.42–0.38)	0.77 ± 0.04 (0.82–0.72)	1.32 ± 0.18 (1.56–1.12)
Labiomere I length	0.26 ± 0.02 (0.30–0.24)	0.51 ± 0.04 (0.56–0.46)	0.68 ± 0.06 (0.76–0.60)	1.01 ± 0.02 (1.04–1.00)	1.37 ± 0.12 (1.48–1.16)
Labiomere II length	0.25 ± 0.02 (0.28–0.24)	0.50 ± 0.01 (0.52–0.50)	0.77 ± 0.04 (0.80–0.72)	1.22 ± 0.08 (1.30–1.10)	1.70 ± 0.12 (1.88–1.56)
Labiomere III length	0.17 ± 0.01 (0.18–0.16)	0.30 ± 0.05 (0.36–0.24)	0.41 ± 0.01 (0.42–0.40)	0.68 ± 0.03 (0.70–0.64)	1.14 ± 0.06 (1.24–1.08)
Labiomere IV length	0.32 ± 0.01 (0.34–0.30)	0.52 ± 0.01 (0.54–0.50)	0.77 ± 0.04 (0.82–0.72)	1.11 ± 0.04 (1.18–1.08)	1.54 ± 0.12 (1.68–1.40)
Antenomere I length	0.14 ± 0.01 (0.16–0.12)	0.18 ± 0.02 (0.20–0.16)	0.24 ± 0.00 (0.24–0.24)	0.39 ± 0.02 (0.40–0.36)	0.60 ± 0.00 (0.60–0.60)
Antenomere II length	0.40 ± 0.00 (0.40–0.40)	0.94 ± 0.03 (0.98–0.90)	1.38 ± 0.11 (1.50–1.22)	2.21 ± 0.06 (2.28–2.12)	3.17 ± 0.22 (3.48–2.92)
Antenomere III length	0.36 ± 0.01 (0.38–0.36)	0.81 ± 0.01 (0.82–0.80)	1.19 ± 0.09 (1.34–1.10)	1.79 ± 0.05 (1.84–1.72)	2.64 ± 0.18 (2.76–2.32)
Antenomere IV length	0.59 ± 0.01 (0.6–0.58)	1.00 ± 0.02 (1.02–0.96)	1.28 ± 0.11 (1.46–1.20)	1.80 ± 0.05 (1.80–1.68)	2.15 ± 0.10 (2.24–2.00)
Pronotal width	0.92 ± 0.02 (0.96–0.90)	1.24 ± 0.07 (1.34–1.16)	2.12 ± 0.18 (2.30-1.82)	3.97 ± 0.23 (4.25–3.75)	7.00 ± 0.47 (7.67–6.50)
Pronotal length	0.20 ± 0.01 (0.22–0.20)	0.41 ± 0.02 (0.44–0.40)	0.70 ± 0.05 (0.74–0.62)	1.34 ± 0.06 (1.40–1.24)	2.34 ± 0.14 (2.48–2.16)
Abdominal width	1.20 ± 0.02 (1.24–1.18)	1.87 ± 0.25 (2.12–1.50)	3.18 ± 0.38 (3.80–2.84)	5.43 ± 0.15 (5.58–5.25)	7.38 ± 0.52 (8.17–6.92)

Table 2: Measurements (mm): mean ± standard deviation (maximum-minimum) of the morphometric characters of nymphs of *Brontocoris tabidus*.

Character	***Brontocoris tabidus* (Signoret)**				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Total length	1.75 ± 0.09 (1.86–1.70)	3.18 ± 0.28 (3.56–2.80)	5.04 ± 0.72 (5.92–4.17)	6.53 ± 0.67 (7.42–5.83)	9.40 ± 0.88 (10.83–8.75)
Head length	0.54 ± 0.06 (0.60–0.48)	0.72 ± 0.08 (0.82–0.60)	1.08 ± 0.12 (1.18–0.94)	1.33 ± 0.11 (1.50–1.22)	1.73 ± 0.13 (1.92–1.60)
Head width	0.67 ± 0.06 (0.70–0.60)	0.96 ± 0.08 (1.00–0.90)	1.29 ± 0.72 (1.30–1.28)	1.71 ± 0.67 (1.92–1.56)	2.18 ± 0.88 (2.28–2.12)
Interocular distance	0.50 ± 0.03 (0.52–0.46)	0.65 ± 0.02 (0.68–0.62)	0.84 ± 0.03 (0.86–0.82)	1.08 ± 0.10 (1.20–0.94)	1.33 ± 0.10 (1.48–1.24)
Labiomere I width	0.15 ± 0.01 (0.16–0.14)	0.20 ± 0.01 (0.22–0.20)	0.37 ± 0.02 (0.38–0.34)	0.47 ± 0.04 (0.54–0.44)	0.66 ± 0.06 (0.72–0.60)
Labiomere I length	0.23 ± 0.03 (0.26–0.20)	0.37 ± 0.02 (0.40–0.36)	0.57 ± 0.06 (0.62–0.50)	0.77 ± 0.13 (0.96–0.64)	0.93 ± 0.04 (1.00–0.88)
Labiomere II length	0.19 ± 0.01 (0.20–0.18)	0.44 ± 0.03 (0.48–0.40)	0.69 ± 0.01 (0.70–0.68)	0.82 ± 0.12 (0.96-0.64)	1.25 ± 0.09 (1.40–1.16)
Labiomere III length	0.19 ± 0.01 (0.20–0.18)	0.30 ± 0.05 (0.38–0.26)	0.49 ± 0.08 (0.56–0.40)	0.66 ± 0.08 (0.76–0.56)	0.89 ± 0.05 (0.96–0.84)
Labiomere IV length	0.27 ± 0.00 (0.28–0.28)	0.39 ± 0.01 (0.40–0.38)	0.55 ± 0.04 (0.60–0.52)	0.70 ± 0.07 (0.76–0.60)	0.90 ± 0.08 (1.00–0.80)
Antenomere I length	0.08 ± 0.00 (0.08–0.08)	0.14 ± 0.02 (0.16–0.12)	0.21 ± 0.01 (0.22–0.20)	0.23 ± 0.01 (0.24–0.22)	0.36 ± 0.03 (0.42–0.34)
Antenomere II length	0.26 ± 0.00 (0.26–0.26)	0.61 ± 0.04 (0.64–0.54)	1.13 ± 0.24 (1.40–0.98)	1.51 ± 0.15 (1.74–1.34)	2.25 ± 0.15 (2.46–2.12)
Antenomere III length	0.23 ± 0.01 (0.24–0.22)	0.49 ± 0.03 (0.52–0.44)	0.75 ± 0.06 (0.80–0.68)	1.06 ± 0.10 (1.20–0.92)	1.43 ± 0.11 (1.60–1.34)
Antenomere IV length	0.42 ± 0.10 (0.44–0.40)	0.56 ± 0.13 (0.60–0.54)	0.88 ± 0.17 (0.90–0.84)	1.02 ± 0.49 (1.10–0.86)	1.26 ± 0.40 (1.38–1.16)
Pronotal width	0.91 ± 0.08 (1.00–0.84)	1.34 ± 0.07 (1.44–1.24)	2.33 ± 0.29 (2.67–2.17)	3.13 ± 0.30 (3.50–2.67)	4.63 ± 0.23 (5.00–4.42)
Pronotal length	0.18 ± 0.02 (0.20–0.16)	0.83 ± 0.04 (0.88–0.80)	0.72 ± 0.07 (0.78–0.64)	0.95 ± 0.08 (1.04–0.84)	1.59 ± 0.26 (2.04–1.36)
Abdominal width	1.37 ± 0.12 (1.50–1.30)	2.16 ± 0.36 (2.64–1.80)	3.39 ± 0.41 (3.67–2.92)	4.35 ± 0.48 (5.00–3.83)	5.77 ± 0.45 (6.50–5.42)

Table 3: Measurements (mm): mean ± standard deviation (maximum-minimum) of the morphometric characters of nymphs of *Marmessulus brasilianus.*

Character	***Marmessulus brasilianus* Schouteden**				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Total length	1.82 ± 0.03 (1.86–1.80)	2.92 ± 0.26 (3.30–2.56)	4.33 ± 0.03 (4.36–4.28)	6.62 ± 0.36 (7.17–6.17)	8.58 ± 0.73 (9.67–7.67)
Head length	0.62 ± 0.03 (0.66–0.60)	0.94 ± 0.04 (1.00–0.90)	1.31 ± 0.05 (1.36–1.24)	1.54 ± 0.08 (1.60–1.44)	2.02 ± 0.04 (2.08-2.00)
Head width	0.74 ± 0.01 (0.74–0.72)	0.99 ± 0.04 (1.04–0.94)	1.40 ± 0.02 (1.42–1.38)	1.80 ± 0.03 (1.84–1.76)	2.32 ± 0.06 (2.40–2.24)
Interocular distance	0.53 ± 0.01 (0.54–0.52)	0.68 ± 0.02 (0.70–0.66)	0.92 ± 0.03 (0.94–0.88)	1.10 ± 0.04 (1.16–1.08)	1.34 ± 0.05 (1.40–1.28)
Labiomere I width	0.15 ± 0.02 (0.18–0.14)	0.23 ± 0.01 (0.24–0.22)	0.30 ± 0.00 (0.30–0.30)	0.46 ± 0.02 (0.48–0.44)	0.64 ± 0.00 (0.64–0.64)
Labiomere I length	0.22 ± 0.01 (0.24–0.20)	0.39 ± 0.02 (0.42–0.36)	0.58 ± 0.01 (0.60–0.56)	0.68 ± 0.04 (0.72–0.64)	0.90 ± 0.02 (0.92–0.88)
Labiomere II length	0.17 ± 0.04 (0.22–0.12)	0.31 ± 0.12 (0.46–0.18)	0.46 ± 0.19 (0.72–0.24)	0.85 ± 0.05 (0.92–0.80)	1.10 ± 0.06 (1.16–1.00)
Labiomere III length	–	–	–	0.40 ± 0.00 (0.40–0.40)	0.54 ± 0.02 (0.56–0.52)
Labiomere IV length	0.27 ± 0.01 (0.28–0.26)	0.41 ± 0.01 (0.42–0.40)	0.57 ± 0.03 (0.60–0.52)	0.80 ± 0.00 (0.80–0.80)	1.06 ± 0.05 (1.16–1.04)
Antenomere I length	0.13 ± 0.01 (0.14–0.12)	0.18 ± 0.02 (0.20–0.16)	0.21 ± 0.01 (0.22–0.20)	0.26 ± 0.02 (0.28–0.24)	0.38 ± 0.02 (0.40–0.34)
Antenomere II length	0.33 ± 0.01 (0.34–0.32)	0.73 ± 0.03 (0.78–0.70)	1.08 ± 0.04 (1.14–1.04)	1.52 ± 0.02 (1.56–1.50)	2.14 ± 0.07 (2.22–2.06)
Antenomere III length	0.29 ± 0.01 (0.30–0.28)	0.62 ± 0.03 (0.64–0.58)	0.89 ± 0.01 (0.90–0.88)	1.23 ± 0.03 (1.26–1.20)	1.59 ± 0.06 (1.66–1.50)
Antenomere IV length	0.64 ± 0.01 (0.66–0.62)	0.90 ± 0.03 (0.94–0.88)	1.17 ± 0.02 (1.20–1.14)	1.41 ± 0.02 (1.44–1.40)	1.72 ± 0.06 (1.80–1.64)
Pronotal width	0.92 ± 0.00 (0.92–0.92)	1.21 ± 0.04 (1.26–1.16)	1.88 ± 0.06 (1.96–1.80)	2.81 ± 0.11 (2.96–2.64)	4.70 ± 0.14 (4.92–4.58)
Pronotal length	0.18 ± 0.00 (0.18–0.18)	0.28 ± 0.03 (0.32–0.24)	0.58 ± 0.04 (0.64–0.54)	0.91 ± 0.03 (0.96–0.88)	1.61 ± 0.07 (1.64–1.48)
Abdominal width	1.24 ± 0.03 (1.28–1.20)	1.87 ± 0.14 (2.08–1.72)	3.16 ± 0.22 (3.40–2.80)	4.36 ± 0.22 (4.68–4.16)	5.82 ± 0.47 (6.50–5.17)

Table 4: Measurements (mm): mean ± standard deviation (maximum-minimum) of the morphometric characters of nymphs of *Podisus fuscescens.*

Character	***Podisus fuscescens* (Dallas)**				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Total length	1.49 ± 0.12 (1.60–1.32)	2.66 ± 0.24 (3.08–2.48)	4.09 ± 0.43 (4.56–3.44)	5.70 ± 0.38 (6.08–5.08)	8.92 ± 0.71 (9.50–7.75)
Head length	0.60 ± 0.02 (0.62–0.58)	0.70 ± 0.08 (0.80–0.60)	0.87 ± 0.05 (0.96–0.82)	1.42 ± 0.08 (1.48–1.28)	1.87 ± 0.02 (1.88–1.84)
Head width	0.62 ± 0.03 (0.66–0.60)	0.90 ± 0.07 (1.00–0.84)	1.21 ± 0.02 (1.24–1.18)	1.60 ± 0.20 (1.72–1.24)	1.93 ± 0.31 (2.20–1.60)
Interocular distance	0.48 ± 0.01 (0.50–0.46)	0.61 ± 0.06 (0.68–0.54)	0.74 ± 0.04 (0.80–0.68)	1.06 ± 0.02 (1.08–1.04)	1.39 ± 0.20 (1.60–1.20)
Labiomere I width	0.15 ± 0.02 (0.18–0.14)	0.20 ± 0.02 (0.24–0.18)	0.31 ± 0.02 (0.34–0.28)	0.47 ± 0.02 (0.48–0.44)	0.69 ± 0.02 (0.72–0.68)
Labiomere I length	0.18 ± 0.00 (0.18–0.18)	0.32 ± 0.03 (0.38–0.30)	0.48 ± 0.03 (0.50–0.44)	0.66 ± 0.05 (0.72–0.60)	0.94 ± 0.07 (1.04–0.88)
Labiomere II length	0.20 ± 0.00 (0.20–0.20)	0.39 ± 0.02 (0.40–0.36)	0.57 ± 0.01 (0.58–0.56)	0.84 ± 0.03 (0.86–0.80)	1.06 ± 0.05 (1.12–1.00)
Labiomere III length	0.18 ± 0.01 (0.18–0.16)	0.27 ± 0.02 (0.30–0.24)	0.47 ± 0.04 (0.52–0.42)	0.58 ± 0.03 (0.60–0.54)	0.90 ± 0.02 (0.92–0.88)
Labiomere IV length	0.26 ± 0.01 (0.26–0.24)	0.41 ± 0.02 (0.44–0.40)	0.60 ± 0.04 (0.64–0.54)	0.69 ± 0.06 (0.76–0.60)	0.96 ± 0.05 (1.00–0.88)
Antenomere I length	0.08 ± 0.00 (0.08–0.08)	0.11 ± 0.01 (0.12–0.10)	0.19 ± 0.01 (0.20–0.18)	0.23 ± 0.03 (0.28–0.20)	0.34 ± 0.04 (0.40–0.30)
Antenomere II length	0.23 ± 0.01 (0.24–0.22)	0.54 ± 0.08 (0.64–0.48)	0.75 ± 0.07 (0.6–40.48)	1.28 ± 0.07 (1.36–1.18)	2.01 ± 0.09 (2.14–1.92)
Antenomere III length	0.19 ± 0.02 (0.20–0.16)	0.42 ± 0.05 (0.50–0.38)	0.58 ± 0.02 (0.62–0.56)	0.91 ± 0.03 (0.94–0.86)	1.35 ± 0.02 (1.38–1.32)
Antenomere IV length	0.40 ± 0.01 (0.42–0.40)	0.58 ± 0.05 (0.64–0.50)	0.72 ± 0.02 (0.74–0.68)	0.98 ± 0.03 (1.00–0.94)	1.19 ± 0.03 (1.22–1.14)
Pronotal width	0.86 ± 0.04 (0.90–0.80)	1.38 ± 0.19 (1.70–1.24)	1.96 ± 0.08 (2.04–1.84)	3.07 ± 0.11 (3.17–2.92)	4.62 ± 0.15 (4.75–4.42)
Pronotal length	0.18 ± 0.00 (0.18–0.18)	0.40 ± 0.05 (0.48–0.36)	0.62 ± 0.07 (0.72–0.56)	0.93 ± 0.04 (1.00–0.92)	1.52 ± 0.11 (1.67–1.42)
Abdominal width	1.09 ± 0.18 (1.32–0.92)	2.02 ± 0.12 (2.16–1.84)	2.78 ± 0.26 (3.20–2.52)	3.83 ± 0.17 (4.00–3.58)	5.42 ± 0.25 (5.83–5.17)

Table 5: Measurements (mm): mean ± standard deviation (maximum-minimum) of the morphometric characters of nymphs of *Podisus nigrispinus.*

Character	***Podisus nigrispinus* (Dallas)**				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Total length	1.19 ± 0.13 (1.40–1.06)	2.30 ± 0.09 (2.48–2.24)	3.44 ± 0.18 (3.92–3.52)	4.82 ± 0.34 (5.42–4.67)	6.08 ± 0.43 (7.00–6.00)
Head length	0.42 ± 0.03 (0.46–0.40)	0.52 ± 0.24 (0.58–0.46)	0.79 ± 0.07 (0.90–0.72)	1.08 ± 0.07 (1.16–1.00)	1.30 ± 0.11 (1.40–1.14)
Head width	0.60 ± 0.01 (0.62–0.58)	0.78 ± 0.04 (0.84–0.74)	1.06 ± 0.04 (1.12–1.02)	1.42 ± 0.04 (1.46–1.36)	1.76 ± 0.05 (1.82–1.70)
Interocular distance	0.43 ± 0.02 (0.46–0.42)	0.52 ± 0.02 (0.54–0.50)	0.69 ± 0.03 (0.72–0.66)	0.88 ± 0.05 (0.92–0.80)	0.99 ± 0.03 (1.02–0.96)
Labiomere I width	0.11 ± 0.02 (0.12–0.08)	0.17 ± 0.01 (0.18–0.16)	0.26 ± 0.02 (0.28–0.24)	0.79 ± 0.03 (0.84–0.76)	1.04 ± 0.05 (1.12–1.00)
Labiomere I length	0.18 ± 0.00 (0.18–0.18)	0.25 ± 0.02 (0.28–0.22)	0.44 ± 0.07 (0.56–0.38)	0.59 ± 0.01 (0.60–0.58)	0.82 ± 0.02 (0.84–0.80)
Labiomere II length	0.18 ± 0.01 (0.20–0.18)	0.31 ± 0.01 (0.32–0.30)	0.50 ± 0.02 (0.54–0.48)	0.76 ± 0.03 (0.80–0.72)	0.92 ± 0.06 (1.00–0.84)
Labiomere III length	0.10 ± 0.01 (0.12–0.10)	0.22 ± 0.02 (0.24–0.20)	0.39 ± 0.04 (0.46–0.36)	0.54 ± 0.03 (0.58–0.52)	0.85 ± 0.07 (0.92–0.80)
Labiomere IV length	0.20 ± 0.01 (0.22–0.18)	0.28 ± 0.02 (0.30–0.26)	0.43 ± 0.05 (0.50–0.38)	0.50 ± 0.08 (0.62–0.40)	0.82 ± 0.04 (0.88–0.80)
Antenomere I length	0.08 ± 0.02 (0.88–0.80)	0.09 ± 0.01 (0.10–0.08)	0.13 ± 0.02 (0.16–0.10)	0.18 ± 0.02 (0.20–0.16)	0.24 ± 0.02 (0.28–0.22)
Antenomere II length	0.19 ± 0.01 (0.20–0.18)	0.43 ± 0.02 (0.46–0.40)	0.73 ± 0.06 (0.80–0.64)	1.14 ± 0.09 (1.24–1.00)	1.69 ± 0.07 (1.78–1.60)
Antenomere III length	0.16 ± 0.01 (0.18–0.14)	0.34 ± 0.02 (0.38–0.32)	0.57 ± 0.02 (0.60–0.54)	0.77 ± 0.04 (0.80–0.70)	1.11 ± 0.08 (1.20–1.02)
Antenomere IV length	0.34 ± 0.02 (0.36–0.32)	0.49 ± 0.05 (0.58–0.44)	0.66 ± 0.03 (0.70–0.64)	0.82 ± 0.04 (0.86–0.76)	0.99 ± 0.05 (1.04–0.92)
Pronotal width	0.80 ± 0.02 (0.82–0.78)	1.08 ± 0.03 (1.12–1.04)	1.73 ± 0.11 (1.88–1.64)	2.62 ± 0.02 (2.64–2.60)	3.83 ± 0.27 (4.08–3.52)
Pronotal length	0.12 ± 0.02 (0.14–0.08)	0.30 ± 0.01 (0.32–0.28)	0.52 ± 0.03 (0.58–0.50)	0.88 ± 0.08 (1.00–0.78)	1.24 ± 0.07 (1.36–1.16)
Abdominal width	0.97 ± 0.05 (1.02–0.90)	1.70 ± 0.10 (1.80–1.60)	2.71 ± 0.28 (3.20–2.48)	3.50 ± 0.24 (3.84–3.20)	4.19 ± 0.25 (4.40–3.92)

Table 6: Measurements (mm): mean ± standard deviation (maximum-minimum) of the morphometric characters of nymphs of *Supputius cincticeps.*

Character	*Supputius cincticeps* (Stål)				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Total length	1.62 ± 0.10 (1.74–1.48)	2.81 ± 0.10 (2.88–2.64)	3.08 ± 0.37 (3.60–2.56)	4.87 ± 0.35 (5.42–4.58)	7.42 ± 1.51 (9.08–5.83)
Head length	0.51 ± 0.01 (0.52–0.50)	0.65 ± 0.29 (0.66–0.62)	0.88 ± 0.08 (1.00–0.82)	1.16 ± 0.03 (1.20–1.14)	1.40 ± 0.29 (1.68–1.06)
Head width	0.66 ± 0.02 (0.68–0.64)	0.92 ± 0.41 (0.98–0.88)	1.10 ± 0.07 (1.20–1.02)	1.52 ± 0.08 (1.60–1.40)	1.80 ± 0.22 (2.00–1.50)
Interocular distance	0.55 ± 0.02 (0.58–0.52)	0.74 ± 0.37 (1.04–0.64)	0.70 ± 0.05 (0.76–0.62)	0.95 ± 0.08 (1.04–0.84)	1.09 ± 0.18 (1.24–0.82)
Labiomere I width	0.14 ± 0.01 (0.16–0.14)	0.21 ± 0.01 (0.24–0.22)	0.26 ± 0.02 (0.28–0.24)	0.40 ± 0.02 (0.44–0.38)	0.54 ± 0.09 (0.68–0.44)
Labiomere I length	0.24 ± 0.00 (0.24–0.24)	0.40 ± 0.02 (0.42–0.38)	0.55 ± 0.05 (0.60–0.52)	0.84 ± 0.02 (0.86–0.80)	1.01 ± 0.08 (1.10–0.90)
Labiomere II length	0.21 ± 0.01 (0.24–0.22)	0.45 ± 0.01 (0.46–0.44)	0.64 ± 0.02 (0.66–0.62)	1.00 ± 0.08 (1.08–0.92)	1.21 ± 0.16 (1.40–1.00)
Labiomere III length	0.14 ± 0.01 (0.16–0.12)	0.28 ± 0.01 (0.30–0.26)	0.37 ± 0.01 (0.38–0.36)	0.52 ± 0.07 (0.58–0.42)	0.76 ± 0.23 (1.02–0.46)
Labiomere IV length	0.19 ± 0.01 (0.20–0.18)	0.26 ± 0.01 (0.26–0.24)	0.33 ± 0.03 (0.36–0.30)	0.42 ± 0.02 (0.44–0.40)	0.56 ± 0.08 (0.66–0.46)
Antenomere I length	0.10 ± 0.00 (0.10–0.10)	0.12 ± 0.00 (0.12–0.12)	0.19 ± 0.02 (0.22:0.16)	0.25 ± 0.04 (0.30–0.22)	0.33 ± 0.04 (0.40–0.30)
Antenomere II length	0.23 ± 0.01 (0.24–0.22)	0.49 ± 0.22 (0.50–0.48)	0.74 ± 0.06 (0.82–0.68)	1.17 ± 0.09 (1.30–1.08)	0.80 ± 0.15 (0.98–0.66)
Antenomere III length	0.21 ± 0.01 (0.22–0.20)	0.30 ± 0.14 (0.34–0.28)	0.50 ± 0.03 (0.54–0.46)	0.75 ± 0.07 (0.86–0.70)	0.50 ± 0.06 (0.54–0.40)
Antenomere IV length	0.35 ± 0.01 (0.36–0.34)	0.51 ± 0.23 (0.52–0.50)	0.62 ± 0.28 (0.64–0.60)	0.79 ± 0.05 (0.86–0.74)	0.46 ± 0.06 (0.50–0.36)
Pronotal width	0.84 ± 0.03 (0.88–0.80)	1.30 ± 0.05 (1.36–1.24)	1.81 ± 0.13 (2.00–1.64)	2.56 ± 0.30 (2.88–2.16)	3.57 ± 0.67 (4.17–2.67)
Pronotal length	0.19 ± 0.01 (0.20–0.18)	0.37 ± 0.01 (0.38–0.36)	1.05 ± 0.13 (1.20–0.88)	1.82 ± 0.25 (2.08–1.58)	2.58 ± 1.25 (3.08–1.92)
Abdominal width	1.17 ± 0.10 (1.24–1.00)	1.93 ± 0.09 (2.00–1.80)	2.35 ± 0.15 (2.60–2.24)	3.29 ± 0.48 (3.80–2.60)	4.70 ± 0.67 (5.58–4.00)

CAPÍTULO III

Revision of *Tynacantha* Dallas with description of two new species (Hemiptera: Heteroptera: Pentatomidae: Asopinae)

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Abstract

Here, *Tynacantha* Dallas is revised and two new species are described from Brazil: *T. cuprea* Brugnera & Grazia sp. nov. and *T. umeridenigrata* Brugnera & Grazia sp. nov. The type material is analyzed, figures, illustrations, a distributional map and a key to the species are provided. The color variation found in *T. marginata* is also discussed.

Key words: Predatory stink bugs, taxonomy, new species

Introduction

Predatory stink bugs are classified in the subfamily Asopinae, usually recognized by having a crassate labium, and by a pair of superior processes on the dorsal rim of pygophore, in addition to which several species present aposematic and bright coloration (Gapud 1991; Thomas 1992; Schaefer 1996; Rider *et al*. 2018). The subfamily is distributed in all the zoogeographical regions and is composed by 64 genera and more than 300 species (Rider et al. 2018; Roca-Cusachs *et al*. 2018; Roell *et al*. 2019), of which 24 genera are known in the neotropics (Thomas 1992; Gapon 2009; Grazia *et al*. 2015). Because of their predatory behavior several species are used as biological control agents in crops, feeding mainly in Lepidoptera and Coleoptera larvae (Zanuncio *et al*. 2014).

Although the biological and economic importance of predatory stink bugs, little attention has been given to their systematics (De Clercq 2000, 2008; Pires *et al*. 2015). Except for the monograph of Thomas (1992) and the revision of *Perillus* Stål, 1862 (Knight 1952), taxonomy of the New World genera of Asopinae is almost restricted to 19th century publications and has been overlooked by recent authors, leaving doubts about the existence of taxonomic problems and uncertainties about species diversity.

Tynacantha Dallas is a Neotropical genus with two known species: *T. marginata* Dallas, 1851 and *T. splendens* Distant, 1889 (see Thomas 1992). The genus is characterized mainly by having the anterolateral margins of pronotum rectilinear, smooth and cream colored (Thomas 1992). *Tynacantha marginata* is a common species, distributed in South America except Chile, Venezuela, Suriname and the Guyanas (Thomas 1992; Grazia *et al*. 2015) and is considered an important agent in biological control, mainly in Brazil (Zanuncio *et al*. 1994; Sanchez *et al.* 2001; Brugnera & Grazia 2018). *Tynacantha splendens* is restricted to Central America, occurring only in Costa Rica and Panama and is a less known species (Thomas 1992).

Here Tynacantha is revised. Lectotypes, original descriptions, and specimens from several institutions were analyzed. The genus is redescribed, and two new species are described from Brazil. The habitus and genital morphology of all the species are fully illustrated; an identification key and a map of distribution are also provided.

Material and methods

Specimens were photographed in multiple focal planes with a Nikon AZ100M stereoscope coupled with a DS-Fi2 digital camera, pictures were stacked in a single focused image using the NIS Elements software.

Genitalia was prepared with heated 10% KOH until clarification, rinsed in water, stained with Congo Red for 30s, preserved in vials with glycerin and pinned with the corresponding specimen. Specimens were observed and measured under light stereomicroscope; measurements [mean ± standard deviation (minimum–maximum)] are given in millimeters. Species distributions were retrieved from the specimen collection labels and mapped on Quantum GIS Lisboa software. When GPS coordinates were not available, localities were georeferenced to the geodetic center of the city based on online global gazetteers. The collection sites were plotted in the Blue Marble Earth's image available by NASA's Earth Observatory.

Terminology of genitalic structures follows Baker (1931), Dupuis (1970), Schaefer (1977), and Gapon & Konstantinov (2006), and Kment & Vilímová (2010) for the external scent efferent system of metathoracic scent glands.

Species of *Tynacantha* are very similar in general and genital morphology (as pointed out by Thomas 1992). Therefore, in order to avoid repetitions, a detailed description of the genus is provided, and the differences among the species are portrayed on the diagnosis of each species.

The following collections are depositories for specimens studied here:

BMNH The Natural History Museum, London, England

BHMH Universidade Federal de Minas Gerais, Museu de História Natural, Belo Horizonte, Brazil

DARC David Rider, North Dakota State University, Fargo, United States of America

DBTC Donald B. Thomas, personal collection, United States of America

EMG Entomologisches Museum Geyer, Insekten Dauerausstellung, Geyer, Germany

ICN Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia

INPA Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

JEE Joseph Eger, personal collection, United States of America

MCNZ Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil

MNRJ Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

MPEG Museu Paraense Emílio Goeldi, Belém, Brazil

MRCC Marcos Roca-Cusachs, personal collection, Barcelona, Spain

MZUSP Museu de Zoologia, Universidade Estadual de São Paulo, São Paulo, Brazil

UFRG Universidade Federal do Rio Grande do Sul, Departamento de Zoologia, Porto Alegre, Brazil

UFVB Universidade Federal de Viçosa, Museu de Entomologia, Viçosa, Brazil

UNAB Universidad Nacional de Colombia, Facultad de Agronomia, Bogotá, Colombia

USNM National Museum of Natural History, Washington DC, United States of America

Results

Taxonomy

Tynacantha **Dallas, 1851**

Tynacantha Dallas, 1851: 106; Stål, 1867: 497; Walker, 1867: 144; Stål, 1870: 56; Schouteden, 1907: 13, 59; Kirkaldy, 1909: 5, 16; Thomas, 1992: 122.

Type species: *Tynacantha marginata* Dallas, 1851, by monotypy

Diagnosis. Anterolateral margins of pronotum rectilinear, concolorous with ventral surface and unpunctured; humeral angles acute, not produced; abdominal spine reaching at most the anterior margin of metacoxae; abdominal venter minutely punctured (Figs 1–2, 4–5, 7–18). Peritreme groove-shaped, surrounded by evaporatorium. Superior layer of ventral rim of pygophore with 1 + 1 acute processes (Figs 20, 25, 30), dorsal rim concave with 1 + 1 sinuous projections (Figs 19, 24, 29). Head of paramere with two branches (Figs 22, 27, 32); capsula seminalis globose; thickening of vaginal intima tube-like with an anterior elliptic projection (Figs 48, 51).

Redescription. Body oval; brown or dark brown dorsally, frequently bright green; ventrally pale yellow, sometimes orange with two or three rows of black spots; legs pale yellow or orange, immaculate (Figs 1–2, 4–5, 7–18). **Head:** rectangular; as long as wide or slightly wider than long; clypeus slightly longer than mandibular plates (Figs 9, 12, 15, 18). Labium slightly surpassing the metacoxae, second segment longest. Antennae five-segmented, second segment the longest. **Thorax:** anterolateral angles of pronotum produced; anterolateral margins of pronotum rectilinear, concolorous with ventral surface and unpunctured; humeral angles acute, not produced (Figs 9, 12, 15, 18). Basal angles of scutellum foveate; frenal margin of scutellum longer than postfrenal margin, apex of scutellum pale calloused or concolorous, reaching the fifth segment of abdomen. Peritreme groove-shaped, apex curved anteriorly and usually with a black spot; evaporatorium on metapleuron surrounding the peritreme, not extending to the lateral margin of thorax; evaporatorium extended onto posterior margin of mesopleuron. Membrane of hemelytra brownish medially or entirely translucent. **Abdomen:** ventral surface unpunctured; abdominal spine reaching at most the anterior margin of metacoxae. Connexival segments brown to dark brown anteriorly and posteriorly, with the medial part pale, or with a lateral line concolorous with the abdominal sternites. Margin of spiracles concolorous with venter. **Male genitalia** (Figs 19–45): Pygophore wider than long; dorsal rim concave, with 1 + 1 projections; inferior layer of ventral rim concave; superior layer of ventral rim concave with 1 + 1 acute processes, convex laterally; parameres with two branches, ventral surface of the internal branch sculptured; superior process of dorsal rim semicircular, with rounded sculptures dorsally; segment X subrectangular; thecal shield longer and wider than basal theca; apex of conjunctival lobes slightly sclerotized; vesica cup-like with 1+1 tabs laterally; secondary gonopore projected. **Female genitalia** (Figs 46–53): Gonocoxites VIII as long as wide, laterotergites VIII triangular; gonocoxites IX rectangular, lateral margins projected over the laterotergites IX; laterotergites IX longer than wide, surpassing the segment X, reaching the sclerite VIII; gonapophyses IX with 1+1 slightly sclerotized areas surrounding the ring sclerites; ring sclerites circular; 1+1 secondary thickenings of gonapophyses IX crescent-like; thickening of vaginal intima tube-like with an anterior elliptic projection; capsula seminalis globose; anterior and posterior annular flanges projected posteriorly; ductus receptaculi proximalis longer than vesicular area.

Remarks. The bright color and the black spots on the ventral surface of abdomen can change after preservation (see Discussion).

Key to species of *Tynacantha* Dallas, 1851

1 Apex of scutellum without a pale and calloused spot; segments of connexivum not alternated, lateral margin concolorous with the abdominal sternites (Figs 1, 7). . . . . *T. marginata* Dallas

- Apex of scutellum with a pale and calloused spot; segments of connexivum alternated brown to dark brown anteriorly and posteriorly, medial area pale (Figs 4, 10, 13, 16). 2

2 Membrane of hemelytra entirely translucent; pale and calloused spot at apex of scutellum occupying half of the postfrenal lobe (Central America) (Figs 4, 10). . . . .*T. splendens* Distant

- Membrane of hemelytra brownish medially; pale and calloused spot of scutellum restricted to the apex of postfrenal lobe (South America) (Figs 13, 16). 3

3 Humeral angles distinctly black and punctured (Fig. 18); intersegmental areas of connexivum light brown; posterior margins of gonocoxites VIII sinuous (Fig. 53). . . . . *T. umeridenigrata* Brugnera & Grazia sp. nov.

- Humeral angles concolorous with pronotum, unpunctured (Fig. 15); intersegmental areas of connexivum black; posterior margins of gonocoxites VIII almost rectilinear (Fig. 50). . . . . *T. cuprea* Brugnera & Grazia sp. nov.

Tynacantha marginata Dallas, 1851

(Figs 1–3, 7–9, 19–23, 34–36, 46–48, 54)

Tynacantha marginata Dallas, 1851: 107; Walker, 1867: 144; Stål, 1870: 56; Schouteden, 1907: 59; Kirkaldy, 1909: 16; De Tella, 1951: 179; Buckup, 1960: 10, 11; Saini & De Coll, 1992: 7, 8; Thomas, 1992: 122, 123; Zanuncio *et al*., gv1994: 67, 71; Moreira *et* *al*., 1995: 255-259; Moreira *et al*., 1996: 253-256; Assis Jr. *et al*., 1998: 247; Kuwahara *et al*., 2000: 8111; Sánchez *et al*., 2001: 213, 214; Zanuncio *et al*., 2002: 1228; Evangelista *et al*., 2003: 682; Zanuncio *et al*., 2004: 359; Oliveira *et al*., 2005: 295; Zanuncio *et al*., 2005: 37; Campos *et al*., 2009: 168; Bunde *et al*., 2010: 85, 86; Picanço *et al*., 2010: 69; Dalvi *et al*., 2011: 1, 2; Buenos *et al*., 2012: 511; Pires *et al*., 2015: 1531; Grazia *et al*., 2015: 688; Dellapé *et al*., 2018: 115, 119; Melo *et al*., 2017: 496; Brugnera & Grazia, 2018: 121, 126; Brugnera *et al*., 2019: 17.

Rhaphigaster albiseptus Germar, ?; Herrich-Schäffer, 1845: 7; Herrich-Schäffer, 1851: Figure 1000; Thomas, 1992: 122.

Podisus albiseptus Herrich-Schäffer, 1851: 339; Herrich-Schäffer, 1853: 168; Stål, 1867: 497; Stål, 1870: 56; Kirkaldy, 1909: 16; Thomas, 1992: 122.

Tynacantha marginata var. *cyanescens* Horváth, 1911: 434; Buckup, 1960: 10, 11; Thomas, 1992: 122.

Tynacantha sanguinolenta Horváth, 1911: 434; Buckup, 1960: 10, 11; Thomas, 1992: 122, 123.

Comments on *Rhaphigaster albiseptus*: The oldest publication where the name appears (that we are aware of) is Herrich-Schäffer (1845), page 7. In this publication, Herrich-Schäffer attributed the name to Germar, but without mention of the year of description. Stål (1867, 1870), Kirkaldy (1909) and Thomas (1992) have all attributed the authorship of *Rhaphigaster albiseptus* to Herrich-Schäffer. Although Herrich-Schäffer did not provide a formal description of this species until 1851, his use of the name in a short key to species in 1845 is enough to validate the name. He also (1851) transferred *Rhaphigaster albiseptus* to the genus *Podisus*, however he still used *Rhaphigaster albiseptus* in the figure legend (Fig. 1000), probably by mistake. Later, Stål (1867: page 497) considered P. albiseptus to be a synonym of *Tynacantha marginata*. Although Herrich-Schäffer's (1845) first valid use of the name *Rhaphigaster albiseptus* is prior to *Tynacantha marginata* (1851), we here consider R. albiseptus to be the senior synonym of *T. marginata*, but based on the confusion surrounding the original description, and because Herrich-Schäffer's name has not been used since Kirkardy, (1909), for the sake of maintaining stability, we believe that *Tynacantha marginata* should continue to be used as the name for this species.

Material examined. Type material: Lectotype ♀ Venezuela, "*Tynacantha marginata*", a, NHMUK 010592371 (BMNH). Additional material: VENEZUELA: 6 ♀ 3 ♂, Aragua, El Limón, 450m. 14, 16, 19.III.1951. F. Fernandez & C. J. Rosales leg. (UFRG); 1 ♀, Aragua, El Limón, 20.XII.1950, C. Prado leg. (UFRG); 1 ♀, Aragua, Henri Pittier National Park, 1100 m, 18.IV.1953, Já Gonz. leg. (UFRG); 1 ♀, Aragua, El Limón, Campo Ceniap, 12.8.1976, Freddy Godoy leg. (UFRG); 2 ♀ 1 ♂, Portuguesa, Acarigua, 20.II.1962, J.J Castilho, leg. (UFRG); 1 ♀, Caracas, D.F., 6.VI.1953, F. Fernandes leg. (UFRG); 1 ♂, Monagas, Jusepín, 50m, 15.IX.1965 (UFRG); Yaracuy, 1 ♂, San Javier, 23.II.1995 (UFRG); 1 ♀, Acaringua (Pimpinela y Sta. Ana), 20-II-62, J.J Castilho, leg. (UFRG); COLOMBIA: 1 ♀, Cundinamarca, San Antonio Del Tequendama, 6.I.1972, N 4°37'04'' W 74°21'15'', 1503 m, J. E. Gutierrez leg. (UNAB); 1 ♀, Antioquia, Santa Barbará, Vda. Damasco, Cerro Amarillo, Fca. La Linda, N 5°47' W 75°34', 1189 m, 6.I.2012, Serna F. leg. (UNAB); BRAZIL: 1 ♀, Pará, Marudá, Ilha Algodoal, 12.VII.1981, Edmar Lima leg. (UFRG); 1 ♀, Pará, Belém, Mocambo, 02.I.1978 (UFRG); 1 ♀, Pará, Belém, Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC) (UFRG); 1 ♀, Pará, Tucuruí, Rio Tocantins, 19.VII.1984, Jacundá leg. (MPEG); 1 ♂, Maranhão, São Luís, 09.IV.1974 (UFRG); 1 ♀, Amazonas, Km 4.5, Am 010, 25.IV.1982, E.F. Ribeiro leg. (INPA); 1 ♀, Bahia, Maracás, 18.VIII.1964, C. Elias leg. (MZSP); 1 ♀, Mato Grosso, Utiariti, Rio Papagaio, 325 m, VII-VIII.1961, K. Lenko leg. (MZSP); 1 ♂, Distrito Federal, Brasília (NMPC); 1 ♀ 1 ♂, Goiás, Morada Nova, 8.VIII.1994, J. C. Zanuncio leg. (UFVB); 1 ♂, Goiás, Corumbá, Fazenda Monjolinho, 8.VI.1942, F. Lane leg. (MZSP); 1 ♀, Espírito Santo, Santa Teresa, 18-23.XII.1967, C. Elias leg. (MZSP); 2 ♂, Minas Gerais, Serra Caraça, 1880 m, XI.1961, Kloss, Lenko, Martins & Silva leg. (MZSP); 1 ♀, Minas Gerais, Sete Lagoas, 26.IV.1984, H. R. Pimenta leg. (BHMH); 1 ♀ 1 ♂, Minas Gerais, Belo Horizonte, Campus UFMG, XI.1997 (BHMH); 2 ♂, Minas Gerais, Uberlândia, 07.III.1997, C. M. Paro leg. (UFRG); 3 ♀, Rio de Janeiro, Rio de Janeiro, 10.II.1943, J. Moraes leg. (MNRJ); 1 ♀, Rio de Janeiro, Itaguaí, km 47, 15.I.1971 M. Silva leg. (UFRG); 1 ♀ 1 ♂, Mato Grosso, near Trivelato, Rio Aripuanã, 300 m, 17/22.III.1977, D. Engleman leg. (UFRG); 1 ♀, São Paulo, Jaguariuna, 07.VII.1981, F. R. Reis leg. (UFRG); 1 ♀ 1 ♂, São Paulo, Indiana, Dirings leg. (MZSP); 1 ♀, São Paulo, Serra da Cantareira (MNRJ); 2 ♀, São Paulo, Paulínia, Lixão, 12.IV.1982, C. Paiva leg. (UFRG); 1 ♀, São Paulo, Campinas, 20.X.1981, B. Geraldo leg. (UFRG); 1 ♀ 1 ♂, São Paulo, Piracicaba, Estalo, X.1983 (UFRG); 1 ♀, São Paulo, Campinas, UNICAMP, VIII.1995, P. N. Patel leg. (UFRG); 2 ♂, São Paulo, Campinas, 28.IV.1982 (UFRG); 1 ♀, São Paulo, Indaiatuba, 04.IX.1981, M. L. E. Kato leg. (UFRG); 1 ♀, Paraná, Guarapuava, 25.X.1985 (MZSP); 1 ♀, Paraná, Curitiba, 4.VII.1973, H. A. Gastal (MCNZ); 1 ♀, Paraná, Cascavel,15.XI.1887, A. R. Panizzi leg. (MCNZ); 1 ♀, Paraná, Fazenda Rio Grande, V.2003, K. Costa leg. (UFRG); 1 ♂, Santa Catarina, Chapecó, 04.IV.1983 (UFRG); 1 ♂, Santa Catarina, Criciúma, Unesc, 20.X.2008, F. M. Bianchi & J. Vicente (UFRG); 1 ♂, Santa Catarina, Nova Teutônia, 10.II.1939, Fritz Plaumann leg. (DARC); 1 ♀, Santa Catarina, Nova Teutônia, 12.XII.1952 (DARC); 2 ♀, Santa Catarina, Nova Teutônia, 300m-500m, II.1981, Fritz Plaumann leg. (MZSP); 2 ♂, Santa Catarina, Nova Teutônia, 4.V.1950 (EMG); 1 ♀, Santa Catarina, Içara, 11.IV.2007, F. S. Martins leg. (UFRG); 2 ♀ 1 ♂, Santa Catarina, Maracajá, Parque Ecológico, 13.XII.2005, T. Bertolin leg.

(UFRG); 9 ♀ 6 ♂, Santa Catarina, Jaguaruna, 24.X.2011, C. Perin leg. (UFRG); 2 ♂, Santa Catarina, Araranguá, Morro dos Conventos, 20.VII.2006, T. Bertolin (UFRG); 3 ♀, Santa Catarina, Nova Veneza, 05.III.2005, P. Daminelli (UFRG); 1 ♀, Rio Grande do Sul, Santo Augusto, 10.IX.2005, R. Moraes leg. (MCNZ); 12 ♀ 6 ♂, Rio Grande do Sul, São Domingos do Sul, Santa Gema, 13.V.2017, R. Brugnera leg. (UFRG); 2 ♀, Rio Grande do Sul, Montenegro, 01.XII.1977, C. H. Buckup leg. (MCNZ); 1 ♂, Rio Grande do Sul, Porto Alegre, XII.1958, Dr. Hüdepohl leg. (EMG); 10 ♀ 6 ♂, Rio Grande do Sul, Porto Alegre, Morro Santana, 21.I.2017, R. Brugnera, leg. (UFRG); 8 ♀ 4 ♂, Rio Grande do Sul, Porto Alegre, UFRGS Campus do Vale, VI.2017, R. Brugnera leg. (UFRG); 1 ♂, Rio Grande do Sul, Porto Alegre, 14.VII.1949 (MCNZ); 1 ♂, Rio Grande do Sul, Triunfo, 14.V.1981, K. Zano leg. (MCNZ); 1 ♀, Rio Grande do Sul, Santa Maria, 07.V.1977, I. C. Canuto leg. (MCNZ); 1 ♀, Rio Grande do Sul, Santa Maria, 02.IV.1984, N. M. Dalmolin leg. (UFRG); 1 ♂, Rio Grande do Sul, Palmares do Sul, 07.VI.2003 (MCNZ); 1 ♀, Rio Grande do Sul, Bagé, 18.VI.1977, H. C. Vaz leg. (MCNZ); 2 ♀ 1 ♂, Rio Grande do Sul, Barra do Quaraí, marco geográfico, 16.V.2003, Bunde & Schwertner leg. (UFRG); 1 ♀, Rio Grande do Sul, Iraí, 19.X.1975, A. Lise leg. (MCNZ); PERU: Amazonas Dept., Cocachimba, vic. Gocta Lodge, S 06°03'22.5'' W 077°53'42.6'', 1815 m, 21-24.X.2012, J. E. Eger (JEE); BOLIVIA: 1 ♀ 1 ♂, Santa Cruz, El Refugio Los Volcanes, 3363 m, 18-24.X.2014, Morris & Wappes leg. (JEE); 1 ♀, Santa Cruz, Potrerillo del Guenda, 400m, 6-8.XII.2011, Morris & Wappes leg. (JEE); 1 ♀, Santa Cruz, Dpt. Refugio Los Vulcones, S 18°06’ W 63°36’, 3400-4200, 16/20.IX.2012, Wappes, Skeiley, Bonaso, Hamel leg. light trap (DBTC); PARAGUAY: 1 ♀ 1 ♂, PARAGUAY: Alto Parana Dept., 21-23.X.1989, G. Arriagada leg. (JEE); 1 ♀, Caazapa Dept., Parque Nac. Caaguazu, 1-8.XII.1990, G. Arriagada leg. (JEE); 1 ♀, Itapus Dept., Encarnacion, 2-28.II.1991, G. Arriagada leg. (JEE); URUGUAY: Artigas, Tres Cruces, 4.VII. 1973, H. A. Gastal leg. (MCNZ); ARGENTINA: Tucuman, Reserva Horco Molle, IX.1997 P. Rebagliati leg. (UFRG).

Diagnosis. Dorsal coloration usually bright green, sometimes light brown; scutellum without a calloused pale spot; lateral margin of connexival segments concolorous with abdominal sternites; usually with three rows of black spots, two located mediolaterally and one in the lateral margin on each segment of ventral abdomen, sometimes the internal row in zigzag; punctures concolorous, deep and close to each other (Figs 1–2, 7, 9); posterior margin of gonocoxites VIII concave (Figs 46, 47); capsula seminalis slightly longer than pars intermedialis; ductus receptaculi distalis as long as pars intermedialis (Fig. 48); inner branch of parameres longer and thinner than outer branch (Fig. 22).

Measurements. Total length, ♀ 11.23 ± 0.95 (7.36–12.64) ♂ 9.36 ± 0.40 (8.42–9.98); width of abdomen across segment III, ♀ 4.16 ± 0.26 (3.76–5.15) ♂ 3.46 ± 0.17 (3.06–3.66); head: length, ♀ 1.96 ± 0.14 (1.71–2.18) ♂ 1.70 ± 0.12 (1.4–2,0); width, ♀ 2.18 ± 0.13 (2,03–2.96) ♂ 2.00 ± 0.11 (1,72–2.18); pronotum: length, ♀ 2.16 ± 0.24 (1.36–2.96) ♂ 1.76 ± 0.15 (1.46–2.06); width, ♀ 4.16 ± 0.30 (3.56–5.77) ♂ 3.46 ± 0.22 (2.16–3.76); scutellum: length, ♀ 2.76 ± 0.17 (2.56–3.28) ♂ 2.26 ± 0.13 (1.96–2.56); width, ♀ 2.66 ± 0.14 (2.26–3.12) ♂ 2.16 ± 0.13 (1.86–3.06); length of antennal segments: I, ♀ 0.27 ± 0.08 (0.20–0.50) ♂ 0.25 ± 0.05 (0.25–0.55); II, ♀ 2.85 ± 0.56 (1.10–3.55) ♂ 2.55 ± 0.29 (1.15–2.95); III, ♀ 2.35 ± 0.53 (1.10–3.15) ♂ 2.25 ± 0.28 (1.05–3.05); IV, ♀ 2.55 ± 0.29 (2.07–3.05) ♂ 2.45 ± 0.17 (2.05–2.75); V, ♀ 1.33 ± 0.17 (1.14–1.85) ♂ 1.23 ± 0.10 (1.00–1.35); length of labial segments: I, ♀ 1.16 ± 0.10 (1.06–1.56) ♂ 0.96 ± 0.13 (0.56–1.16); II, ♀ 1.26 ± 0.19 (0.96–1.96) ♂ 1.11 ± 0.08 (0.95–1.26); III, ♀ 0.76 ± 0.08 (0.55–0.96) ♂ 0.66 ± 0.03 (0.55–1.76); VI, ♀ 0.66 ± 0.07 (0.25–0.83) ♂ 0.56 ± 0.05 (0.35–0.66).

Distribution. Venezuela (Monagas, Aragua, Yaracuy, Distrito Capital, Portuguesa, Táchira), Colombia (Cundinamarca, Antioquia), Ecuador, Brazil (Pará, Maranhão, Amazonas, Bahia, Mato Grosso, Distrito Federal, Goiás, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Peru, Bolivia, Paraguay, Argentina (Corrientes, Formosa, Jujuy, Misiones, Salta (Dellapé et al. 2003), Tucumán), Uruguay (Fig. 54).

Tynacantha splendens **Distant, 1889**

(Figures 4–5, 10–12, 24–28, 37–39, 56)

Tynacantha splendens Distant, 1889: 321; Schouteden, 1907: 59; Kirkaldy, 1909: 16; Thomas, 1992: 123; Cumbra *et al*., 2018: 5.

Material examined. Type material: Lectotype ♂, PANAMA, Bugaba, 800-1500 ft. Champion, B.C.A., Hem. I. Tynacantha splendens Dist.", NHMUK 010592342. (BMNH); Additional material: 3 ♂ COSTA RICA, Turrialba, Collection Schield-Burgdorf (USNM).

Diagnosis. Dorsal coloration dark with bright green or blue reflections (Figs 4, 10, 12); abdominal sternites with two rows of black spots, one in the lateral margin and one mediolateral (Figs 5, 11); apex of scutellum with a pale calloused spot, occupying half of the postfrenal lobe; punctures concolorous, shallow and spaced; membrane of hemelytra entirely translucent; intersegmental areas of connexivum concolorous with dorsal corium; branches of parameres as long as wide (Fig. 27).

Measurements. Total length, ♂ 9.60 ± 0.07 (9.44–9.60); width of abdomen across segment III, ♂ 4.68 ± 0.08 (4.56–4.80); head: length, ♂ 1.84 ± 0.08 (1.76–2.00); width, ♂ 1.92 ± 0.08 (1.84–2.08); pronotum: length, ♂ 2.20 ± 0.01 (2.20–2.24); width, ♂ 4.80 ± 0.21 (4.80–5.28); scutellum: length, ♂ 3.40 ± 0.09 (3.36–3.60); width, ♂ 3.04 ± 0.16 (2.88–3.32); length of antennal segments: I, ♂ 0.36 ± 0.01 (0.32–0.36); II, ♂ 1.28 ± 0.01 (1.24–1.28); III, ♂ 1.06 ± 0.02 (1.04–1.08); IV, ♂ 1.20; V, ♂ 1.24; length of labial segments: I, ♂ 1.20 ± 0.01 (1.16–1.20); II, ♂ 1.48 ± 0.06 (1.44–1.60); III, ♂ 1.00 ± 0.01 (1.00–1.04); VI, ♂ 0.76 ± 0.01 (0.76–0.80).

Distribution. Costa Rica and Panama (Fig. 56).

Remarks. Female unknown.

Tynacantha cuprea **Brugnera & Grazia sp. nov.**

(Figures 13–15, 29–33, 40–42, 49–51, 55)

Holotype ♂, BRAZIL, Pará, Belém, UFPA, 15.XI.2013 (MZUSP). Paratypes: 1 ♂ 1 ♀, BRAZIL, Pará, Belém, CEPLAC (UFRG). 1 ♀, BRAZIL, Pará, Belém, CEPLAC (MZUSP).

Diagnosis. Dorsal coloration light brown, scutellum with a calloused, crescent-like pale spot; punctures deep and close to each other; intersegmental areas of connexivum light brown (Figs 13–15); inner branch of parameres slightly longer than outer branch (Fig. 32); sutural margins of gonocoxites VIII juxtaposed; posterior margins of gonocoxites VIII almost rectilinear (Figs 49–50); capsula seminalis distinctly longer than pars intermedialis (Fig. 51).

Measurements. Total length, ♀ 11.96 ± 0.12 (11.84–12.08) ♂ 10.36 ± 0.28 (10.08–10.64); width of abdomen across segment III, ♀ missing ♂ 4.98 ± 0.02 (4.96–5.00); head: length, ♀ 2.14 ± 0.02 (2.12–2.16) ♂ 2.04 ± 0.04 (2.00–2.08); width, 2.14 ± 0.02 (2.12–2.16) ♂ 2.04 ± 0.04 (2.00–2.08); pronotum: length, ♀ 2.66 ± 0.14 (2.52–2.80) ♂ 2.28 ± 0.12 (2.16–2.40); width, ♀ 6.04 ± 0.20 (5.84–6.24) ♂ 5.32 ± 0.12 (5.20–5.44); scutellum: length, ♀ 4.28 ± 0.12 (4.16–4.40) ♂ 3.50 ± 0.10 (3.40–3.60); width, ♀ 3.92 ± 0.12 (3.80–4.04) ♂ 3.12 ± 0.08 (3.04–3.20); length of antennal segments: I, ♀ 0.34 ± 0.02 (0.32–0.36) ♂ 0.34 ± 0.02 (0.32–0.36); II, ♀ 1.54 ± 0.10 (1.44–1.64) ♂ 1.52 ± 0.04 (1.48–1.56); III, ♀ 1.38 ± 0.10 (1.28–1.48) ♂ 1.30 ± 0.02 (1.28–1.32); IV, ♀ missing ♂ 1.40; V, ♀ missing ♂ 1.44; length of labial segments: I, ♀ 1.46 ± 0.06 (1.40–1.52) ♂ 1.34 ± 0.06 (1.28–1.40); II, ♀ 1.92 ± 0.08 (1.84–2.00) ♂ 1.80; III, ♀ 1.00 ± 0.00 (1.00–1.00) ♂ 0.98 ± 0.02 (0.96–1.00); VI, ♀ 0.80 ♂ 0.76 ± 0.04 (0.72–0.80).

Etymology. From *cupreus* (Latin), in reference to the coppery color of dorsal surface.

Distribution. BRAZIL (Pará) (Fig. 55).

Tynacantha umeridenigrata **Brugnera & Grazia sp. nov.**
(Figures 16–18, 52–53, 55)

Holotype ♀, BRAZIL, Rondônia, Ouro Preto, V. 1980, A. C. Mendes leg., (MZUSP).

Diagnosis. Dorsal coloration brown, apex of scutellum with a calloused, crescent-like pale spot, humeral angles black and punctured; punctures black, deep and close to each other; intersegmental areas of connexivum black (Figs 16–18); posterior margins of gonocoxites VIII sinuous (Figs 52–53).

Measurements. Total length, ♀ 11.92; width of abdomen across segment III, ♀ 5.80; head: length, ♀ 2.00; width, ♀ 2.00; pronotum: length, ♀ 2.40; width, ♀ 5.60; scutellum: length, ♀ 3.80; width, ♀ 3.32; length of antennal segments: I, ♀ 0.28; II, ♀ 1.44; III, ♀ 1.28; IV, ♀ missing; V, ♀ missing; length of labial segments: I, ♀ 1.28; II, ♀ 1.60; III, ♀ 1.04; VI, ♀ 0.92.

Etymology. From *umeri* (Latin) and *denigratum* (Latin), in reference to the darkened color of humeral angles.

Distribution. Brazil (Rondônia) (Fig. 55).

Remarks. Male unknown.

Discussion

According to Thomas (1992), and supported by our results, *Tynacantha* species are mainly diagnosed by the anterolateral margins of pronotum rectilinear, calloused and unpunctured (Thomas, 1992, this work). These features occur in other Neotropical genera of Asopinae like *Tyrannocoris* Thomas, 1992 (anterolateral margins of pronotum rectilinear), and some *Podisus* Herrich-Schäffer, 1851 species (anterolateral margins of pronotum calloused), but never in combination. The new species are described in *Tynacantha* upon the presence of these pronotal characteristics and also the genital morphology.

Tynacantha marginata is the most easily recognized species of the genus, by the absence of pale calloused spot in the scutellum and the lateral margin of connexivum concolorous with ventral abdomen. *Tynacantha splendens* and the two new species here described share the presence of pale calloused spot in the scutellum, but can be distinguished by male and female genitalia and their distribution. Thomas (1992) pointed out that there would be no significant differences between the male genitalia of *T. splendens* and *T. marginata*. Indeed they are very similar, but we found some differences in the morphology of pygophore and parameres (Fig. 3) that aid species recognition. Additionally, the female genitalia is likewise useful for identification, mainly the shape of gonocoxites XII (Fig.5).

Several species of Asopinae exhibit a bright coloration and sometimes aposematic colors like orange and red (Schaefer 1996). Dorsally, *T. marginata* and *T. splendens* can be bright green or blue. All the four specimens of *T. splendes* analyzed exhibit an iridescent color. In *T. marginata*, the specimens can be brown or iridescent green, the latter described as the variety *cyanescens* (Horváth, 1911). Brown specimens are usually very old preserved, so the bright coloration may disappear or be influenced by preservation conditions.

The ventral surface of *T. marginata* is also variable in color. We analyzed several males and females and observed that about one-third of the females are orange ventrally, while the males are always pale yellow. This orange morph was described by Horváth (1911) as a different species (*T. sanguinolenta* Horváth, 1911) and synonymized under *T. marginata* by Buckup (1960). We reared *T. marginata* in laboratory (Brugnera & Grazia 2018) and observed that both adult males and virgin adult females are always pale yellow, but females usually turn to orange after copulation and the intensity of the orange color increases with the age (R. Brugnera personal observation). The functions (if any) of this dimorphism are unknown and developing studies involving the behavior of *T. marginata* can clarify this issue.

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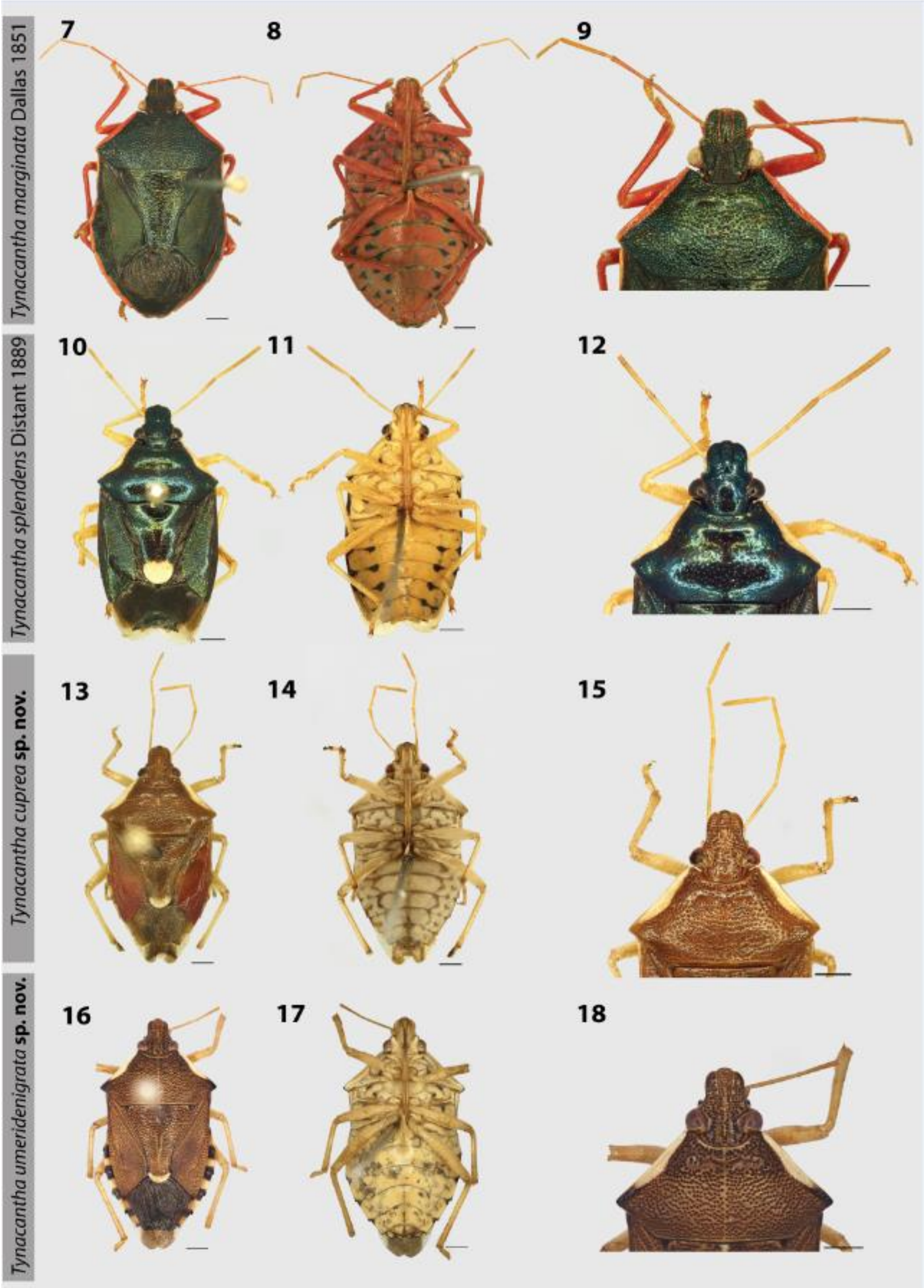
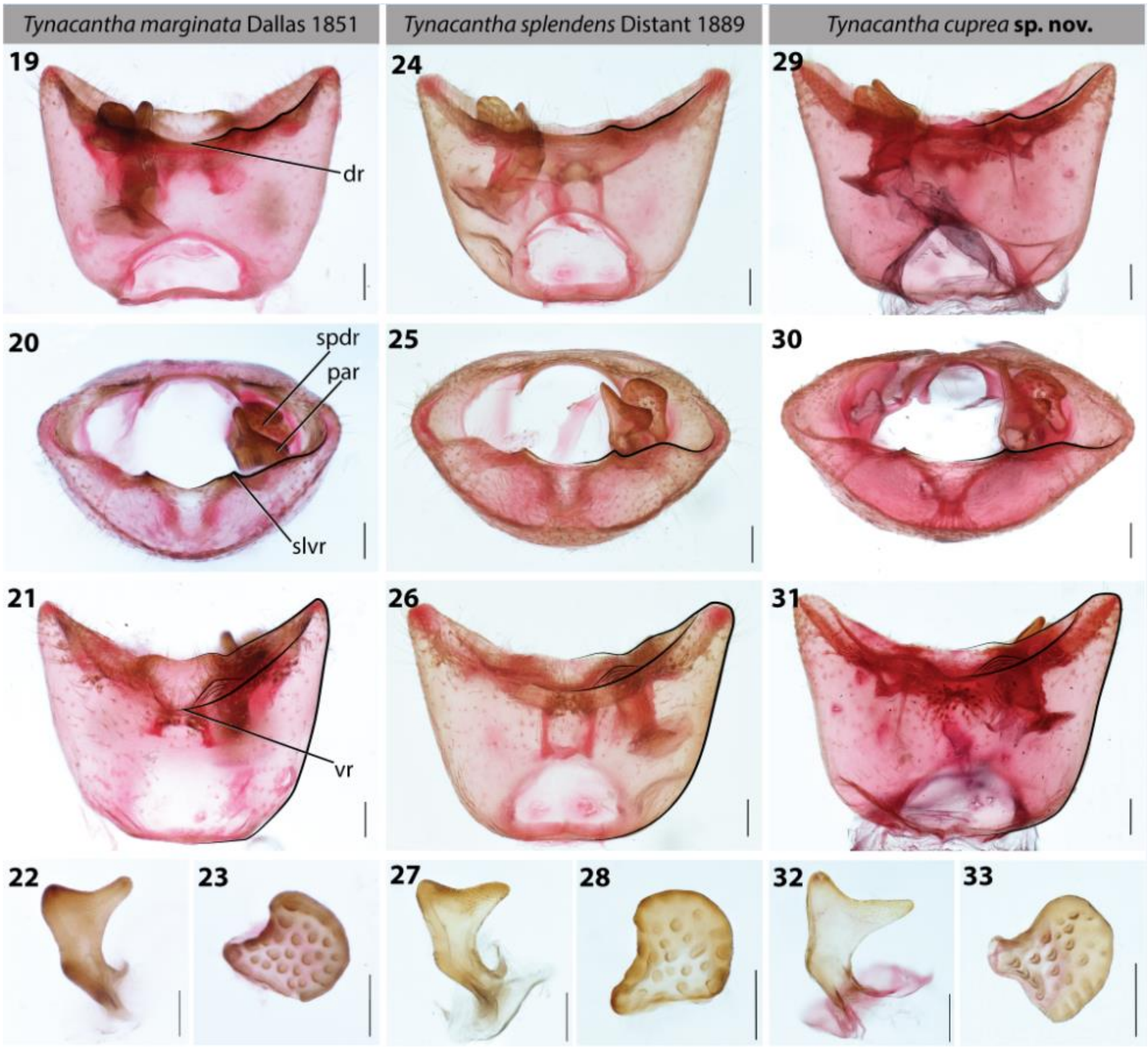
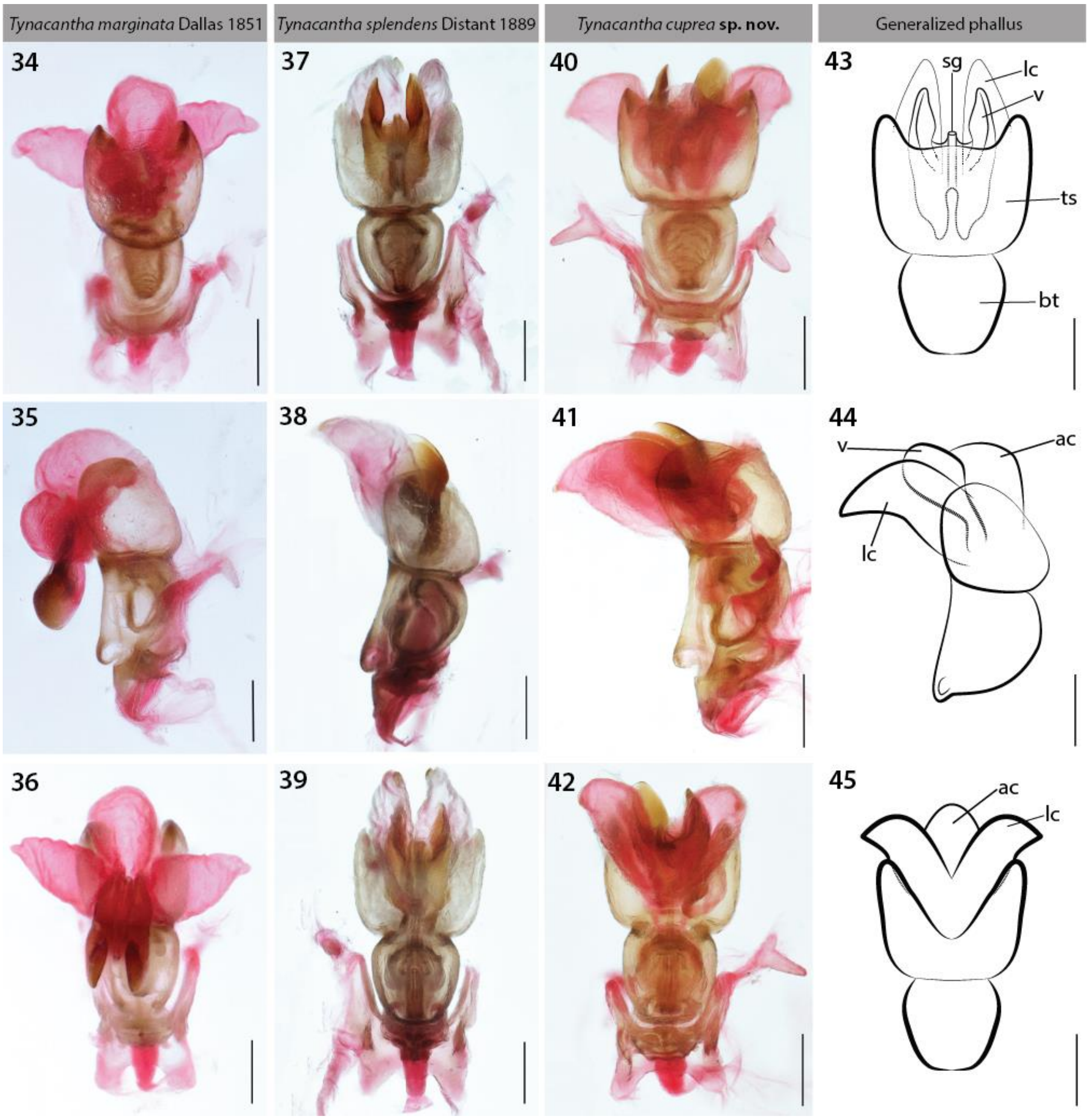
FIGURES 1–6. Lectotypes of *T. marginata* and *T. splendes* and their respective labels. 1–3, *Tynacantha marginata*. 4–6, *Tynacantha splendens*. (photos by T. Roell)



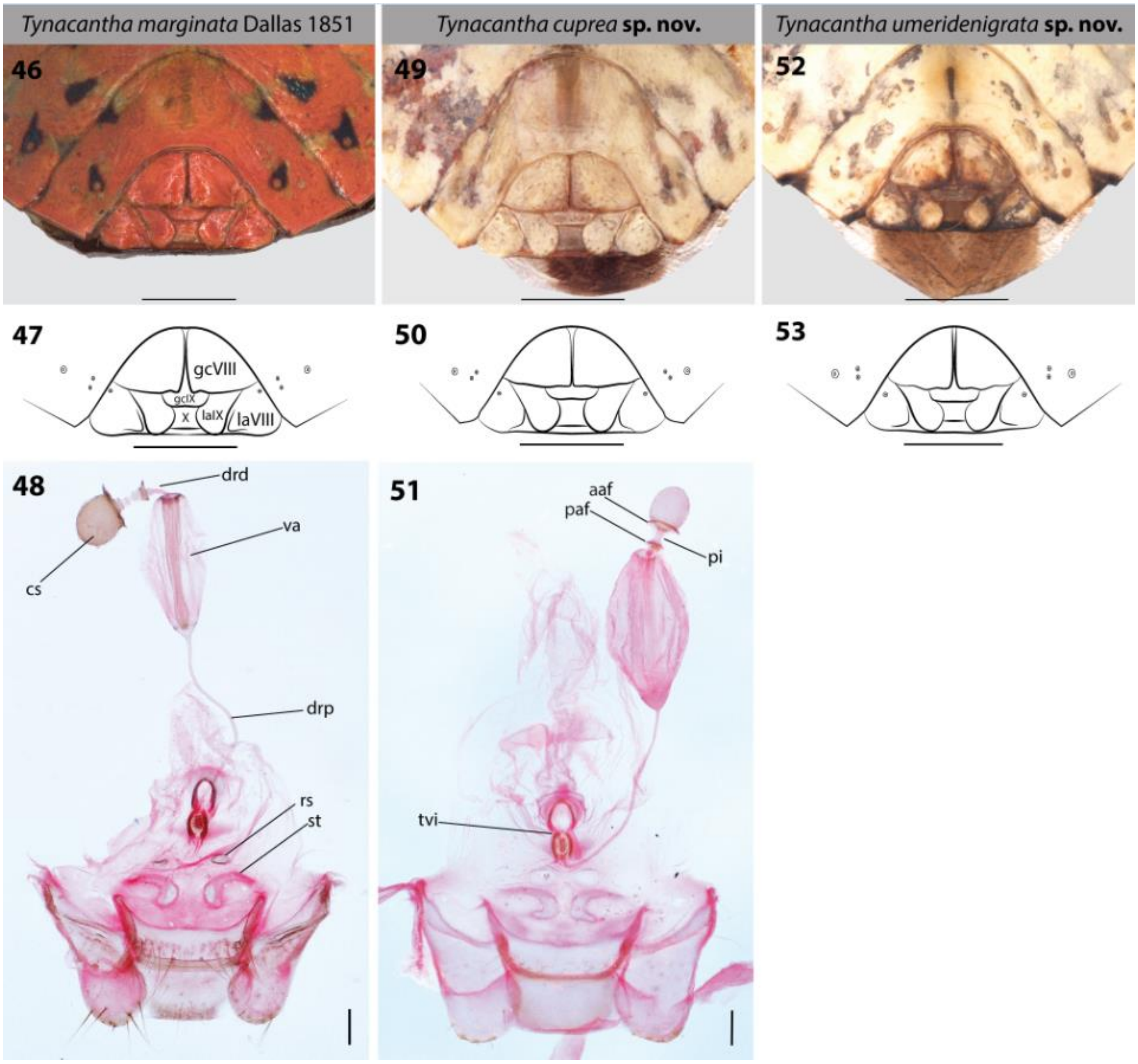
FIGURES 7–18. Habitus of species of *Tynacantha* in dorsal, ventral and head + pronotum views, respectively. 7–9, *Tynacantha marginata*; 10–12, *Tynacantha splendens*; 13–15, *Tynacantha cuprea* **sp. nov**.; 16–18, *Tynacantha umeridenigrata* **sp. nov**. Scale bars: 1 mm.



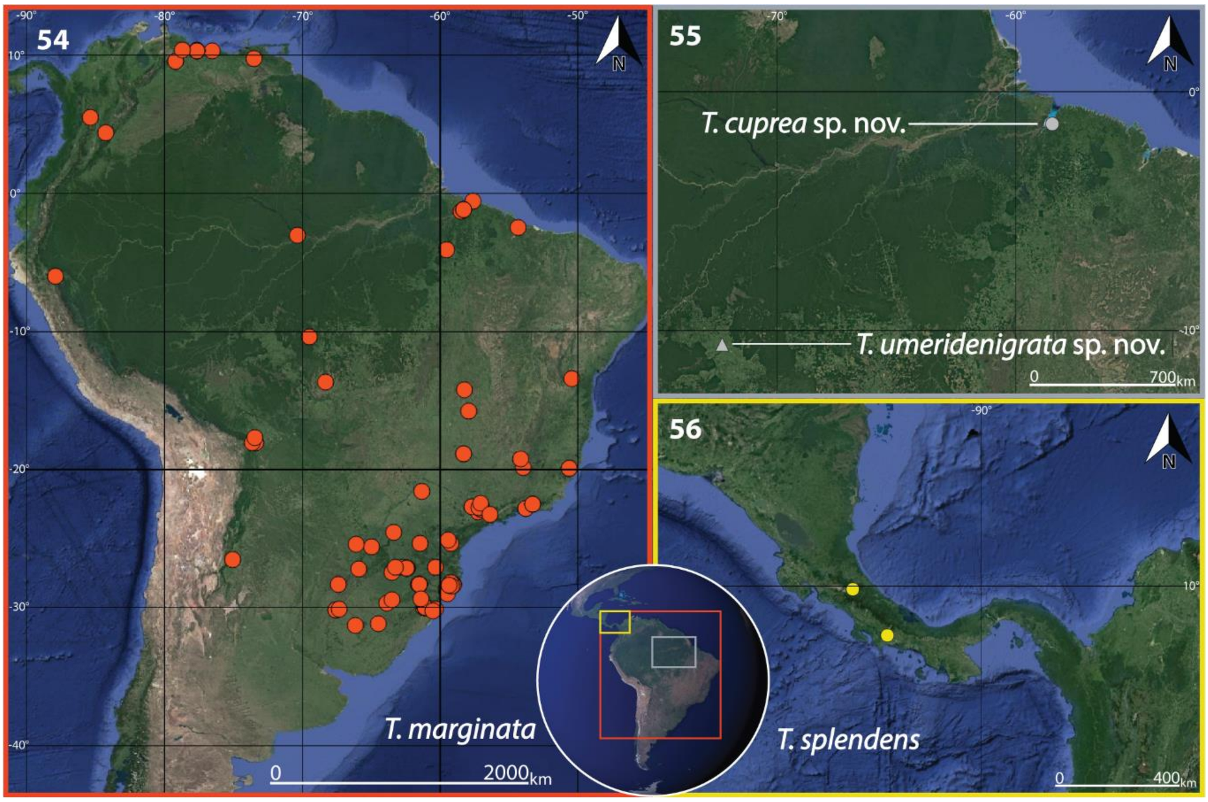
FIGURES 19–33. Pygophore of species of *Tynacantha*. Pygophore in dorsal (19, 24, 29), posterior (20, 25, 30), and ventral (21, 26, 31) views. Left paramere (22, 27, 32). Left superior process of dorsal rim (23, 28, 33). 19–23, *Tynacantha marginata*; 24–28, *Tynacantha splendens*. 29–33, *Tynacantha cuprea* **sp. nov.**. Abbreviations: dr = dorsal rim; par = paramere; slvr = superior layer of ventral rim; spdr = superior process of dorsal rim; vr = ventral rim. Scale bars: 19–21, 24–26, 29–31 = 1 mm; 22–23, 27–28, 32–33 = 0,1 mm



FIGURES 34–45. *Phallus* of species of *Tynacantha*. *Phallus* in dorsal (34, 37, 40, 43), lateral (35, 38, 41, 44), and ventral (36, 39, 42, 45) views. 34–36, *Tynacantha marginata*; 37–39, *Tynacantha splendens*; 40–42, *Tynacantha cuprea* **sp. nov.**; 43–45, generalized *phallus*. Abbreviations: ap = apical conjunctiva; bt = basal theca; lc = lobes of conjunctiva; sg = secondary gonophore; ts = thecal shield; v = vesica. Scale bars: 0,1 mm.



FIGURES 46–53. Female external and internal genitalia of *Tynacantha*. Genital plates (46–47, 49–50, 52–53). Internal genitalia (48, 51). 46–48, *Tynacantha marginata*; 49–51, *Tynacantha cuprea* **sp. nov.**; 53–53, *Tynacantha umeridenigrata* **sp. nov.**. Abbreviations: aaf = anterior annular flange; cs = capsula seminalis; drd = ductus receptaculi distalis; drp = ductus receptaculi proximalis; paf = posterior annular flange; pi = pars intermedialis; rs = ring sclerites; st = secondary thickening of gonapophyses IX; tvi = thickening of vaginal intima; va = vesicular area Scale bars: 46–47, 49–50, 52–53 = 1 mm; 48–51 = 0,1 mm.



FIGURES 54–56. Geographic distribution of the species of *Tynacantha*. 54, *Tynacantha marginata*; 55, *Tynacantha cuprea* **sp. nov.** and *Tynacantha umeridenigrata* **sp. nov.**; 56, *Tynacantha splendens*.

CAPÍTULO IV

Taxonomic modifications in *Tylospilus* Stål (Hemiptera: Pentatomidae: Asopinae): redescription of *T. nigrobinotatus* (Berg), description of a new species and an updated identification key for the genus

[Brugnera et al. (2020). Zootaxa, 4766 (1): 128–138, doi.org/10.11646/zootaxa.4766.1.6]

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Abstract

The systematics of the New World Asopinae genera is still not completely understood, thus hampering their study in many areas of biological science. *Tylospilus* Stål is one of the less known genera among New World predatory stink bugs, despite its common occurrence and potential as a biological control agent in crops. Here, we make a contribution to the knowledge of *Tylospilus*; the species *Tylospilus nigrobinotatus* (Berg, 1879) is redescribed, and based upon the examination of type specimens, *T. armatus* Thomas, 1992 is considered to be a junior synonym of the above species. Furthermore, a new species is herein described, and an updated identification key for the species of Tylospilus is provided.

Key words: Heteroptera, predatory stink bugs, new synonymy, taxonomy

Introduction

Tylospilus Stål, 1870, is one of 64 genera included in the pentatomid subfamily Asopinae (Thomas 1992, 1994; Roca-Cusachs *et al*. 2019). The genus currently comprises eight species, most of which distributed in the Neotropical region, the only exception being *T. acutissimus* Stål that also occurs in the southern United States (Grazia *et al*. 2015). Species of *Tylospilus* are relatively small in size (~ 8–10 mm long); they can usually be recognized by the abdominal tubercle surpassing the metacoxae, the peritreme of the external scent efferent system relatively short, reaching less than half the width of the metapleuron (Thomas 1992), and by the presence of pale callosities on the body, especially on the head, pronotum, and scutellum.

Known as predatory stink bugs, the asopines are comprised of about 300 species, which are recognized mainly by the subquadrate shape of the head in dorsal view; the crassate labium; the presence of a pair of processes on the dorsal rim of male pygophore, and by the phallus composed by basal theca and a thecal shield (Gapud 1991; Thomas 1992; Rider *et al*. 2018; Roell *et al*. 2019. The remarkable crassate labium is probably an adaptation for the predatory behavior of these bugs. This feature is observed in most genera of the subfamily, however, *Tylospilus* species present a thinner labium, and has been considered to possibly be secondarily phytophagous (Stoner *et al.* 1974; Rider *et al*. 2018). Hypothesized to have evolved from a phytophagous ancestor (Gapud 1991), many species of predatory stink bugs have conserved plant-feeding habits, believed to be mainly to obtain water and nutrients during periods of prey scarcity (De Clercq 2008; Grazia *et al*. 2015); however, it may not be related to the thickening of labium, which remains to be investigated.

Despite increased human interest in the use of predatory stink bugs as natural control agents in crops (De Clerqc 2000, 2008; Zanuncio *et al*. 2014; Roca-Cusachs *et al*. 2020), very few modern taxonomic revisions in this group have been undertaken recently (Brugnera *et al*. 2020). The systematic knowledge of most asopinae genera is still incipient, with the majority being known only from original descriptions, and from the taxonomic compilations of Schouteden (1907) and Thomas (1992, 1994). These studies, although advancing the knowledge concerning this subfamily, have still left unknown may problems associated with systematics of the Asopinae, thus highlighting the importance of continued studies with the taxonomic and phylogenetic issues associated with this group.

Tylospilus has been historically poorly studied. The latest taxonomic contribution to the genus was that by Thomas (1992), who described the new species, *T. armatus*, based on specimens from Argentina. Biological aspects of *T. acutissimus* were studied by Stoner *et al*. (1974), and the immature stages of *T. cloelia* Stål [as *T. nigrobinotatus* (Berg)] by Saini (1992). Except for *T. megaspilus* (Walker) which is known only from the holotype and appears to be quite rare, the other species seem to be quite common, and may be excellent model organisms for further studies for their potential as biological control agents, especially regarding their preference for small-sized prey. This may be especially true for *Tylospilus nigrobinotatus*, which is widely distributed in austral South America (Dellapé *et al*. 2003).

The current identification of this species is difficult due to past deficient diagnoses, and also due to the sharing of similar characteristics with other species of the genus, thus contributing to unclear species delimitations.

Aided by the examination of the two syntypes of *T. nigrobinotatus*, one paratype of *T. armatus*, and a series of specimens deposited at The Natural History Museum of the United Kingdom (NHMUK), we redescribe *T. nigrobinotatus*, considering *T. armatus* Thomas as a junior synonym. The other seven species currently known in the genus are recognized, including a new species, *Tylospilus armatusimilis* sp. nov., which is described herein. Based on the new proposed changes within this genus, we provide an updated identification key for species of *Tylospilus*, including images of all species.

Material and methods

Images of type and non-type specimens of *Mormidea nigrobinotata* were taken in the Museo de La Plata, Argentina (MLP) (Figs 1–6) using a digital camera mounted on a Nikon SMZ1000 stereomicroscope, and stacked with Helicon Focus software. Type specimens in the Natural History Museum of United Kingdom (NHMUK) (Figs 11–16) were taken using a Canon EOS 5D SR camera mounted with a Canon Macro Lens EF 100mm 1:2.8 L IS USM, controlled with Helicon Remote software. Images of a paratype of *Tylospilus armatus* (Figs 7–10) were received from Donald B. Thomas. Other specimens were photographed by Gervásio S. Carvalho, Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Brazil, with the digital camera Leica DMC2900 (Leica, Wetzlar, Germany) coupled to a stereomicroscope.

Genitalia were prepared with 10% heated aqueous KOH (~80 °C) for five minutes, and stained with Congo Red solution (5, 3 mg/10 ml H2O) for 30 seconds (Brugnera et al. 2020). Drawings were made with the aid of a camera lucida coupled to a stereomicroscope, and then digitally scanned and edited with Adobe Illustrator (Adobe Systems, Inc., San Jose, California, USA). Specimens were observed and measured under light stereomicroscope, and the measurements [mean ± standard deviation (minimum-maximum)] were given in millimeters. Terminology follows Baker (1931), Dupuis (1970), Schaefer (1977), and Gapon & Konstantinov (2006) for genitalic structures; and Kment & Vilímová (2010) for the external scent efferent system.

Regarding the similarities between *T. nigrobinotatus* and *T. armatussimilis* **sp. nov.**, only *T. nigrobinotatus* is fully redescribed. The main differences between the two species are presented in Table 1.

The following collections are depositories for the specimens studied here: **BHMH**, Museu de História Natural, Universidade Federal de Minas Gerais, Brazil; **DBT**, Donald B.

Thomas, personal collection, United States of America; **JEE**, Joseph E. Eger, personal collection, United States of America; **NHMUK**, The Natural History Museum, United Kingdom; **MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Argentina; **MNHNM**, Museo Nacional de Historia Natural, Montevideo, Uruguay; **MLP**, Museo de La Plata, Argentina; **MZUSP**, Museu de Zoologia, Universidade de São Paulo, Brazil; **UFRG**, Universidade Federal do Rio Grande do Sul, Departamento de Zoologia, Brazil.

Results

Taxonomy

Tylospilus nigrobinotatus **(Berg, 1879)**

Figures 1–19, 23, 25–27, 31–33, 37–41

Mormidea nigro-binotata Berg, 1879: 279.
Podisus (*Tylospilus*) *nigrobinotatus*: Berg 1884: 19.
Podisus nigro-binotatus: Lethierry & Severin 1893: 219.
Podisus Borellii [sic] Montandon, 1895: 5. syn. by Thomas, 1992: 117.
Apateticus (*Eupodisus*) *Borellii* [sic]: Schouteden 1907: 71.
Apateticus (*Tylospilus*) *nigrobinotatus*: Schouteden 1907: 73; Kirkaldy 1909: 22.
Apateticus (*Podisus*) *borellii*: Kirkaldy 1909: 18.
Tylospilus nigrobinotatus: Thomas 1992: 117; Coscarón & Grazia 1996: 24.
Tylospilus armatus Thomas, 1992: 121. **NEW SYNONYMY**

Types examined. *Mormidea nigro-binotata* Berg, 1879: Lectotype ♀ (here designated for taxonomic stability), labels: “Buenos Aires”, “Typus”, “1419”, “Museo La Plata” (MLP). (Figs 1–3)

Mormidea nigro-binotata Berg, 1879: Paralectotype ♀ (here designated for taxonomic stability), labels: “*Podisus nigrobinotatus* Berg”, “BuenAir. Günther”, “Typus”, “1419”, “Museo La Plata” (MLP). (Figs 4–6)

Tylospilus armatus Thomas, 1992: Paratype ♀, labels: “Pque. Nac. El Palmar Entre Rios Argent. Bordón leg. 12 I 1981”, “Paratype *Tylospilus armatus* Thomas” (DBTC). (Figs 7–10). Holotype (not examined) deposited in Universidad Nacional Autónoma de México—UNAM.

Non-types examined. ARGENTINA: Salta 1 ♀, 3–8Kms SW Campo Quijano, 17+18.III.1995, H. & A. How den leg. (DBTC); **Entre Ríos** 1 ♀, Paraná, I.1921, Gómez del

Río leg. (MACN); 1 ♀ Gualeguachú, 19.IV.1924, Excurs. Prof. M. B. Yurado (MACN); **Santa Fe** 2 ♀ 4 ♂, Rosario (MACN); 1 ♀ 1 ♂, Rosario, A. Stévenin leg. (MACN); 1 ♂ 19.I.1929, Bridarolli leg. (MACN); **Buenos Aires** 1 ♀ 3 ♂, J. Boso leg. (MLP); 1 ♂, Isla Martín García, IV.1938, M. J. Viana (MACN); 1 ♂, Capital, 1946, A. A. Pirán leg. (UFRG); 2 ♀ 1 ♂, Buenos Aires (NHMUK) (Figs 11–16).

Redescription. General body coloration reddish brown dorsally and pale brown ventrally. Body densely punctured with pale calloused and dark spots dorsally and ventrally (Figs 17–19, 23, 40–41). **Head:** (Figs 18, 23) wider than long; mandibular plates and clypeus subequal in length; width of head across eyes greater than anterior angle of pronotum. Ocelli situated posterior to compound eyes. Proximal half with 1+1 black, longitudinal stripes. Labial segments uniformly brown; apex of labium surpassing mesocoxae, but not reaching metacoxae; proportion of labial segments: I<II>III=IV. Antennomeres uniformly brown; proportion of antennomeres: I<II>III>IV>V. **Thorax:** (Figs 17, 23) Anterior angles of pronotum projected; anterolateral margins of pronotum crenulated, distinctly paler than disc on anterior two-thirds. Humeral angles strongly developed, produced laterad, upwardly-directed, acute, and darker on apices, each with a posterior tooth. Pronotum more than three times wider than long. Posterior angles of pronotum projected. Scutellum triangular, length of frenal subequal to postfrenal lobe; anterior angles with 1+1 pale calloused spots, sometimes reaching constriction of scutellum; foveae dark brown, as wide as ocelli; lateral margins of constriction of scutellum with 1+1 black macules. Each corium longer than scutellum, reaching anterior margins of connexivum VI; posterior margins of coria rectilinear; hemelytral membranes dark brown mesially, surpassing apex of abdomen; apex of radial veins with 1+1 impunctate black spots, equal to or larger than diameter of a compound eye. Ostiolar peritremes disc-like, elevated, dark at apices; median furrow of each surpassing half the length of peritreme; each metapleural evaporatorium surrounding associated peritreme, but not reaching lateral margin of pleuron; each mesopleural evaporatorium restricted to posterior margin of mesopleuron, reaching lateral mesopleural margin. Impunctate pale, elevated calloused spots at median portion of mesopleura and metapleura (right after peritreme). Legs brown, with apices of tibiae and tarsi dark brown. **Abdomen:** (Figs 18, 19) Pale brown ventrally, with reddish punctures. Intersegmental areas of connexivum dark brown, with posterior and anterior regions black, lateral outer margins of connexival segments pale; each (II–VII) anterior and posterior angles of ventrolateral segments of connexivum bearing a black spot; 1 + 1 lateral and interconnected black spots on III-VII segments; a mesial row of black spots on IV–VII segments. Spiracles light brown. Abdominal tubercle reaching posterior margins of mesocoxae. **Female genitalia:** (Figs 25–27) Laterotergites VIII subtriangular; laterotergites IX longer than wide, surpassing segment X, reaching posterior margin of sclerite VIII; posterior margins of laterotergites VIII and IX rounded; segment X subrectangular; gonocoxites IX subrectangular, posterior margin distinctly convex; gonocoxites VIII as wide as long, mesial margins parallel, juxtaposed, posterior margins sinuous; posteromesial region of gonocoxites VIII with 1+1 acute projections, distinctly visible in lateral view. Internal gonapophyses IX with 1+1 secondary sickle-like thickenings; thickening of vaginal intima with anterior region somewhat conical and posterior region horseshoe-like; ring sclerites absent; proximal part of *ductus receptaculi* slightly shorter than vesicular area; distal part of *ductus receptaculi* longer than *pars intermedialis*; *capsula seminalis* elliptical, slightly longer than *pars intermedialis*. **Male genitalia:** (Figs 31–33, 37–39) pygophore cup-like, as wide as long; anterior opening subtriangular, reaching dorsal rim; dorsal rim, concave with a median projection in dorsal view; ventral rim strongly concave mesially in ventral view; lateral margins of ventral rim with 1 + 1 concavities; parameres spatulated with apices acute, inner directed in posterior view; superior processes of dorsal rim subquadrate, with globose dorsal sculptures restricted to lateral margins. *Phallus* with thecal shield and basal theca subequal in length, thecal shield slightly wider than basal theca; anterior margin of thecal shield with a mesial concavity in dorsal view; 1+1 lobes of conjunctiva; vesica with 1 + 1 tabs inner directed; *ductus seminis distalis* not developed beyond vesica.

Comments. Berg (1879: 270–280) described *Mormidea nigro-binotata* from at least two specimens, indicating that he examined both sexes. We located two female specimens in MLP, one of which is much smaller (Figs 4–5). Because Berg gave a wide range of measurements, he may have assumed that the smaller specimen was a male, and as such believed that he had a male and a female in front of him (assuming that females are usually much larger than males). The male syntype was not located in the MLP. On the other hand, three specimens were located in NHMUK, one male and two female specimens collected in Buenos Aires. These specimens are of historical value, but we cannot assume that the male specimen found in the collection is the actual syntype male from Berg. Specimens found in MLP are of different sizes, but the labels are similar; therefore, we assume that these specimens are the syntypes from Berg, and we speculate that Berg errored regarding the gender assignment of his specimens. We herein designate the largest specimen (Figs. 1–3) as the lectotype, and the smaller specimen (Figs. 4–6) as the paralectotype.

Podisus (*Tylospilus*) *borellii* Montandon, 1895 was described from one female specimen, collected in Salta, Argentina (Montandon, 1895: 5); this species was later synonymized with P. nigrobinotatus by Thomas, 1992. We have not been able to examine the holotype of P. borellii (the institution of deposition is unknown). We, however, based on the detailed description provided by Montandon, accept the synonymy proposed by Thomas (1992).

Measurements: (n=5). Head length: 1.3 ± 0.13 (1.1–1.5), width: 1.43 ± 0.07 (1.3–1.5); pronotum length: 1.72 ± 0.26 (1.5–2.1), width: 5.38 ± 0.66 (4.5–6.2); scutellum length: 1.9 ± 0.26 (1.5–2.1), width: 2.11 ± 0.22 (1.8–2.4); antennomeres length: I 0.22 ± 0.05 (0.2–0.3), II 0.8 ± 0.0 (0.8–0.8), III 0.65 ± 0.5 (0.6–0.7), IV 0.6 ± 0.0 (0.6–0.6); V 0.5 ± 0.0 (0.5–0.5); labial segments length: I 0.67 ± 0.05 (0.6–0.7), II 0.77 ± 0.05 (0.7–0.8), III 0.6 ± 0.00 (0.6–0.6), IV 0.59 ± 0.08 (0.5–0.6); abdominal length: 4.93 ± 0.81 (4.0–5.5), width: 4.03 ± 0.64 (3.3–4.3); total length: 6.4 ± 0.85 (5.6–8.0).

Distribution: Argentina (Salta, Entre Ríos, Santa Fe, Buenos Aires). Thomas (1992) also cited Brazil and Uruguay, which were not confirmed in this study.

Tylospilus armatusimilis **Brugnera, Paim & Grazia**

Figures 20–22, 24, 28–30, 34–36

Holotype. URUGUAY: Colonia ♀, Ruta 21 km 184.5, Piedra de Los Indios, 30.XII.2005, beating Schinus, G. J. Wibmer leg. (MNHNM).

Paratypes. URUGUAY: Colonia 1♂, Same data as Holotype (MNHNM); 1 ♀, Ruta 21 km 184.5, Piedra de Los Indios, 25.XII.2002, G. J. Wibmer leg. (JEE); 1♀, Piedra de Los Indios, 23.XII.2002, G. J. Wibmer leg. (MZUSP); 3 ♀ 1♂, Ruta 21, km 194, Arroyo San Pedro, 9.II.1989, C. W. & L.O'Brien & G. Wibmer leg (UFRG); 2 ♀, Ruta 21, km 194, Arroyo San Pedro, 28.XII.1991, G. Wibmer leg. (JEE).

Diagnosis. Similar to *T. nigrobinotatus* in general aspects, *T. armatusimilis* can be recognized by the anterolateral margins of the pronotum concolorous with the pronotal disc; humeral angles shorter and slender, laterally directed (Figs 20–22, 24); black spots on the apices of radial veins distinctly smaller than in *T. nigrobinotatus* (Fig. 20), and lateral row of black spots on the urosternites restricted to the anterior margin of each urosternite (Fig. 22); females have a well-defined rounded projection on gonocoxites XIII (Figs 28, 29), secondary thickening of gonapophyses IX sickle-like (Fig. 30), anterior projection of thickening of vaginal intima v-shaped (Fig. 30) and *capsula seminalis* elliptical (Fig. 30); in males, the mesial portion of ventral rim slightly concave (Fig. 33), and superior process of dorsal rim of pygophore subrectangular (Fig. 35). A differential diagnosis between *T. nigrobinotatus* and *T. armatusimilis* **sp. nov.** is presented on table 1.

Measurements: (n=10). Head length: 1.2 ± 0.10 (1.1–1.5), width: 1.6 ± 0.07 (1.5–1.7); pronotum length: 1.7 ± 0.15 (1.4–1.9), width: 5.55 ± 0.43 (4.7–6.0); scutellum length: 2.7 ± 0.19 (2.3–2.9), width: 2.45 ± 0.18 (2.4–2.8); antennomeres length: I 0.22 ± 0.05 (0.2–0.3), II 0.82 ± 0.5 (0.8–0.9), III 0.65 ± 0.5 (0.6–0.7), IV 0.6 ± 0.0 (0.6–0.6); V 0.5 ± 0.0 (0.5–0.5); labial segments length: I 0.75 ± 0.05 (0.7–0.8), II 0.85 ± 0.04 (0.8–0.9), III 0.58 ± 0.03 (0.5–0.6), IV 0.59 ± 0.08 (0.5–0.6); abdominal length: 3.97 ± 1.07 (3.2–5.8), width: 3.8 ± 0.95 (3.1–5.3); total length: 7.5 ± 0.50 (7.0–8.4).

Etymology. From *armatus* (Latin) and *similis* (Latin) in reference to *T. armatus* described by Thomas (1992), here considered to be a junior synonym of *T. nigrobinotatus*.

Distribution: Uruguay (Colonia).

Key to the species of *Tylospilus* Stål, 1870 (modified from Thomas, 1992)

1. Longitudinal pale yellow stripe on clypeus and midline of pronotum present; humeral angles concolour with disc of pronotum. 2

- Longitudinal pale yellow stripe on clypeus and midline of pronotum absent (if present, never in both clypeus and pronotum); humeral angles discolour with disc of pronotum. 3

2. Humeral angles length distinctly greater than diameter of eye. *T. distans* Bergroth (Fig. 42)

- Humeral angles length subequal to the eye diameter. . . . . *T. peruvianus* (Horváth) (Fig. 43)

3. Humeral angles distinctly forwardly directed . . . . *T. acutissimus* Stål (Fig. 44)

- Humeral angles laterally directed.. 4

4. Clypeus contrastingly black or fumose; pro-, meso-, and metapleura lacking pale callosities. . . . . *T. chilensis* (Spinola) (Fig. 45)

- Clypeus concolour with mandibular plates; pro-, meso-, and/or metapleura with pale callosities 5

5. Anterior half of anterolateral margins of pronotum pale calloused, smooth. 6

- Anterolateral margins of pronotum not calloused, crenulated. 7

6. Scutellum with an entire black macula on the constriction portion; urosternites with pale calloused spots on all segments. . . . . *T. megaspilus* (Walker) (Fig. 47)

- Scutellum with 1+1 black bands on the constriction portion; urosternites pale yellow, without callosities. . . . . *T. cloelia* Stål (Fig. 46)

7. Humeral angles strongly developed with apices dorsally directed; black spots on apices of radial veins equal to eye diameter; 1+1 pale calloused spots posterior to ostiolar peritremes present; a mesial row of black spots on urosternites IV–VII. . . . . *T. nigrobinotatus* Berg (Figs 17–19)

- Humeral angles developed more laterally; black spots on apices of radial veins smaller than eye diameter; pale calloused spots posterior to ostiolar peritremes absent; VII urosternite with a mesial black spot . . . . *T. armatusimilis* Brugnera, Paim & Grazia sp. nov. (Figs 20–22)

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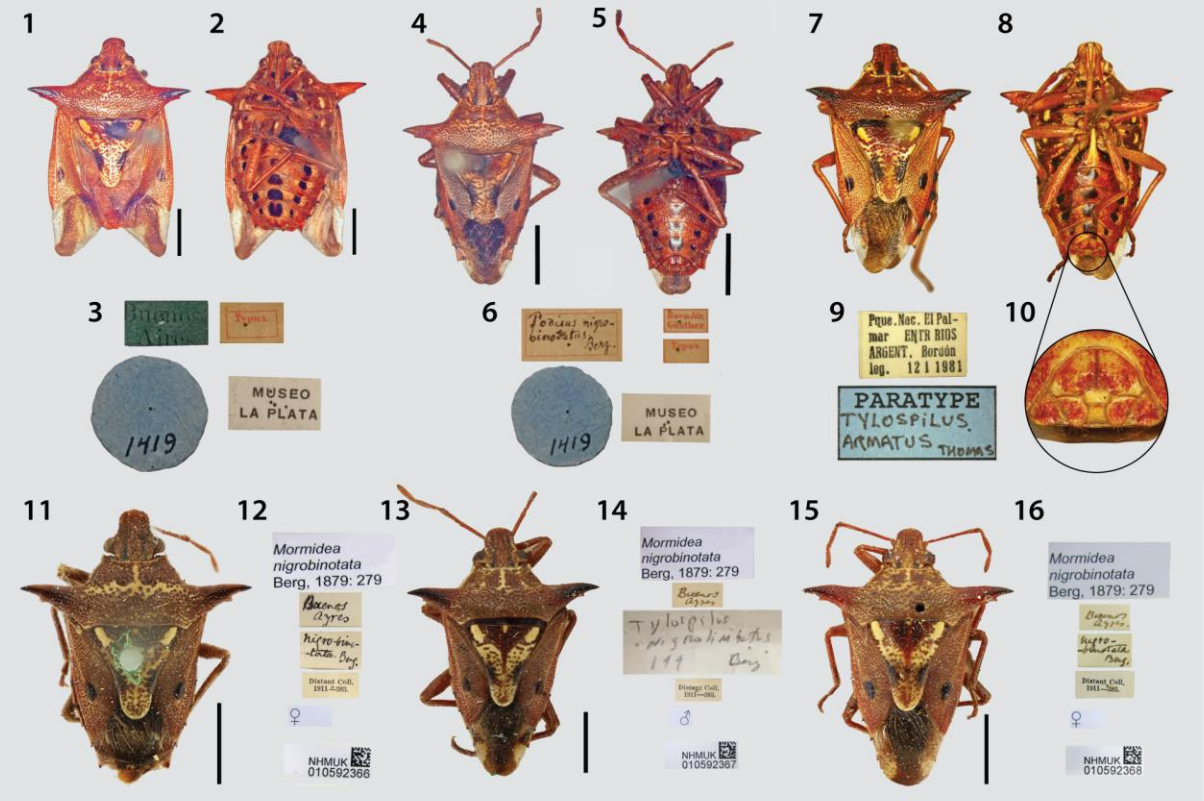
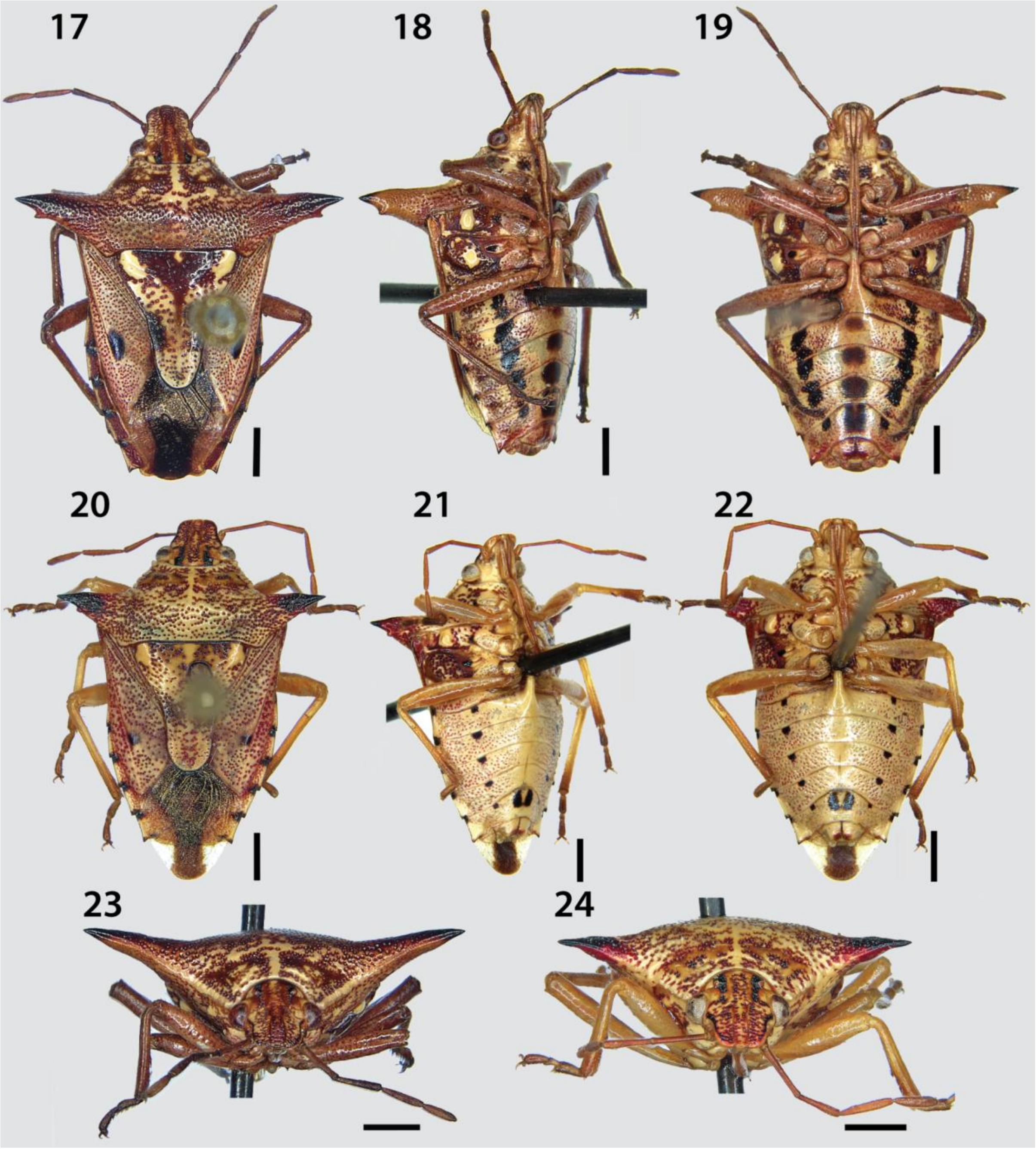
TABLE 1. Differential diagnosis to *T. nigrobinotatus* and *T. armatusimilis*.

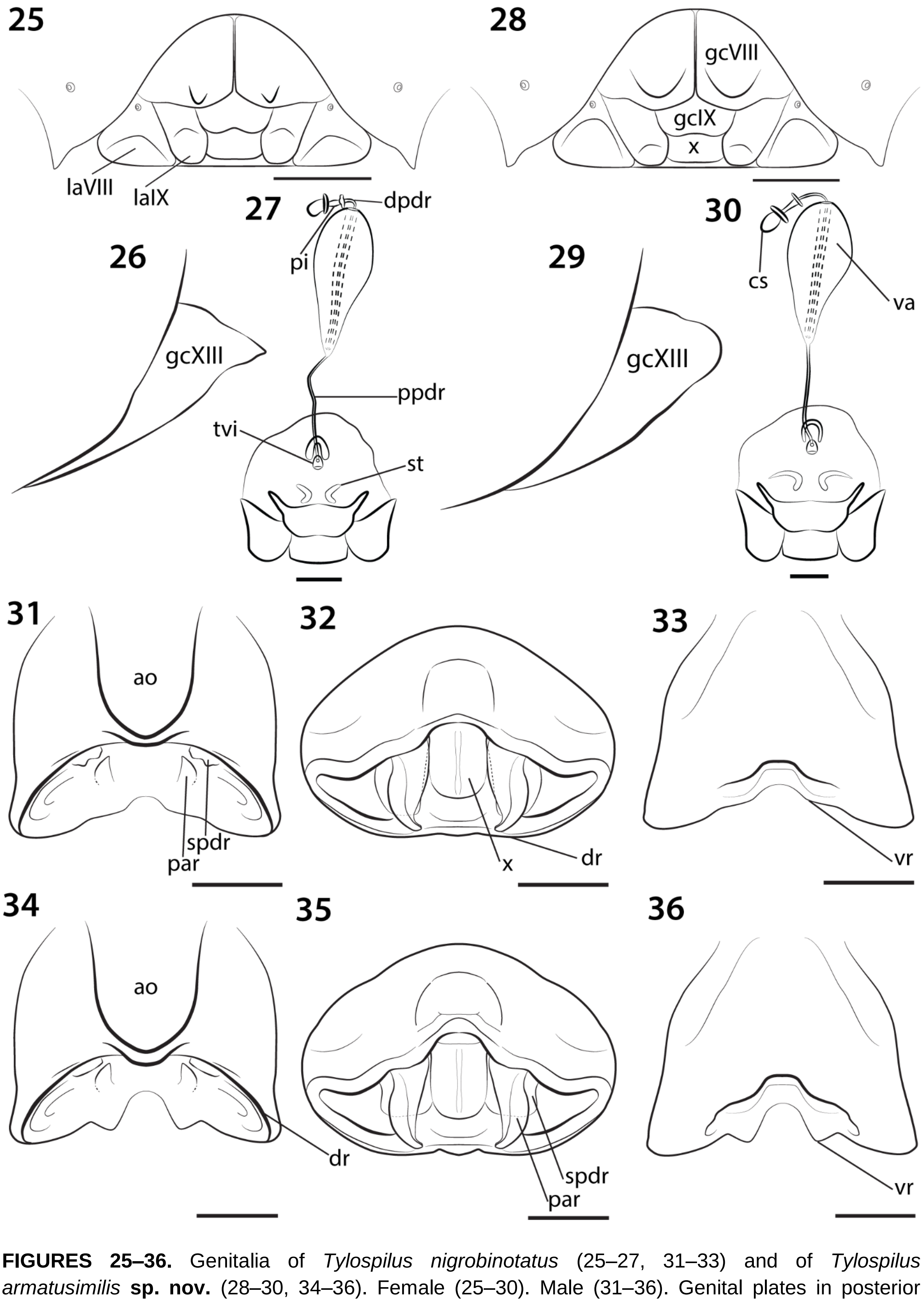
Characters	***T. nigrobinotatus* Berg**	***T. armatusimilis* sp. nov.**
Anterolateral margins of pronotum	Distinctly pale (Fig. 23)	Concolour with disc (Fig. 24)
Humeral angles	Longer and robust, upward directed (Figs 17, 23)	Shorter and slender, laterally directed (Figs 20, 24)
Black spots on apex of radial vein	Size equal to eye diameter (Fig. 17)	Size smaller than eye diameter (Fig. 20)
Posterior margin of corium	Rectilinear (Fig. 17)	Slightly concave (Fig. 20)
Pale calloused spot on metasternum	Present (Fig. 18)	Absent (Fig. 21)
Median row of black spots on ventral abdomen	From IV to VII segment (Fig. 19)	Restricted to VII segment (Fig. 22)
Lateral row of black spots on ventral abdomen	Larger, interconnected (Fig. 19)	Smaller, restrict to the anterior margin of segments (Fig. 22)
Projection on gonocoxites VIII	Acute (Figs 25–26)	Rounded (Figs 28–29)
Secondary thickening of gonapophyses IX	Boomerang-like (Fig. 27)	Sickle-like (Fig. 30)
Anterior projection of thickening of vaginal intima	Horseshoe-like (Fig. 27)	V-shaped (Fig. 30)
Capsula seminalis	Truncate (Fig. 27)	Elliptical (Fig. 30)
Mesial portion of ventral rim of pygophore	Strongly concave (Fig. 33)	Slightly concave (Fig. 36)
Superior process of dorsal rim of pygophore	Subquadrate (Fig. 32)	Subrectangular (Fig. 35)



FIGURES 1–16. Type and historical specimens of *Tylospilus nigrobinotatus* and its respectives labels. 1–6, Lectotype and Paralactotype of *Mormidea nigrobinotata* deposited at Museo de La Plata, Argentina; 7**–**10, paratype of *Tylospilus armatus* deposited at D. B. Thomas personal collection, United States; 10, external female genitalia; 11–16, non-types with historical value of *Mormidea nigrobinotata* deposited at The Natural History Museum, United Kingdom. Scales bars: 2mm.

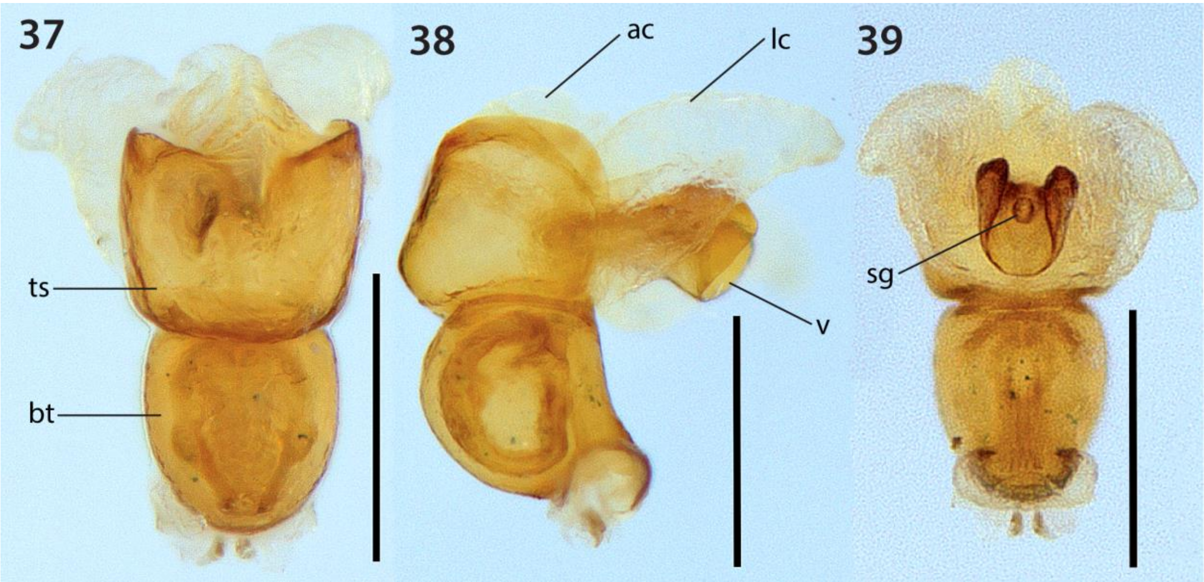


FIGURES 17–24. Habitus of *Tylospilus nigrobinotatus* (17–19, 23) and of *Tylospilus armatusimilis* **sp. nov.** (20–22, 24). Dorsal (17, 20), lateral (18, 21), ventral (19, 22) and frontal (23, 24) views. Scale bars: 1 mm.



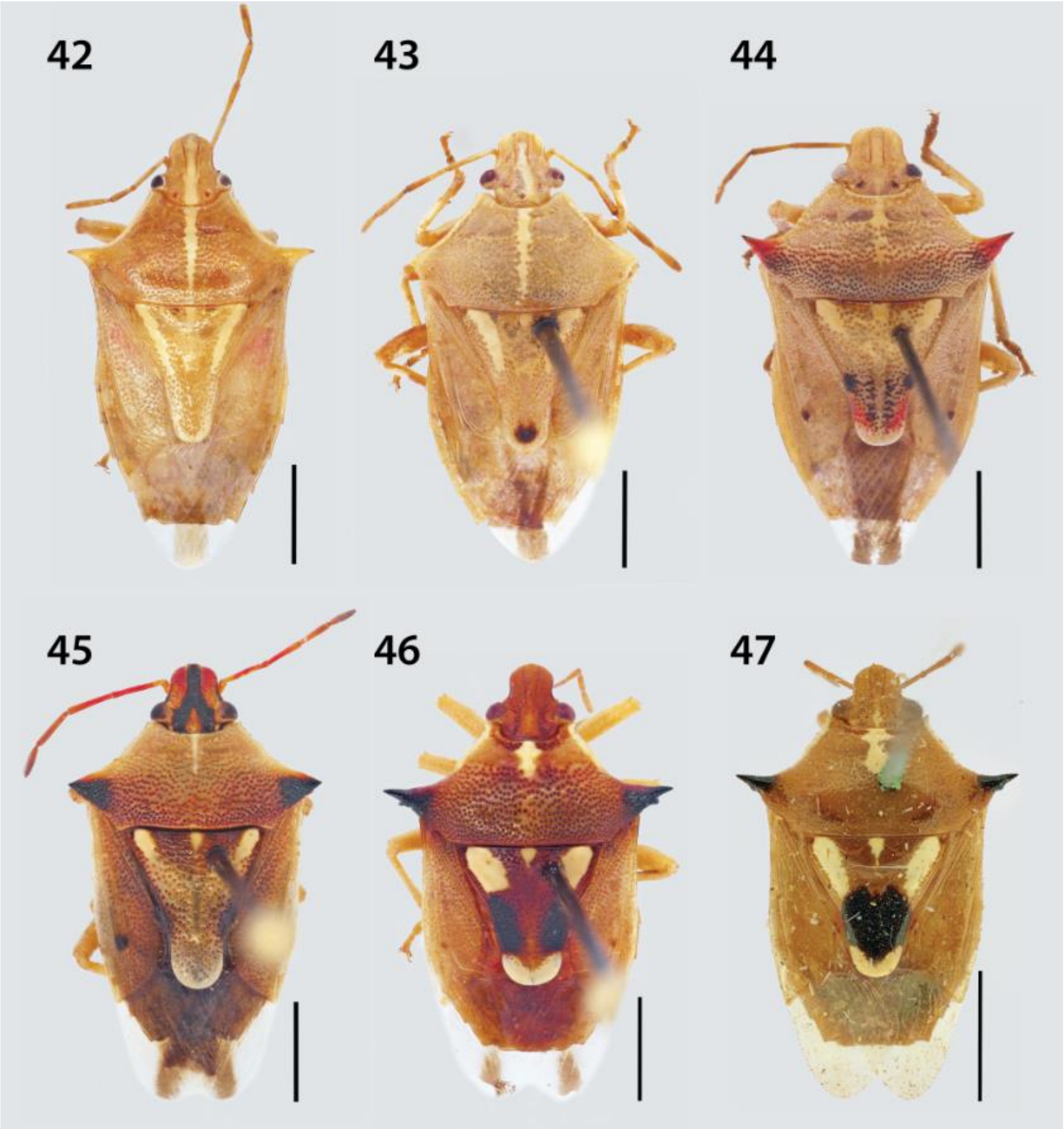
FIGURES 25–36. Genitalia of *Tylospilus nigrobinotatus* (25–27, 31–33) and of *Tylospilus armatusimilis* **sp. nov.** (28–30, 34–36). Female (25–30). Male (31–36). Genital plates in posterior view (25, 28). Gonocoxites VIII in lateral view (26, 29). Internal genitalia (27, 30). Pygophore in dorsal (31, 34), posterior (32, 35) and ventral (33, 36) views. Abbreviations: ao = anterior opening; cs = capsula seminalis; dpdr = distal part of ductus receptaculi; dr = dorsal rim; gcVIII = gonocoxites VIII; gcIX = gonocoxites IX; laVIII = laterotergites VIII; laIX = laterotergites IX; par = paramere; pi = pars

intermedialis; ppdr = proximal part of ductus receptaculi; spdr = superior process of dorsal rim; st = secondary thickening of gonapophyses IX; tvi = thickening of vaginal intima; va = vesicular area; vr = ventral rim; x = abdominal segment X. Scale bars: 25, 28 = 0.5 mm; 26–27, 29–36 = 0.25 mm.



FIGURES 37–39. Phallus of *Tylospilus nigrobinotatus*. Dorsal (37), lateral (38) and ventral (39) views. Abbreviations: ac = apical conjunctiva; bt = basal theca; lc = lobes of conjunctiva; sg = secondary gonophore; ts = thecal shield; v = vesica. Scale bars: 0.25 mm.

FIGURES 40–41. Habitus of live specimen of *Tylospilus nigrobinotatus*. Photos by Roberto Güller, obtained in Reserva Municipal de Ribera Norte, Buenos Aires – Argentina, 2017.



FIGURES 42–47. Dorsal view of *Tylospilus* species, with institution of deposition and place of collect of each specimen between parenthesis. *T. distans* (BHMH, Brazil—Mariliéria) (42); *T. peruvianus* (DBT, Bolivia—Santa Cruz de la Sierra) (43); *T. acutissimus* (JEE, United States—Pinal County) (44); *T. chilensis* (JEE, Chile—Coquimbo) (45); *T. cloelia* (JEE, Brazil—Ariquemes) (46); *T. megaspilus* (Holotype, NHMUK 010592365 Brazil—Santarém) (47). Scale bars: 2 mm.

CAPÍTULO V

Taxonomy of widespread Neotropical species of *Podisus* Herrich-Schäffer (Hemiptera: Pentatomidae: Asopinae): redescription of *P. distinctus* (Stål, 1860) and revalidation of *P. fuscescens* (Dallas, 1851)

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Abstract

Some species of *Podisus* Herrich-Schäffer have a confuse taxonomic history with several modifications and loss of information over time. The genus has been considered a taxonomic dumping ground in Asopinae, and its current species composition is doubtful. After examining the type specimens of *Telepta distincta* Stål, *Arma submarginata* Walker, *Arma mo*nospila Walker, *Arma fuscescens* Dallas, *Arma caliginosa* Walker, *Arma turbida* Walker and *Podisus mellipes* Bergroth, we redescribe and revalidate *A. fuscescens* as *Podisus fuscescens* rev. stat., previously considered a junior synonym of *Podisus sagitta* (Fabricius). The taxonomic status, morphology and distribution of *P. fuscescens* and *P. distinctus* are updated and illustrated. *Arma caliginosa*, *A. turbida* and *Podisus mellipes* become synonyms of *P. fuscescens*. Additionally, *Arma submarginata* Walker is removed from its synonymy with *Podisus ventralis* (Dallas) and treated as a synonym of *P. distinctus. Podisus signoreti* Fallou is removed from its synonymy with *P. distinctus* and treated as *species inquirenda*.

Key words: *Arma*, *Telepta*, systematics, predatory stink bugs, nomenclatural acts

Introduction

Asopinae is a subfamily of Pentatomidae composed of 65 genera and 298 species whose representatives are recognized by their predatory behavior, feeding mainly on larvae of Lepidoptera and Coleoptera, and acting as biological controllers in natural and modified areas (Thomas 1992, 1994; De Clercq 2000, 2008; Rider *et al*. 2018; Roca-Cusachs 2019; Brugnera *et al*. 2019a). The members of Asopinae are distributed in all zoogeographical regions except for the Arctic and the Antarctic (Thomas 1992, 1994; Rider *et al*. 2018). Apart from the revision of few Asian (e.g. Zhao *et al*. 2013, 2018; Roca-Cusachs *et al*. 2018, 2019) and African (Roell *et al*. 2019) genera, the two monographs by Thomas (1992, 1994), and the recent revision of *Tynacantha* Dallas (Brugnera et al. 2019a), the taxonomy of the group has received little attention lately, especially the New World taxa (Rider et al. 2018).

Podisus Herrich-Schäffer, 1851 is the most diverse genus in Asopinae, currently with 32 species distributed in the Neotropical and Nearctic regions (Thomas 1992; Gapon 2009). The biology of several *Podisus* species has been studied in the Americas over the past several decades, with some of those species being considered important agents in biological control programs, mainly *P. maculiventris* (Say, 1831) in North America, *P. nigrispinus* (Dallas, 1851), *P. sagitta* (Fabricius, 1794) and *P. distinctus* (Stål, 1860) in Central and South America (De Clercq 2000, 2008; Pires 2015; Grazia *et al*. 2015). *Podisus distinctus* [sensu Thomas (1992)] has been the target of several studies regarding biological control (e.g. Soares 2008; Zanuncio *et al*. 2014), physiology (e.g. Tavares *et al*. 2017), and morphology (e.g. Sá *et al*. 2013; Matesco *et al*. 2014), mainly in Brazil, and referred to as the most common species of the genus (Thomas, 1992).

The confusion in the taxonomic history of Asopinae is emphasized by several modifications, as properly explained by Thomas (1992) in his monograph on the New World taxa (see also Schouteden 1907; Kirkaldy 1909; Thomas 1994). Thomas (1992) improved significantly the knowledge about Asopinae by examining specimens from several institutions and including primary types, especially those deposited at The Natural History Museum, London, United Kingdom that houses many type specimens of Asopinae. However, the types deposited in some collections like the Swedish Museum of Natural History (NHRS) were not examined by Thomas, including the oldest ones described by Carolus Stål, resulting in some misunderstandings. Thomas (1992) organized *Podisus* into morphological groups of species and, among his new taxonomic combinations, he treated *Arma caliginosa* Walker, 1867, *Arma turbida* Walker, 1867, *Podisus mellipes* Bergroth, 1891 and *Podisus signoreti* Fallou, 1891 as junior synonyms of *P. distinctus*; *Arma fuscescens* Dallas, 1851 as junior synonym of *Podisus sagitta*; and *Arma submarginata* Walker, 1867 as junior synonym of *Podisus ventralis* Dallas, 1851.

According to our interpretation, the delimitation of *P. distinctus* by Thomas (1992: 90–91) was based on the types of *A. caliginosa* and *A. turbida*, deposited in the NHMUK, and on the descriptions of *P. mellipes* by Becker & Grazia (1977) and Hildebrand (1987). However, after examining the type material and consulting the original descriptions of each species mentioned above, we conclude that *Podisus fuscescens* is a valid species having *A. caliginosa*, *A. turbida* and *P. mellipes* as junior synonyms. Furthermore, we consider *A. submarginata* a junior synonym of *P. distinctus*, and *Podisus signoreti* a *species inquirenda*.

Here, new taxonomic concepts and illustrated redescriptions for *Podisus distinctus* and *Podisus fuscescens* **rev. stat.** are provided. A map with the species geographical distribution is also included.

Material and methods

Images of type specimens (Figs 4–15, 19–24) were taken in NHMUK using a Canon EOS 5D SR camera mounted with Canon Macro Lens EF 100mm 1:2.8 L IS USM controlled with Helicon Remote software; stacking was done with Helicon Focus software. Other images from type specimens were received from Gunvi Lindberg (NHRS) (Figs 1–3) and Laurent Fauvre (MNHN) (Figs 16–18). Non-type specimens were photographed at the Universidade Federal do Rio Grande do Sul, Brazil with a Nikon AZ100M coupled with a Nikon DS-Fi2 digital camera, in multiple focal planes; pictures were stacked in a single focused image using the NIS Elements software (Figs 25–47, 49, 51,53).

Genitalia were prepared with 10% heated aqueous KOH solution (~80 ºC) for five minutes, and stained with Congo Red solution (5.3 mg/10 ml H2O) for 30 seconds. Specimens were observed and measured under light stereomicroscope, and the measurements [mean ± standard deviation (minimum–maximum)] are given in millimeters.

Terminology of genital structures follows Baker (1931), Dupuis (1970), Schaefer (1977), and Gapon & Konstantinov (2006).

The distribution records were taken from the collecting labels of the examined material, and complementary records for *P. fuscescens* rev. stat. were obtained from the literature, where *P. fuscescens* was identified as *P. distinctus* (Thomas 1992, Dellapé *et al*. 2003, Henry & Wilson 2004, Ortega-León & Aguilera 2013, Lupoli 2019).

The records were mapped on QGIS Lisboa software, version 2.18.21. When GPS coordinates were not available, localities were georeferenced to the geodetic center of the city based on online global gazetteers.

The following collections are depositories for the specimens studied here:

AMNH American Museum of Natural History, New York, United States of America

EMG Entomologisches Museum Geyer, Insekten Dauerausstellung, Geyer, Germany

FIOC Fundação Instituto Oswaldo Cruz, Rio de Janeiro, Brazil

ICN Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia

JEE Joseph Eger, personal collection, Tampa, United States of America

MACN Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina

MCNZ Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil

MIZA Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez, Maracay, Venezuela

MNHN Muséum National d’Histoire Naturelle, Paris, France

MNRJ Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

MPEG Museu Paraense Emílio Goeldi, Universidade Federal do Pará, Belém, Brazil

MPUJ Museo Javeriano de Historia Natural, Pontificia Universidad Javeriana, Bogotá, Colombia

MZUSP Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil

NHMUK The Natural History Museum, London, United Kingdom

NHRS Naturhistoriska Riksmuseet, Stockholm, Sweden

NMPC National Museum, Prague, Czech Republic

UFES Departamento de Biologia, Universidade Federal do Espírito Santo, Vitória, Brazil

UFRG Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

UFVB Museu de Entomologia, Universidade Federal de Viçosa, Viçosa, Brazil

UNAB Universidad Nacional de Colombia, Facultad de Agronomia, Bogotá, Colombia

Results

***Podisus distinctus* (Stål, 1860)**

Telepta distincta Stål, 1860: 11; Thomas 1992: 90 (Syntype male in NHRS, Figs 1–3).

Arma distincta: Walker 1867: 137.

Arna [*sic*] *submarginata* Walker, 1867: 139; Thomas 1992: 99 **NEW SYNONYMY** (removed from the synonymy with *Podisus ventralis* (Dallas, 1851) proposed by Thomas 1992: 99) (Holotype female in NHMUK, Figs 4–6).

Podisus (*Telepta*) *distinctus*: Stål 1867: 497; Thomas 1992: 90.

Podisus (*Podisus*) *distinctus*: Stål 1870: 51; Thomas 1992: 90.

Podisus submarginatus: Lethierry & Severin 1893: 219; Thomas 1992: 99.

Apateticus (*Eupodisus*) *distinctus*: Schouteden 1907: 71; Thomas 1992: 90.

Apateticus (*Eupodisus*) *submarginatus*: Schouteden 1907: 72; Thomas 1992: 99.

Apateticus (*Podisus*) *distinctus*: Kirkaldy 1909: 19.

Apateticus (*Podisus*) *submarginatus*: Kirkaldy 1909: 21; Thomas 1992: 100.

Podisus distinctus: Thomas, 1992: 90; Aldrich 1995: 1033, 1036–1040; Zanuncio *et al*. 1997: 483–487; Aldrich *et al*. 1997: 1–3, 6–11; Oliveira *et al*. 1999: 77–80; Magalhães *et al.* 2002: 445–447; Dellapé *et al*. 2003: 8; Henry & Wilson 2004: 75, 76, 79, 80; Lacerda *et al*. 2004: 237–241; Matos Neto *et al*. 2004: 101–107; Santos *et al*. 2004: 213, 215–219; Torres *et al*. 2006: 3; Causton *et al*. 2006: 136; Soares *et al*. 2009: 30–32; Guedes *et al*. 2009: 170–175; Campos *et al*. 2009: 168; Araújo *et al*. 2011: 560–564; Zanuncio *et al*. 2011: 608–612; Grazia & Schwertner 2011: 713; Weiler *et al*. 2012: 188; Zanuncio *et al*. 2013: 39–43; Barbosa *et al*. 2012: 1–5; Sá *et al*. 2013: 282–286; Matesco *et al*. 2014: 351, 353, 360–362, 364, 374; Abreu *et al*. 2015: 22–24; Martínez *et al*. 2015: 1514–1520; Ricalde *et al*. 2015: 2126, 2127, 2129; Tavares *et al*. 2017: 35–39; Melo *et al*. 2017: 496; Brugnera *et al*. 2019b: 16; Lupoli 2019: 76, 77, 81, 85, 87.

Types examined: *Telepta distincta* Stål, 1860: Syntype #m, labels: “Brasil”, “F. Sahtt”, “Type.”, “Typus”, “NHRS-GULI 000067359” (NHRS) (Figs 1–3).
Arma submarginata Walker, 1867: Holotype #f, labels: “Tejuca, Jan/1857. H. Clark.”, “37. *Arna submarginata*.”, “Type”, “Holotype”, “NHMUK 010592336” (NHMUK) (Figs 4–6).

Non-types examined: BRAZIL: Minas Gerais 2 #m, Carmos do Rio Claro, Carvalho leg. (MNRJ); **Espírito Santo** 1 #m, Domingos Martins, 17.X.2018, D. S. Martins leg. (UFES); **Rio de Janeiro** 1 #f, Distrito Federal [Rio de Janeiro], Carvalho leg. (MNRJ); Tejuca [Rio de Janeiro], I.1857, H. Clark leg. [010938846] (NHMUK) **São Paulo** 1 #f, Paranapiacaba, 25.II.1962, L. Stowbunenko leg. (MZUSP); 1 #m, Salesópolis, Est. Biol. Boracéia, 21–22.X.1989, Exc. DZUSP leg. (MZUSP); **Santa Catarina** 5 #m 3 #f, Araranguá, 30.IX.2009, Bianchi, F. M. leg. (UFRG); 2 #m 2 #f, Araranguá, 24.IV.09, Bianchi, F. M. & Perin C. leg. (UFRG); **Rio Grande do Sul** 8 #f, Maquiné, 4.VI.2011, -29.6103, -50.1946, Bianchi, F. M. leg. (UFRG); 2 #m, Torres, P. E. Itapeva Mata Sul, 12.I.2005, L. Moura & I. Heydrich leg. [177390, 177379] (MCNZ).

Diagnosis. Anterolateral margin of pronotum tumescent on anterior two-thirds, pale or reddish, crenulated; humeral angles directed upward and slightly backward, acute and darker at apex, with a posterior minute tooth (Figs 1, 4, 25, 27). Paramere with two branches equally long and acute at apex, inner branch without ventral sculptures, posterior margin of paramere concave (Figs 32, 37); superior process of dorsal rim subrectangular, with striated dorsal sculpturing (Fig 38); thecal shield and basal theca subequal in length, thecal shield wider than basal theca (Figs 41–43). *Capsula seminalis* finger-like, longer than distal part of *ductus receptaculi*; 1 + 1 secondary thickening of gonapophyses IX boomerang-like (Figs 49–50).

Redescription. Body dorsally brown and usually paler ventrally, with dark brown punctures (Figs 1–2, 4–5, 25–27). **Head:** longer than wide and densely dark brown punctured; mandibular plates and clypeus subequal in length; width of head across eyes longer than anterior width of pronotum; ocelli situated posterior to the eyes (Fig. 27). First three labial segments pale brown, last segment dark brown; apex of labium reaching metacoxae; proportion of antennal segments: I<II>III>IV (Figs 5, 26). Antennae brown, IV segment usually pale yellow; proportion of antennal segments: I<II>III<IV>V (Fig. 27). **Thorax:** anterolateral margins of pronotum tumescent on anterior two-thirds, pale or reddish and crenulated; humeral angles directed upward and slightly backward, acute and darker at apex, with a posterior tooth. Scutellum triangular, frenal portion longer than postfrenal portion, apical margin usually with a pale line. Corium longer than scutellum, reaching anterior margin of abdominal segment VI; hemelytral membrane dark brown mesially, surpassing apex of abdomen (Figs 1, 4, 25, 27). Legs usually pale yellow, sometimes with dark spots on femur. Peritreme discal-type, curved anteriorly; metapleural evaporatorium surrounding the peritreme, not reaching the lateral margin of pleuron; mesopleural evaporatorium reaching the lateral margin of pleuron. **Abdomen:** connexival segments dark with pale spots medially; apex of connexival segments projected posteriorly. Abdominal tubercle reaching the posterior margin of metacoxae; females usually with a row of dark brown spots in the middle of urosternites IV-VII (Figs 2, 5, 26). **Male genitalia:** pygophore cup-like; anterior opening subtriangular; dorsal rim concave and projected medially in dorsal view; superior layer of ventral rim sinuous in ventral view; inferior layer of ventral rim concave; paramere with two branches equally long and acute at apex, inner branch without ventral sculpturing, posterior margin of paramere concave; superior processes of dorsal rim subrectangular, with striated dorsal sculptures (Figs 31–33, 37–38). *Phallus* with thecal shield and basal theca subequal in length, thecal shield wider than basal theca; apex of 1+1 lobes of conjunctiva slightly sclerotized; vesica with 1+1 lateral flaps; *ductus seminis distalis* located between the flaps of vesica, posteriorly directed, ending on a secondary gonopore

(Figs 41–43). **Female genitalia:** gonocoxites VIII as long as wide, sutural margins parallel and juxtaposed, posterior margins sinuous; laterotergites VIII trapezoidal; gonocoxites IX rectangular, posterior margin slightly convex, lateral margins over the laterotergites IX; laterotergites IX longer than wide, obtuse apically, surpassing the segment X, reaching the posterior margin of laterotergites VIII; segment X subrectangular (Figs 47–48). Internal genitalia with *capsula seminalis* finger-like, longer than distal part of *ductus receptaculi*; posterior annular flange located above the base of *capsula seminalis*; posterior region of distal part of *ductus receptaculi* dilated ; proximal part of *ductus receptaculi* twice longer than vesicular area; ring sclerites circular; 1+1 secondary thickening of gonapophyses IX boomerang-like; thickening of vaginal intima with anterior region somewhat conical and posterior region cylindrical. (Figs 48–50).

Measurements. Males: (n = 8). Head length: 1.73 ± 0.07 (1.65–1.85), width: 1.96 ± 0.08 (1.82–2.04); pronotum length: 2.20 ± 0.10 (2.04–2.30), width: 6.13 ± 0.29 (5.54–6.40); scutellum length: 3.12 ± 0.15 (2.89–3.40), width: 2.83 ± 0.10 (2.72–3.00); length of antennal segments: I 0.27 ± 0.04 (0.18–0.30), II 1.40 ± 0.07 (1.28–1.50), III 0.92 ± 0.09 (0.80–1.10), IV 1.23 ± 0.09 (1.10–1.30); V 1.18 ± 0.05 (1.12–1.24); length of labial segments: I 0.95 ± 0.04 (0.86–0.98), II 1.21 ± 0.05 (1.14–1.30), III 0.93 ± 0.02 (0.90–0.96), IV 0.82 ± 0.06 (0.72–0.92); length of abdomen: 4.15 ± 0.18 (3.90–4.41), width: 4.33 ± 0.19 (4.09–4.59); total length: 9.45 ± 0.31 (9.00–9.90). **Females:** (n = 9). Head length: 1.97 ± 0.12 (1.75–2.14), width: 2.15 ± 0.13 (1.87–2.36); pronotum length: 2.50 ± 0.20 (2.12–2.75), width: 7.03 ± 0.46 (6.11–7.76); scutellum length: 3.68 ± 0.40 (3.15–4.40), width: 3.29 ± 0.24 (2.90–3.75); length of antennal segments: I 0.30 ± 0.04 (0.22–0.34), II 1.64 ± 0.18 (1.44–2.00), III 0.99 ± 0.12 (0.80–1.16), IV 1.41 ± 0.13 (1.24–1.62); V 1.17 ± 0.07 (1.08–1.25); length of labial segments: I 1.01 ± 0.05 (0.94–1.10), II 1.37 ± 0.10 (1.20–1.50), III 1.04 ± 0.06 (0.90–1.12), IV 0.90 ± 0.05 (0.82–0.95); length of abdomen: 5.14 ± 0.27 (4.60–5.52), width: 5.25 ± 0.40 (4.60–5.85); total length: 10.55 ± 0.72 (9.20–11.68).

Distribution. Brazil (Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Santa Catarina, Rio Grande do Sul) (Fig. 56).

Comments. Thomas (1992) considered *Arma submarginata* Walker, 1867 (= *Podisus distinctus* Stål, this work) (Figs 4–6) a synonym of *Arma ventralis* Dallas, 1851 (currently *Podisus ventralis* (Dallas)). We examined the type of *Arma ventralis* (Figs 19–21, female, deposited in NHMUK) and concluded they are not synonyms; *Arma submarginata* is actually a synonym of *P. distinctus*, here redescribed. *Podisus distinctus* and *P. ventralis* can be differentiated by: the anterolateral margins of pronotum more tumescent in *P. distinctus*; the anterior half of the posterior margin of gonocoxites VIII strongly concave in *P. ventralis* and sinuous in *P. distinctus*; the branches of the parameres shorter and with rounded apex in *P. ventralis* (see Thomas, 1992: Fig. 96), and longer with acute apex in *P. distinctus* (Fig. 37).

The tumescent anterolateral pronotal margins of *P. distinctus* are similar to the species of the *congrex* group proposed by Thomas (1992), who characterized it by the "pronotal margin inflated, rugulose". Due to the lack of a phylogenetic hypothesis for the *Podisus* species, the possible relatedness of *P. distinctus* with species of the *congrex* group is yet unclear.

***Podisus fuscescens* (Dallas, 1851), REVISED STATUS**

Arma fuscescens Dallas, 1851: 102; Walker 1867: 134; Kirkaldy 1909: 19; Thomas 1992: 87 (Lectotype female in NHMUK, Figs 7–9) (removed from the synonymy with *P. sagitta* (Fabricius, 1794) proposed by Thomas 1992: 87).

Telepta fuscescens Stål, 1862: 90 (part.) (Homonym) (Synonymized by Stål 1870: 51).

Arma caliginosa Walker, 1867: 138; Kirkaldy 1909: 18; Thomas 1992: 90 **NEW SYNONYMY** (Holotype female in NHMUK, Figs 10–12) (removed from the synonymy with *P. distinctus* (Stål, 1860) proposed by Thomas 1992: 90).

Arma turbida Walker, 1867: 140; Kirkaldy 1909: 21; Thomas 1992: 90 **NEW SYNONYMY** (Holotype female in NHMUK, Figs 13–15) (removed from the synonymy with *P. distinctus* (Stål, 1860) proposed by Thomas 1992: 90).

Podisus (*Podisus*) *fuscescens*: Stål 1867: 497; Stål 1870: 50.

Podisus mellipes Bergroth, 1891: 217; Lethierry & Severin 1893: 218; Kirkaldy 1909: 19; Becker & Grazia–Vieira 1977: 63; Hildebrand 1987: 88; Thomas 1992: 90 **NEW SYNONYMY** (Holotype male in MNHN, Figs 16–18) (removed from the synonymy with *P. distinctus* (Stål, 1860) proposed by Thomas 1992: 90).

Podisus caliginosa: Lethierry & Severin 1893: 217; Kirkaldy 1909: 18; Thomas 1992: 90.

Podisus turbidus: Distant 1900: 59; Kirkaldy 1909: 21; Thomas 1992: 90.

Apateticus (*Eupodisus*) *fuscescens*: Schouteden 1907:71; Thomas 1992: 88.

Apateticus (*Eupodisus*) *caliginosus*: Schouteden 1907: 71; Thomas 1992: 90.

Apateticus (*Eupodisus*) *mellipes*: Schouteden 1907: 71; Costa Lima 1940: 49; Thomas 1992: 90.

Apateticus (*Eupodisus*) *turbidus*: Schouteden 1907: 72; Thomas 1992: 90.

Apateticus (*Podisus*) *caliginosa*: Kirkaldy 1909: 18; Thomas 1992: 90.

Apateticus (*Podisus*) *fuscescens*: Kirkaldy 1909: 19; Thomas 1992: 88.

Apateticus (*Podisus*) *mellipes*: Kirkaldy 1909: 19; Thomas 1992: 90.

Apateticus (*Podisus*) *turbidus*: Kirkaldy 1909: 21; Thomas 1992: 90.

Podisus (*Podisus*) *mellipes*: Buckup 1960: 13; Thomas 1992: 90.

Comments on *Telepta fuscescens* Stål, 1862: This species was first synonymized by Stål 1870: 50–51 with *Podisus* (*P.*) *fuscescens* (=*Arma fuscescens*) (Dallas, 1851). Based on the specimens (two females) used by Stål to describe *Telepta fuscescens*, Distant (1880) concluded that only part of the specimens would be synonyms of *Podisus fuscescens* (Dallas). Therefore, Distant (1880: 83) described *Podisus affinis* Distant for one of the females to correct the homonymy between *Arma fuscescens* Dallas and *Telepta fuscescens* Stål (in part). Distant (1880: 38) stated: "Stål considered the above synonymous with *P.* (*Arma*) *fuscescens*, Dallas. It, however, differs at once from that species by the pronotal spines, which are not emarginate or notched as in *P. fuscescens"*. We examined the syntype of *Podisus affinis* Distant deposited in NHMUK, and we agree with Distant's decision.

Types examined: *Arma fuscescens* Dallas, 1851: Lectotype #f, labels: "48 11", "mexico" "7. *Arma fuscescens*,", "a", "Type", "Lectotype", "NHMUK 010592323" (NHMUK).

Arma caliginosa Walker, 1867: Holotype #f, labels: "Constancia Jan/1857. H. Clark.", "35. *Arma caliginosa*.", "Type", "Holotype", "NHMUK 010592321" (NHMUK).

Arma turbida Walker 1867: Holotype #f, labels: "Saunders 65.13", "43. *Arma turbida*", "Type", "Holotype", "NHMUK 010592336" (NHMUK).

Podisus mellipes Bergroth, 1891: Holotype #m, labels: "Brésil", "Museum Paris MNHN(EH) 24476", "TYPE", "MUSEUM PARIS collection FALLOU", "*Podisus mellipes* Bergroth, 1891" (MNHN).

Non-types examined: HONDURAS: El Paraíso 1 #f, Yuscaran, Rio Aguacote, 2800m, 12.V.1993, L. Stanee & R. Miller leg. (JEE); **PANAMA: Chiriquí** 1 #f, 8k N of Cont'l Divide, 15.V.1996, Wappes Huether & Morris leg. (JEE); **COLOMBIA**: **Putumayo** 1 #m 1 #f, Santa Rosa, Kofan Indian Village, Rio S. Miguel, 2–15.X.1970, P. Burchard & B. Malkin leg. [00319676, 00319677] (AMNH); 1 #f, Mocoa, Rumiyaco, N1°11'84.0", W76°38'65.3", 600 m, 03.III.2016, J. Mora leg. (UNAB); **Cundinamarca** 1 #f, La Veja, 26.IV.1974, A. B. Lotero.leg. [55942] (ICN); **Valle del Cauca** 1 #m, Restrepo, Vereda Rio Bravo, 900m, 9.II.1984, I. de Arévalo.leg. [55954] (ICN); 2 #f 1#m, Buga, Laguna de Sonso, N 03.88340°, W76.34908°, 965 m, 1–2.III. 2017, L. Girón, C. Castillo, M. Nepto leg. [24228, 3487, 52591] (MPUJ); **Caquetá** 1 #f, San José del Fragua, V. Vergel, F. Lagos, N 01°20'23", W75°59'01", 402 m, 03.VI.2013, J. Gamboa leg. (UNAB); **Caldas** 1 #f Palestina, Vda. Santágueda, Granja Montelindo, 1010 m, N 5°03'38.82" W 74°40'12.21", 12.IV.2012, A. Caballero leg. (UNAB); **Meta** 1 #f, Cumaral, Vda. El Yari, N4°16', O73°29', 452 m, 04.VIII.2014, C. Zamora leg. (UNAB); **Tolima** 1 #m, Chaparral N 3º43'39" W 75°50'10", 854 m, 03.I.2004, Malagon C, Triviño C. leg. (UNAB) **VENEZUELA: Miranda** 2 #f, 2km SW Caucagua, 300 m, 3.VII.1998, O'Brien & G.Wibner leg. (JEE); **Mérida** 1 #f, South of Chiguara, 17.VI.1986, 450 m, P. H. Freylaq & M. A. Gaiani leg. (JEE); **Yaracuy** 1 #f, 24 km west Nirgua, 1300 m, 4.VIII.1988, O'Brien & G. Wibner leg. (JEE); **Zulia Kasmera** 1 #f, Rio Yasa, Sierra de Perija, 19.IX.1961, C. J. Rosales & F. Fernandez leg. (MIZA); **BRAZIL: Pará** 1 #m 1 #f, Jacareacanga, XII.1968, M. Alvarenga leg. [00319678, 00319679] (AMNH); 1 #f, Tucuruí, Rio Tocantins, 01.VII.1984, A. A. Nunes leg. (MPEG); 1 #f, Serra Norte, Est. do Fofoca, 08.V.1984, M. F. Torres leg. (MPEG); 1 #f, Serra Norte, Manganês, 24.VI.1985, M. F. Torres leg. (MPEG); **Mato Grosso** 2 #f, Sinop, S12°31', W55°37', X.1974, M. Alvarenga leg. (AMNH); **Rondônia** 1 #f, 62 km SW Ariquemes, Nr. Fzda. Rancho Grande, 6–15.XII.1990, D. A. Rider & J. E. Eger leg. (JEE); 1 #f 62 km SW Ariquemes, Nr. Fzda. Rancho Grande, 12.IX.1992, U. Schmitz, BL Trap (JEE); 1 #f, Forte Príncipe da Beira, 19.XI–3.XII.1967, G. R. Kloss leg. (MZUSP); **Goiás** 2 #m 1 #f, Jataí, Faz. Aceiro, X.1962, Exp. Dep. Zool. (MZUSP); **Minas Gerais** 1 #f, Viçosa, 06.V.1990, G. A. R. Melo leg. (UFVB); 1 #f, Campos Altos, Fazenda Heron Reges, 1023m, S19°53'17", W44°47'25", 13–15.XI.2005, Victor, Evaldo, Lorena, Fiuza leg. (UFVB); 1 #f, Cambuquira, Lopes & Gomes leg. (MNRJ); **Rio de Janeiro** 1 #f, Glória [Rio de Janeiro], 20.XI.1949, J. C. Leite leg. (FIOC); 1 #m, Corcovado, Guanabara [Rio de Janeiro], X.1975, C. A. Campos leg. (MNRJ); 1 #m, Corcovado, 25.XI.1952, Zajciv leg. (FIOC), **São Paulo** 1 #f, Barueri, 14.II.1955, V. Lenha leg. (MNRJ); 1 #f, Teodoro Sampaio, XIII.1973, F. H. Oliveira leg. (AMNH); 1 #f, Campinas, 07.XI.1976, M. R. Marques leg. (UFRG); 1 #f, Barueri, 5.VI.1966, K. Lenko leg. (MZUSP); 1 #f, Campinas, 18.VI.1986 (UFRG); 1 #f, São José dos Campos, XII.1934, H. S. Lopes leg. (MNRJ); 2 #f, São Paulo, Mráz leg. (NMPC); **Paraná** 1 #f, Bituruna, I.1946, Staviarski leg. (MNRJ); 4 #f 2 #m, Londrina, 02.II.1999, J.J. da Silva leg. (UFRG); 1 #f 1 #m, Ponta Grossa, XII.1938, Camargo leg. (MZUSP); 1 #m, Pinhão, Rio Bragança, 26.X.1991, R. P. Rocha leg. (UFRG); **Santa Catarina** 1 #m, Jaguaruna, 23.XI.2011, C. Perin leg. (UFRG); 2 #f, Maracajá, Pq. Ecológico, 19.IV.2006, T. Bertolin leg. (UFRG); 7 #f 4 #m, Maracajá, Pq. Ecológico, 27.IX.2005, T. Bertolin leg. (UFRG); 1 #f, Seara [Nova Teutônia], 27°11', 52°23', 09.II.1937, L. Fritz Plaumann leg. (MNRJ); 1 #m, Seara [Nova Teutônia], XI.1966, F. Plaumann leg. (MZSP); 1 #m 1 #f, Seara [Nova Teutônia], 1.XII.1944, 26.X.1950 (NMPC); 4 #f 4 #m, Seara [Nova Teutônia], 27°11', 52°23', 01.XII.1959, L. Fritz Plaumann leg. (AMNH), 1 #m 1 #f, Seara [Nova Teutônia], 27°11', 52°23', VII.1948, H. Ruckes leg. (AMNH); **Rio Grande do Sul** 1 #f, Santa Maria, 26.X.1979, R. Lúcia leg. (UFRG); 1 #f, Santa Maria, 28.XI.1977, D. Link leg. (UFRG); 3 #m 2 #f, Santa Maria, 25.X.1979, Luiz F. Flores leg. (UFRG); 1 #f, Santa Maria, 2.X.1986, H. Ritter leg. (UFRG); 1 #f, Porto Alegre, 16.IX.1982, M. Becker leg. (UFRG); 1 #m, Porto Alegre, 20.VIII.1995, A. F. Silva leg. (UFRG); 1 #f, Porto Alegre, Campus do Vale - UFRGS, 18.II.2017, R. Brugnera & P. Cremonese leg. (UFRG); 2 #f 1 #m, Porto Alegre, 30.III.1959 (MAGP); 1 #f, Porto Alegre, Campus do Vale - UFRGS, 18.II.2017, R. Brugnera leg. (UFRG); 1 #m, Porto Alegre, Belém Novo, 7.XI.1983, R. Hildebrand leg. (UFRG); 1 #f, Porto Alegre, 09.X.1958, Hudepohl leg. (NMPC); 1 #m, Chapada, 17.XI.1986, J. L. Richter leg. (UFRG); 2 #m, Derrubadas, Pq. Flor. Est. Turvo, 22.XII.1982, S. Bonatto leg. (UFRG); 1 #f, Lajeado, 11.X.1986, A. Siqueira leg. (UFRG); 1 #f, Derrubadas, P. E. Do Turvo, Trilha Salto Yucumã, 19.IV.2004, J. L. C. Bernardes leg. (UFRG); 1 #f, Derrubadas, P. E. do Turvo, S. Yucumã, 04.II.2009, Weiler, L. & Simões, F. leg. (UFRG); 2 #f, Novo Hamburgo, 15.IV.1988, C. J. Becker leg. (UFRG); 2 #f 1 #m, Campo Bom, 19–20.V.1986, C. J. Becker leg. (UFRG); 1 #f, Maquiné, Gruta, 13.XII.2007, L. Moura leg. (UFRG); 1 #f, Ijuí, 22.I.2003, F. L. Santos leg. (UFRG); 1 #f, Catuípe, 20.X.2003, F. L. Santos leg. (UFRG); 2 #f, Caxias do Sul, Vila Oliva, 16.I.1960 (MAGP); 1 #f, Taquari, 12.X.1986, C. Bayer leg. (UFRG); Rio Grande, Est. Ecol. Taim, 02.IX.1986, A. Lise leg. [Col. MCN. 49208] (MCNZ); 1 #f, Triunfo, Parque Copesul, Trilha do Pórtico, 07.XII.2005, A. Barcellos leg. [Col. MCN 178627] (MCNZ); 1 #f, Tenente Portela, 17.I.1985, A. Lise leg. [Col. MCN 48438] (MCNZ); 8 #m 12 #f, São Domingos do Sul, 13.V.2017, R. Brugnera leg. (UFRG); **ECUADOR: Napo** vic. Puerto Misahuali, lat 1°2'4.2"S, lon 77°39'49.2"W, 1650–1900 m, mercury vapor & ultraviolet lights, 6-19.IX.1998, J.E. Eger leg. (JEE); 1 #m, Coca, 250m, 03.IV.1982, G. Onore leg. [010938871] (NHMUK); **Pichincha** 2 #f, Tinalandia, 12 km east Sto. Domingo de Los Colorados, 2500 m, 11–17.V.1986, J. E. Eger leg. (JEE); **PERU: Huánuco** 1 #m, Puente Cinchavito, 25 km south Tingo Maria, 3400 m, 11–17.IV.1987, J. E. Eger leg. (JEE); 1 #f, Tingo Maria, Tingo Maria National Park, 660 m, 11–17.IV.1987, J. E. Eger leg. (JEE); 1 #f, Cueva de las Pavas Canyon, 8 km south Tingo Maria, 2600 m, 11–17.IV.1987, J. E. Eger leg. (JEE); 1 #m, Panguana, Rio Llullapichis, Rio Pachitea, S 9°37', W 74°56', 28.IX–06.X.2000, E.G. Burmeister, E. Diller, T. Kothe & W. Schlang leg. [Coll. #2016080471] (EMG); 2 #m, Forsch. Station "Panguana", Rio Llullapichs, S 9°37', W 74°56', 260 m, 20.IX–05.X.2013, K. Arnold leg. [Coll. #2015040905, 2015040801] (EMG); 1 #f, Tingo Maria, Roadside veg. Los Cuervos road, S. W. of town, 2000ft, 13.VIII.1971, P.S. & H. L. Broomfield B.M. 1971-486 [010938903] (NHMUK); **San Martín** 2 #f, Tarapoto vic. Cordillera Escalera Lodge, S 06°28'08.1", W 076°21'16.4", 432 m, mercury vapor & ultraviolet lights, 11–13.X.2002, J. E. Eger leg. (JEE); 2 #m 2 #f, 500 m, 8°25', 76°25', 2011, S. M. Delzo leg. (UFRG); **BOLIVIA: La Paz** 1 #m 1 #f, Guanay, X.1993, G. Arriagada leg. (JEE); **Santa Cruz** 1 #m, Buena Vista, Flora & Fauna Hotel, 26-27.X.2000 ,R. Morris leg. (JEE); 3 #m 2 #f, El Cairo, 5 km west Buena Vista, ultraviolet light, 16-18.X.2004, J.E. Eger leg. (JEE); 2 #f, Buena Vista, Flora & Fauna Hotel, 14-26.XI.2003, Morris, Nearns, & Wappes leg. (JEE); **El Beni** 1 #f, 15–20 km east Rurrenabaque, 13–19.X.2004, R.F. Morris & J.E. Wappes leg. (JEE); **Cochabamba** 1 #f 1#m, Region Chaparé, 400 m, XI.1949, Dirings leg. (MZUSP); **PARAGUAY: Distrito Capital** 1 #m, Asunción, 11-30.X.1990, G. Arriagada leg. (JEE);

Caazapá 1 #m 1 #f, Parque Nac. Caaguazu, 1-8.XII.1990, G. Arriagada leg. (JEE); **Paraguarí** 1 #m, Parque Nac. Ybycui, 16.XII.1990, G. Arriagada leg. (JEE); **Alto Paraná** 2 #f, 19–20.X.1989, G. Arriagada leg. (JEE); 2 #f, Reserva Biol. Tati Yupi., 12–29.XI.1990, G. Arriagada leg. (JEE); **Central** 1 #f, Capiatá, 15.X.2006, C. Aguilar leg. (JEE); **Caaguazú** 1 #m, Repatriacion, 28.IX.2005, C. Aguilar leg. (JEE); **Guairá** 1 #f, Paso Yobai, 01.III.1951, 280m, J. Foerster leg. [010938852] (NHMUK); **ARGENTINA: Corrientes** 2 #f 2 #m, S. Tomé, G. Pellerano leg. (MACN); **Misiones** 1 #f, Puerto Iguazú, XI.1945, Duret leg. (UFRG); 1 #m 1 #f, Eldorado, 02.X.1964, A. Kovacs leg. [00319660, 00319666] (AMNH); 1 #f 1 #m, Victoria, 11.XI.1964, A. Kovacs leg. [00319662, 00319663] (AMNH); 1#m 2 #f, Mado Puerto, Magdalena, 11.III.1964, A. Kovacs leg. [00319664, 00319665, 00319666] (AMNH).

Diagnosis. Anterolateral margins of pronotum concolor with disc, crenulated; humeral angles acute and laterally produced, with a well-developed posterior tooth (frequently appearing a bifid humeral angle) (Figs 7–8, 10–11, 13–14, 16–17, 28–30). Head of paramere subtriangular in posterior view, mesial part of posterior margin slightly elevated, apex of paramere branches rounded (Figs 35, 39); superior process of dorsal rim reniform, with globose dorsal sculpturing (Fig 40); thecal shield longer and wider than basal theca; vesica grooved medially (Figs 44–46). *Capsula seminalis* ellipsoid; proximal part of *ductus receptaculi* and vesicular area subequal in length; distal part of *ductus receptaculi* slightly longer than *pars intermedialis* and *capsula seminalis* combined; ring sclerites absent (Figs 53–54).

Redescription. Body usually dark brown dorsally and brown or dark brown ventrally with dark brown punctures, females frequently almost black dorsally and ventrally (Figs 7–8, 10–11, 13–14, 16–17, 28–30). **Head:** longer than wide and densely dark brown punctured; mandibular plates and clypeus subequal in length; width of head across eyes longer than anterior width of pronotum; ocelli situated posteriorly to the eyes (Fig. 30). First labial segment frequently paler than posterior segments; apex of labium reaching metacoxae; proportion of labial segments: I<II>III:IV (Figs 8, 11, 14, 17, 29). Antennae brown, anterior portion of IV segment usually pale yellow; proportion of antennal segments: I<II>III<IV>V. **Thorax:** Anterolateral margins of pronotum concolor with disc, crenulated; humeral angles acute and laterally produced, with a well-developed posterior tooth (frequently appearing a bifid humeral angle). Scutellum triangular, frenal portion longer than postfrenal portion. Corium longer than scutellum, reaching the anterior margin of abdominal segment VI; hemelytral membrane dark brown mesially, surpassing the apex of abdomen (Figs 7, 10, 13, 16, 28). Legs paler than body or dark brown. Peritreme disc-type, curved anteriorly; metapleural evaporatorium surrounding the peritreme, not reaching the lateral margin of pleura; mesopleural evaporatorium reaching the lateral margin of pleura. **Abdomen:** anterior and posterior portions of connexival segments dark brown with the mesial portion paler, or connexivum entirely dark brown; apex of connexival segments projected posteriorly. Abdominal tubercle reaching anterior margins of metacoxae. **Male genitalia:** pygophore cup-like; anterior opening oval; dorsal rim concave, with 1 + 1 projections; superior layer of ventral rim convex in posterior view and concave in ventral view, with 1 + 1 lateral projections; inferior layer of ventral rim concave, depressed medially; head of paramere subtriangular in posterior view, mesial part of posterior margin slightly elevated, apex of paramere branches rounded, ventral surface of the internal branch sculptured; superior process of dorsal rim reniform, with globose dorsal sculptures (Figs 34–36, 39–40). *Phallus* with thecal shield longer and wider than basal theca; lobes of conjunctiva slightly sclerotized apically; vesica grooved medially (Figs 44–46). **Female genitalia:** gonocoxites VIII as long as wide, sutural margins parallel and juxtaposed, posterior margins concave; laterotergites VIII triangular; gonocoxites IX rectangular, posterior margin slightly convex to rectilinear, lateral margins over the laterotergites IX; laterotergites IX longer than wide, rounded apically, surpassing the segment X, not reaching the posterior margin of laterotergites VIII; segment X subrectangular (Figs 51–52). Internal genitalia with *capsula seminalis* ellipsoid, longer than *pars intermedialis*; anterior annular flange laterally projected; posterior annular placed slightly before base of *capsula seminalis*; distal part of *ductus receptaculi* slightly longer than *pars intermedialis* and *capsula seminalis* combined; proximal part of *ductus receptaculi* and vesicular area equally long; ring sclerites absent; 1+1 secondary thickenings of gonapophyses IX very close to the thickening of vaginal intima, reniform; thickening of vaginal intima with anterior region cylindrical and posterior region tube-like (Figs 53–54).

Measurements. Males: (n=10). Head length: 2.04 ± 0.09 (1.92–2.24), width: 2.32 ± 0.10 (2.11–2.43); pronotum length: 2.64 ± 0.17 (2.35–2.86), width: 6.77 ± 0.50 (5.98–7.52); scutellum length: 3.79 ± 0.31 (3.21–4.10), width: 3.38 ± 0.21 (3.00–3.65); length of antennal segments: I 0.31 ± 0.04 (0.25–0.38), II 1.63 ± 0.10 (1.47–1.79), III 1.17 ± 0.16 (0.85–1.34), IV 1.59 ± 0.13 (1.37–1.72); V 1.27 ± 0.11 (1.08–1.45); length of labial segments: I 1.11 ± 0.09 (1.00–1.24), II 1.43 ± 0.11 (1.22–1.56), III 1.10 ± 0.05 (1.00–1.18), IV 1.05 ± 0.05 (0.95–1.12); length of abdomen: 4.86 ± 0.37 (4.22–5.20), width: 5.16 ± 0.36 (4.53–5.60); total length: 10.66 ± 0.61 (9.50–11.31). **Females:** (n=10). Head length: 2.20 ± 0.09 (2.01–2.32), width: 2.43 ± 0.06 (2.33–2.52); pronotum length: 2.94 ± 0.20 (2.55–3.12), width: 7.35 ± 0.38 (6.56–7.92); scutellum length: 4.36 ± 0.25 (3.92–4.72), width: 3.88 ± 0.19 (3.50–4.16); length of antennal segments: I 0.33 ± 0.06 (0.20–0.41), II 1.78 ± 0.09 (1.68–1.95), III 1.17 ± 0.16 (0.84–1.32), IV 1.64 ± 0.11 (1.44–1.80); V 1.31 ± 0.05 (1.28–1.40); length of labial segments: I 1.20 ± 0.05 (1.12–1.24), II 1.52 ± 0.07 (1.40–1.60), III 1.20 ± 0.07 (1.12–1.28), IV 1.08 ± 0.05 (1.02–1.15); length of abdomen: 6.04 ± 0.41 (5.20–6.64), width: 6.18 ± 0.42 (5.60–6.80); total length: 11.66 ± 0.60 (10.70–12.30).

Distribution. Mexico (Puebla, Oaxaca), **Honduras**, **Panama**, **Colombia** (Putumayo, Caquetá, Cundinamarca, Meta, Valle del Cauca, Caldas, Tolima), **Venezuela** (Miranda, Yaracuy, Mérida, Zulia Kasmera), **French Guiana** (Kourou, Saül), **Brazil** (Pará, Mato Grosso, Rondônia, Goiás, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), **Ecuador** (Pichincha, Napo, Galápagos), **Peru** (San Martín, Huánuco), **Bolivia** (Pando, El Beni, La Paz, Cochabamba, Santa Cruz), **Paraguay** (Central, Caaguazú, Distrito Capital, Alto Paraná, Caazapá, Paraguarí, Guairá), **Argentina** (Buenos Aires, Misiones, Tucumán, Corrientes) (Fig. 55).

Comments. For the determination of the species and to conclude that *P. fuscescens* and *P. sagitta* are not synonyms, the type of *Arma monospila* Walker, 1862 (= *Podisus sagitta*) (Figs 22–24, female, deposited in NHMUK) was examined. The main differences between *P. sagitta* and *P. fuscescens* **rev. stat.** are: labial segment IV contrastingly darker than the preceding (last three segments darker than segment I in *P. fuscescens*), anterolateral margins of pronotum paler than disc (concolor in *P. fuscescens*), humeral angles acute and strongly produced forward (laterally produced in *P. fuscescens*), color of ventral surface pale yellow (brown or dark brown in *P. fuscescens*), posterior margins of gonocoxites VIII sinuous (concave in *P. fuscescens*), head of parameres with two branches (Thomas 1992: Fig. 86) (subtriangular in *P. fuscescens*, Fig. 39), superior processes of dorsal rim subrectangular (reniform in *P. fuscescens*). The shape of the paramere's head in *P. fuscescens* is unique among *Podisus* species, lacking the concavity on the mesial part of the posterior margin (not forming two branches), being an important characteristic for the species identification.

Podisus signoreti **Fallou, 1891, SPECIES INQUIRENDA**

Podisus signoreti Fallou, 1891: 6; Kirkaldy 1909: 21; Thomas 1992: 90.
Apateticus (*Eupodisus*) *signoreti*: Schouteden 1907: 71; Thomas 1992: 90.
Apateticus (*Podisus*) *signoreti*: Kirkaldy 1909: 21; Thomas 1992: 90.

Comments. Thomas (1992) synonymized *Podisus signoreti* Fallou, 1891 with *P. distinctus* Stål, based on a description by Begroth (1911). We were not able to find the type specimen of *P. signoreti*. Fallou's collection should be deposited in the Muséum National d'Histoire Naturelle in Paris (Rider 2019); we asked Dr. Dominique Pluot-Sigwalt and Dr. Eric Guilbert from MNHN who reported the type of *P. signoreti* is missing in the collection and is apparently lost. Based on our interpretation, both the descriptions by Fallou (1891) and Bergroth (1911) are insufficient to conclude that *P. signoreti* is a synonym of *P. fuscescens*

rev. stat.. The features described by both authors may represent intraspecific variations and can match characteristics of many species in the genus, precluding its undoubtful identification. Thus, we propose to treat *P. signoreti* as *species inquirenda*.

Discussion

We examined in this work several type specimens of *Podisus,* the most diverse genus of predatory stink bugs. Based on the syntype of *Telepta distincta* (Figs 1–3) conserved at NHRS, we observed that the specimen has none of the diagnostic characteristics of the types of its previous synonyms *A. caliginosa* (Figs 10–12), *A. turbida* (Figs 13–15) and *P. mellipes* (Figs 16–18)*,* especially the most remarkable of them: the tumescent anterolateral margins of pronotum, already described by Stål (1860: 11) and clearly visible in the type of *T. distincta*. In order to revalidate a synonym species of *P. distinctus* (*sensu* Thomas, 1992), we found a species previously synonymized with *P. sagitta*, *A. fuscescens* (Figs 7–9), and we conclude that *Podisus fuscescens* **rev. stat.** is a valid species having *A. caliginosa*, *A. turbida*, and *P. mellipes* as junior synonyms. The same characteristics of *T. distincta* were found in the type of *A. submarginata* (Figs 4–6), previously synonymized with *P. ventralis*. Then, we consider *A. submarginata* now as a junior synonym of *P. distinctus*. *Podisus signoreti*, also a previous synonym of *P. distinctus*, cannot be assigned to any other species since the type is lost, and so we treat it as *species inquirenda*.

The pronotum uniformly colored with serrulate anterolateral margins in *A. caliginosa* and *A. turbida* were used by Thomas (1992: 90) as characteristics of *P. distinctus*, and are presented in his identification. This misinterpretation possibly reflects erroneous identifications of specimens as *P. distinctus* (*sensu* Thomas, 1992) in several subsequent studies (see list of synonyms). Considering the revalidation of *Podisus fuscescens*, with *A. caliginosa*, *A. turbida* and *P. mellipes* as its junior synonyms, all the aforementioned works should be viewed as possibly referring to *P. fuscescens* **rev. stat.**.

P. fuscescens **rev. stat.**, here revalidated, is now the most widespread *Podisus* species, distributed throughout most of the Neotropical region, from Mexico to Argentina, including the pacific islands of Galápagos (Fig. 55). *P. distinctus* (*sensu* this work) has a much more restricted geographical distribution, perhaps associated with the Atlantic Rain Forest, being registered only from southeastern and south of Brazil (Fig. 56).

The results in this work show the dissimilarities in the morphology among *P. fuscescens* and *P. distinctus*. The pronotum and genitalia features like the superior processes of the dorsal rim, and *phallus* in males; vesicular area, ring sclerites, *capsula seminalis* and proximal part of *ductus receptaculi* in females are distinctly different among the two species. Being considered a taxonomic dumping ground in Asopinae, the species of *Podisus* are highly diverse in their overall morphology which possibly reflects on the difficulties to establish a conclusive diagnosis for the genus based on its current classification and calls into question its monophyly, which remains to be investigated.

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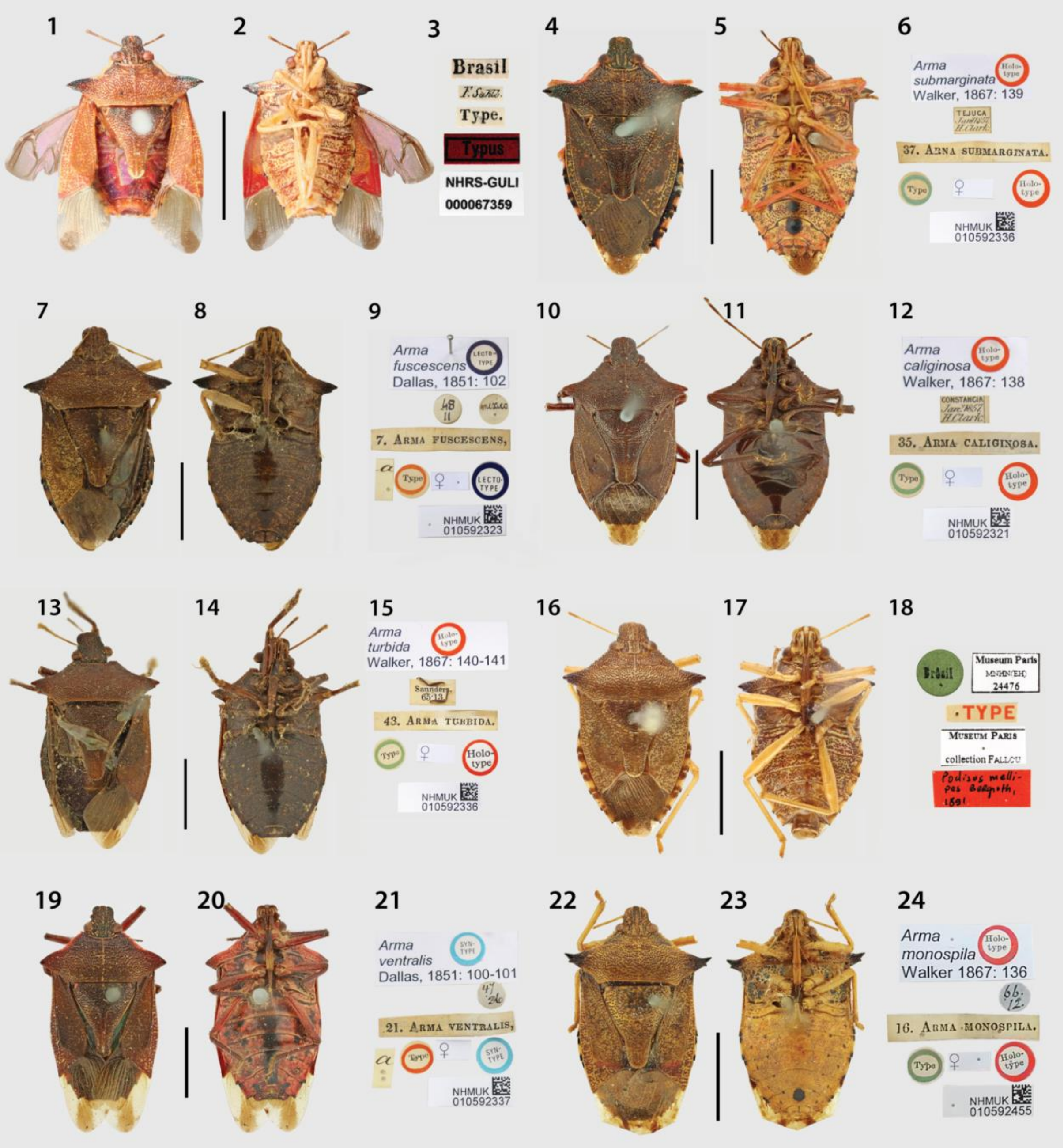
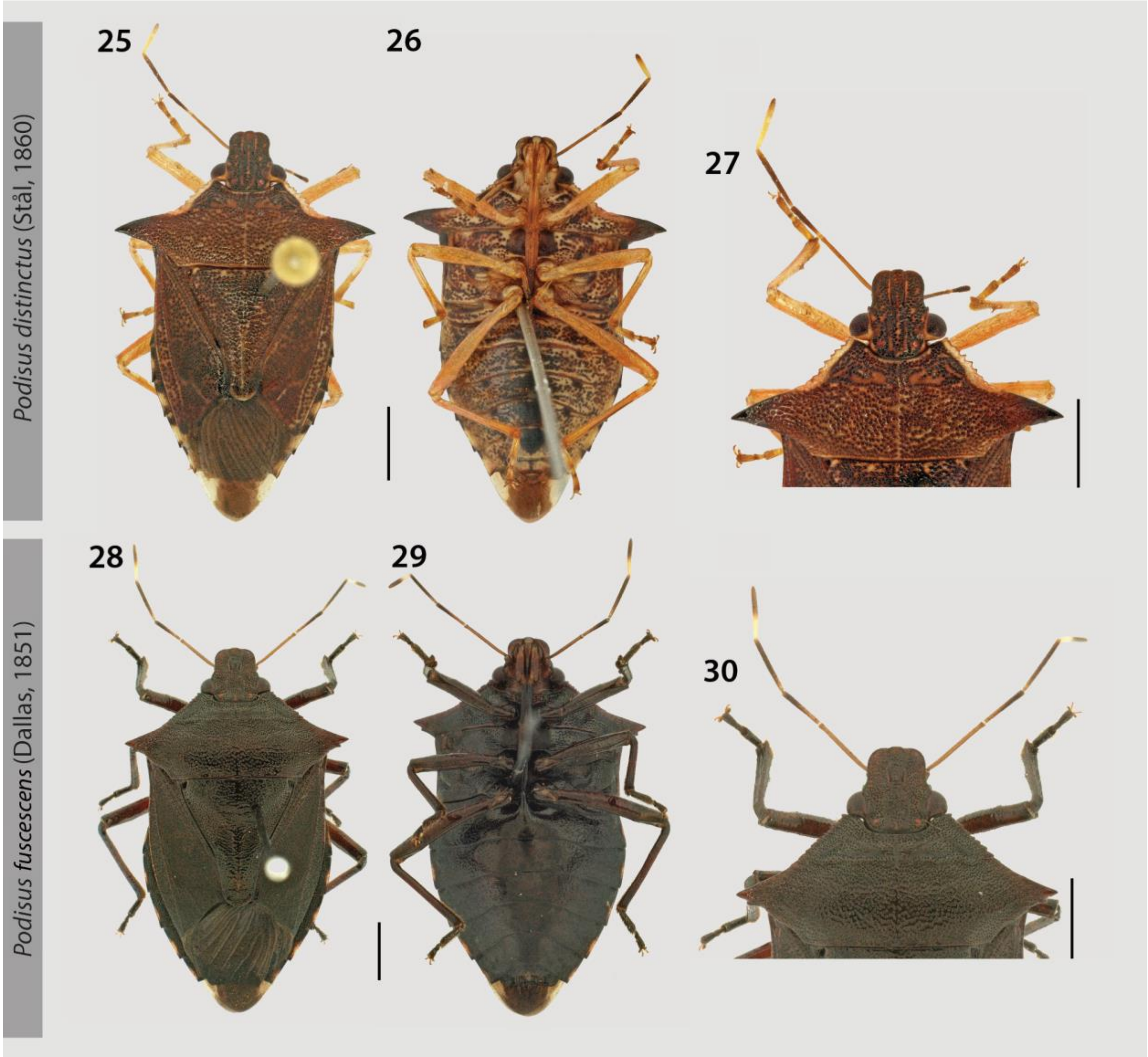
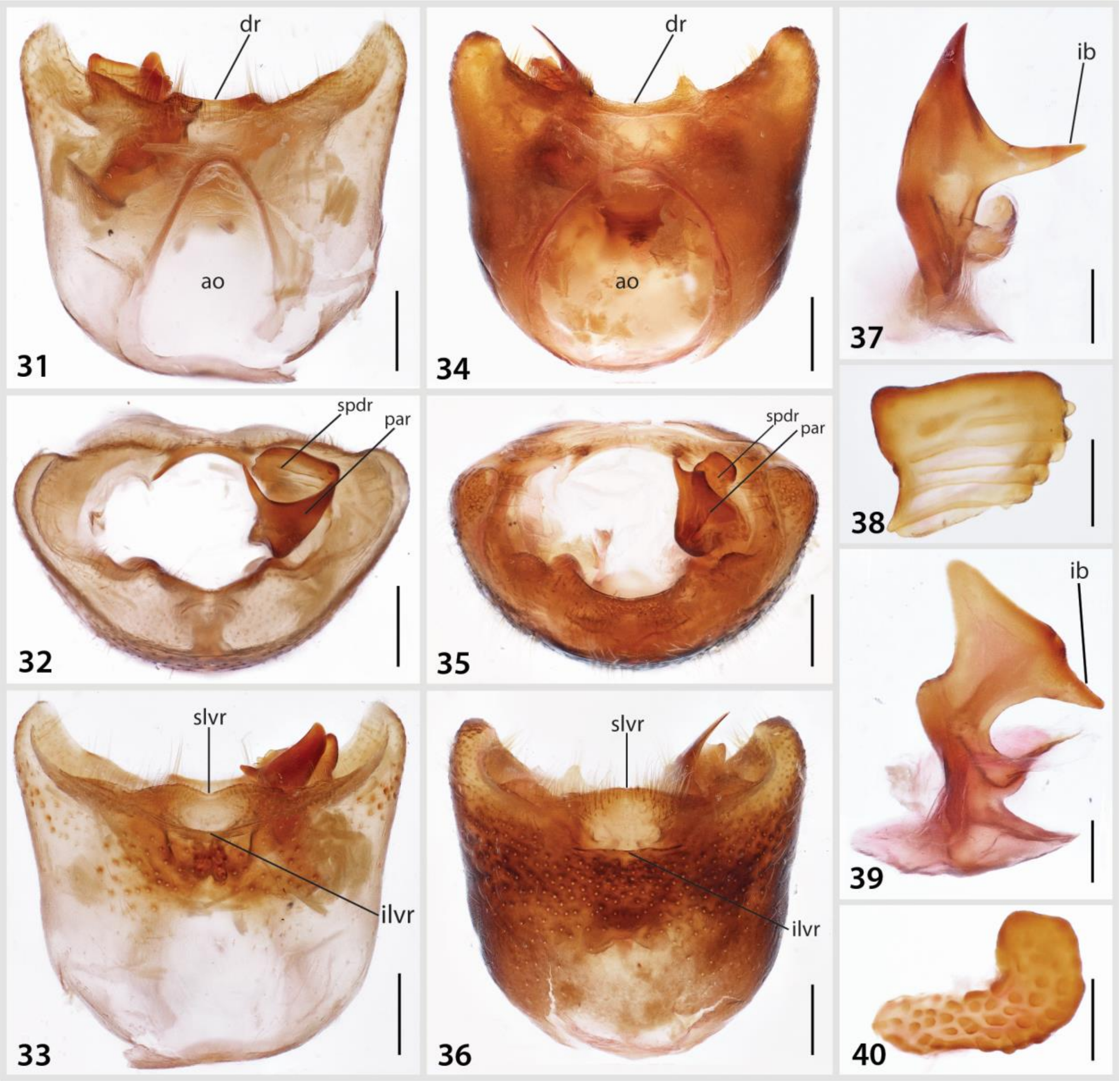


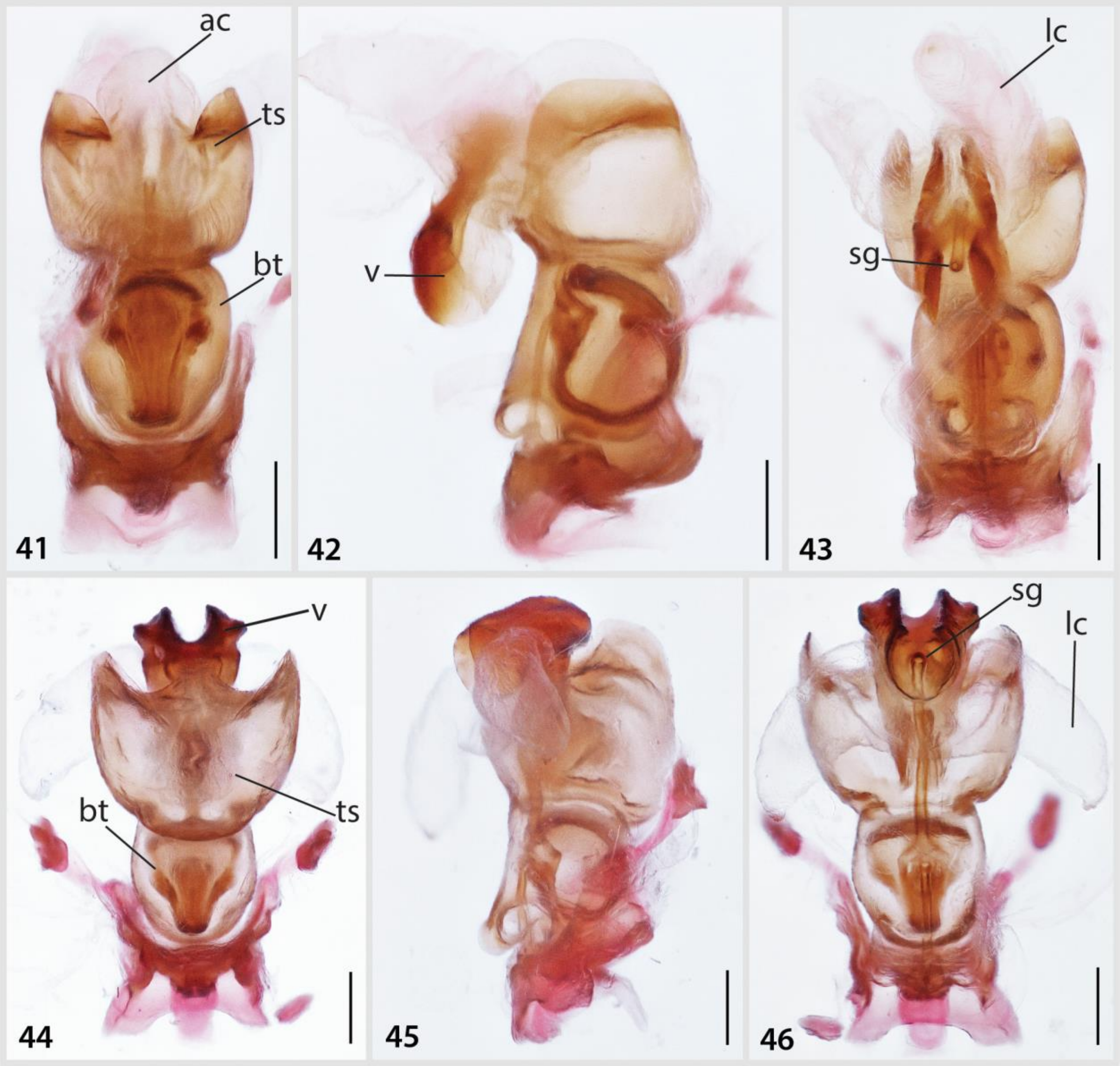
FIGURES 1–24. Type specimens examined in ventral and dorsal views, with their respectives labels. 1–3, *Telepta distincta*; 4–6, *Arma submarginata*; 7–9, *Arma fuscescens*; 10–12, *Arma caliginosa*; 13–15, *Arma turbida*; 16–18 *Podisus mellipes*; 19–21 *Arma ventralis*; 22–24 *Arma monospila*. 1–3, Photographed by Gunvi Lindberg (© 2019 Naturhistoriska riksmuseet); 16–18, Photographed by Laurent Fauvre (© 2019 Muséum National d'Histoire Naturelle); original photos cropped, light levels and contrast adjusted. Scale bars: 4 mm.



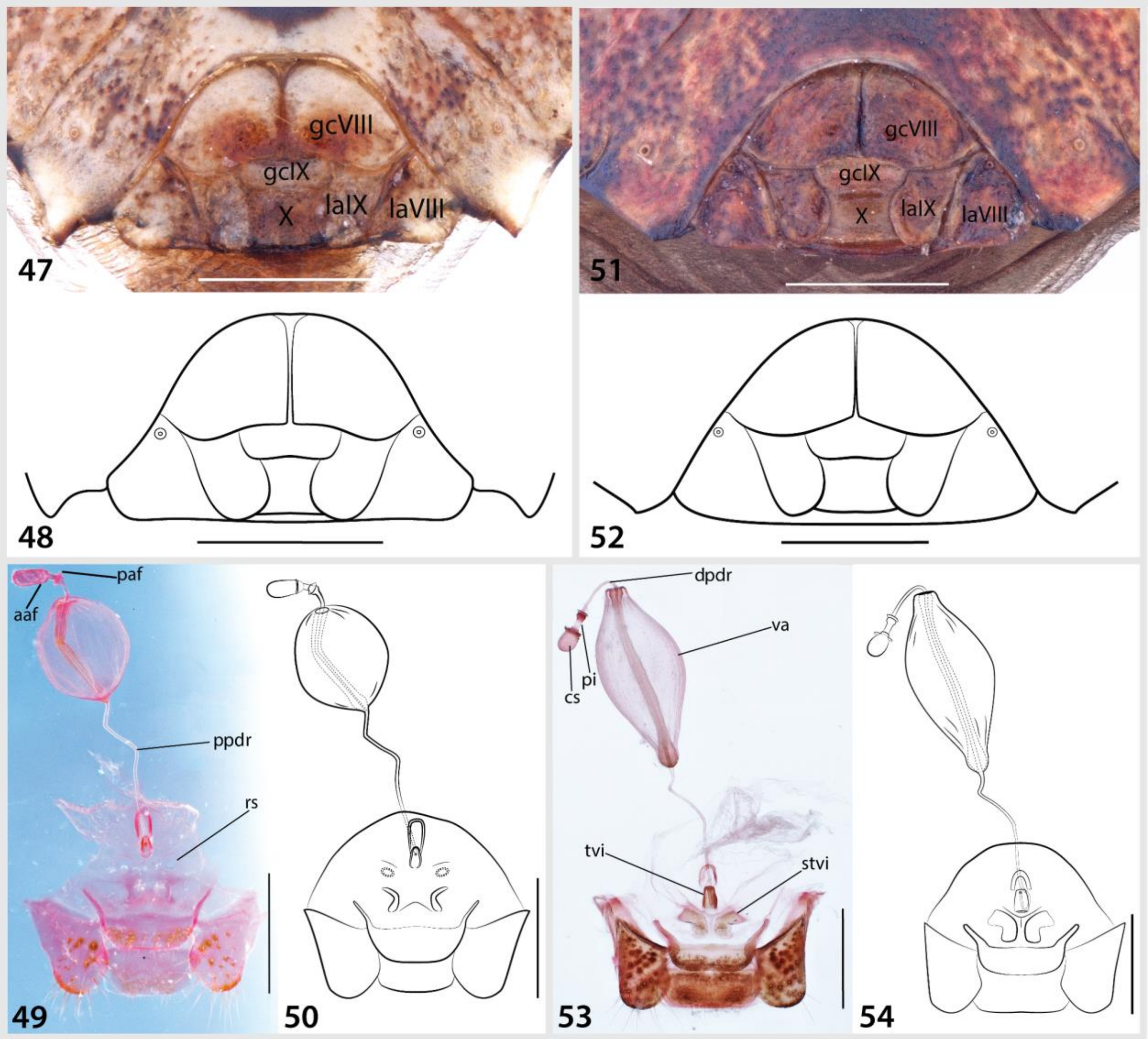
FIGURES 25–30. Habitus of *Podisus distinctus* (25–27) and *Podisus fuscescens* (28–30). Dorsal (25, 28), ventral (26, 29) and head + pronotum (27, 30) views. Scale bars: 2 mm.



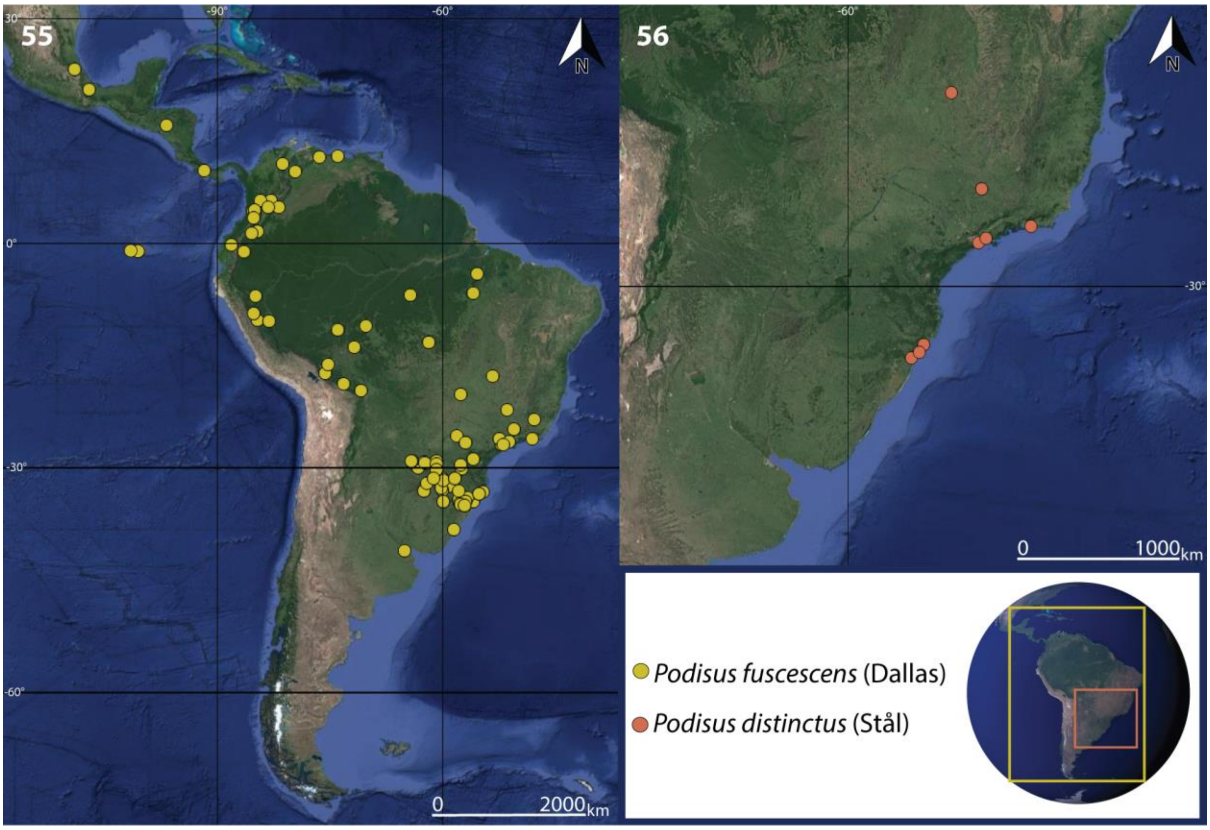
FIGURES 31–40. Pygophore, paramere and superior process of dorsal rim of *Podisus distinctus* (31–33, 37–38) and of *Podisus fuscescens* (34–36, 39–40). Pygophore in dorsal (31, 34), posterior (32, 35) and ventral (33, 36) views. Paramere (37, 39). Superior process of dorsal rim (38, 40). Abbreviations: ao = anterior opening; dr = dorsal rim; ib = inner branch; par = paramere; slvr = superior layer of ventral rim; ilvr = inferior layer of ventral rim; spdr = superior process of dorsal rim. Scale bars: 31–36= 0,2 mm; 37–40 = 0,1 mm.



FIGURES 41–46. Phallus of *Podisus distinctus* (41–43) and of *Podisus fuscescens* (44–46). Dorsal (41, 44), lateral (42, 45) and ventral (43, 46) views. Abbreviations: ac = apical conjunctiva; bt = basal theca; lc = lobes of conjunctiva; sg = secondary gonophore; ts = thecal shield; v = vesica. Scale bars: 0,1 mm.



FIGURES 47–54. Female genitalia of *Podisus distinctus* (47–50) and of *Podisus fuscescens* (51–54). Genital plates in posterior view (47–48, 51–52). Internal genitalia (49–50, 53–54). Abbreviations: aaf = anterior annular flange; cs = capsula seminalis; dpdr = distal part of ductus receptaculi; gcVIII = gonocoxites 8; gcIX = gonocoxites 9; laVIII = laterotergites 8; laIX = laterotergites 9; paf = posterior annular flange; pi = pars intermedialis; ppdr = proximal part of ductus receptaculi; rs = ring sclerites; st = secondary thickening of gonapophyses IX; tvi = thickening of vaginal intima; va = vesicular area; X = 10th abdominal segment. Scale bars: 47–48, 51–52 = 1 mm; 49–50, 53–54 = 0,1mm.



FIGURES 55–56. Geographic distribution of *Podisus fuscescens* (55, yellow spots) and of *Podisus distinctus* (56, orange spots).

Conclusão geral

No capítulo I, estudou-se a morfologia dos ovos e ninfas, a história natural e a variação de coloração na fase adulta de *Oplomus catena* (Drury), a partir de espécimes criados em laboratório, e de coleção. Concluíu-se que a morfologia dos ovos é semelhante a já descrita para *Oplomus cruentus* (Burmeister) e algumas espécies de *Stiretrus* Laporte, sugerindo que a morfologia do ovo pode ter significância para a sistemática em níveis supragenéricos. As ninfas apresentam morfologia distinta, principalmente a partir do terceiro ínstar, quando adquire coloração irridescente e azulada. O primeiro instar apresenta a combinação de coloração preta e vermelha, típica de Asopinae. Também a partir do terceiro ínstar, as ninfas apresentam o desenvolvimento de uma protuberância no fêmur e o ápice das placas mandibulares se torna angulado, assim como observado em adultos. No estágio adulto, quatro padrões diferentes de coloração foram identificados, sendo que três deles foram observados nos espécimes criados em laboratório, sugerindo que não há relação entre os padrões e diferentes populações ou com a distribuição da espécie. Observações do hábito alimentar de *O. catena* em laboratório e a comparação com a literatura, sugerem ainda que a espécie apresenta hábito generalista, predando principalmente larvas de Lepidoptera e Coleoptera.

No capítulo II, é apresentada uma compilação de dados de literatura sobre estágios imaturos (ovos e ninfas) de Asopinae, juntamente com a busca por informações de história natural e morfologia a partir de fotografias publicadas em plataformas de ciência cidadã. Ainda, a partir de um viés comparativo, foi incluída a descrição da morfologia dos imaturos de seis espécies criadas em laboratório. Cinquenta e uma publicações foram selecionadas, que representam 41 espécies e 30 gêneros de Asopinae. Informações de categorias previamente selecionadas foram identificadas, destacadas, e listadas em uma tabela. Os dados demonstram que há descrições morfológicas dos ovos e ninfas de pelo menos 28 espécies, informações sobre história natural somam 26, e espécies submetidas a criação em laboratório 28. O compilado permite a visualização de quais espécies são mais estudadas, e quais táxons necessitam de mais investimento em pesquisa. A busca por fotografias em plataformas de ciência cidadã possibilitou o reconhecimento de pelo menos 40 espécies, a maioria com ocorrência nas regiões Neotropical (52.94%) e Paleártica (35.29%). A identificação das espécies nas plataformas, com base na literatura apresentada, possibilita o acesso destas informações ao público não acadêmico, contribuindo para a popularização da ciência. Ainda, a morfologia comparada permite a elucidação de algumas características diagnósticas presentes nos imaturos e que são importantes para identificação a nível específico (principalmente para as espécies mais conhecidas) e de gênero.

No capítulo III, o gênero *Tynacantha* Dallas é revisado taxonomicamente, e duas espécies novas são descritas. O exame de exemplares oriundos de 17 diferentes coleções científicas permitiu reconhecer quatro espécies no gênero, e ampliar a distribuição conhecida da espécie mais comum, *Tynacantha marginata* Dallas, 1851. *T. marginata* e *Tynacantha splendens* Distant, 1889 foram redescritas, *Tynacantha cuprea* Brugnera & Grazia, 2019 e *T. umeridenigrata* Brugnera & Grazia, 2019 foram descritas a partir de exemplares provenientes da região amazônica no Brasil. O gênero pode ser facilmente reconhecido pela morfologia das margens anterolaterais do pronoto, que são retilíneas, calosas, sem pontuação, e de coloração pálida.

No capítulo IV, a espécie *Tylospilus nigrobinotatus* (Berg, 1879) é redescrita e *Tylospilus armatus* Thomas, 1992 é classificada como seu sinônimo júnior. A redescrição permitiu o reconhecimento de uma nova espécie (*Tylospilus armatussimilis* Brugnera, Paim & Grazia, 2020) proviniente da região de Colonia, no Uruguai. Embora as duas espécies sejam morfologicamente similares, foi possível reconhecer diversas características que as diferenciam, dentre elas as margens anterolaterais do pronoto distintamente pálidas em *T. nigrobinotatus* a da mesma cor do pronoto em *P. armatusssimilis*, além da morfologia da genitália de ambos os sexos.

No capítulo V, o status taxonômico de uma importante espécie utilizada em estudos sobre controle biológico é corrigido: *Podisus fuscescens* (Dallas, 1851). A espécie que antes era chamada de *Podisus distinctus* (Stål, 1860), foi redescrita e teve sua área de distribuição atualizada, passando a ser a espécie com a mais ampla distribuição no gênero, ocorrendo desde o México até a região de Buenos Aires na Argentina. É destacada a importância de consultar exemplares-tipo na tomara de decisões taxonômicas, além da análise da genitália interna e externa de ambos os sexos. Este estudo foi a primeiro a investigar a genitália interna e externa de diferentes espécies do gênero, possibilitando verificar variações em ambos os sexos, reforçando a hipótese de não-monofilia de *Podisus* Herrich-Schäffer.

No capítulo VI, o registro de ocorrência de *Podisus sagitta* (Fabricius, 1795) em Minas Gerais apresentado por Oliveira-Júnior et al. 2020 é corrigido. Em uma nota científica, é destacada a distribução da espécie e características que permitem a diferenciação de *Podisus nigrispinus* (Dallas, 1851) com *P. sagitta* é apresentada.

ANEXO I

Occurrence of the Yellow Spotted Stink Bug *Erthesina fullo* (Thunberg) (Hemiptera: Pentatomidae) in Brazil, a polyphagous species from Asia

[Brugnera et al. (2021). Neotropical Entomology: 51, 325–329, doi.org/10.1007/s13744-021-00924-9]

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Abstract

In recent years, the management of invasive stink bugs (Pentatomidae) has been a challenge in many regions of the world, including the Neotropical, where four non-native species were detected in the last two decades. Species with invasive potential include the Yellow Spotted Stink Bug, *Erthesina fullo* (Thunberg). It is polyphagous and is known to cause damages to fruit crops in Southeast Asia. Herein, we report for the first time the occurrence of *E. fullo* in Brazil (Santos, São Paulo). Nymphs and adults have been recorded nearby the Harbor of Santos, since November 2020. A fifth instar nymph was collected and reared until adulthood. The insect was found feeding on *Inga* sp. leaves (Fabaceae), a plant restricted to the Neotropical Region. The detection of multiple specimens in Santos, plus their ability to feed on native and or on cultivated plants, may represent a threat to the Brazilian agribusiness and environment.

Keywords: pest management, invasive species, iNaturalist, citizen science, hitchhiking species

Stink bugs (Pentatomidae) include some species with invasive potential (McPherson 2018). Among the characteristics that allow some species of stink bugs to establish in non-native environments, include their polyphagous habits, and their ability to survive under unfavorable conditions (as overwintering), currently magnified by the climate changes (Panizzi 2015; Esquivel et al. 2018). The more recent case of an invasive pentatomid is the Brown Marmorated Stink Bug (BMSB), *Halyomorpha halys* (Stål). It is currently widespread in different regions of the world, causing problems in agriculture, the environment, and people's homes (Lesley et al. 2012, Inkley 2012). In the Americas, other important invasive species include *Bagrada hilaris* (Burmeister), *Murgantia histrionica* (Hahn), and *Piezodorus guildinii* (Westwood) (McPherson 2018).

At least four non-native species of stink bugs have been reported in the Neotropics, which invasive status are still uncertain in some cases: *Agonoscelis puberula* Stål, reported in Mexico, Jamaica, and Dominican Republic (Thomas et al. 2003); *B. hilaris* in Chile (Faúndez et al. 2016); *Chroanta ornatula* (Herrich-Schäffer) in Dominican Republic and Venezuela (Perez-Gelabert and Thomas 2005; Cazorla-Perfetti and Morales-Moreno 2019); and *H. halys* in Puerto Rico and Chile (Segarra-Carmona et al. 2015; Faúndez and Rider 2017). Additionally, the cosmopolitan *Nezara viridula* (L.) is widely distributed in the region, recorded since the end of the 18th century (Esquivel et al. 2018). This list also includes other true bugs, such as the Black Bean Bug, *Brachyplatys subaeneus* (Westwood) (Plataspidae) detected in Panamá in 2012 (Aelio et al. 2012), and currently widespread in other countries of the Central, North, and South America (Añino et al. 2020, Eger et al. 2020); and the Kudzu Bug (Plataspidae) *Megacopta cribraria* (F.) which have been recorded in the Southern United States since 2009 (Eger et al. 2018).

Among the stink bug species with potential to invade new regions, the Yellow Spotted Stink Bug (YSSB), *Erthesina fullo* (Thunberg), has been highlighted in the last few years (Mi et al. 2020). It is native from the Palearctic Region and recorded in Bangladesh, China, India, Indonesia, Japan, Myanmar, Sri Lanka, and Vietnam (Rider 2006, CABI), including other countries of Southeast Asia (website iNaturalist.org - GBIF) (Fig. 1A). The YSSB is a polyphagous species, feeding on leaves, flowers, shoots, or fruits of at least 57 plants from 29 families (Mi et al. 2020). It is a large species, with males reaching 220-230 mm (Wang 2015). The head is long and acuminate, mostly black with a yellow midline that extends to the pronotum. Adult body coloration is black, with yellow spots in the dorsal surface, including connexivum, tibia, and tarsus (Fig. 2C-E). The labium always exceeds hind coxae, reaching the third up to the fifth urosternite.

In 2014, a specimen of *E. fullo* was found in Temuka, New Zealand (Mitchel 2014), however, now records were not detected. Since 2017, it has been recorded in Tirana and Durrës, Albania, where it was able to reproduce and survive (Lupoli et al. 2020, 2021). These records call attention to the hitchhike ability of YSSB, by using containers and other types of cargo to reach new regions, as observed in *H. halys* (Aigner and Kuhar 2016).

Here, we report for the first time the presence of *E. fullo* in the Neotropical Region based on four records found in Santos, São Paulo State, Southeastern Brazil. The first record, a fourth instar nymph (Fig 2A), was observed, photographed, and submitted to the iNaturalist website in November 2020 by Y. Lima. The nymph was found in a tree of *Inga* sp. (Fabaceae) in the urban area, ca. 200 m from the harbor of Santos, one of the major harbors in Brazil (Fig 1C, red spot). On February 19, 2021, a fifth instar nymph was found on the same tree, which was photographed and collected (Fig. 2B). The nymph was maintained in a plastic pot, fed *ad libitum* with *Inga* sp. leaves and a piece of moistened paper. The specimen molted to adult (Fig. 2C-E) on February 22, a female kept in the plastic pot up to February 26. Then, it was cold anesthetized in a freezer and stored in alcohol 99%. The specimen was deposited in the Hemiptera collection of the Museu de Zoologia, Universidade de São Paulo (MZSP 190221).

In a second observation, a photograph of an adult was published on the iNaturalist website (www.inaturalist.org/observations/73412688) on April 9, 2021, located at a place nearby of the previous record (Fig. 1C, green spot). Two other records were identified in the Facebook group “Insetos do Brasil” dated April 24 and May 11, 2021, without a specific location in the Santos area.

The detection of multiple live specimens, nymphs, and adults of *E. fullo* in Brazil, indicates a possible establishment of the species in the city of Santos. All records were registered near the harbor, suggesting that they reached Brazil on shiploads. Located on the coast of the Atlantic Ocean and with a tropical climate, the annual average temperature up to 20 °C found in Santos, may allow a multivoltine seasonal phenology to the species, as observed in southern China (Zhou et al. 2000).

In its native range, *E. fullo* is recorded in 57 host plants of 29 families, mostly trees and other perennial hosts (Mi et al. 2020). Most important, the YSSB host range include important crops such as apple, apricot, cherry, grape, kiwifruit, macadamia, peach, pear, plum, pomegranate, and some woody ornamentals. The pest status can vary and depends on the region and the associated crop. Significant damages to kiwifruit (Shaanxi province) and pear (Hebei, Henan and Shaanxi province) are reported in China (Mi et al. 2020). The species is also pointed as a potential nuisance pest. On the other hand, there is no record of the YSSB on any important commodity crops, such as corn, cotton, and soybean, which in Brazil include other native stink bugs as major pests (e.g. Panizzi 2015, Sosa-Gómez et al. 2020).

Nevertheless, considering the polyphagous habits of *E. fullo*, the plant diversity, and the extensive and varied agricultural activity in Brazil, surveillance of the species is an important step toward its management. The installation of traps in the area and the constant inspection of citizen science initiatives, such as iNaturalist and other online resources, are important tools to contribute to the identification and monitoring of this stink bug, as demonstrated to *B. subaenus* (Eger et al. 2020), *H. halys* (Maistrello et al. 2016), and *E. fullo* (Lupoli et al. 2020).

Authors' contributions

RB and CSF planned and designed the study and wrote the manuscript. YL made the observation and the photographs (Fig. 2), and reviewed the manuscript. JG designed and reviewed the manuscript. All authors read and approved the manuscript.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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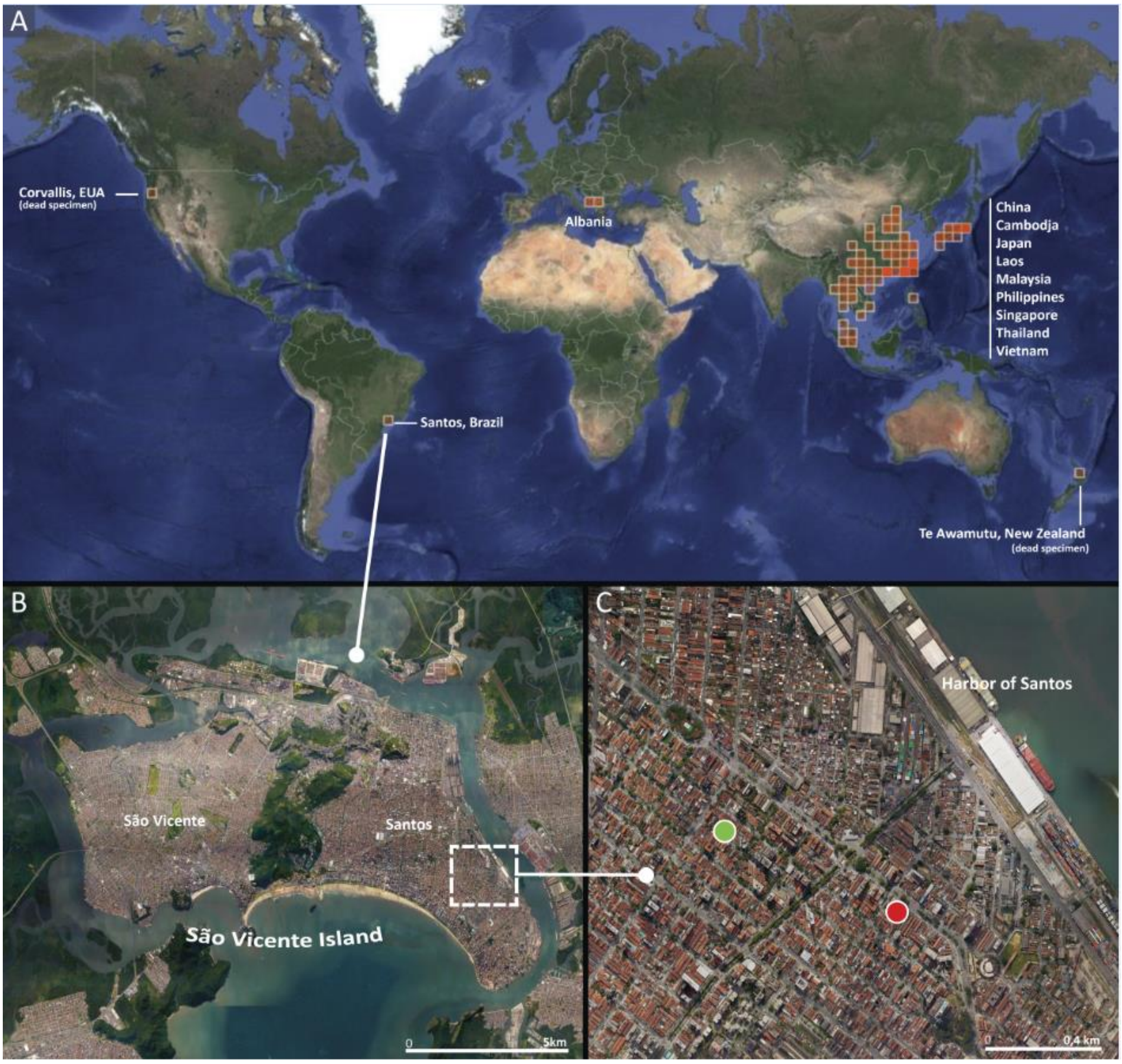

Fig. 1 General distribution of *Erthesina fullo* (Thunberg), with new records found in Brazil. A World map with the occurrences of *Erthesina fullo* according to 2190 (accessed on May 31, 2021) Researchgrade observations registered in iNaturalist.org. B Map of the São Vicente Island in São Paulo State, southeastern Brazil. C Observations of *Erthesina fullo* near the Harbor of Santos; green spot represent the collected specimen (latitude − 23.9 S, longitude − 46.3 W); red spot represent the iNaturalist observation by @giuliano1

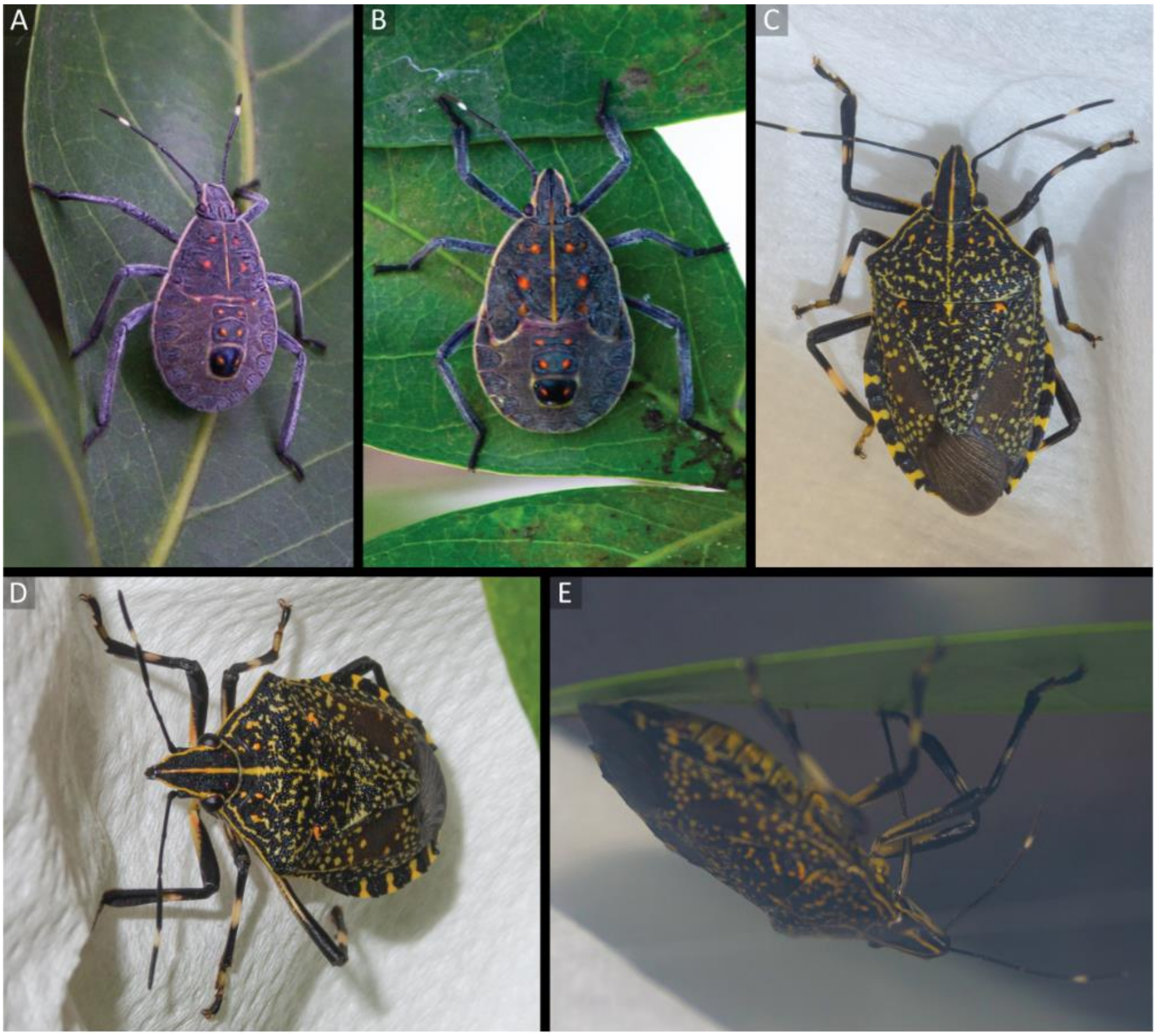

Fig. 2 Collected specimen. A Fourth instar nymph. B Fifth instar nymph. C–E Adult female, deposited in the Hemiptera Collection of Museu de Zoologia of Universidade de São Paulo (MZSP 190221); C Dorsal view. D Frontal view. F Lateral view, feeding of *Inga* sp. leaves.

ANEXO II

Podisus sagitta (Fabricius) does not occur in Brazil: a corrigendum to Oliveira-Júnior et al. 2021

[Brugnera et al. (2022). Brazilian Journal of Biology, 84, doi.org/10.1590/1519-6984.255757]

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Among the 65 genera of predatory stink bugs currently described, *Podisus* Herrich-Schäffer is one with the most taxonomic incongruences. The genus is the most speciose of the subfamily with 35 species described, presenting a great morphological variety and several taxonomic arrangements throughout its history (Thomas, 1992; Brugnera et al., 2020; Roell et al., 2021). Some species are the target of studies regarding biological control, mainly *P. maculiventris* (Say, 1831) in North America, and *P. nigrispinus* (Dallas, 1851), *P. sagitta* (Fabricius, 1794), and *P. fuscencens* (Dallas, 1851) in Central and South America. The last three belong to the sagitta group, which can be recognized by the acute humeral angles, with a noticeable posterior projection (Thomas, 1992). *Podisus nigrispinus* is commonly found in all regions of Brazil and applied in different types of researches (Pires et al., 2015). *P. fuscescens* (identified as *P. distinctus* (Stål) in the last two decades) is also widely found in Brazil and is easily distinguished from *P. nigrispinus* by morphological characteristics of the pronotum and genitalia (Brugnera et al., 2020). *Podisus sagitta* is northern distributed and very similar to *P. nigrispinus*, being sympatric in Costa Rica, Panama, Colombia, and Venezuela (Thomas, 1992; Castro-Huertas et al. 2015).

Oliveira-Júnior et al. (2021) present a new record for *Podisus sagitta* (Fabricius, 1794) in Brazil, including information about its natural history based on specimens reared under laboratory conditions. The first determination of the species was made in 2016 by Dr. Jocélia Grazia as cited by Oliveira-Júnior et al. (2021). In 2016, Dr. Jocélia provided the identification based on Thomas's identification key and description (1992). More recently, with new studies and access to type specimens of *Podisus*, the diagnostic delimitations of this species have been clarified, providing a more precise identification (Brugnera et al., 2020). During the review process of the manuscript of Oliveira-Júnior et al. (2021), the identification made in 2016 was corrected to *Podisus nigrispinus* (Dallas, 1851); however, it was published incorrectly as *P. sagitta*. This note aims to correct that misidentification.

This is not the first time that *Podisus nigrispinus* and *Podisus sagitta* are confounded. De Clercq and Degheele (1995) also reported the same misidentification of specimens collected in Surinam (Clercq and Degheele, 1990). *P. nigrispinus* and *P. sagitta* are very similar in the overall morphology, including the parameres of male genitalia. They can be distinguished mainly by the shape and coloration of the pronotum. The anterolateral margins of the pronotum present a distinct coloration and are concave in *P. nigrispinus*, which varies from pale to red, always differing from the pronotal disc (Figs 1d, f). *P. sagitta* does not present this feature, being the anterolateral margins of pronotum sinuous and concolorous with the disc (Figs 1a, c). Additionally, *P. sagitta* usually present the humeral angles anteriorly directed (Fig. 1c), instead of laterally directed as observed in *P. nigrispinus* (Fig. 1f). In addition, females of *P. sagitta* present a single dark spot in the VII sternite (Fig. 1b), instead of a series of spots from III to IV sternites usually observed in females of *P. nigrispinus* (Fig. 1e).

The known species distribution (country records) is: *Podisus sagitta* - United States (Texas, Florida, and New Mexico), Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Cuba, Bahamas, Jamaica, Dominican Republic, Haiti, Puerto Rico, Saint Vincent and the Grenadines, Curaçao, Trinidad and Tobago, Colombia, and Venezuela (Thomas, 1992; Castro-Huertas et al. 2015; GBIF) (Fig. 2). *Podisus nigrispinus* - Costa Rica, Panama, Colombia, Venezuela, Ecuador, Surinam, Guyana, French Guiana, Brazil, Peru, Bolivia, Argentina, Paraguay, and Uruguay (Thomas, 1992; Dellapé et al. 2003; Lupoli, 2019; GBIF) (Fig. 2).

In summary, the results presented by Oliveira-Júnior et al. (2021) must be assigned to *P. nigrispinus* and not to *P. sagitta*. We warn that the classification of *Podisus* is currently unresolved, including the genus monophyly, the diagnosis of species and the available identifications keys. Thus, the identification of the species needs to be done with caution to avoid future misinterpretations.

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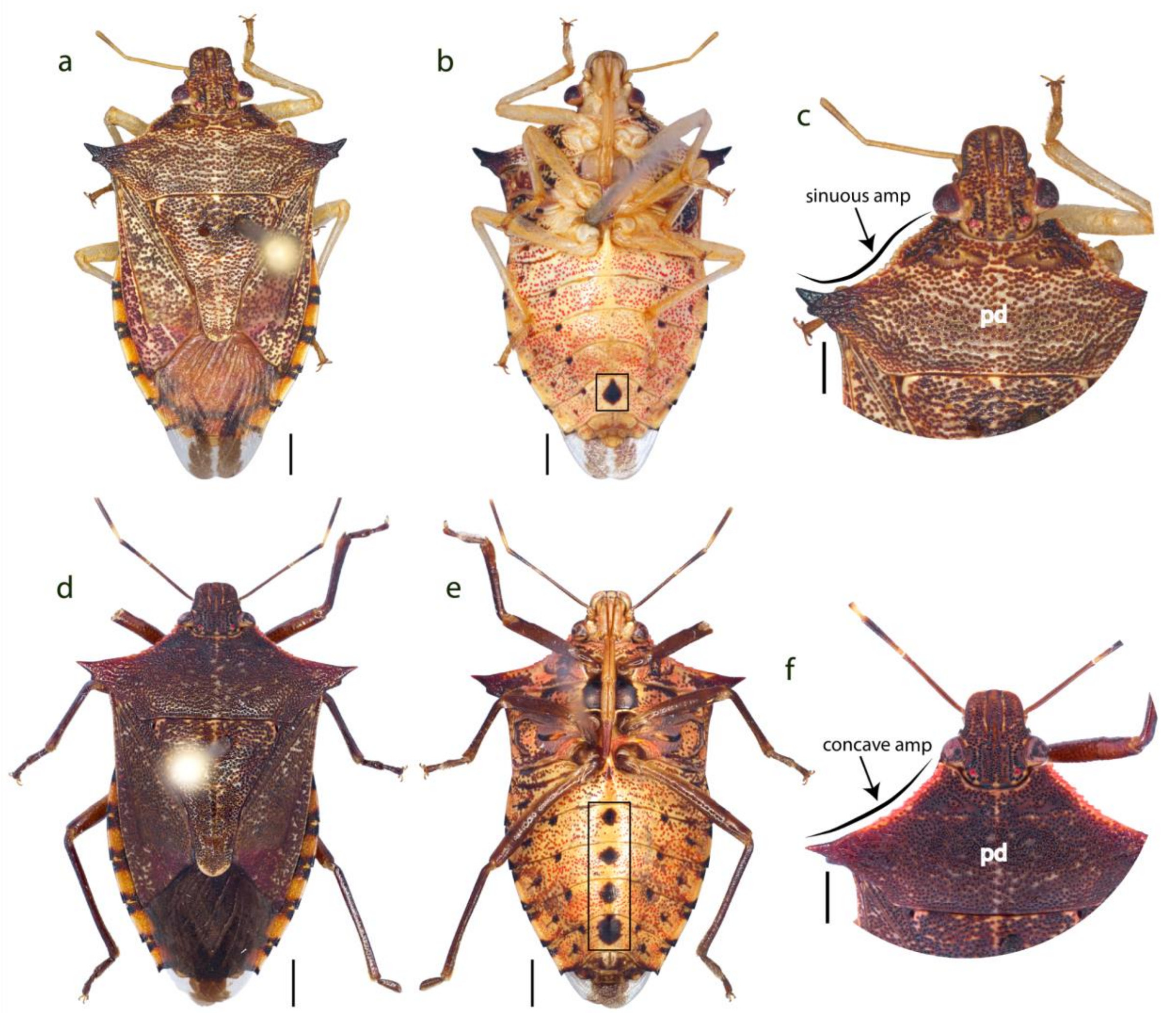

Figure 1. Habit of *Podisus sagitta* (a-c) and *Podisus nigrispinus* (d-e). a, d, dorsal view. b, e, ventral view. c, f, head and pronotum in dorsal view. amp = anterolateral margin of pronotum. pd = pronotal disc. Squares in the figures b and e represent the distribution of dark spots in the female sternites.

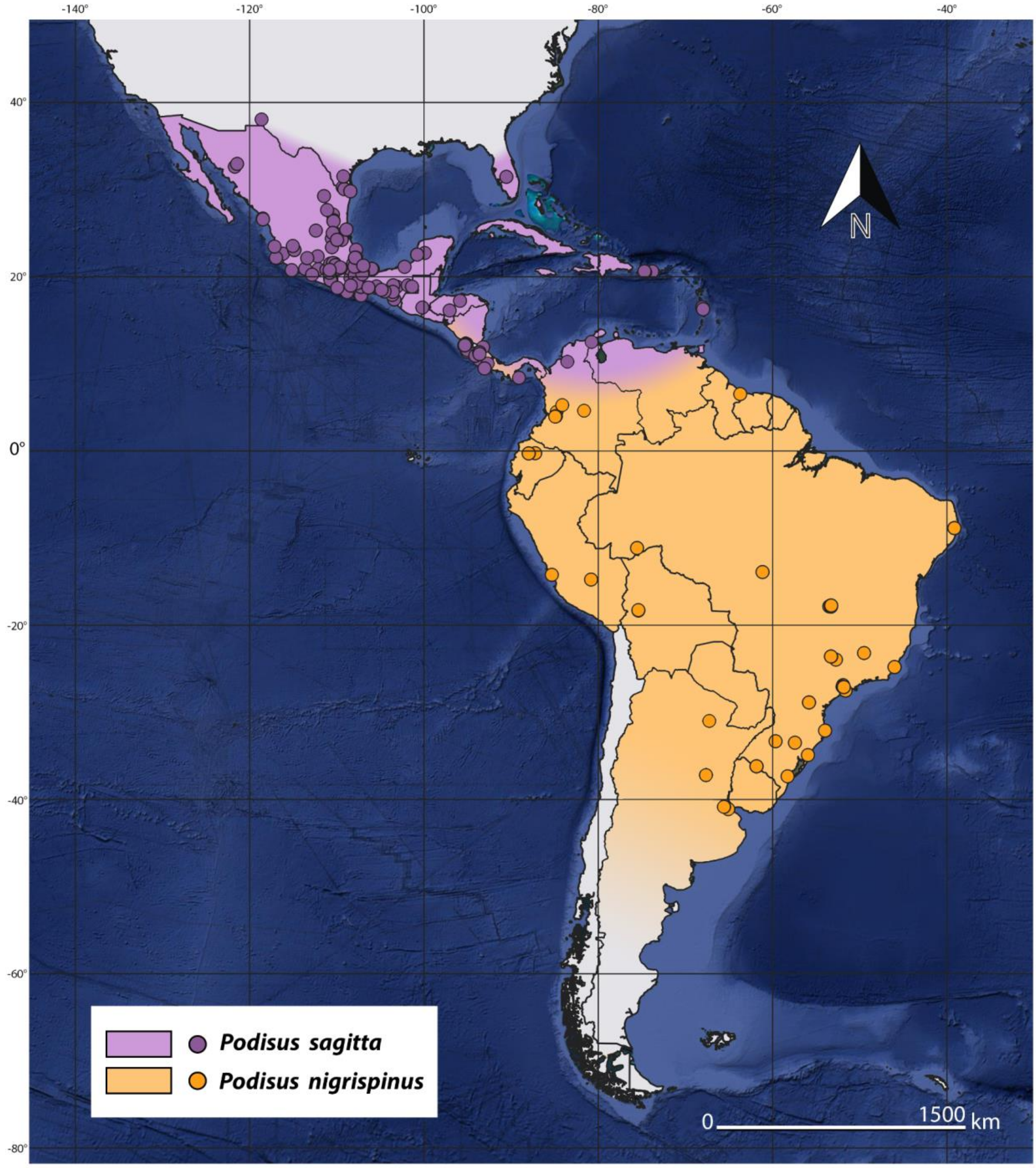

Figure 2. General distribution of *Podisus sagitta* (Fabricius) and *Podisus nigrispinus* (Dallas) in the American continent. Spots represent GBIF occurrences.